Hillcoat, Suzanne Kathleen (2024) ***Investigating morphometry, growth patterns, and interactive behaviour of dwarf minke whales in the Great Barrier Reef: insights from diver-operated stereo-video systems.*** **PhD Thesis, James Cook University.**

Investigating morphometry, growth patterns, and interactive behaviour of dwarf minke whales in the Great Barrier Reef: Insights from diver-operated stereo-video systems

Suzanne Kathleen Hillcoat
BSc (University of Guelph, Canada)
MSc (James Cook University, Australia)

August 2024

In fulfilment of the requirements for the degree of

Doctor of Philosophy

College of Science and Engineering

James Cook University

Acknowledgements

Writing is tragically a solo effort but it takes a village to bring a PhD to fruition. I'd like to thank my village:

First I'd like to thank my supervisors for the time and expertise they've given to me and this thesis. I've learned so much from each of you. Alastair, you've taught me that every word counts (both written and spoken!), to choose them carefully, and how to tell a story like few others can. Naomi, your scientific rigour and technical writing skills have made me a better scientist and have made me so proud of this thesis. Matt, thank you for always being the first to read my drafts and for encouraging me to zoom out and widen my perspective. Your input and expertise have made my discussion sections in particular infinitely better.

The Minke Whale Project has an uncanny ability to secure the most amazing people. I'm exceptionally grateful for Gena Williams, Martha Kusetic, and Emily Daley – I'll never forget your support while I was 'in the trenches'. The dozens of volunteers who assisted me with field data collection and photo-ID are too numerous to name but I am thankful for each and every one of you and would still be matching photos of whales if it weren't for you all. Claire Barr – I cannot begin to convey the depths of my gratitude for you. I feel privileged to know you and cannot wait to see what the future holds for you.

There are so many other important people who have unofficially contributed to this thesis through their emotional (and occasionally financial!) support. My parents, who raised me to believe I can do anything. My sister, Sarah, who has been a constant source of strength throughout this journey and who makes me laugh like no one else. My brother-in-law Nate, who I look forward to getting to know better in the years to come. My nieces Zoë and Penny – I never knew I could love someone I'd never met. The friends back in Canada who always make time to catch up with me no matter how short my trip is, especially Steph, Belinda, Malynn, and Mallory.

The friends I’ve made while at JCU are some of the most incredible people on this planet. Kevin Bairos-Novak, Katie Peterson, Rachel Miller, and Gena Williams in particular have done some heavy emotional lifting over the years, and while distance and circumstance may separate us, our friendships will always be cherished. Brooke D’Alberto, Chloë Boote, Brittany Dewdney, Carolyn Wheeler, and Ketki Jog, I’ll forever be thankful that our dogs (or just mine) brought us together. My constant companion, Kara the tropical husky - you are my emotional support fluff.

This thesis would not have been possible without the extensive and long-standing support of the swim-with minke whales tourism operators in Cairns and Port Douglas, Australia, especially Divers Den, Eye to Eye Marine Encounters, Mike Ball Dive Expeditions, ProDive, and Tusa Dive. I appreciate the assistance of the crews and passengers who have supported our field data collection, and the friendships I have made with some of you have been a highlight of this journey. I would also like to thank Jim Seager from SeaGIS for his patient advice and feedback. I am particularly indebted to Susan Sobtzick for pioneering this work with dwarf minke whales and for freely sharing her data and ideas.

Finally, to my partner, Elliot, and my stepdaughter Maggie. Nothing I have attempted to write feels like enough, so I will just take the easy way out and say thank you and I love you. Even if you don’t let Kara on the bed.

Statement of the Contribution of Others

Financial Support

James Cook University Postgraduate Scholarship
Great Barrier Reef Marine Park Authority Reef Guardians Grant
College of Science and Engineering Competitive Research Training Grant
Minke Whale Project
Cod Hole And Ribbon Reefs Operators Association (CHARROA) in-kind support

Statistical and Analytical Support

Dr Naomi Gardiner
Dr Kevin Bairos-Novak
Dr Tasmin Rymer

Supervision

Dr Naomi Gardiner
Dr Alastair Birtles
Dr Matt Curnock

Editorial Support

Dr Kevin Bairos-Novak
Dr Naomi Gardiner
Dr Alastair Birtles
Dr Matt Curnock
Dr Tasmin Rymer

Abstract

An understanding of the biology and behaviour of a species or population is an important consideration for developing conservation and management strategies. The discovery of a seasonal aggregation of dwarf minke whales (*Balaenoptera acutorostrata* subsp.) in the northern Great Barrier Reef (GBR) has led to the development of a lucrative swim-with dwarf minke whales tourism industry and has also facilitated dedicated research on this population. Despite significant advancements in knowledge, many knowledge gaps remain, particularly regarding the population structure, growth rates, and social behaviours of these whales, largely due to the challenges associated with traditional observation methods. Most commonly, cetaceans are studied from vessels and aerial vehicles (i.e., drones). However, the unpredictable surfacing behaviour of dwarf minke whales and the remoteness and prevailing weather conditions of the GBR aggregation area have precluded the use of dedicated research vessels and aerial techniques for these whales. Alternatively, the in-water access provided to the aggregation from permitted dive tourism operators in Cairns and Port Douglas offers a low-cost opportunity for researchers to observe dwarf minke whales underwater. This thesis employs underwater videogrammetry techniques, using a diver-operated stereo-video (SDOV) system, to explore several aspects of dwarf minke whale biology and behaviour, offering novel insights into population demographics, growth patterns, and interactive behaviour of these understudied cetaceans. This research advances our understanding of these enigmatic whales and provides suggestions for conservation and management strategies. This thesis also offers baseline data for future research and population monitoring, and methodological recommendations for further advancements.

Chapter 1 provides a general introduction to dwarf minke whales and the swim-with dwarf minke whales tourism industry in the GBR. In this chapter I outline the current state of knowledge of this undescribed subspecies as well as the knowledge gaps that remain.

Chapter 2 provides the general methods used for field data collection in this thesis, via permitted swim-with dwarf minke whales tourism vessels in the GBR.

Chapter 3, the first data chapter of this thesis, focused on the methodological refinement of underwater photogrammetry techniques for measuring dwarf minke whales. Stereo systems are generally preferred over single-camera systems, but direct comparison studies have only evaluated these techniques on small fauna. Thus, a controlled trial was performed to determine whether using a SDOV system confers an advantage over a single-camera system under the operational conditions expected when observing dwarf minke whales. Measurements made via SDOV were significantly more precise, and the ability for the SDOV system to account for parallax error (i.e., when the target measurement is not absolutely perpendicular to the camera) mitigated a significant methodological constraint associated with single-camera methods. This chapter demonstrates the importance of standardisation in ensuring the reliability and comparability of morphometric data across studies. The recommendations derived from this methodological trial can also serve as valuable guidelines for future research involving medium-sized cetaceans and in-water access.

In **Chapter 4**, the application of a SDOV system and the methodological protocols developed in Chapter 3 facilitated the measurement of nine morphological features of dwarf minke whales observed during in-water interactions in the GBR across multiple years. This novel approach enabled the investigation of allometric growth patterns and the identification of proxies for total body length, providing foundational insights into the demographic structure and potential health status of this population, and the opportunity to expand historically limited sample sizes in future research, such as known sex identifications. Furthermore, the baseline estimates of body condition derived from these data offer valuable metrics for ongoing population monitoring and conservation assessments in the region.

Chapter 5 investigated the drivers of interactive behaviour exhibited by dwarf minke whales during swim-with interactions and risks associated with such behaviour. Specifically, whale-swimmer approach distances were measured using a SDOV system, and generalised mixed methods modelling and regression techniques were employed to investigate external and internal factors influencing interactive behaviour (nine variables were assessed). This study found that as interactions progress and individual whales make more passes by swimmers, whale-swimmer approach distances decrease, demonstrating that the whales exhibit increasing attraction to humans, at least in the short term. Approach distances also decreased with increasing whale group size. These factors can be loosely monitored in real-time by vessel crew to assess and manage the risk of harm associated with increasingly close whale-swimmer approaches. Increased encounter oversight during long and large encounters is recommended as a strategy for mitigating the increased risk of harm to both swimmers and whales associated with very close interactions. This highlights the utility of adaptive management approaches as research progresses to ensure that best practices are continually informed by the latest scientific evidence. While demographic factors such as age (by proxy of length) and sex were also evaluated, individual differences in whale behaviour persisted, suggesting that individual traits such as personality and/or boldness may be driving much of the variation in behaviour observed in this study. This indicates a need for continued research to better understand the complexities of interactive behaviour in dwarf minke whales.

Chapter 6 presents the general discussion, synthesising the findings of this thesis to provide a comprehensive overview of their implications for the conservation and monitoring of dwarf minke whales in Australia. This chapter integrates the results from previous chapters, emphasising how these findings contribute to a broader understanding of dwarf minke whale behaviour, population dynamics, and threats in the Great Barrier Reef. This

chapter also outlines future research directions and suggests targeted management strategies that could enhance the protection of this unique whale population.

Overall, this thesis offers critical insights into the biology and behaviour of dwarf minke whales. It establishes a baseline for continued research on this undescribed subspecies and demonstrates the value of tourism vessels as platforms of opportunity for studying free-ranging cetaceans. It also demonstrates how advanced techniques such as stereo-videogrammetry can be used in the absence of applicable traditional behavioural methodologies, underscoring the need for innovative research approaches. Despite Australia's national and international commitments to marine conservation, there are currently no formal policies specifically addressing dwarf minke whales. By integrating biology, behaviour, and ecology, this study enhances our general understanding of dwarf minke whales, providing essential data to support conservation and management in the Great Barrier Reef.

Table of Contents

ACKNOWLEDGEMENTS I

STATEMENT OF THE CONTRIBUTION OF OTHERS III

ABSTRACT IV

TABLE OF CONTENTS VIII

LIST OF TABLES XIV

LIST OF FIGURES XVI

1 CHAPTER 1: GENERAL INTRODUCTION AND LITERATURE REVIEW 1

1.1 WHALE WATCHING 2

1.1.1 Trends and economic value 2

1.1.2 Platforms of opportunity 3

1.1.3 Potential impacts of whale-watching 5

1.2 SWIM-WITH WHALES TOURISM 6

1.2.1 Concerns and research regarding swimming with whales 7

1.3 RESEARCH OPPORTUNITIES FROM SWIM-WITH-WHALES PROGRAMS 10

1.3.1 Morphometry 10

1.3.2 Photogrammetry 11

1.3.3 Array comparison of underwater photogrammetry systems 14

1.4 DWARF MINKE WHALES 18

1.4.1 Significance of the Great Barrier Reef for dwarf minke whales 19

1.4.2 Swim-with tourism facilitating research 20

1.5 RESEARCH AIMS, OBJECTIVES, AND THESIS STRUCTURE 23

2 CHAPTER 2: GENERAL MATERIALS AND METHODS 26

2.1 STUDY SITE 27

2.1.1 Aggregation area 27

2.1.2 Remote site access: swim-with dwarf minke whale tourism platforms of opportunity 29

2.2 DATA COLLECTION 31

2.2.1 Equipment and calibration methods 31

2.2.2 General field protocols 33

2.3 DATA PRE-PROCESSING 36

2.3.1 Photo-identification 36

2.3.2 Photogrammetry 40

2.3.3 Sex identification 45

2.4 DATA SUMMARY 46

2.5 QUALITY CONTROL AND ERROR MITIGATION PROCEDURES 46

2.5.1 Mis-matches 46

2.5.2 Whale body flexure 48

2.5.3 Exclusion of poor quality measurements 49

3 CHAPTER 3: DEVELOPING PROTOCOLS FOR IN-WATER MORPHOMETRIC MEASUREMENTS OF DWARF MINKE WHALES USING STEREO-VIDEOGRAMMETRY 51

3.1 INTRODUCTION 52

3.1.1 Morphometry 52

3.1.2 Techniques for measuring cetaceans 52

3.1.3 Measurements of dwarf minke whales 54

3.1.4 Aims 55

3.2 METHODS 56

3.2.1 Study site and species 56

3.2.2 Technical equipment and calibration methods 56

3.2.3 Control trial filming protocol 57

3.2.4 Whale filming protocol *58*

3.2.5 Image and measurement processing *59*

3.2.6 Data analysis *65*

3.3 RESULTS 67

3.3.1 Stereo-videogrammetry: Control measurements *67*

3.3.2 Single-camera vs. stereo-image techniques *71*

3.4 DISCUSSION 75

3.4.1 Recommended protocols for SDOV filming of dwarf minke whales *79*

3.4.2 Detecting change over time (growth and body condition) *82*

3.4.3 Conclusion *84*

4 CHAPTER 4: COMPARATIVE MORPHOMETRICS 85

4.1 INTRODUCTION 86

4.1.1 Morphometry applications *86*

4.1.2 Knowledge gaps for dwarf minke whales *88*

4.1.3 Objective and research questions *90*

4.2 METHODS 91

4.2.1 Overview *91*

4.2.2 Field site & data collection *93*

4.2.3 Data pre-processing: photo-identification *93*

4.2.4 Data processing: extracting morphometric values *93*

4.2.5 Data analysis *94*

4.3 RESULTS 98

4.3.1 Photo-identification and sex *98*

4.3.2 Descriptive morphometrics and allometry *98*

4.3.3 Ontogenic growth and allometric scaling *102*

4.3.4 Body condition *106*

4.3.5 Growth *109*

4.3.6 Long-term demographic trends 111

4.4 DISCUSSION 113

4.4.1 Chapter summary 113

4.4.2 Ontogenic allometry 115

4.4.3 Predictors of total body length 116

4.4.4 Body condition 118

4.4.5 Growth 120

4.4.6 Long-term demographic trends 123

4.4.7 Limitations 125

4.4.8 Conclusion and future research directions 126

5 CHAPTER 5: INVESTIGATING INTERACTIVE BEHAVIOUR BY DWARF MINKE WHALES DURING SWIM-WITH ACTIVITIES IN THE GREAT BARRIER REEF .. 128

5.1 INTRODUCTION 129

5.1.1 Animal behaviour 129

5.1.2 Measuring behavioural responses of animals to human presence 130

5.1.3 Behaviour of dwarf minke whales 131

5.1.4 Whale-swimmer approach distances 132

5.1.5 Knowledge gaps 134

5.1.6 Identifying potential predictors of whale-swimmer approach distance 135

5.1.7 Aims 140

5.2 METHODS 141

5.2.1 Study site and data collection 141

5.2.2 Data pre-processing 142

5.2.3 Variable selection and categorisation 144

5.2.4 Data analysis 146

5.3 RESULTS 150

5.3.1 Approach distance and encounter overview 150

5.3.2 Close approaches ... 151

5.3.3 Repeat passes ... 153

5.3.4 Group variables ... 155

5.3.5 Individual variables ... 157

5.4 DISCUSSION ... 161

5.4.1 Chapter overview ... 161

5.4.2 Repeat passes and closer approaches ... 162

5.4.3 Repeat encounters vs repeat passes ... 163

5.4.4 Potential drivers of individual variation ... 164

5.4.5 Non-significant variables ... 165

5.4.6 Significance of closer approaches and increased attraction ... 166

5.4.7 Implications for tourism management ... 167

5.4.8 Limitations ... 168

5.4.9 Unresolved questions and further research recommendations ... 169

5.4.10 Conclusion ... 169

6 CHAPTER 6 GENERAL DISCUSSION ... 171

6.1 INTRODUCTION ... 172

6.2 THESIS SUMMARY ... 172

6.2.1 Study 1 summary: Developing protocols for in-water stereo-videogrammetry data collection ... 173

6.2.2 Study 2 summary: Comparative morphometrics of dwarf minke whales ... 174

6.2.3 Study 3 summary: Drivers of interactive behaviour of dwarf minke whales ... 174

6.3 LONG-TERM DEMOGRAPHIC CHANGES ... 175

6.3.1 Behavioural change: desensitisation to human interactions? ... 176

6.3.2 Environmental/ecological stressors ... 177

6.3.3 Challenges in resolving these issues ... 178

6.4 CONTRIBUTION TO CONSERVATION AND MONITORING OF DWARF MINKE WHALES . 180

6.4.1 Increased accuracy and precision of measurements *181*

6.4.2 New methodologies to increase sample sizes *182*

6.4.3 Identified changes in dwarf minke whale population demographics *183*

6.5 IMPLICATIONS FOR SWIM-WITH DWARF MINKE WHALE TOURISM IN THE GREAT BARRIER REEF 184

6.6 FUTURE RESEARCH RECOMMENDATIONS RESULTING FROM THIS THESIS 184

6.6.1 Developing automated methodologies for reducing analytical time costs *184*

6.7 CONCLUDING REMARKS 187

REFERENCES 189

APPENDIX A: WHALE SIGHTING SHEET 240

APPENDIX B: IMAGE GRADING FOR PHOTO-IDENTIFICATION OF DWARF MINKE WHALES 241

APPENDIX C: TOTAL BODY LENGTH (TBL) MEASUREMENTS 243

APPENDIX D: WIDTH AT WIDEST POINT (WWP) MEASUREMENTS 247

APPENDIX E: TOTAL BODY LENGTH (TBL) MEASUREMENTS OF MULTI-YEAR RESIGHTED WHALES 248

APPENDIX F: CLOSE APPROACHES 248

List of Tables

Table 2.1: Details of data collection field trips.. 30

Table 2.2: Rationale for the selection of morphologic features to be measured......................... 42

Table 3.1: Criteria used for attaining measurements of dwarf minke whales from footage of a single-camera ('single') and stereo-image ('stereo') systems and schematic of measurements on a dwarf minke whale from a dorsal view.. 61

Table 3.2: List of excluded total body length (TBL) measurements due to poor quality............ 64

Table 3.3: Accuracy and precision of stereo-image measurements of an 8 m PVC pipe marked at 1 m intervals, measured at distances from 1.230 m – 14.788 m. 68

Table 3.4: Comparative accuracy and precision of control measurements using single-camera videogrammetry and stereo-videogrammetry... 72

Table 3.5: Whale measurement summaries from single-camera and stereo-image methods...... 73

Table 4.1: Morphometric measurement summaries by measurement type………………….......102

Table 4.2: Prediction equations of five morphometric features for total body length (TBL) and their corresponding 95% prediction intervals..105

Table 4.3: SDF and FW measurements relative to TBL, by sex..107

Table 4.4: Measurements of a calf from the 2017 sampling period..108

Table 4.5: Relative width measurements of dwarf minke whales, standardized by total body length (TBL), and the variability of each measurement type across individuals.................................110

Table 4.6: Growth of features on whales measured across multiple years...............................113

Table 4.7: Size range of measured whales (total body length, TBL) from previously collected data (2006 and 2007, Sobtzick 2010) and 2017 (this study)..115

Table 5.1: Encounter statistics for the top five dwarf minke whale encounter locations in the Great Barrier Reef. Data aggregated from 2003 – 2008. 139

Table 5.2: Description and categorisation of independent variables modelled....................... 145

Table 5.3: Second-order Corrected Akaike Information Criterion (AICc) scores of 1-, 2-, and 3-fixed effect(s) Generalised Linear Mixed Models assessing the effect of external variables on whale-swimmer approach distance...156

Table 5.4: Second-order Akaike's Information Criterion (AICc) scores of Generalised Linear Mixed Models (GLMMs) assessing the effect of TBL on whale-swimmer approach distance............158

Table 5.5: Second-order Akaike's Information Criterion (AICc) scores of Generalised Linear Mixed Models (GLMMs) assessing the effect of sex on whale-swimmer approach distance. 159

Table 5.6: Second-order Akaike's Information Criterion (AICc) scores of Generalised Linear Mixed Models (GLMMs) assessing the effect of sex on whale-swimmer approach distance. 159

List of Figures

Figure 1.1. Schematic of measurement determination using underwater videogrammetry with a single camera and distance sensor. *16*

Figure 1.2. Geometry of a typical stereo diver-operated video (SDOV) frame. *17*

Figure 2.1. Section of the Great Barrier Reef where most sightings of dwarf minke whales occur. *28*

Figure 2.2. Technical equipment used for videogrammetry data collection. *32*

Figure 2.3. The main features used for photo-identification of individual dwarf minke whales in the Great Barrier Reef. *38*

Figure 2.4. Schematic of a dwarf minke whale (dorsal view) identifying the nine morphological features selected for measurement and the reference points used to measure each feature. *41*

Figure 2.5. Precision of replicate total body length (TBL) measurements for all measured whales in 2017 sampling period. *48*

Figure 3.1. Accuracy and precision of stereo-image measurements of an 8 m PVC pipe marked at 1 m intervals, measured at distances from 1.230 m – 14.788 m. *69*

Figure 3.2. Minimum distance range (m) required for length measurements of large object sizes (1-10 m long) using the effective field-of-view (eFOV) of paired stereo-video cameras (i.e., the horizontal width of the overlapping FOV between cameras). *70*

Figure 3.3. (a) accuracy (as mean error) and (b) precision (as coefficient of variation) of replicate 5 m PVC pipe measurements at three approach distances (i.e., ranges): 'close' (6 m), 'medium' (9 m), and 'distant' (12 m). *71*

Figure 4.1. Schematic of a dwarf minke whale (dorsal view) with the nine morphological features selected for measurement………………………………………………………………..................*94*

Figure 4.2. Mean total body length (TBL) of SDOV-measured whales, 2017..........................*104*

Figure 4.3. Simple linear regression of total body length (TBL) and (a) snouth-to-dorsal-fin length (SDF); (b) caudal fluke width (FW), (c) snout-to-blowholes length (SBH), (d) width at eyes (WE), and width at widest point (WWP)...*106*

Figure 4.4. Median ± inter-quartile ranges of relative caudal fluke width (FW) as a per cent of total body length (TBL) by sex for dwarf minke whales with both FW and TBL measurements……………………………………………………………………………………………108

Figure 4.5. Median ± inter-quartile ranges of measurements of (a) width behind eyes (WBE) and width at eyes (WE); (b) width at pectoral fin anterior insertion point (WAP); width at pectoral fin posterior insertion point (WPP); (c) coefficient of variation of replicate WBE and WE measurements; and (d) coefficient of variation of replicate WAP, WPP, and WWP measurements…………………………………………………………………………………………….111

Figure 4.6. Annual relative total body length (TBL) growth of individual whales as a function of initial body length (m)..114

Figure 4.7. Percentage of measured dwarf minke whales in 0.5 m length classes by sampling year...116

Figure 4.8. Example aerial photograph for measuring body condition of a right whale using a custom-written GUI in MATLAB...123

Figure 5.1. Distribution of whale-swimmer approach distances (m) of all measured passes in 2017 (n = 1118 passes by 121 whales)..151

Figure 5.2. Median ± 25% inter-quartile ranges of approach distances (m) by "close approachers" (≤ 3 m, n = 365 passes) and "non-close approachers" (> 3 m, n = 753 passes).........................152

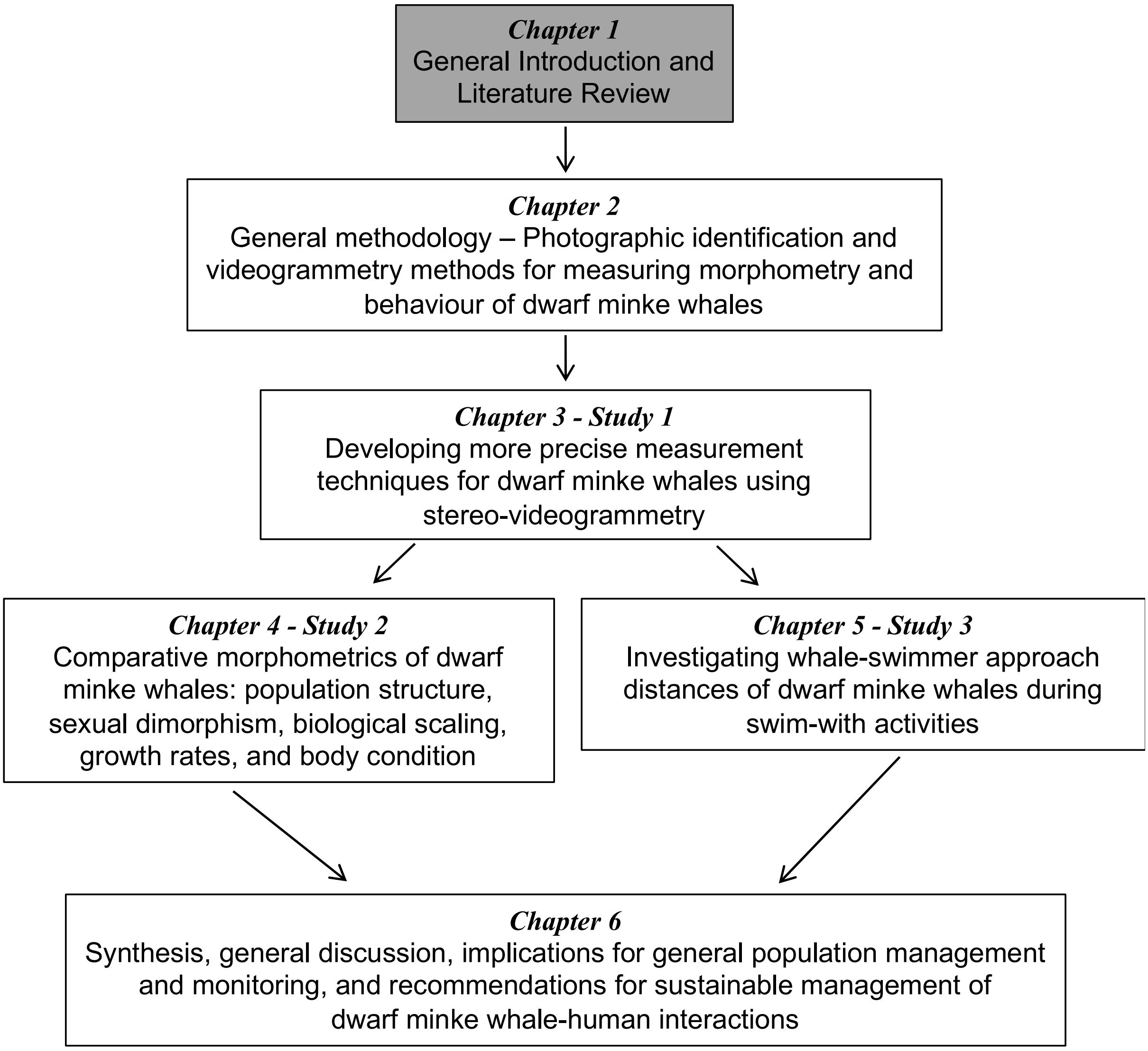
Figure 5.3. Number of measured passes per whale across 21 encounters in 2017 (N = 121). 153

Figure 5.4. a) Log mean approach distance (m) per whale by log number of passes per whale; and b) Log minimum approach distance (m) per whale by log number of passes per whale, across all encounters in 2017...154

Figure 5.5. Modelled relationship (mean ± 95% CI) of mean whale-swimmer approach distance (m) by time in encounter across five theoretical encounters of differing group sizes. 161

1 CHAPTER 1:

GENERAL INTRODUCTION AND LITERATURE REVIEW



Preamble

In this chapter I provide a general introduction to cetacean research from platforms of opportunity. I describe the usefulness and value of such platforms as well as the limitations incurred from these mixed-priority expeditions. I introduce the swim-with dwarf minke whale tourism industry in the Great Barrier Reef and the long-standing support this industry has provided to research scientists and the Minke Whale Project in particular. I discuss the limited knowledge of dwarf minke whale population biology and behaviour, the previous research undertaken on these topics, the remaining knowledge gaps, and outline the aims and objectives of this thesis to further scientific understanding in these areas.

1.1 Whale watching

1.1.1 Trends and economic value

The 20th century saw a widespread shift in the type of economic value provided by whales. Commercial whaling, once a lucrative worldwide industry, was dramatically reduced due to depleted stocks, which led the International Whaling Commission to declare a temporary, worldwide moratorium on whaling in 1986 (Stedman, 1990). This moratorium was extended indefinitely in 1990 and remains in place today (IWC, 2014). On the other hand, whale watching tourism experienced continuous growth since it began in the 1950s through the 1990s (Hoyt, 2001). In 2008, an estimated 12.9 million people worldwide participated in whale watching trips, and the industry generated an estimated revenue of over $2 billion USD (Cisneros-Montemayor et al., 2010; O’Connor et al., 2009), representing the highest-value cetacean-related activity for the global economy (Parsons, 2012). Further, many of these industries operate in poor and developing countries where economic opportunity is limited (Hoyt, 2001; O’Connor et al., 2009). Given the historical trend of this industry’s continuous growth, the economic value of whale watching is probably even higher today

(Finkler & Higham, 2020). Thus, the increasing economic significance of whale watching not only reflects a paradigm shift away from commercial whaling but also demonstrates the value of non-extractive use of cetaceans, contributing substantially to global economies and, providing economic value to impoverished regions and people.

Scientists are provided with platforms of opportunity to conduct research that may be otherwise prohibitively expensive (i.e., due to vessel hire costs and/or access to remote sites), and tourism operators benefit financially as consumers worldwide are increasingly demanding sustainable practices from tourism (Technavio, 2022). Due to these economic and research values, banning whale-watching tourism may not be a realistic option for mitigating the potential risks of these activities. Alternatively, continued collaboration between tourism and scientific research, particularly research that focuses on sustainability and safety of these operations, may offer an alternative approach that supports both the economic and scientific values of whale-watching tourism.

1.1.2 Platforms of opportunity

In addition to the economic value of whale-watching tourism, this industry also provides important opportunities to advance cetacean research. The inaccessibility of many marine environments often makes studying wild cetaceans challenging. This is particularly true for those occurring predominantly offshore, where the cost of sending a dedicated research vessel can be prohibitively expensive (Kiszka et al., 2007). As a result, ‘platforms of opportunity’ are commonly utilised, which refer to vessels that already access an area of interest for another reason. Vessels used as platforms of opportunity for studying cetaceans have included ferries (Aniceto et al., 2016), whale-watching boats (Kiszka et al., 2007), fishing vessels (Cox et al., 2003), and other research vessels (Djiba et al., 2015). This working relationship can be mutually beneficial to stakeholders, as it provides researchers low-cost access to their study animals while providing financial benefit to tourism operators as consumers worldwide are increasingly demanding sustainable practices from tourism (Technavio, 2022).

Platforms of opportunity are useful for a range of research applications including photo-identification studies, species distribution patterns, parameters of energetic expenditure (e.g., swim speed, breathing rates), and even the study of whale-watching activities themselves (IWC, 2000; Stack & Currie, 2022; Williams et al., 2006). Vessels that regularly frequent the same areas, such as whale watching vessels or ferries, can be particularly valuable by enabling long-term monitoring and research studies that would otherwise be financially unfeasible (Parsons & Brown, 2017). Tourism vessels are particularly suitable as a platform of opportunity for cetacean research as they have a shared goal of encountering wildlife.

While platforms of opportunity can be extremely useful for facilitating low-cost research, there are limitations and biases associated with conducting research from these vessels. Temporal and spatial data can be biased, as the vessels' schedules are usually dictated by the main activity of the vessel and not the needs of the research (Kiszka et al., 2007). Thus, many established sampling methods cannot be used from these platforms (Mann, 1999), limiting the repeatability and comparability of studies (Sobtzick, 2010). Furthermore, vessels often disturb cetaceans (Bejder et al., 1999; Bejder & Samuels, 2003; Fiori et al., 2019; Nowacek et al., 2007), consequently biasing abundance and behavioural data. While disturbance is not specific to platforms of opportunity, it is an important consideration for any boat-based cetacean research. Finally, invasive research techniques will likely be discouraged, particularly from whale-watching vessels to reduce the risk of negatively impacting the tourism experience (i.e., by deterring the target animals). Thus, mostly passive observational studies are conducted using these platforms.

1.1.3 Potential impacts of whale-watching

Due to its non-extractive nature, whale-watching is logically more sustainable than whaling. Nonetheless, it can still have negative consequences to whale populations. Evidence has shown that whale-watching can disturb the animals they seek to interact with (Avila et al., 2015; Connor & Smolker, 1985; Constantine et al., 2004; Magalhães et al., 2002). Common disturbance responses of dolphins and whales to approaching vessels include altering their direction and speed of travel (Bejder et al., 2006), compacting their groups (Bejder et al. 1999; Bejder et al., 2006), and increasing their aerial behaviour (Magalhães et al., 2002). Disturbed animals spend less time on critical activities such as resting, socialising, and feeding (Constantine et al., 2004; Lusseau, 2003a; Steckenreuter et al., 2012; Stockin et al., 2008). There is also evidence of life-history stage related differences in response to boat-based tourism in southern right whales (*Eubalaena australias*; Lundquist et al., 2013), sperm whales (*Physeter macrocephalus*; Magalhães et al., 2002), killer whales (*Orcinus orca*; Williams et al., 2002), and several species of dolphin (Constantine, 2001; Tseng et al., 2011). Further, compliance with whale-watching regulations is often low (Fiori et al., 2019; Hoarau et al., 2020; Parsons, 2012). Therefore, understanding the behavioural responses of wildlife associated with tourism is imperative for effective management, as they can be used as indicators of disturbance (Frohoff, 2004).

While short-term behaviour changes have been studied extensively, the longer-term – and potentially negative - impacts of these changes are mostly unknown (Bejder, 2005; Bejder & Samuels, 2003). This is partly due to the difficulty of distinguishing between the effects of human presence and other potentially confounding variables such as natural mortality, immigration/emigration, and other stressors (Bain et al., 2002; Bejder, Samuels, Whitehead, Gales, et al., 2006; Corkeron, 2004). Furthermore, much of the research investigating impacts of tourism has focused on dolphins, and specifically bottlenose dolphins (*Tursiops* sp.), since they are the most targeted species for tourism (Constantine et al., 2004; Samuels et al., 2000). Comparatively little is known about the impacts of cetacean-watching that target other dolphins and whales, particularly those involving baleen whales.

Though animals may exhibit disturbance responses to whale-watching, those same animals may become habituated to human presence over time. Habituation is characterised as an enduring decrease in a response due to repeated exposure to a stimulus without subsequent reinforcement (Nisbet, 2000; Thorpe, 1963). Whales and dolphins that become de-sensitised or habituated towards human presence may be at a greater risk of experiencing harassment (Samuels et al., 2003; Samuels & Bejder, 2004), collisions with vessels (Bejder & Samuels, 2003), and entanglement in fishing gear or marine debris (Knowlton et al., 2012; Lien, 2009). Increased tolerance of humans could also result in closer encounters, increasing the risk for accidental injuries.

1.2 Swim-with whales tourism

Swim-with-whales (SWW) tourism is a relatively new subset of the whale-watching industry. This activity involves placing people in the water for the purpose of swimming with or observing wild cetaceans. SWW programs are controversial within public opinion and amongst stakeholders (Finkler & Higham, 2020). A review of the literature concerning swim-with programs concluded that they can be highly invasive (IWC, 2001). This activity can also pose risks to the human participants (IWC, 2013). Due to the potential risks to both the whales and the people, SWW has been banned in many countries (Carlson, 2011). Despite the ban, this industry has experienced rapid growth in popularity in recent years (O’Connor et al., 2009), including – under special permit – in some countries where the activity is otherwise banned (e.g., Australia, Canada). The full extent of SWW programs throughout the world is unknown, but a 2016 study found at least 75 possible with operators in existence across the world and suspected that many more undocumented operations exist (IWC, 2015). Nine species of whales are confirmed targets of SWW operations across seven countries (Gero et al., 2016).

1.2.1 Concerns and research regarding swimming with whales

While the SWW industry has experienced significant growth in recent decades, research remains lacking (Gero et al., 2016; Hoyt, 2018; IWC, 2015; Stack et al., 2021). Concern exists regarding multiple aspects of SWW activities, including the safety of both humans and animals, the effects on animal behaviour, and cumulative impacts of multiple stressors (Bejder & Samuels, 2003; Birtles, Arnold, et al., 2002; Machernis et al., 2018; Samuels et al., 2003). Dolphin-watching (including swim-with programs) has been better studied, and in several cases, behaviour changes and negative impacts have been observed (Bejder et al., 2009; Bejder, Samuels, Whitehead, Gales, et al., 2006; Bejder & Samuels, 2003; Constantine, 2001; Higham et al., 2009; Samuels & Bejder, 2004). Similar investigations into SWW programs have been repeatedly called for (Birtles, Arnold, et al., 2002; Fiori et al., 2019; Lundquist et al., 2013; Sprogis et al., 2020; Stack et al., 2021).

1.2.1.1 Risks to whales

Research findings have begun to identify the behavioural changes and risk of harm to both human and animal participants of swim-with activities. Many SWW programs directly target swims with mother-calf pairs (Gero et al., 2016), a practice that is highly discouraged (Birtles et al., 2008; Hoarau et al., 2020; Kessler & Harcourt, 2012). In the presence of tourism vessels and human swimmers, humpback whale (*Megaptera novaeangliae*) cows and calves in Tonga spent less time resting and more time diving than when observed away from tourism activities (Fiori et al., 2019). Similar disturbance responses have been reported during humpback whale swim-with activities in Australia (Sprogis et al., 2020; Stack et al., 2021), at Reunion Island in the Indian Ocean (Hoarau et al., 2020), and during swims with right whales (*Eubalaena australis*) in Argentina (Lundquist et al., 2013; Vermeulen et al., 2012). These behavioural changes almost certainly increase energy expenditure for these animals during this critical life-history stage, which could have flow-on impacts to reproductive fitness and survivability (Bejder & Samuels, 2003; Finkler & Higham, 2020). Further, the cumulative impacts of these behaviour changes, along with other known stressors, such as those due to climate change (e.g., declining food availability in the Antarctic; Agrelo et al., 2021; Flores et al., 2012; Konishi et al., 2008, 2013; Nicol et al., 2008; van Weelden et al., 2021), could result in significant declines in health (i.e., body condition), fecundity, and survival for those individual whales and/or populations. However, due to the practical considerations of such research including time, cost, logistics, and ethical consideration, these long-term effects are challenging to study (Bejder, 2005). As such, most impact studies focus on direct behavioural responses (Bejder et al., 2009; National Academies of Sciences, 2017).

1.2.1.2 Risk to humans

Injuries to human participants during swim-with whale activities have also been documented in several locations, although incidents are likely under-reported. In Australia, at least three swimmers have been struck by the pectoral fin of a humpback whale – two in Ningaloo Reef and one off the Rowley Shoals of Western Australia – each incident involving a mother with a calf (Barra et al., 2020; Sprogis et al., 2017). Agonistic displays directed towards swimmers have also been frequently observed in Tonga, suggesting that the whales may perceive the swimmers as a threat (Fiori et al., 2020). In Ningaloo Reef, these “high-risk” behaviours (e.g., agonistic behaviours and breaching) occur significantly more often near vessels and/or swimmers (Sprogis et al., 2017), further substantiating this hypothesis.

Compliance may also be a contributing factor to the risk of injury during swim-with whales activities. A swimmer was struck by the pectoral fin of a humpback whale in Tonga after attempting to touch the whale (Fiori et al., 2020). The influence of social media has been proposed as a driver of non-compliance behaviours, as the desire to capture and share unique experiences encourages individuals to seek out closer and more intimate interactions with wildlife (Pagel et al., 2020). These incidents, which are likely much more frequent due to underreporting and limited data capture, substantiate safety concerns for both whale and human participants in swim-with whale activities.

1.2.1.3 Encounter time limits as a risk mitigation strategy

Most whale-watching tourism activities, whether in-water or boat-based, impose maximum time limits on encounters with individual animals. These interaction time limits are generally applied as a precautionary approach to minimise potential impacts and/or disturbance to the animals, particularly in the absence of data on long-term or cumulative impacts. The Australian National Guidelines for Whale and Dolphin Watching (2017) outline “specific issues to be considered when developing or reviewing swimming operations”, and these include “maximum cumulative time with a pod, individual or population per day” and “maximum time for each interaction” (pg. 16). Higham et al. (2009) also recommend consideration of contact time with focal animals. Many whale watching activities are limited to a maximum of 1 - 1.5 hours with a whale or group, such as in Tonga (Fiori et al., 2020), Western Australia (Sprogis et al., 2017), and Québec, Canada (Chion et al., 2013). However, the effectiveness of this intervention is questionable, with low levels of regulatory compliance found in multiple countries (Kessler & Harcourt, 2013; Mallard, 2019; Sitar et al., 2016), no regulation in others, and many unlicensed operators (Gleason & Parsons, 2019; O'Connor et al., 2009).

1.3 Research opportunities from swim-with-whales programs

Despite their potential risks, SWW programs offer expanded research opportunities for studying cetaceans. Due to the in-water access they provide, research from these platforms is not limited to what can be observed from above-water, as with vessel-based whale-watching and research. For example, most photo-identification (photo-ID) images of cetaceans have been historically taken from boats. As a result, photo-ID studies were limited to species with distinguishing features on body parts that break the surface, such as the tail flukes of humpback whales (Katona et al., 1979), dorsal fins of bottlenose dolphins (Würsig & Würsig, 1977), or the saddle patch of orcas (Dahlheim et al., 2008). Further, opportunities to take appropriate images from vessels are limited to those brief instances when both a) the animal is surfacing, b) the specified body part is visible, and c) suitably oriented for ID. When in-water access is available, these limitations on collecting photo-identification data can be mitigated or eliminated altogether. Thus, SWW programs, despite their inherent risks, present valuable opportunities for cetacean research, offering unique in-water access that transcends the constraints imposed by traditional vessel-based and aerial observation methods.

1.3.1 Morphometry

In-water access to cetaceans also lends itself particularly well to the study of morphometry. Biological morphometry describes the quantitative size and shape of an organism (Stower et al., 1960). This involves the numeric measures of external physical features, for example body and appendage lengths, and the relationships between these features. Morphometry can be studied at different organizational levels (e.g., an individual organism, a particular life-history stage, an entire species or taxonomic group, etc.) to help understand a range of biological characteristics of an individual or population unit, such as age, sexual maturity and ecological function. Body size has been identified as one of the most important factors contributing to an individual or species' function and performance (Schmidt-Nielsen, 1984). Thus, precise morphometric measurements are paramount to understanding many key characteristics for a population or species.

Historically, lethal sampling, either scientifically or opportunistically from strandings and commercial whaling, has provided most morphometric measurements of large whales (Kato et al., 2022; Kato & Fujise, 2000; Mackintosh & Wheeler, 1929; Yablokov, 1994). These data can be useful, but strandings and incidental deaths are unpredictable, uncommon, and are often biased towards sick, very old or very young animals (Caughley, 1966; Dunstan et al., 2008). Further, length estimates from Antarctic whales are generally considered to be poor (Best, 1984), and evidence suggests widespread falsification of both catch and length data throughout the 20th century (Clapham & Ivashchenko, 2009, 2016; Ivashchenko & Clapham, 2015; Yablokov, 1994). Therefore, data from these sources cannot be relied upon to provide accurate insights into wild cetacean populations. The use of these methodologies declined throughout the 20th century due to concerns over costs, biases, declining populations, and moral values/ethics (Baker et al., 2000; Clapham & Ivashchenko, 2009; Clapham, 2016).

1.3.2 Photogrammetry

As the use of lethal sampling techniques began to decline, the use of less invasive, indirect techniques arose to measure live cetaceans at sea. Researchers begun using photogrammetry (the science of making measurements from photographs or video footage) to derive length estimations of marine vertebrates in the 1980s (Best & Rüther, 1992; Klimley & Brown, 1983; Perryman & Lynn, 1993; Perryman & Westlake, 1998). These applications allowed systematic in situ collection of data and provided larger and more representative sample sizes of animal populations than historical sampling methods. Photogrammetry techniques have proven useful for a range of research objectives for cetaceans including population estimates (Fettermann et al., 2022), investigating body condition (Christiansen et al., 2023; Vermeulen et al., 2023), monitoring entanglements (Ramp et al., 2021; Stewart et al., 2021), health assessments (Apprill et al., 2017; Pirotta et al., 2017), behavioural studies (Orbach et al., 2020; Torres et al., 2020), and taxonomic classification (Leslie et al., 2020). Thus, the transition to non-lethal sampling techniques has provided a more sustainable approach to the study of wild cetaceans that has since enabled diverse research objectives across a range of applications.

Photogrammetry data can be collected from several different platforms. Initially, photogrammetry of cetaceans was primarily boat-based (Dawson et al., 1995) or from occupied aerial vehicles (Best & Rüther, 1992; Cubbage & Calambokidis, 1987; Ratnaswamy & Winn, 1993). More recently, advances in drone technology have facilitated the development of low-cost unoccupied aerial vehicle (UAV) photogrammetry techniques (Bierlich et al., 2021, 2023; Burnett et al., 2019; Christiansen et al., 2016; Goebel et al., 2015; Gray et al., 2019; Krause et al., 2017; Torres et al., 2020; Vermeulen et al., 2023). Now, UAV-based photogrammetry is one of the most widely utilised techniques for measuring body size, growth, and condition of cetaceans (Castrillon & Bengtson Nash, 2020).

1.3.2.1 Constraints associated with common methods

While boat-based and aerial techniques are useful, they require specific environmental and behavioural conditions, limiting their widespread application. These techniques generally require very calm weather, with wind potentially interfering with aircraft flight (Duffy et al., 2018; Gao et al., 2021)and wave action interfering with views of the animals (Best & Rüther, 1992; Christiansen et al., 2016). These platforms also require specific surfacing behaviour by the target animals to avoid underestimation of length due to dorso-ventral body flexure; ideally, the animals will be stretched out at the surface (Christiansen et al., 2018). Further, aerial- and boat-based photogrammetry are generally limited to dorsal views only, since these techniques rely exclusively on surfacing behaviour. Finally, many boat-based photogrammetry studies have relied upon allometric extrapolation of various morphological dimensions to estimate full-body length (e.g., tail fluke width), as the entire body is typically not visible from boat-based vantage points (Dawson et al., 1995; Durban & Parsons, 2006; Growcott et al., 2012; Jaquet, 2006; Ortega-Ortiz et al., 2022). However, considerable variation in allometric scaling exists for some cetacean species (Spitz et al., 2000; Tomilin, 1967), and allometric relationships are unknown for others. As such, the application of boat-based and aerial measurements is limited to those species for which allometric relationships are well established, or the animal's behaviour and weather conditions allow for straight, full-body measurements. The appropriateness of these platforms thereby varies by both species and location, and there are many circumstances under which neither option is viable.

1.3.2.2 Alternative methods: Underwater photogrammetry

Alternatively, underwater, diver-operated photogrammetry systems have been used for morphometric research for a wide variety of marine fauna when in-water access is available (Gibson et al., 2016). Animals successfully measured using these techniques include several shark species (Klimley & Brown, 1983; Rohner et al., 2011; Smith et al., 2015), southern bluefin tuna (*Thunnus maccoyii*; Phillips et al., 2008), reef manta rays (*Manta alfredi*; Deakos 2010), humpback whales (*Megaptera novaeangliae*; Spitz et al., 2000). Given adequate water visibility and approach distance, the entire length of an animal can often be photographed, eliminating the error associated with morphometric scaling and extrapolation often required with boat-based and aerial techniques. Further, in-water access potentially allows the animals to be photographed from many different angles, thus providing increased measurement capabilities over aerial and boat-based platforms (Koopmans & Wijffels, 2008). Diver-operated systems can also be relatively inexpensive compared to occupied aerial surveying and/or vessel hire, generally requiring only simple photographic and measurement equipment mounted to a sturdy frame, similar to UAV systems. Therefore, swim-with programs offer an opportunity to expand the application of underwater photogrammetry techniques, particularly where costs are otherwise prohibitive and where above-water methodologies are unsuitable.

1.3.3 Array comparison of underwater photogrammetry systems

1.3.3.1 Single-camera photogrammetry

Several variations in physical photogrammetric systems exist. These can be broadly split into two categories: single-camera systems and stereo systems. Single-camera techniques use one camera in an underwater housing and either a sensor to determine the distance from the camera to the target animal (termed the "range") (Figure 1.1), or an object of known size for scale near the target animal. For diver-operated systems the sensor is usually a depth sounder (Dunstan et al., 2008; Spitz et al., 2000, 2002), for aerial surveys an altimeter (Best & Rüther, 1992; Ratsimbazafindranahaka et al., 2021), and for boat-based photogrammetry a laser rangefinder (Jaquet, 2006; Wong & Auger-Méthé, 2018). First, a calibration is performed, during which a two-dimensional object of known size (e.g., a PVC pipe) is filmed at known ranges, to determine the camera lens angle. The trigonometric relationship between the range and the camera lens angle allows the field-of-view (FOV) to be calculated. Subsequently, the length of the animal (or another morphometric feature) can be estimated based on the proportion of the FOV it uses (usually by counting pixels).

An additional calibration is required to identify and correct any image distortion, such as barrel distortion or image stretching (Clarke & Fryer, 1998; Dunbrack, 2006a; Dunstan et al., 2008; Sobtzick, 2010; Spitz et al., 2000). For this calibration, a uniform two-dimensional grid consisting of small squares (2-5cm) is filmed at sufficiently close range that it fills the entire FOV of the camera. The length of each square is calculated using the same formulae as for length measurements, and the comparison between expected (i.e., real) and measured (i.e., calculated) size allows a regression equation to be derived to correct for detected distortion.

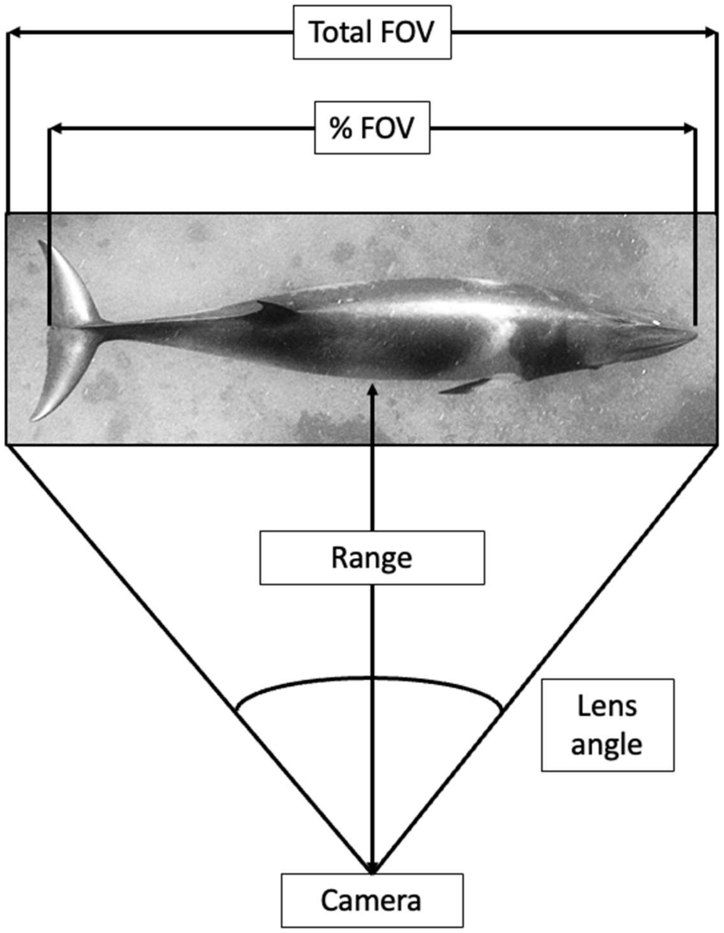


Figure 1.1. Schematic of measurement determination using underwater videogrammetry with a single camera and distance sensor. Adapted from Dunstan et al. (2008).

1.3.3.2 Stereo-photogrammetry

Stereo photogrammetry uses paired cameras, fixed on a rigid bar/frame a known distance apart, so that the field-of-views of both cameras overlap (Figure 1.2; Klimley Brown, 1983; Shortis & Harvey, 1998). Some cameras are mounted parallel to each other (e.g., Klimley & Brown 1983; Bräger et al., 1999); however, most studies of marine megafauna mount the cameras at a small, inwardly converging angle to maximise the overlapping field-of-view (e.g., Shortis & Harvey, 1998; Smith et al., 2015). The further the cameras are separated (termed the “base separation”), the more precise measurements are

(Shortis & Harvey, 1998). Conversely, portability decreases with increased base separation, and thus a trade-off exists that should be considered on a case-by-case basis. Photo or video footage can be taken (i.e., photogrammetry or videogrammetry); if taking video, post-field selection of still images is required for analysis. System calibrations and footage analysis are more complicated than those for single-camera and paired-laser methods and are usually conducted using calibration tools and computer software designed specifically for these purposes (e.g., computer program SeaGIS 2016a; see Chapter 2).

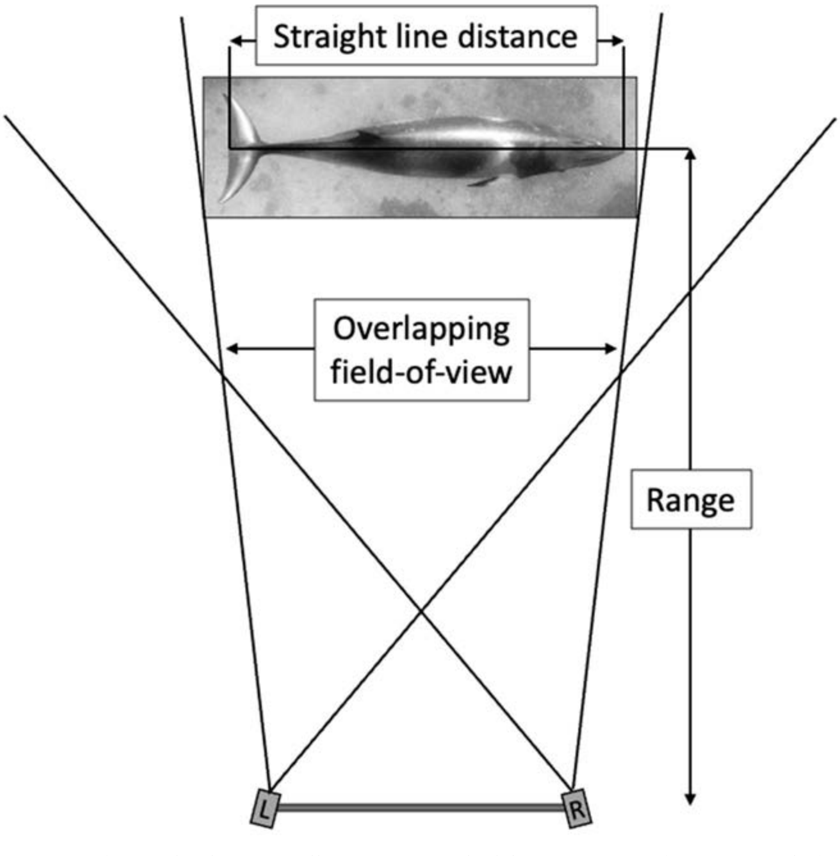


Figure 1.2. Geometry of a typical stereo diver-operated video (SDOV) frame. L = left camera, R = right camera. Adapted from Shortis & Harvey (1998).

Stereo-image techniques generally produce more accurate and precise measurements compared to other methods (Harvey et al., 2002). The ability for stereo systems to correct for parallax error (i.e., the underestimation of length that occurs when the measurement plane is not exactly parallel to the camera plane) is likely to be a significant contributor to the increased quality of SDOV measurements over other systems. This feature confers an additional advantage, as the animal is not required to be absolutely perpendicular to the camera(s) (Harvey et al., 2002; Jaquet, 2006), which may increase the quantity of suitable footage for making measurements. Dawson et al. (1995) have argued that the accuracy and precision for stereo photogrammetry is likely approaching the most accurate measurements possible for open ocean conditions, when known biases are corrected for. The advances made in recent decades to stereo-image technology are considered a significant contribution to the effectiveness and management of marine ecosystems for conservation objectives (Gibson et al., 2016).

1.4 Dwarf minke whales

The dwarf minke whale (*Balaenoptera acutorostrata* subsp.) is the second smallest baleen whale, born at approximately 2 m in length and growing to a maximum measured length of 7.8 m (Arnold, 1997; Best, 1985). Dwarf minke whales are distributed throughout the southern hemisphere, including Antarctica, and were first acknowledged by science in 1985 (Arnold et al., 1987; Best, 1985; Kasamatsu et al., 1993). Prior to this, there were only scattered reports of a “white-flippered form” of the southern hemisphere minke whale (*Balaenoptera bonaerensis*; Arnold et al. 1987). Despite sharing its range with the southern hemisphere minke, comparisons of the external colour patterning suggest a closer relation to the ordinary (northern hemisphere) minke whale (Arnold et al., 1987; Best, 1985), of which there are two described subspecies (*Balaenoptera a. acutorostrata* and *B. a. scammoni*).

Genetic and osteological data corroborate this finding (Milmann et al., 2021; Pastene et al., 2010; Ramirez-Flores et al., 2019; Rice, 1998). The exact taxonomic status of the dwarf minke whale remains unresolved, and it is currently considered an undescribed subspecies of the ordinary minke whale.

1.4.1 Significance of the Great Barrier Reef for dwarf minke whales

The only known predictable aggregation of dwarf minke whales occurs seasonally in the Great Barrier Reef (GBR), Australia (Arnold, 1997). After migrating from the Antarctic (Birtles et al., 2015), a minimum of several hundred animals aggregate in the Ribbon Reefs each year, with approximately 15% of photo-identified individuals re-sighted in subsequent years (Birtles et al., 2001; Sobtzick, 2010). Similar inter-annual site fidelity has been observed in other baleen whales at wintering grounds and summer feeding grounds (Hoelzel, 1998; Stevick et al., 2006; Valenzuela et al., 2009).

While aggregating in the GBR, dwarf minke whales are unusually inquisitive, readily approaching vessels and divers and often maintaining contact for prolonged periods (Arnold, 1997; Arnold & Birtles, 1999; Birtles, Arnold, et al., 2002). This gathering likely serves as a mating ground for these otherwise solitary animals. While courtship behaviours are frequently observed, copulation has never been recorded (Birtles, Arnold, et al., 2002; Gedamke, 2004; Mangott, 2010). The inquisitive behaviour of dwarf minke whales in the GBR was first documented in the 1980s (Arnold et al., 1987). In the 1990s, the liveaboard dive tourism industry expanded operations into the winter months, and they began to regularly observe this inquisitive behaviour (Arnold, 1997). From 1996, dedicated swim-with trips were advertised. A permit system was introduced by the Great Barrier Reef Marine Park Authority (GBRMPA) in 2003, with nine permits issued. This cap remains in place today.

1.4.2 Swim-with tourism facilitating research

Almost all dedicated field research on dwarf minke whales occurs through this small tourism industry. Permitted operators regularly provide berth spaces for researchers on their liveaboard vessels throughout their “minke season” (a 6 – 9 week period each June and July across the mid-peak of the seasonal aggregation period). The reliance on platforms of opportunity is primarily driven by limited funding for dedicated research on dwarf minke whales. However, the remoteness of the aggregation area is also a contributing factor, increasing the logistical and financial demands of operating a dedicated research vessel in this location.

The research facilitated by tourism operators on dwarf minke whales has been multidisciplinary, investigating various aspects of: (1) the sustainable management of the swim-with tourism industry (e.g., Arnold & Birtles, 1999; Birtles, Arnold, et al., 2002; Birtles et al., 2001; Curnock, Birtles, & Valentine, 2013; Valentine et al., 2004); (2) external features and colour patterns (e.g., Arnold et al., 2005; Hutchings et al., 2023; Konovalov et al., 2020); (3) basic population demographics (e.g., Dunstan et al., 2008; Sobtzick, 2010); and (4) behaviour of the whales during swim-with tourism interactions (e.g., Mangott, 2010; Mangott et al., 2011; Valentine et al., 2004). Elsewhere, data have been collected opportunistically from various sightings, strandings, and cetacean surveys throughout the southern hemisphere including the Southern Ocean/Antarctica (Acevedo et al., 2011; Kasamatsu et al., 1993), South America (Andriolo et al., 2010; Di Beneditto et al., 2018; Hassel et al., 2003; Milmann et al., 2023), South Africa (Best, 1985), New Zealand (Dawson & Slooten, 1990), and other parts of Australia (Arnold et al., 1987). Additionally, some data have come from whaling records (Kasamatsu et al., 1993; Kato et al., 2022; Kato & Fujise, 2000), but these data should be treated with caution (see section 1.3.1).

1.4.2.1 Citizen science contributions: photo-identification imagery

Citizen science has played an integral role in developing James Cook University's (Minke Whale Project; MWP) long-term photo-identification database of dwarf minke whales sighted in the Great Barrier Reef. Many passengers, including vessel crew, are hobbyist photographers, and others simply wish to document their wildlife encounters. Tourism operators also employ professional photographers to document passengers' wildlife encounters, who then sell their imagery to the passengers as a souvenir of their experience. As a result, numerous cameras are usually in the water at any given time during an interaction, sometimes up to several dozen. This provides an enormous opportunity for data collection from tourism vessels. The value of such image donations to augment photo-identification research was demonstrated by Sobtzick (2010) who found that citizen science footage comprised over two thirds of the high-quality imagery used for photo-ID of dwarf minke whales. Additionally, some whales were identified exclusively from citizen science imagery (i.e., not captured in researcher imagery), and thus would have otherwise been missed. As a result, everyone on board these trips is encouraged to donate copies of their underwater imagery to support the MWP's photo-identification research, and are briefed by vessel crew and researchers on how to take useful ID photos. Some many thousands of donated photos and videos are collected each season, often orders of magnitude more imagery than collected by researchers alone. During the 2006 field season, citizen science imagery accounted for approximately 70% of the high-quality imagery used for photo-identification purposes by the Minke Whale Project (Sobtzick, 2010).

1.4.2.2 Potential impacts and risks of swimming with dwarf minke whales

The uniquely inquisitive nature of dwarf minke whales distinguishes their swim-with interactions from those with other cetaceans. Unlike most swim-with whales (SWW) interactions worldwide, which are typically initiated by humans and last only a few minutes (Gero et al., 2016), encounters with dwarf minke whales are characterised by voluntary approaches by the whales themselves and can span several hours (Arnold & Birtles, 1999; Curnock, Birtles, & Valentine, 2013). As a result, some of the closest known whale-human approaches and longest interaction durations in SWW tourism activities are with dwarf minke whales in the Great Barrier Reef (Birtles & Mangott, 2011; Samuels et al., 2003). While this behaviour highlights the uniqueness of these interactions, it also raises concerns about the potential risks of harm to both the humans and whales (Birtles, Arnold, et al., 2002; Birtles et al., 2001). The prolonged duration and close proximity of these encounters substantiates a strong research focus on understanding the dynamics of swim-with encounters with dwarf minke whales.

1.4.2.3 Knowledge gaps

Despite decades of research in the Great Barrier Reef, significant knowledge gaps remain for dwarf minke whales, including overall population size, structure and trajectory, life history parameters, reproductive biology, and migratory patterns. Extensive effort has been made to study and enhance the sustainability and safety of the swim-with tourism industry in the Great Barrier Reef. Numerous research programs and studies have sought to identify the risks of these interactions to both the people and the whales (Curnock, 2010; Curnock, Birtles, & Valentine, 2013; Curnock et al., 2019; Sobtzick, 2010; Valentine et al., 2004), and a collaborative management strategy including multiple stakeholders has allowed this research to directly inform industry governance and management (Birtles et al., 2001, 2010, 2014; Birtles, Valentine, et al., 2002; Curnock, 2010; Curnock, Birtles, Valentine, et al., 2013; Valentine et al., 2004). With a suite of protocols already employed by the industry to mitigate risk and increase passenger safety, several risk assessments have concluded that the overall risk of harm to swimmers and whales is low; however, the potential for habituation is a major concern (Birtles, Arnold, et al., 2002; Curnock, Birtles, Valentine, et al., 2013). Certain individual animals have exhibited evidence of short-term behavioural changes, approaching swimmers closer both as an encounter progresses and across subsequent encounters within a season (Mangott, 2010; Mangott et al., 2011). More research is needed to determine the extent of these changes, their long-term implications, and the broader behavioural trends within encounters with dwarf minke whales.

The inquisitive behaviour of the whales, coupled with the accessibility facilitated by the tourism industry, have provided ideal conditions to employ underwater photogrammetry techniques for the study of dwarf minke whales in the Great Barrier Reef. A specialised photo-identification methodology for dwarf minke whales has been developed over numerous years (see Chapter 2 section 2.3.1), and initial measurements of total body length on live dwarf minke whales were made using single-camera techniques in the mid-2000s (Dunstan et al., 2008; Sobtzick, 2010). By combining photo-identification and body length measurements, these studies enabled the first ever population size estimates for dwarf minke whales, insights into demography, behaviour, and population structure in the Great Barrier Reef, and preliminary data on live animal growth rates. Given the broad utility of morphometric data, ongoing collection would be worthwhile, particularly for enabling monitoring of important population trends over time with multiple time series data. Further, methodological enhancements could yield more robust measurements and broaden measurement capabilities beyond total body length.

1.5 Research aims, objectives, and thesis structure

In this thesis, I aimed to increase the quality and quantity of morphometric data of dwarf minke whales and developed species-specific protocols to facilitate this. I also built on previous research by combining measurement science, photo-identification, and behavioural research to develop a deeper understanding of dwarf minke whale demography, growth patterns, and behaviour during swim-with activities.

This thesis has two overarching aims:

(1) To increase the quality and quantity of morphometric measurements of dwarf minke whales, and

(2) Increase our understanding of dwarf minke whale biology and behaviour using these improved measurement techniques.

To achieve these aims, I developed three objectives, each corresponding to a data chapter in this PhD thesis:

Objective 1: To develop more precise measurement techniques for dwarf minke whales

Study 1 – Chapter 3. In Chapter 3, I trialled the replacement of a single-camera photogrammetry system with a stereo system for making morphometric measurements of dwarf minke whales in the Great Barrier Reef. I compared measurement quality between both systems, using data collected in this study via a diver-operated stereo-video (SDOV) system and those collected by Sobtzick (2010) via a single-camera system. I then developed additional protocols to optimise the filming and measurement process for small- to medium-sized cetaceans, and dwarf minke whales in particular. This Chapter formed the basis for all following data Chapters, as these new techniques and protocols are followed throughout.

Objective 2: To investigate demographic and temporal differences in morphometry parameters of the interacting dwarf minke whale population in the Great Barrier Reef

Study 2 – Chapter 4. In Chapter 4, I explored the morphometric relationships between several body measurements of dwarf minke whales using the stereophotogrammetry filming and analytical techniques developed in Chapter 3. I investigated population structure, biological scaling, sexual dimorphism, growth rates, body condition, and I investigated long-term demographic trends by comparing body length measurements to data from previous studies.

Objective 3: To investigate the drivers of interactive behaviour of dwarf minke whales during swim-with tourism activities in the Great Barrier Reef

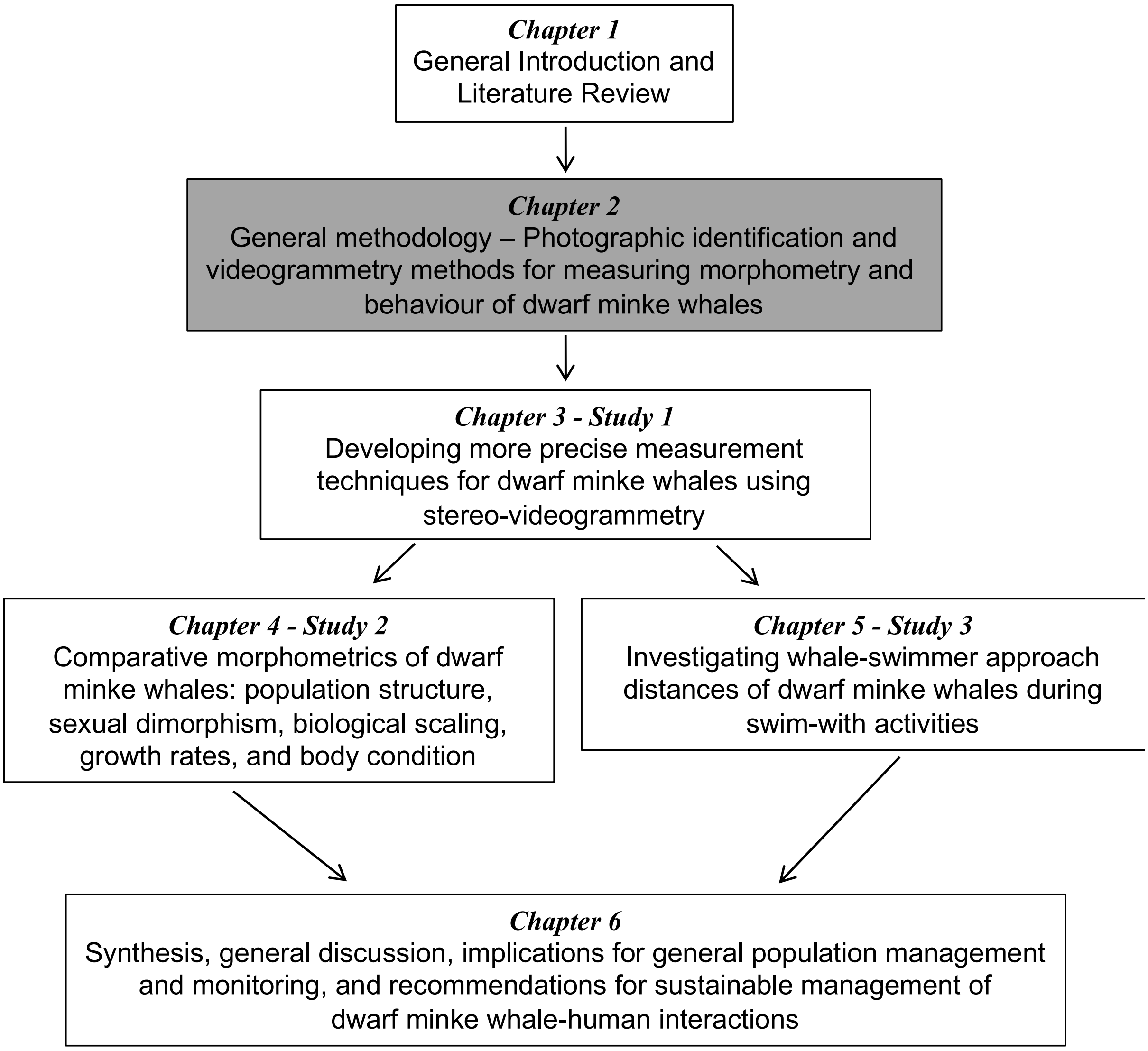
Study 3 – Chapter 5. In Chapter 5, I used the same SDOV system and measurement software to investigate variation in behaviour of dwarf minke whales during tourism activities in the Great Barrier Reef. I measured the approach distances of whales to swimmers during in-water interactions and use mixed methods modelling and regression analysis to identify potential drivers of this inquisitive behaviour, using approach distance as a proxy.

Finally, in Chapter 6, I provide a summary of my major research findings, their contribution to the biological understanding of dwarf minke whales, and the potential implications for the conservation of dwarf minke whales and management of the swim-with tourism industry in the Great Barrier Reef. I also provide future research recommendations to further contribute to these fields.

All data chapters (Chapters 3-5) were written in a format to enable publication in peer reviewed journals, as recommended in James Cook University's Higher Degree by Research Thesis Preparation Guidelines. Chapter 3 was published in Marine Mammal Science in 2020 (doi: 10.1111/mms.12724). Minimal edits have been made to Chapter 3 post-publication; some Introduction and Methods text has been removed and paraphrased in Chapters 1 and 2 of this thesis, to minimise repetition.

2 CHAPTER 2:

GENERAL MATERIALS AND METHODS



Preamble

This chapter describes the general field methodologies and data collection protocols used in this thesis. The field protocols were developed by James Cook University's Minke Whale Project over years of utilising endorsed swim-with liveaboard tourism vessels as platforms of opportunity to study the dwarf minke whales that aggregate in the Great Barrier Reef each year and are described in Birtles, Arnold, et al., (2002). I evaluated these protocols in the context of my research aims and further developed them to support my specific data collection requirements and needs.

2.1 Study site

2.1.1 Aggregation area

Dwarf minke whales have been sighted throughout much of the Great Barrier Reef Marine Park, from north of Lizard Island (14°36S) to the Swain Reefs (22°S) (Arnold, 1997). Most sightings, as well as the inquisitive behaviour that enables the success of the swim-with tourism industry, occur almost exclusively in the Ribbon Reefs region near Lizard Island (Fig. 2.1). More specifically, over half of all reported dwarf minke whale sightings occur in the outer lagoon region area Ribbon Reefs 9 and 10 (Curnock, Birtles, & Valentine, 2013). Ninety percent (90%) of these sightings occur during austral winter in the months of June and July. Sightings are most common in the Great Barrier Reef, and their characteristic inquisitive and aggregate behaviour that facilitates such success in the swim-with tourism industry appear to be particularly localized there (Birtles, Arnold, et al., 2002; Curnock, Birtles, & Valentine, 2013; Mangott et al., 2011). This region and seasonal occurrence is often referred to by researchers and tourism operators as the "aggregation area", and will be referred to as such herein.

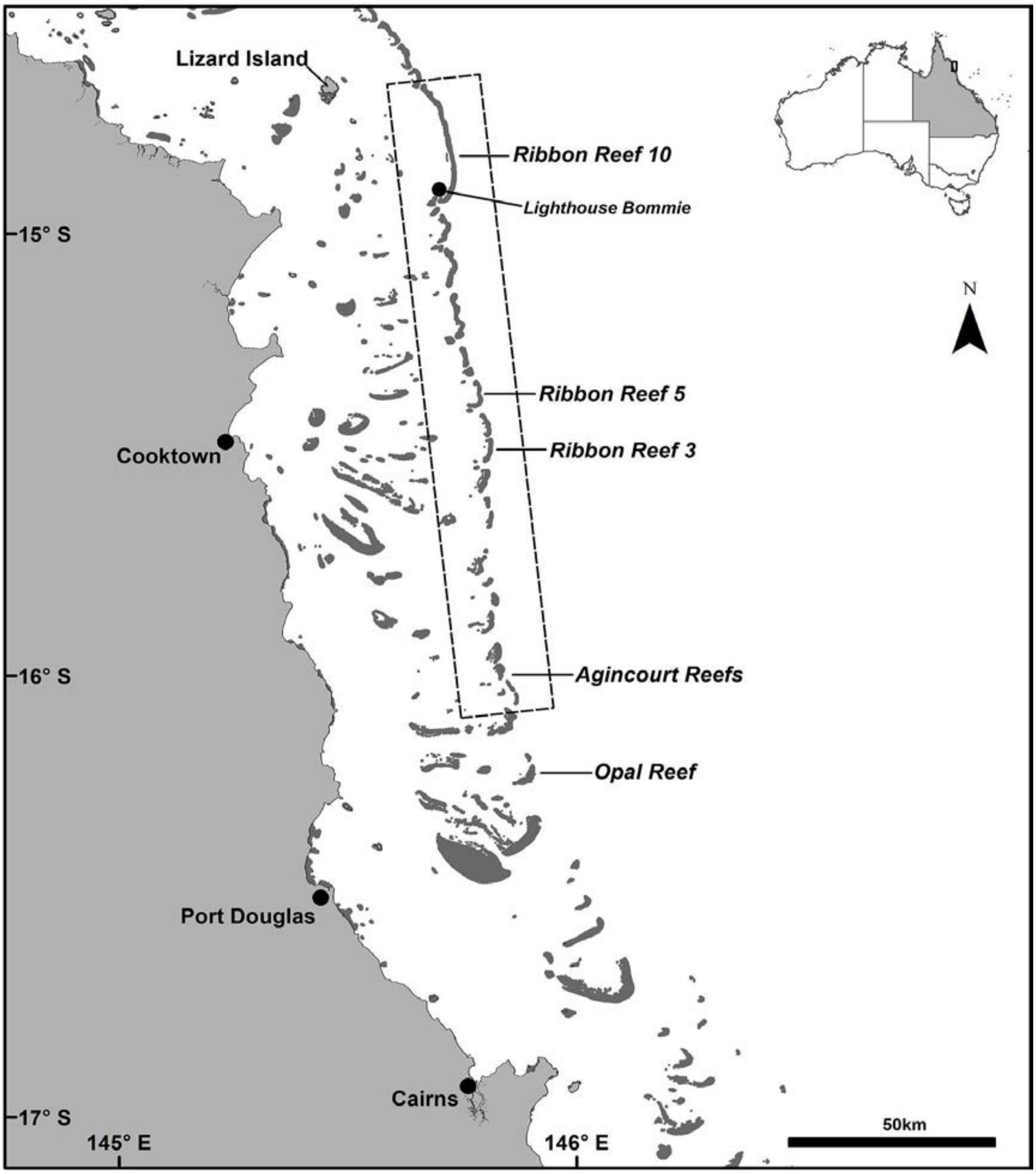


Figure 2.1. Section of the Great Barrier Reef where most sightings of dwarf minke whales occur. Swim-with tourism vessels operate in the dashed area to the west of the outer Ribbon and Agincourt reef complexes. Vessels depart from Cairns and on their northerly steam begin to regularly encounter dwarf minke whales near Ribbon Reef 3, with the highest sightings frequency at dive sites close to Ribbon Reef 10.

2.1.2 Remote site access: swim-with dwarf minke whale tourism platforms of opportunity

Dedicated dwarf minke whale research has been facilitated through in-kind support from the swim-with tourism industry in North Queensland. Specifically, tourism operators have allocated vessel berth space for researchers aboard their trips to the aggregation area. Occasionally, media expeditions and private charters have also supported this research, and these opportunities have been utilised ad hoc to collect additional field data. However, the majority of site access is provided through mutually beneficial relationships with regular tourism operators. During the three field seasons of this study (2017 – 2019), all but one field trip were aboard regular tourism vessels, and one was a private charter arranged for a media documentary (Table 2.1). Some vessels provided a single berth per trip to researchers, while others provided space for up to three researchers per trip.

2.1.2.1 Trip overview and vessel itinerary

Swim-with dwarf minke whale tourism trips are combined activity trips, including reef SCUBA diving and swimming with whales when encountered. Through years of experience and frequent crew exchange amongst operators, endorsed liveaboard vessels have developed similar schedules for these dedicated “minke trips”. Generally, four to five reef dives are scheduled each day, some of which may be exchanged with swimming with whales if they are encountered. Most in-water interactions with dwarf minke whales begins when one or more whales approach a stationary vessel already moored or anchored at a dive site. As a result, selection of dive sites is based on a combination of both SCUBA dive suitability and probability of a whale encounter. If weather conditions and passenger diving experience are suitable,

Table 2.1: Details of data collection field trips.

Permittee/Sponsor	Vessel name	Length	Cruising speed	Passenger capacity	Itinerary overview	Data collection trip dates
Mike Ball Dive Expeditions Pty Ltd	***Spoilsport***	29 m	12 kn	31	3- and 4-day trips to the Ribbon Reefs. Departed Cairns on Thursdays and Lizard Island on Mondays throughout June and July.	8 – 15 June 2017 22 – 29 June 2017 14 – 21 June 2018 6 – 13 June 2019 4 – 11 July 2019
Divers Den Investments Pty Ltd (now operating as Entrada Travel Group Pty Ltd)	***Ocean Quest***	37 m	13 kn	48 (reduced to 35 for swim-with minke trips)	4-day liveaboard trips to the outer reefs. Spent day 1 at outer reef dive sites off Cairns, spent days 2-4 in Ribbon Reefs. Departed Cairns on Fridays throughout June and July.	16 – 20 June 2017 7 – 11 July 2017 14 – 18 July 2017 8 – 12 June 2018 22 – 26 June 2018 6 – 10 July 2018 13 – 17 July 2018 27 – 31 July 2018 21 – 25 June 2019 28 June – 2 July 2019 12 – 16 July 2019
ICG Australia Pty Limited (now operating as Entrada Travel Group Pty Ltd)	***Spirit of Freedom***	37 m	12 kn	24	3-day liveaboard trips to the outer reef. Spent day 1 at outer reef dive sites off Cairns, spent days 2-3 in Ribbon Reefs. Departed Cairns on Mondays, returned Thursdays, throughout June and July.	4 – 7 June 2018 23 – 26 July 2018
Great Latitude Pty Ltd (vessel permittee), Nine Entertainment Co Pty Ltd	***ARGO***	39 m	10 kn	18	4-day liveaboard trip to the Ribbon Reefs. Departed Yorkey’s Knob 20 July; 4 days in the Ribbon Reefs, returned 25 July (media expedition private charter)	20 – 25 July 2017

the sites with the highest probability of encountering dwarf minke whales, such as Lighthouse Bommie and Steve's Bommie, are almost certainly visited at least once every trip (Curnock, Birtles, & Valentine, 2013). Whales are occasionally spotted by someone while the vessel is steaming and, depending on the vessel's schedule and conditions at the location (e.g., depth, current, visibility), the vessel may stop to see if the whale(s) will interact. Dedicated swim-with trips generally commence in the first week of June each year and run through the last week of July, guided by consistent yearly "peak season" sightings histories (Birtles et al., 2014). Sightings occasionally occur outside of these dates, particularly at the end of May and beginning of August. However, whales sighted at these times are noticeably less interactive, with fewer whales per encounter and shorter encounter durations.

2.2 Data collection

2.2.1 Equipment and calibration methods

The diver-operated stereo-video (SDOV) unit used in this thesis was purchased from SeaGIS, a measurement science software and hardware company (Fig. 2.2). This frame had a base separation of 800 mm and was fitted with two GoPro Hero 4+ Silver action cameras enclosed in waterproof housings. GoPro camera settings used were 1920 x 1080 resolution, 30 fps, and medium FOV. These settings were chosen in consultation with J. Seager, the developer of the SeaGIS camera systems and measurement software. Calibration equipment consisted of a 1 x 1 x 0.5 m purpose-built calibration "cube" and a 1.2 m measurement "scale bar", both covered in high-contrast targets of known separation, also supplied by SeaGIS.

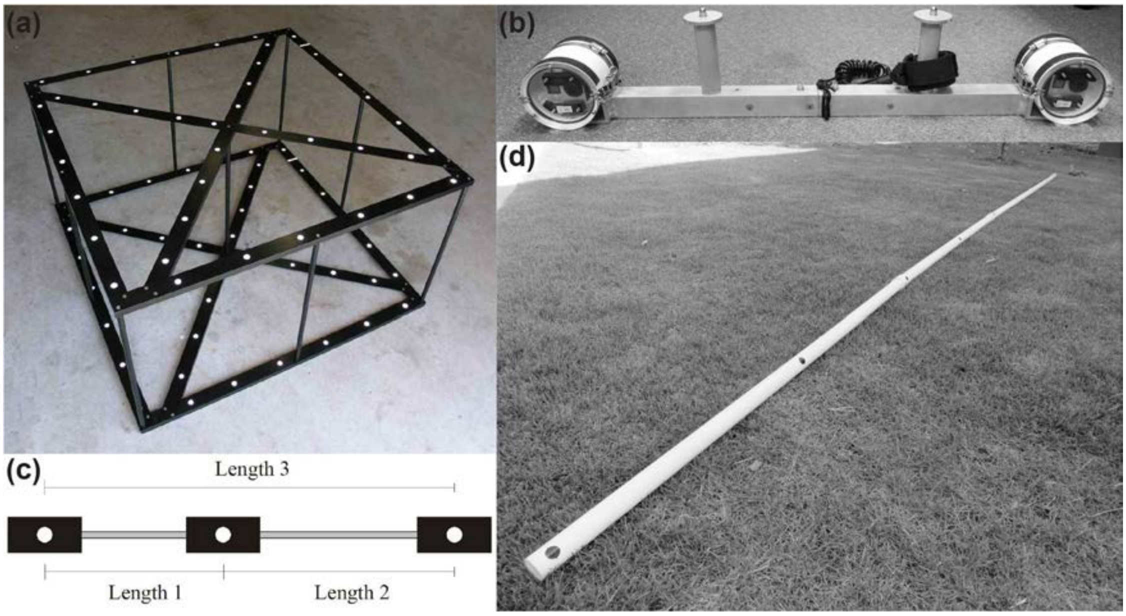


Figure 2.2. Technical equipment used for videogrammetry data collection. a) Three-dimensional cube used for calibration of stereo-videogrammetry system; b) diver-operated stereo video (SDOV) camera system (frame + GoPro cameras); c) schematic of calibrated scale bar used to assess SDOV system calibration accuracy and stability (Length 1 = 0.4582 m, Length 2 = 0.7526 m, Length 3 = 1.2108 m); and d) PVC pipe used in pool trial, with marked points for reference every 1 m. (a) and b) reprinted from Seager (2016a); Seager (2016b).

Calibrations were conducted in a large swimming pool prior to each field season. SeaGIS recommended to re-calibrate whenever cameras are replaced or substantially bumped. Thus, one additional mid-season calibration was required during the 2017 sampling period due to a camera flooding occurrence. The calibration process is described in detail in SeaGIS (2016a) and involves recording video footage of the calibration cube with the SDOV system. During calibration the cube was rotated and filmed at 20 pre-determined orientations at approximately 2 m distance. This allowed the cube to fill as much of the overlapping field of view as possible from both cameras (see Chapter 1 section 1.3.3.2), from herein referred to the “effective field of view, or eFOV”, ensuring that the entire eFOV can be calibrated. Following the cube filming, the 1.2 m scale bar was filmed at multiple orientations and distances to enable post-field validation of the calibration procedure (i.e., to compare estimated vs actual lengths). The integrity of the system's calibration was validated periodically throughout each field season by re-filming the scale bar under typical field conditions (i.e., in an open ocean setting). After the calibration data collection, footage was processed through the SeaGIS suite (see section 2.3.2.1). This completed the calibration process.

2.2.2 General field protocols

2.2.2.1 Encounter overview

A dedicated surface watch for whales was conducted each day while at sea, generally from the top deck of the vessel at a height of approximately 7 – 10 m. Watch was kept throughout daylight hours, from approximately 6:30 am - 6:30 pm in June-July. When a whale was sighted near the vessel, one to two nylon ropes with floats were deployed from the vessel, usually attached at the stern, which trailed behind the vessel on the surface. A crew member or researcher then entered the water to see if the whales would interact. Once a whale was confirmed as sighted underwater, an *in-water interaction* began (Birtles, Arnold, et al., 2002; Mangott, 2010) and passengers entered the water. As part of the endorsed operators' permit conditions, all swimmers, including crew and researchers, are required to hold onto the surface rope (Birtles et al., 2008). Whales typically swim around vessels in large loops and tend to aggregate specifically around swimmers (Mangott, 2010). Anywhere from 1 to 20 individual whales may be sighted at a time and are visible from distances up to 20-40 m underwater (depending on localized conditions). In-water interactions in the vicinity of Ribbon Reefs Nos. 9 and 10, where the majority occur, typically last between 3 – 4 hours (Sobtzick, 2010). Occasionally, encounters up to 12 hours have been recorded in this area (Birtles, pers. comm.).

Most often, in-water interactions occurred while the vessel was moored or anchored at a dive site. Occasionally, if whales were sighted while steaming, the engines were stopped and a *drift encounter* occurred. Provided the wind speed was sufficiently calm and wind direction was suitable (i.e., to not drift into an island or onto a reef), the crew deployed one or two surface ropes without mooring or anchoring the vessel. The vessel would slowly drift in the wind, and whales would often follow along or join the encounter as the vessel drifted through the aggregation area. All legal obligations for endorsed operators and swimmers during encounters with dwarf minke whales can be found in the industry's Code of Practice (Birtles et al., 2008).

2.2.2.2 Photogrammetry filming protocols

Once an in-water interaction was underway, cameras were turned on and locked into their housings in the SDOV frame. Before entering the water, a synchronising hand gesture was filmed to enable post-field synchronisation of the video footage (e.g., a quick clap of the hands or pinching of the fingers). I then entered the water as soon as possible with the SDOV system and remained in the water for the duration of the interaction. To correct for any potential desynchronisation due to video drift (Seager, 2016d), the synchronising hand gesture was repeated periodically throughout filming periods, roughly every 15 min. I positioned myself at the end of the surface rope whenever possible for consistency, to film the encounter from the same general position relative to other swimmers and the vessel.

I remained in the water and continued filming whenever whales were present, until either the encounter ended or the camera battery life ended. Returns to the boat were kept as brief and infrequent as possible, for example, to recharge and swap cameras, use the bathroom, or warm up briefly during long encounters. If more than one researcher was present on a vessel, then returns to the boat were staggered so that at least one researcher was always in the water during an interaction.

Encounters ended when either a) a whale was not seen underwater for over 30 min or b) passengers were instructed by the crew to exit the water for other reasons, such as dusk falling or the itinerary requiring a move to another location. Due to the GoPro cameras being fixed into the SDOV housings, batteries could not be exchanged without removing the cameras. Removing the cameras was not feasible as this would require recalibration (Seager, 2016b). Thus, the camera battery life dictated the end of the photogrammetry data collection for that interaction. To maximise filming capacity, battery extension packs were fitted to the cameras, allowing up to approximately 3.5 hours of filming when fully charged. Details of how I further modified the standard researcher data collection protocols for the requirements of this study (i.e., to obtain footage suitable for measuring morphometrics and approach distances) will be found in Chapter 3 (section 3.4.1). Encounter and environmental data for each encounter were recorded on a Whale Sighting Sheet (Appendix A), a standardised data sheet developed by the Great Barrier Reef Marine Park Authority (GBRMPA) and James Cook University which permit holders are required to complete for every swim-with interaction with dwarf minke whales.

2.2.2.3 Photo-identification data

Passengers and crew were encouraged to donate copies of any imagery of dwarf minke whales they collected with their personal cameras during each trip. The presence of multiple photographers enables a larger portion of an interaction to be photographed, which can be quite spread out if long or multiple ropes are used. Surface ropes can be up to 50 m in length, well beyond the limits of typical underwater visibility in this area. Thus, some swimmers may observe and photograph some individual animals that others did not see or capture. Therefore, collecting passenger and crew imagery donation was a high priority for this research. When a battery depleted in the SDOV system, I exited the water, exchanged the SDOV system with a regular underwater camera to capture supplemental photo-identification imagery. When multiple researchers were present, they prioritised time in-water to collect additional photo-identification imagery.

2.2.2.4 Methodological limitations

Data for this research were collected from commercial tourism vessels (i.e., ‘platforms of opportunity’), not dedicated research vessels – which would be prohibitively expensive. While encountering dwarf minke whales was an advertised priority for each trip, sampling of the study area was non-systematic. Steaming between dive sites was not always linear, to search for whales. Whales sighted while steaming were not always attempted to be swam with, due to scheduling constraints and suitability of the location and/or vessel.

Since interactions with dwarf minke whales rely on voluntary approaches of whales, it is possible that some whales in this aggregation avoided interacting and were thus not available to be identified (Sobtzick, 2010). However, given that dwarf minke whales aggregate around vessels and swimmers (Mangott et al., 2011), and most sightings turn into encounters (Birtles et al., 2014), even those from several kilometres away, it is reasonable to assume that most dwarf minke whales using this aggregation area were available to be identified (Sobtzick, 2010).

2.3 Data pre-processing

2.3.1 Photo-identification

All field imagery was first pre-processed for photo-identification of individual whales, following procedures outlined in Sobtzick (2010). Photo-identification data were utilised across all data chapters in this thesis. The photo-identification process for dwarf minke whales is species-specific, as it relies on classification of unique colour patterns (Arnold et al., 2005), but is generally similar to other cetacean ID processes (e.g., Franklin et al., 2020; Fujiwara & Caswell, 2001; Katona et al., 1979), particularly blue whales (*Balaenoptera musculus*) (Calambokidis & Barlow, 2004; Sears et al., 1990). Although variation in colour patterns can be seen all over the body, photo-identification of dwarf minke whales has focused on the pectoral flippers and the flank just above the pectoral flippers (Fig. 2.3). The high contrast between light and dark patches in this area makes it desirable for photo-ID, as the patterns are more likely to appear clearly in imagery (Birtles et al., 2001). Furthermore, the colour patterns of this area are particularly variable (Arnold et al., 2005; Hutchings et al., 2023), and as such are likely to reduce Type I errors (false positives; mismatches), which occur when two photographs are falsely concluded to be of the same animal (Sobtzick, 2010; Urian et al., 2015). Additional markings were also used to assist with photo-ID, such as scars from possible predatory attacks or vessel strikes (Birtles, Arnold, et al., 2002).

Whale imagery collected by researchers, passengers, and crew were reviewed by myself or one of several student volunteers who were trained specifically for photo-identification of dwarf minke whales. This was completed one encounter at a time. Photos were first graded for 1) quality and 2) amount of identification information contained in the photo on a scale developed for photo-ID of sperm whales (*Physeter macrocephalus*; Arnbom, 1987) and utilised by Sobtzick (2010) for photo-identification of dwarf minke whales

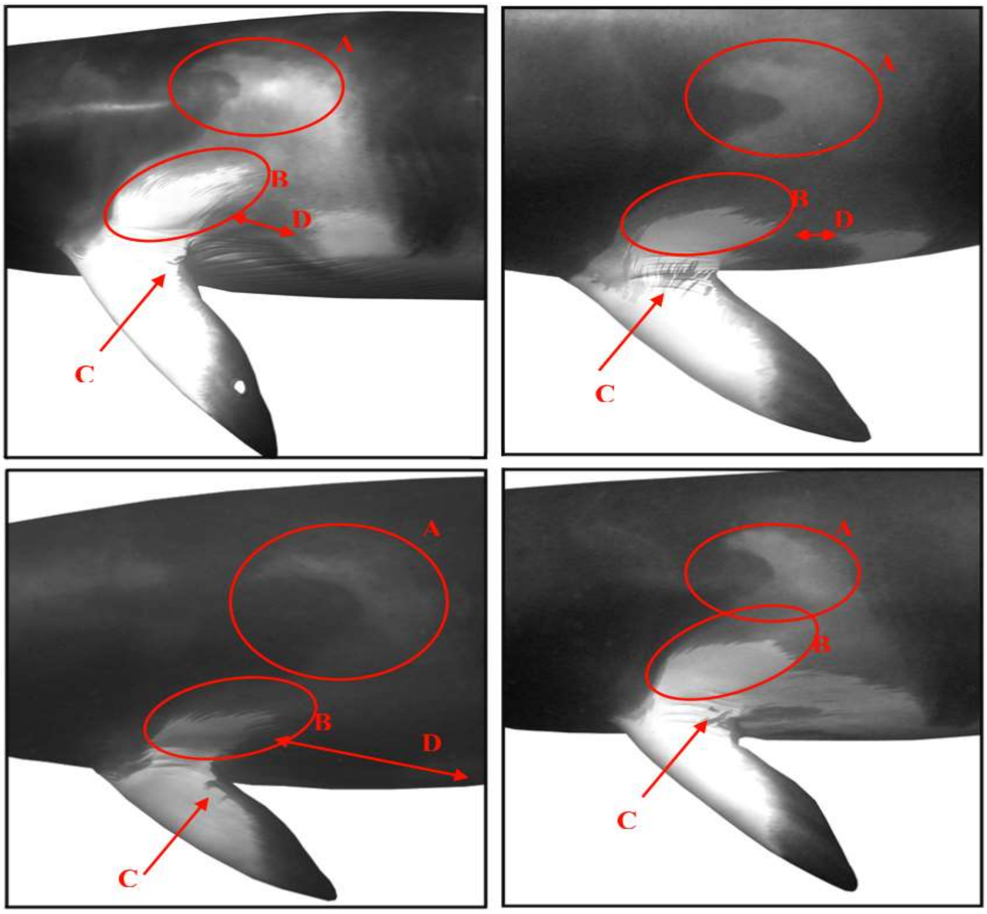


Figure 2.3. The main features used for photo-identification of individual dwarf minke whales in the Great Barrier Reef. A: thorax patch (tip shape, indentation); B: speckling in shoulder blaze; C: speckling in flipper blaze; D: extent of attachment of the axillary patch to the thorax patch. Reprinted from Sobtzick (2010).

(Appendix B). Imagery falling below the chosen level of acceptable quality and information was rejected to reduce the likelihood of Type II errors (false negatives; missed matches). A positive whale ID match was made between two images when at least three unique features could be identified in both images. If sufficient features could not be identified, that photo was classified as “unknown ID”. A reference library of high quality photos was collated for every identified whale, and each ID match across multiple encounters was reviewed by a second trained researcher or volunteer.

Whale IDs were categorised as “complete” IDs when both the left and right sides of that individual were identified. When only one side of a whale was identified, that whale ID was categorised as a “left-only” or “right-only” partial ID. It is likely that many of the left-only partial IDs represent the same individuals as the right-only partial IDs, but that the available imagery was simply insufficient to link them together as the same animal. Thus, to prevent double-counting of individuals, only the partial ID category with the higher number of IDs was used in each data analysis in this thesis (i.e., left-only *or* right-only, never both). The side used could be different for each analysis depending on the subset of IDs required for that analysis (e.g., all identified whales vs measured-only whales vs sexed-only whales, etc.).

2.3.1.1 Sub-sampling of photo-identification imagery

Due to the time-intensive nature of the manual photo-identification process, a complete review of all photos of all encounters was not possible. Encounters with both a low number of estimated whales (i.e., 5 whales or less) and a high number of photos (i.e., more than 1000 images) were sub-sampled.

The following protocols were developed to select which images would be reviewed in these sub-sampled encounters:

1. Photographers within an encounter were priority ranked based on their relevant experience and expertise: 1) researchers, 2) onboard photographer(s)/videographer(s), 3) other vessel crew, and 4) passengers
2. Images from priority photographers were selected to cover as much of the encounter duration as possible (i.e., include photos from the beginning, middle, and end of the encounter in case new individuals joined part-way through an encounter)
3. After researcher photos were analysed, additional photographers’ photos were reviewed until no new whales were identified in 100 photos.

A total of three encounters were sub-sampled following this protocol.

2.3.1.2 Limitations

While generally reliable, photo-ID studies do have some limitations. Some photo-ID studies only enable the identification of a subset of the population (Auger-Méthé & Whitehead, 2007). This can occur when the distinguishing features are only present on some animals, such as scarring (Gowans & Whitehead, 2001), if markings change over time, or if they are too simple to distinguish individual animals from each other (Hammond, 1990; Urian et al., 2015). Fortunately, the colour patterns on dwarf minke whales remain stable over at least several years and are sufficiently complex to allow for unequivocal identification of individuals (Arnold et al., 2005; Birtles, Arnold, et al., 2002; Hutchings et al., 2023; Sobtzick, 2010). Additional protocols developed for quality control and error mitigation purposes are described in section 2.5.

2.3.2 Photogrammetry

2.3.2.1 Calibration footage

Calibration footage was processed in “CAL”, one of two computer programs in SeaGIS’s photogrammetric software suite. The step-by-step user guide provided with the program was followed for calibration processing (Seager, 2016b). Briefly, I manually identified every target that was visible on the calibration cube in both the left and right camera footage in each of the 20 orientations filmed during the calibration. This enabled the program to compute a calibration-specific file for each camera to be imported into EventMeasure. These files enabled true distances to be measured in any footage that was suitable for that particular calibration (see section 2.2.1).

2.3.2.2 Whale measurement assessment trial

Before conducting measurements, an initial assessment was necessary to determine the feasibility of measuring morphologic features on dwarf minke whales. Therefore, a preliminary experimental review of the footage was undertaken. After reviewing approximately half of the stereo imagery collected in the first sampling period (2017), consisting of over 18 h of video footage, nine features were ultimately selected (Fig. 2.4) based on a qualitative assessment of usefulness and measurability (Table 2.2).

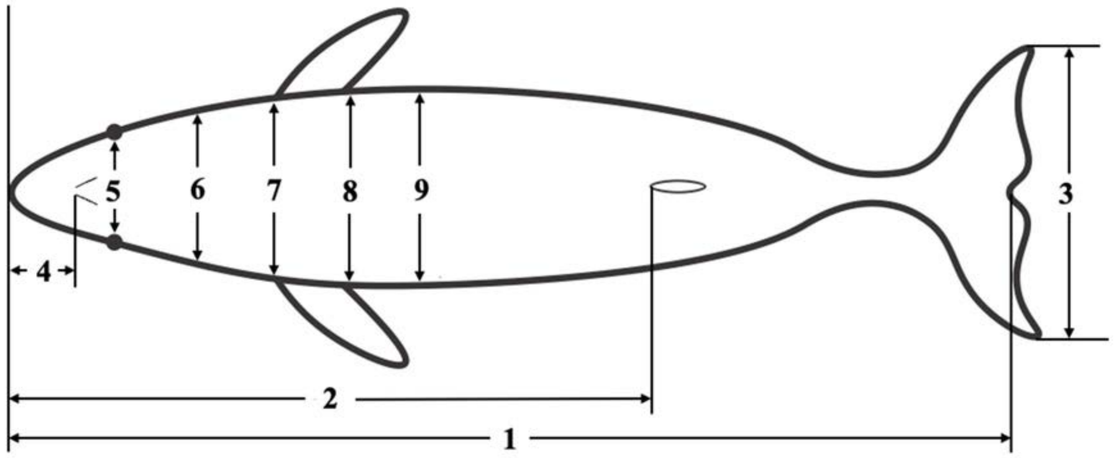


Figure 2.4. Schematic of a dwarf minke whale (dorsal view) identifying the nine morphological features selected for measurement and the reference points used to measure each feature. **1** = Total body length (TBL), **2** = Snout-to-dorsal-fin length (SDF), **3** = Fluke width (FW), **4** = Snout-to-blowhole length (SBH), **5** = Width at eyes (WE), **6** = Width behind eyes (WBE), **7** = Width at anterior insertion point of pectoral fin (WAP), **8** = Width at posterior insertion point of pectoral fin (WPP), **9** = Width at widest point (WWP).

Table 2.2: Rationale for the selection of morphologic features to be measured.

Morphologic feature: reference points used	**Usefulness** Practical applications/biological/ecological significance	**Measurability** Does this feature have discrete and visible reference points that can be identified in SDOV footage? How visible is this feature during in-water interactions?
Total body length (TBL): tip of snout, caudal notch	• Proxy for age (relative and, eventually, absolute) • Life-history and population demographics (Christiansen et al., 2018; Dunstan et al., 2008) • Growth rates (Christiansen et al., 2014; Fortune et al., 2012) • Only in-situ measurements previously collected for dwarf minke whales (Dunstan et al., 2008; Sobtzick, 2010), and thus comparable to previous studies	• Discrete reference points • Dependent on: a) swimming behaviour (cannot be measured during any active swimming behaviour, only during gliding behaviour, due to dorso-ventral (DF) body flexure); b) orientation (an absolutely lateral view obscures the caudal notch, and DF flexure is more difficult to detect from dorsal views); and c) approach distance (cannot be measured during approaches closer than ca. 3.5 m as the entire length of the body cannot be filmed)
Snout to dorsal fin (SDF): tip of snout, anterior dorsal fin insertion point	• May be a reliable proxy for length (Mead & Payne, 1975) • Useful because TBL cannot always be measured due to DF flexure, which particularly affects the tail region, and entire body length not fitting in frame	• Discrete reference points • Slightly more achievable than TBL because it is: a) less impacted by DF flexure (e.g., can be measured during some active swimming behaviour, i.e., when the tail is beating but the rest of the body remains straight, as well as during gliding behaviour); b) visible from all lateral and dorsal views; and c) measurable at closer approach distances (e.g., as close as ca. 2.5 m)
Fluke width (FW): lateral tips of caudal flukes	• May be a reliable proxy for length, e.g., sperm whales (Jaquet, 2006), humpback whales (Sousa-Lima & Groch, 2010) • Relationship may provide insights into feeding behaviour (Woodward et al., 2006)	• Discrete reference points • Decreased precision when measured from lateral view (i.e., parallax error, see Chapter 3 section 3.2.6)
Snout to blowhole (SBH): tip of snout, anterior margin of LHS blowhole crease	• Proxy for length of head (Whitehead & Payne, 1978) • Allometric growth: length of head relative to TBL (i.e., SBH:TBL ratio) may decrease with age (Pittenger, 1990)	• Discrete reference points • Blowhole crease is thin and not visible in distant passes or when water clarity is poor

Width at eyes (WE): lateral margin of each eye at middle/widest point	• Proxy for width of head • Likely to be unaffected by body condition (i.e., determined by skull width, not fat stores), thus may provide a relatively standardized width measurement	• Discrete reference points • Only visible from dorsal view
Width behind eyes (WBE): halfway between WE and WAP	• Probable location of blubber accumulation (Konishi, 2006), and thus potential indicator of body condition	• Requires on-screen measurement of point halfway between WE and WAP (thus also only measurable if WE and WAP are measured) • Only visible from dorsal view
Width at anterior pectoral fin insertion point (WAP): anterior pectoral fin insertion point	• Not particularly known for blubber accumulation, thus possible standardized width measurement for comparison to other width measurements which are more likely to vary with changes in body condition	• Discrete reference points • Requires specific swimming behaviour for reference points to be visible (i.e., pectoral fins must be near or fully extended) • Only visible from dorsal view
Width at posterior pectoral fin insertion point (WPP): posterior pectoral fin insertion point	• Same as WAP	• Discrete reference points • Requires specific swimming behaviour for reference points to be visible (i.e., pectoral fins must be near or fully extended) • Only visible from dorsal view
Width at widest point (WWP): visible estimation of widest point at approximately mid-body length	• Probable location of blubber accumulation (Konishi, 2006), and thus potential indicator of body condition	• No discrete reference points • Determination of widest point may be different in LHS and RHS video frames due to different perspectives • Only visible from dorsal view

2.3.2.3 Whale measurements

All body measurements of whales were processed in EventMeasure, the second program in SeaGIS's measurement suite. The user guide for this program was followed (Seager, 2016d), which outlines general (i.e., not whale-specific) procedures for making three-dimensional straight-line measurements. Measurements were made by pausing the videos on suitable frames and manually identifying pairs of points representing the desired measurement(s) in both videos. Ideal images for morphometric body measurements occurred when a whale passed 1) directly below the cameras, 2) with minimal/no body flexure, and 3) between approximately 4 - 12 m (4 m being the approximate distance at which the entire length of a whale could be seen in both images, and 12 m being the approximate distance when precision decreased to an unacceptable level and water clarity and/or light rendered the reference points difficult to identify). Lateral-view passes were also acceptable for some measurements, but not all (e.g., total body length could be obscured because the caudal flukes obscured the caudal notch). The software program then converted the point coordinates into three-dimensional object space (x, y, and z), and computed the straight-line distance between paired points. For each measurement, the photo-ID reference library was manually consulted to identify the whale being measured (when the footage was of sufficient quality to make a positive ID). Repeat measurements were obtained whenever possible (i.e., during repeat passes of sufficient quality).

2.3.2.4 Approach distances

Whale-swimmer approach distances were also measured from the stereo footage in EventMeasure. Each time a whale swam past the videographer (i.e., myself), it was termed a 'pass' or an 'approach'. Measurements were made by pausing the videos at the closest estimated point of each pass and selecting a "reference point" on the body that was visible in both stereo-videos. When a whale passed by side-on (i.e., a lateral view), the reference point was usually a feature on the shoulder blaze. When a whale passed underneath (i.e., dorsal view), the anterior dorsal fin insertion point or a visible scar on the dorsal surface was used. When present, recent cookie-cutter shark bites were useful reference points as they can be bright white and very visible for a number of weeks or months before they re-pigment (Birtles, Arnold, et al., 2002; Jones, 1971). Once the reference point was selected in both videos, the software computed the distance from the mid-point between the two cameras to the selected reference point, termed the ‘range’. This measurement was used as a proxy for whale-swimmer approach distance. This process was repeated several times for each pass to determine the true closest point of the pass, and the measurement made at this point was saved. A pass was considered complete when a whale changed directions and began to move closer to the researcher after having moved away (i.e., representing the beginning of a new pass), or when the whale was no longer visible due to underwater visibility (i.e., left the field of view).

2.3.3 Sex identification

Sex identification of dwarf minke whales can be made opportunistically either in-water or from photo or video imagery. As with other cetaceans, the sex of a dwarf minke whale can be identified by the relative positioning of the urogenital slit to the anus (Berta et al., 2005; Best, 1985). Thus, a sex identification requires the observer or photographer to obtain a clear view or image of the ventral surface of a whale. This area is only visible to an observer at the surface when a whale performs one of a small number of specific behaviours, such as a “belly presentation”, “headrise”, or “barrel roll” (Mangott, 2010). These behaviours are relatively rare; therefore, sex can only be determined incidentally and has been determined for a maximum of approximately one-third of dwarf minke whales in previous photo-identification studies (Sobtzick, 2010).

2.4 Data summary

Videogrammetry imagery was collected for 21 encounters in 2017, 17 encounters in 2018, and 20 encounters in 2019. While the initial objective of this study was to analyse all footage collected across the three sampling periods, to obtain morphometric measurements and whale-swimmer approach distances from every suitable pass that was filmed, imagery processing (photo-identification and measurements) took considerably longer than anticipated. Consequently, after completion of processing of the 2017 data (approximately 40 hours of videogrammetry footage and 15,000 regular photos and videos), I had to refocus my analyses more strategically. Photo-identification was successfully completed for all three sampling periods. Therefore, I used re-sightings of whales across all three years to obtain time series data of those animals. Analyses of newly identified whales and approach distances were only measured from 2017. Over 10,000 photos and videos were reviewed for photo-identification for each of the three sampling years, facilitating the identification of over 140 unique individuals. A total of 1,327 morphometric measurements were made on 104 dwarf minke whales, and over 1,100 whale-swimmer approach distances were obtained for this thesis.

2.5 Quality control and error mitigation procedures

2.5.1 Mis-matches

Positive identification of individual dwarf minke whales can be nearly unequivocal with high–quality footage showing colour patterns in clear detail (e.g., good visibility and lighting, close proximity to the animal). However, distant passes or poor lighting conditions in photo or video footage can potentially result in the mis-identification of animals (i.e., a false positive or negative). While several protocols were followed to ensure that these types of errors are minimised (see section 2.3.1), the risk cannot be eliminated entirely. If a high degree of certainty can be established for the most difficult of identifications, then we can logically presume a high degree of confidence across *all* identifications. Thus, a third researcher was given a subset of de-identified images from 10 of the most distant identifications from the first sampling period (2017). These photos were checked against the existing photo-ID database (containing over 400 unique dwarf minke whales), and each image was either matched to an existing whale in the database or classified as a "new whale". This resulted in a 100% agreement with the initial identification process (which already requires confirmation by two trained researchers/volunteers). Therefore, I concluded that there is generally a high degree of confidence across all identifications.

Another opportunity to identify instances of whale identity mis-identification arose when replicates of morphometric measurements were achieved for a given animal. Poor replicate precision may indicate a measurement outlier or could potentially represent a mis-identification of the individual whale during that pass. For example, if two or more TBL measurements were achieved for a particular animal, and there was poor precision amongst them, then one (or more) of those measurements may have been a mis-identification of a whale of a different size. Precision (as CV) was calculated for all measurements with replicates and plotted in histograms with 0.5% CV intervals (Fig. 2.5). Potential outliers were visually apparent as increased counts of replicates with poor precision. I reviewed the video footage of each pass during which a measurement was made to confirm or reject the assigned ID. Following this approach, two mis-identifications were found each of TBL, SDF, and FW measurement types and subsequently corrected ($N_{TBL} = 82$, $N_{SDf} = 88$, $N_{FW} = 53$).

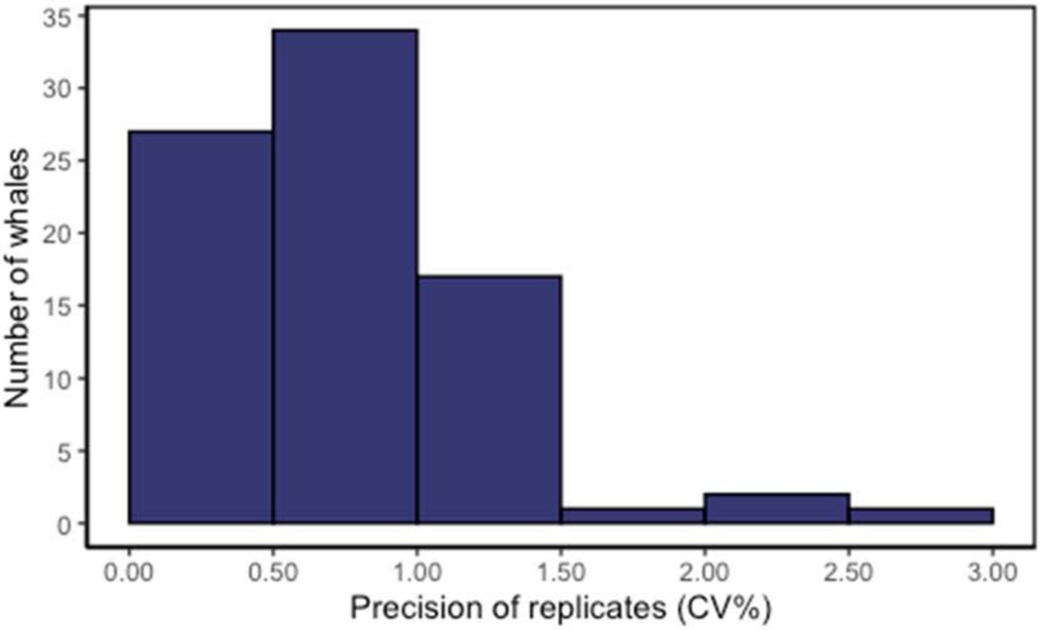


Figure 2.5. Precision of replicate total body length (TBL) measurements for all measured whales in 2017 sampling period. All replicates with CV > 2.00% were investigated to identify potential Type I errors (i.e., mismatches).

2.5.2 Whale body flexure

Dorso-ventral body flexure occurs when a whale is swimming and can result in an underestimate of body length. While topside images (i.e., dorsal view) were ideal for measurements as they generally provided the clearest view of the required reference points (i.e., tip of the snout and the caudal notch), dorso-ventral body flexure was difficult to determine from this perspective. Previous studies could not identify dorso-ventral body flexure in dwarf minke whales from standalone photographs but were able to detect this flexure from video imagery (Dunstan et al., 2008; Sobtzick, 2010). Thus, each potentially measurable pass was reviewed slowly in Eventmeasure (0.25 x - 0.5 x speed) or stepped through frame-by-frame, and sections with detectable flexure were rejected. Lateral body flexure can also occur, but is much less common (Dunstan et al., 2008) and was easily detectable in dorsal view images. Such sections were also rejected.

2.5.3 Exclusion of poor quality measurements

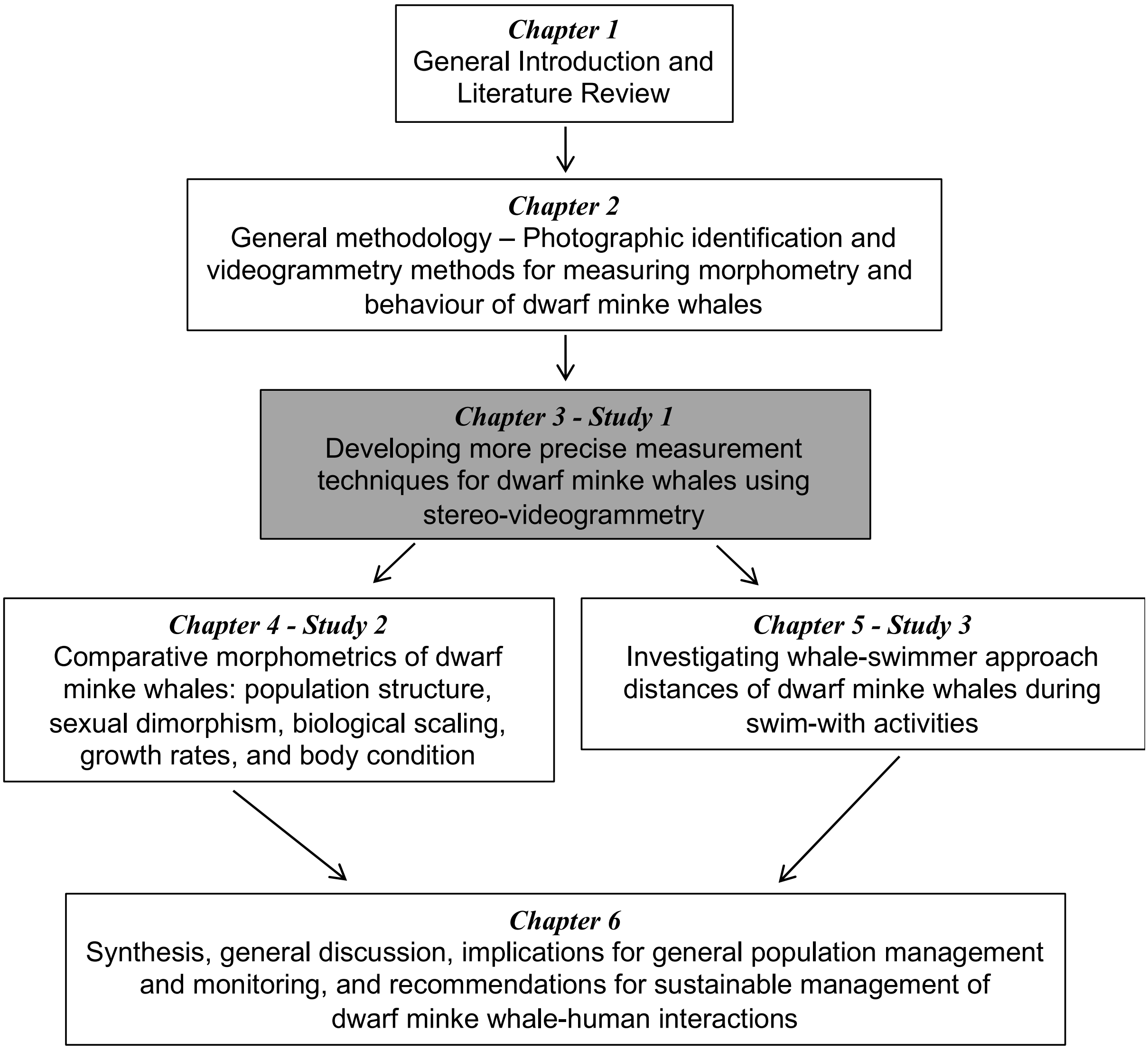
EventMeasure provides outputs that indicate the internal quality of each measurement:

1. RMS (Root Mean Square) intersection: This value represents the least squares fit for all points in the measured length. This provides a mathematical indication of the consistency of the network solution used to compute the calibration parameters, camera locations and orientations (Shortis, 2015). Theoretically the RMS value should be 0; however, *in situ,* values less than 10 mm are ideal, values between 10 mm and 20 mm are questionable, and values greater than 20 mm should generally be rejected (SeaGIS, 2016b). Variables that will impact RMS values are poor synchronisation of videos, measurement distance, and imprecise selection of reference points.
2. Software precision: This output provides a numerical confidence interval (±) around the precision of an individual measurement estimate. It is a "mathematically derived estimate based on the physical camera properties, the three-dimensional intersection geometry, and an image measurement precision of 1 pixel" (SeaGIS, 2016b p. 96). Since each image pixel represents more real-life space as range increases, this measure of precision is expected to worsen with increased range. Note that this precision is not the same as the calculated precision of replicates of the same measurement on an individual whale or calibration check length. In the absence of replicate measures, this can be used as an indicator of precision for a single measurement.

Exclusion of poor measurements was undertaken in accordance with recommendations from SeaGIS (2016b). This generally occurred during distant passes, as the measurement reference points became progressively more difficult to identify. When a measurement output contained a poor quality indicator (RMS greater than 20 mm; SeaGIS, 2016b), the measurement was deleted and re-attempted until the measurement outputs indicated sufficient quality.

3 CHAPTER 3:

DEVELOPING PROTOCOLS FOR IN-WATER MORPHOMETRIC MEASUREMENTS OF DWARF MINKE WHALES USING STEREO-VIDEOGRAMMETRY



3.1 Introduction

3.1.1 Morphometry

Investigating the body size and shape (i.e., morphometrics) of animals provides insights into a range of biological and ecological features of a species (Peters, 1986). Determining growth rates and size at sexual maturity can provide insights into population and social structures (Shane et al., 1986), reproduction, and other life history characteristics (Blueweiss et al., 1978). Morphometry can also be used to assess body condition/fitness and provide insights into sublethal (i.e., energetic) threatening processes such as declining food availability (Bradford et al., 2012; Christiansen et al., 2016, 2020; Lockyer, 1986; Miller et al., 2012). Concerns for cetacean populations are increasing due to several threats, including anthropogenic disturbance (Evans, 1996; Natural Resource Management Ministerial Council, 2005; Pirotta et al., 2018) and climate change, in particular the effects of changes in food availability for baleen whales in high latitude feeding areas (Fabry et al., 2009; Tulloch et al., 2019). Morphometric study represents an opportunity to monitor the health of cetacean populations in the face of these escalating threats. Further, by detecting declines in health prior to the onset of significant mortality, monitoring body condition potentially allows time for a management response to avert population decline.

3.1.2 Techniques for measuring cetaceans

While the use of unoccupied aerial vehicles (UAVs or drones) for morphometry research has increased dramatically in recent years, these methods are heavily dependent on weather conditions, particularly wind and precipitation (Gao et al., 2021). Most drones cannot withstand winds over approximately 20 knots (Ranquist et al., 2017). These methods also require predictable surfacing behaviour of the target animals, who must be resting at the surface in clear waters (e.g., Christiansen et al., 2018), or, alternatively, allometric growth patterns must be known for scaling relationships between measurable features (e.g., caudal fluke width or blowhole-to-dorsal-fin length) and the target feature(s) (e.g., total body length, (Dawson et al., 1995; Leslie et al., 2020; Ortega-Ortiz et al., 2022). Thus, drone-based techniques are not always suitable. Alternatively, when in-water access is available, diver-operated systems have been used to measure cetaceans (Dunstan et al., 2008; Shortis & Harvey, 1998; Spitz et al., 2000).

3.1.2.1 Underwater photogrammetry array comparison

Direct comparative studies of stereo-image vs single-camera photogrammetry techniques have only been evaluated on small fauna (reef fishes up to ~50 cm in length) (Harvey et al., 2002). While stereo-image systems generally produce more accurate and precise measurements than single-camera systems, it is unknown whether the advantages scale up to operational conditions applicable to dwarf minke whales (e.g., animals larger than 2 m, measured from distances up to 15 m away). Further, selection of equipment calibration techniques can have a significant impact on measurement quality as well. For small fauna, three-dimensional calibration techniques have higher accuracy and precision than the two-dimensional methods (Boutros et al., 2015; Shortis, 2015). Optimizing precision is particularly important for detecting growth or changes in body condition, as precision represents the certainty around each set of replicate measurements (e.g., yearly measurements of the same animal). In other words, higher precision confers more reliability around the difference between each set of replicate measurements, and thus increases the sensitivity with which true change can be detected. Thus, if the advantages scale up to operational conditions applicable to dwarf minke whales, then a stereo system combined with a 3D calibration (vs a 2D calibration) may be the ideal choice for underwater, diver-operated photogrammetry research. With both increased accuracy and precision, this methodology may be useful for conducting ongoing and detailed (individual based) monitoring of cetacean populations to provide management agencies informative data on the population's health (i.e., body condition), supplementing existing density assessments, and serve as an early warning indicator of declining population status.

3.1.3 Measurements of dwarf minke whales

The swim-with dwarf minke whales tourism industry in the Great Barrier Reef provides researchers with a "platform of opportunity" to study this population (see Chapters 1 and 2). Consistently strong winter trade winds and unpredictable surfacing behaviour of the whales has made both aerial and boat-based platforms unsuitable for most photogrammetry and morphometry purposes. Alternatively, the highly interactive nature of the whales while present in the region has facilitated the application of in-water measurement techniques. The first in situ length estimations of live dwarf minke whales were produced using single-camera techniques and a 2D calibration (Dunstan et al., 2008; Sobtzick, 2010). Measurements were obtained using an underwater rangefinder mounted to a video camera in an underwater housing, similar to the equipment and techniques used by Spitz et al. (2000) for measuring humpback whales (Megaptera novaeangliae).

The total body lengths (TBL) of 140 individual dwarf minke whales were measured, enabling preliminary insights into the demography of the "interacting population" (Dunstan et al., 2008; Sobtzick, 2010). While calibration trials showed that a high degree of accuracy can be attained using this technique, the precision of repeat measurements of individual animals was shown to be variable, with some replicates differing by up to 0.49 m or ~8% in body length (Sobtzick, 2010), limiting the value of this technique in longer-term studies on growth and body condition.

Monitoring body condition of dwarf minke whales has not previously been undertaken. As such, it is unknown how well girth measurements serve as an indicator of inter-annual change in body condition for this subspecies. For common minke whales (*Balaenoptera acutorostrata*), interannual changes in overall prey abundance have only correlated weakly with body condition (measured as both girth and blubber index) (Haug et al., 2002). For the Antarctic minke whale (*Balaenoptera bonaerensis*), girth just posterior to the eyes has been shown to be a suitable indicator of body condition (Konishi, 2006). I aim to measure two-dimensional width as a proxy for girth and assess the quality of these measurements for monitoring interannual changes.

3.1.4 Aims

In this study I sought to develop a robust methodological technique for making precise in-water morphometric measurements of cetaceans. First, I conducted a control trial to compare the quality of calibration and in-situ whale body length measurements between single-camera and stereo-image photogrammetry techniques to determine the most suitable approach for obtaining in-water measurements of dwarf minke whales. Next, I investigate whether a combined SDOV unit and 3D calibration technique can achieve sufficient precision to enable monitoring of growth and body condition. From addressing these aims, I developed methodological protocols to optimize data collection and analysis of morphometric data to reliably monitor individual and population level changes over time.

3.2 Methods

3.2.1 Study site and species

A detailed description of the study site and species can be found in Chapters 1 and 2. An initial control trial using a diver-operated stereo-video (SDOV) system was conducted in the public swimming pool at James Cook University, Townsville, Australia prior to the first sampling period. Dwarf minke whale photo-identification and photogrammetry imagery were collected during the winter aggregation period (June and July) in the northern Great Barrier Reef, Australia for both this study (collected in 2017) and for the previously collected photogrammetry comparison data from Dunstan et al. (2008) and Sobtzick (2010; 2006 – 2008).

3.2.2 Technical equipment and calibration methods

3.2.2.1 Stereo equipment and calibration

A detailed description of the technical equipment used in this study, including the diver-operated stereo-video SDOV unit, cameras and settings, and calibration equipment and procedures can be found in Chapter 2 section 2.2.1 and in Seager (2016a). Briefly, the calibration cube was rotated and filmed underwater at 20 pre-determined orientations, at a distance that allowed the cube to fill as much of the effective field of view (i.e., overlapping across both cameras) as possible. Immediately following each cube calibration, the 1.2 m check bar was filmed for validation.

3.2.2.2 Comparison data equipment and calibration

The single-camera photogrammetry equipment and calibration methods from both pool trials and field environments are detailed in Dunstan et al. (2008) and Sobtzick (2010). This single-camera technique requires a sonar rangefinder be attached to the camera to determine the distance from the camera to the object (i.e., whale or calibration device). Object length was subsequently determined using the geometric relationship between the occupied field-of-view, the range, and the subtended camera lens angle, as well as a calibration to correct for radial distortion from the wide-angle video camera lens (see Chapter 1 section 1.3.3.1).

3.2.3 Control trial filming protocol

A robust photogrammetry methodology produces both highly accurate and highly precise measurement estimates (Harvey et al., 2002). Provided that replicate estimates can be acquired for a target object or animal, precision can be assessed. However, since photogrammetry techniques make *indirect estimates* of true length, when true length is unknown - as when measuring free-ranging cetaceans - accuracy cannot be assessed. Therefore, to obtain estimates of accuracy for a photogrammetry technique, control measurements of known lengths are required. For this, a control pool trial was conducted to assess the accuracy of measurement estimates produced by the SDOV system.

An 8 m length of PVC pipe was marked at 1 m intervals and filmed with the SDOV system in the public swimming pool at James Cook University, Townsville, Australia. The 8 m length of PVC pipe was chosen to encompass the entire range of expected morphometric measurements on dwarf minke whales. This includes lengths as small as 1-2 m, for example the distance from the snout to the blowholes or the length of a newborn calf of ~ 2 m, to beyond the longest length recorded of 7.8 m (Best, 1985). The PVC pipe was filmed at regular distance intervals throughout the pool, from approximately 1 – 15 m, at which point the targets on the PVC pipe were no longer visible. This range of distances covers the operational ranges at which dwarf minke whales have successfully been measured (Dunstan et al., 2008; Sobtzick, 2010). At each distance interval, the SDOV system was rotated approximately 20 degrees in the horizontal and vertical planes, for a total of five orientations, simulating non-perpendicular passes: straight on, left camera forward, right camera forward, left camera up, right camera up. This process is similar to the calibration methods in Seager (2016a).

Single-camera system control measurements of a known object length were conducted similarly in Sobtzick (2010). The accuracy and precision of known target length measurements were later compared between stereo and single-camera systems.

3.2.4 Whale filming protocol

The SDOV filming methods employed in this thesis followed the swim-with protocol and in-water methodology described by Dunstan et al. (2008) and Sobtzick (2010). These methods are also described in detail in Chapter 2 section 2.2.2. Briefly, when whales were sighted near the vessel, the videographer (myself) entered the water on snorkel and attached to the vessel via a 30-50 m surface rope, usually at the trailing end for a consistent filming position. The whales typically soon began to approach the vessel and swimmer(s) to a visible distance underwater (i.e., closer than 10 m with water visibility usually 15-25 m). Using an *ad libitum* sampling protocol, continuous in-water video footage was collected when whales were present, until either the encounter ended (i.e., a whale was not seen underwater for over 30 min or the vessel had to depart) or the camera battery life ended (after approximately 3.5 hr).

3.2.5 Image and measurement processing

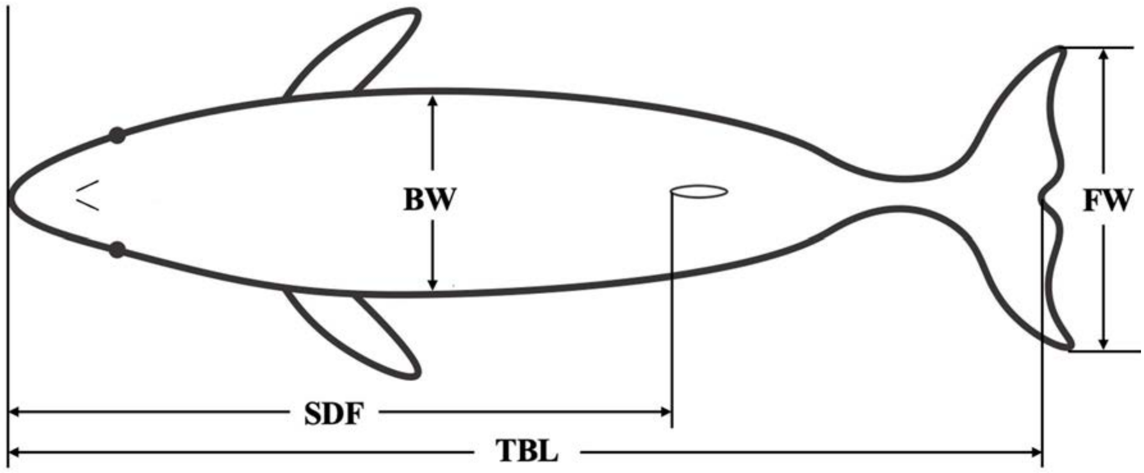
All whale imagery was pre-processed for photo-identification of individual animals (see Chapter 2 section 2.3.1). Single-camera footage processing methods are detailed in Dunstan et al. (2008) and Sobtzick (2010). Data on control measurements, whale length and whale approach distances (Table 3.1) were extracted for comparison with SDOV measurements. SDOV imagery from calibration, control, and field footage was processed using SeaGIS's photogrammetric computer software suite "CAL" (Seager, 2016a) and "EventMeasure" (Seager, 2016c), following the step-by-step user guides (Seager, 2016b, 2016d). This process is described in detail in Chapter 2 section 2.3.2. A brief summary follows.

Stereo-image calibration footage (i.e., paired video of the 3D cube) was processed in CAL. CAL computed a bundle adjustment file that was then imported into EventMeasure to enable estimates of true distance in the video footage. All measurement footage (i.e., footage of the check bar, PVC pipe, and whales) was imported into EventMeasure and stepped through frame-by-frame to synchronize the paired videos. Measurements of whales and check bars were made by pausing the videos on suitable frames and manually identifying pairs of "reference points" in both videos to compute the straight-line distance between them. On the calibration cube, check bar, and PVC pipe, the high contrast targets were used as reference points. On the whales, physical features were used as reference points (

Table 3.1). Reference points were chosen to represent morphometric measurements of interest and particularly those that might be most suitable for assessing growth and body condition (such as total body length and maximum body width), or as potential proxies for total body length (such as fluke width or snout-to-dorsal-fin length).

Table 3.1: Criteria used for attaining measurements of dwarf minke whales from footage of a single-camera ('single') and stereo-image ('stereo') systems and schematic of measurements on a dwarf minke whale from a dorsal view.

Measurement	**Reference points used**	**Body orientation and criteria required for measurement**
Total body length (TBL) *single, stereo*	Tip of snout to caudal notch	Dorsal or lateral view (caudal notch must be visible)
Fluke width (FW) *stereo*	Tip to tip of tail flukes	Dorsal view
Body width (BW) *stereo*	Widest point (by visual estimation, just posterior to pectoral fins)	Dorsal view
Snout-to-dorsal-fin length (SDF) *stereo*	Tip of snout to anterior dorsal fin insertion point	Dorsal or lateral view
Approach distance/range *single, stereo*	Closest identifiable point or marking	The closest point of any visible pass



Imagery of each individual whale was viewed at 0.5 x speed and screened for ideal frames from which to take desired measurements (i.e., a morphometric measurement or an approach distance). When an appropriate frame occurred, the video was paused and the appropriate reference points were selected. Using the bundle adjustment generated from the calibration process, EventMeasure software then converted the reference point coordinates into three-dimensional object space (*x*, *y*, and *z*) and computed the straight-line distance between the paired points. For each measurement, EventMeasure also provided a 'range' output; being the calculated distance from the cameras to the midpoint of the object being measured.

For total body length (TBL) and snout-to-dorsal-fin length (SDF) measurements, images were sought when the whale's dorso-ventral body flexure was limited and the whale was in a 'glide' position (i.e., not actively swimming). A whale's body flexure during swimming – either dorso-ventral from tail propulsion or lateral from turning - can result in an underestimate of its body length and other transverse features (e.g., snout-to-dorsal-fin length, SDF). During some passes, dwarf minke whales 'glide' by without actively swimming, showing little to no dorso-ventral body flexure. Detecting body flexure and reducing subsequent measurement errors was done (in both single and stereo video footage) by watching the animal's motion at slow speed and taking measurements at the estimated point of least flexure (e.g., Dunstan et al., 2008; Phillips et al., 2008), or not making a measurement during that pass if an ideal frame did not occur. Dorsal and lateral passes were reviewed slowly (0.25 x - 0.5 x) or stepped through frame-by-frame, and sections with detectable flexure were rejected (in both single and stereo video footage).

In the stereo video footage, the closest point of each pass was used as a proxy for approach distance (i.e., an approximation of how close the whales approach swimmers in the water). To determine this point, an entire pass was viewed at 0.5 x speed and then scrubbed back to the estimated closest approach of the whale. The videos were paused at this point and a single-point measurement was made by selecting a reference point on the whale that was visible in both videos. When a whale passed by side-on (lateral view), this reference point was generally a distinct mark of high contrast colour pattern on their shoulder. When a whale passed underneath (dorsal view) either the anterior dorsal fin insertion point, or a visible pattern or scar on the dorsal surface was used. To determine the actual closest point of each pass, the procedure was repeated several times around this estimated closest point, and distance range outputs compared. The single closest distance range measurement was retained and used as a proxy for approach distance for that pass.

3.2.5.1 Measurement quality and exclusion of poor measurements

EventMeasure provides several outputs that indicate the internal quality of each measurement (see Chapter 2 section 2.5 and Seager, 2016d). Initial exclusion of poor measurements was done in accordance with recommendations from Seager (2016d) which provides guidelines for reviewing and excluding measurements based on these quality outputs (see Chapter 2 section 2.5.3). These protocols were followed and unsuitable measurements were determined through a review process before being rejected. This generally occurred at greater ranges, as the targets became progressively more difficult to identify. When a measurement output contained a poor quality indicator, the measurement was deleted and re-attempted until the measurement outputs indicated sufficient quality. If, after several attempts, a measurement of sufficient quality could not be achieved, the measurement for that video frame was abandoned. Measurements with marginal quality indicators were also investigated as recommended (e.g., 10 mm < RMS < 20 mm). Examination of these marginal measurements resulted in the further exclusion of three measurements (Table 3.2).

Table 3.2: List of excluded total body length (TBL) measurements due to poor quality.

Measurement ID	Whale ID	Feature	Rationale
16	SH002	TBL	RMS > 20 mm (as recommended by Seager (2016d)
259	SH015	TBL	Range > 10 m, replicate > 10 cm larger than others (n=6), RMS > 10 mm
347	MW3104	TBL	RMS > 20 mm (as recommended by Seager (2016d)
368	MW3106	TBL	RMS > 20 mm (as recommended by Seager (2016d)
373	MW3108	TBL	RMS > 20 mm (as recommended by Seager (2016d)
398	MW3104	TBL	Poor quality imagery (difficult to locate caudal notch)
413	MW3112	TBL	Poor quality imagery (difficult to locate caudal notch)

Note. RMS = Root Mean Square.

Through the examination of marginal measurements, I made the following observations, which led to the development of a protocol for excluding marginal measurements:

1. All total body length (TBL) measurements with RMS values greater than 20 mm, (which indicate poor quality and are recommended to be excluded), were made at a ranges greater than 10 m.
2. However, acceptable measurements were still possible and often made at ranges greater than 10 m. Mean error of PVC pipe measurements made at 9 - 10 m range was generally below -2%, and precision of replicate whale TBL measurements was not impacted by range within the operational ranges (5 - 12 m) of this study.
3. As range increased, accuracy and precision decreased. Accuracy decreased systematically in a linear function such that size is progressively slightly

> overestimated. Thus, the further away a measurement was made, the more likely it overestimated the true length of that feature.

As a result, additional TBL measurements were also excluded if all of the following criteria were met:

1) Range > 10 m, AND

2) RMS value > 10 mm, AND

3) the measurement was suspiciously larger than other replicates (e.g., >10 cm).

Measurements made when the reference points were not clearly visible were also excluded. This occurred when image quality was poor and due a combination of factors such as backlighting, water visibility, movement and/or orientation of the whale obscuring the view of the caudal notch.

3.2.6 Data analysis

Accuracy, precision, the effect of distance range and replication requirements were determined for control trials using measurements of known object length (the PVC pipe). To ensure equal sample sizes for each object length size, replicates were subsampled down to the lowest number of replicates for an object length size (i.e., 7). One measurement made at each distance range was used, and remaining replicates were randomly selected. SDOV results for accuracy and precision were compared to single-camera results using percent error (to compare accuracy) and coefficient of variation (to compare precision) at specified ranges. Two-tailed t-tests assuming unequal variances were conducted. SDOV measurements made at ranges less than 3.5 m and greater than 14.5 m were excluded from this particular analysis to match the distance profile available in the (Sobtzick, 2010) data but presented elsewhere. To assess the effect of distance on measurement quality (i.e., precision), the “range” output for each measurement was evaluated. This output provides an estimate of the distance at which each measurement was made.

To determine the minimum whale-swimmer approach distance required to make a measurement of a given length, an “effective field-of-view” (eFOV) must be established. This is the true object size that can be seen in the overlapping sections of video across both SDOV cameras. When identifiable objects lined up with the left and right extent of the overlapping sections of video (e.g., markers on the PVC pipe or pool lane markers or tiles), they were used as reference points and the distance between them was measured (as well as the range). The distance between these reference points approximates the maximum object size that can be measured at that range. This was done at 1.220 m, 3.372 m, 5.678 m, and 7.396 m, and fitted to a linear regression for extrapolation to other approach distance distances and object sizes. Technically, measurements slightly larger than the eFOV can be made, as the stereo technique allows and accounts for parallax error (i.e., off-perpendicular targets); however, measurement quality decreases as this angle increases (Seager, 2016c; Shortis & Harvey, 1998).

To investigate the effect of increasing replicates on accuracy and precision of a control target, a subset of PVC pipe measurements was sampled iteratively with replacement using a bias-corrected bootstrap method in the analytical program RStudio. The 5 m length data were used, as most measured dwarf minke whales were between 4 - 6 m in length in the previous data set (mean_{TBL} = 5.71 m ± 0.70SD, N = 102) (Sobtzick, 2010). Three range categories were compared from 1-10 replicates: close (6-7 m), medium (9-10 m), and distant (12-13 m). Means ± SD were drawn from the simulated data, with 10,000 iterations for each range category and replicate combination.

3.3 Results

3.3.1 Stereo-videogrammetry: Control measurements

3.3.1.1 Accuracy and precision

Using the SDOV system at ranges up to 15 m in a control situation, accuracy and precision in measuring known object length were both high, with mean raw error and variation (*CV*) both below 2.5% for all object sizes (Table 3.3). When SDOV control measurements were stratified across range (i.e., the distance at which the measurement was made), a range effect became apparent (Fig. 3.1a). Accuracy and precision of known object length measurements were inversely related to the distance at which the measurement was made, with error and variation progressively increasing with range, indicative of a systematic bias. A slight object size effect was also observed in the SDOV control measurements (Fig. 3.1b); however, this effect was not statistically significant ($T_{270} = 1.97$. $p = 0.79$). Further, this object size effect may simply be an artefact of the range effect, as larger objects required a greater range to fit within the cameras' field of view for measuring.

To correct for the systematic range effect bias, a linear regression was fitted to the raw measurement error data which was then used to develop the following measurement correction factor:

$$a = m(0.999296 - 0.001687r)$$

where a = adjusted measured length, m = raw measured length, and r = range (Table 3.3, Figure 3.1).

Table 3.3: Accuracy and precision of stereo-image measurements of an 8 m PVC pipe marked at 1 m intervals, measured at distances from 1.230 m – 14.788 m.

Interval length (m)	*n*	**Mean raw measured length ± *SD*** (m), **Mean raw error**, ***Raw coefficient of variation*** (*CV*)	**Mean adjusted measured length ± *SD*** (m), **Mean adjusted error**, ***Adjusted coefficient of variation*** (*CV*)
1.00	*7*	1.019 m ± *0.021* 1.81% *2.02%*	1.003 m ± *0.014* 0.32% *1.39%*
2.00	*7*	2.026 m ± *0.020* 1.26% *0.99%*	1.998 m ± *0.008* -0.10% *0.41%*
3.00	*7*	3.041 m ± *0.012* 1.36% *0.36%*	2.990 m ± *0.014* -0.34% *0.47%*
4.00	*7*	4.059 m ± 0.020 1.45% *0.50%*	3.993 m ± 0.030 -0.19% *0.75%*
5.00	*7*	5.065 m ± *0.070* 1.26% 1.39%	4.979 m ± *0.080* -0.44% 1.60%
6.00	*7*	6.106 m ± *0.037* 1.73% *0.60%*	6.010 m ± *0.040* 0.16% *0.67%*
7.00	*7*	7.133 m ± *0.068* 1.86% *0.95%*	7.016 m ± *0.043* 0.22% *0.61%*
8.00	*7*	8.189 m ± *0.112* 2.30% *1.37%*	8.030 m ± *0.089* 0.37% *1.10%*

Note. *n* = number of repeat measurements. Mean error represents degree of accuracy and *CV* represents level of precision.

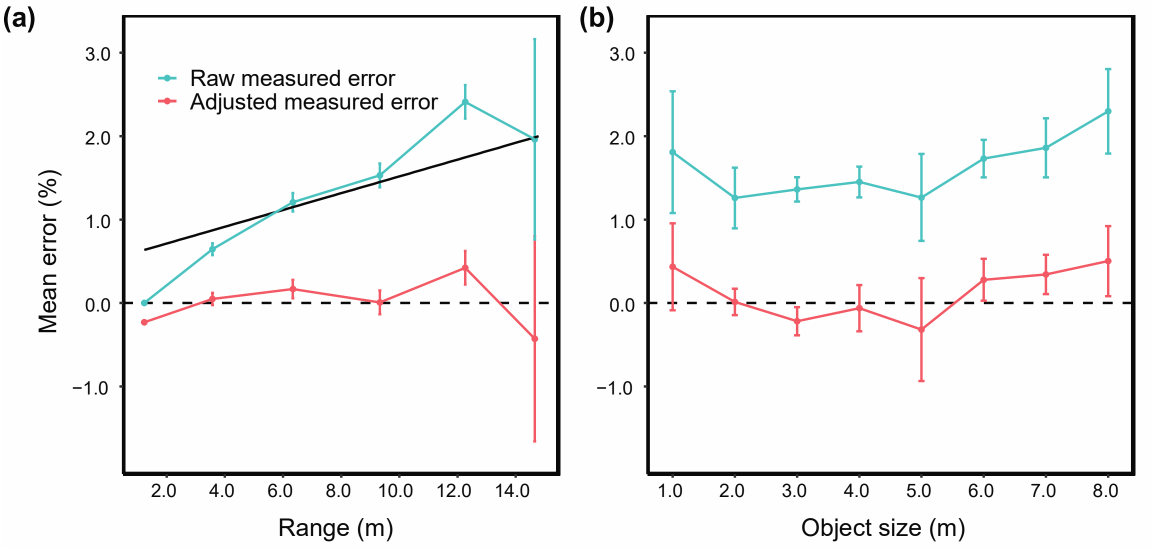


Figure 3.1. Accuracy and precision of stereo-image measurements of an 8 m PVC pipe marked at 1 m intervals, measured at distances from 1.230 m – 14.788 m. Error bars represent precision of replicates as standard error. Black line represents line of best fit for raw measured error. Equation represents linear regression fit of SDOV-estimated error to range, which was used to develop a measurement correction factor: $a = m(0.999296 - 0.001687r)$, where a = adjusted measured length, m = raw measured length, and r = range).

3.3.1.2 Distance range

To obtain a length measurement of 1 m (i.e., to obtain an effective field-of-view of 1 m) with in situ stereo-videogrammetry, a minimum approach distance (i.e., range) of approximately 1.2 m was required (Fig. 3.2). Via extrapolation, a 4 m whale requires an approach distance of just over 3 m for a TBL measurement, and a 7 m whale required approximately 5.5 m. In 2017, 99.2% of measured whale passes (N = 708) occurred at ranges greater than 3 m, and 87.0% of passes occurred at ranges greater than 5.5 m (i.e., sufficiently distant that the TBL of a large dwarf minke whale could fit in the FOV).

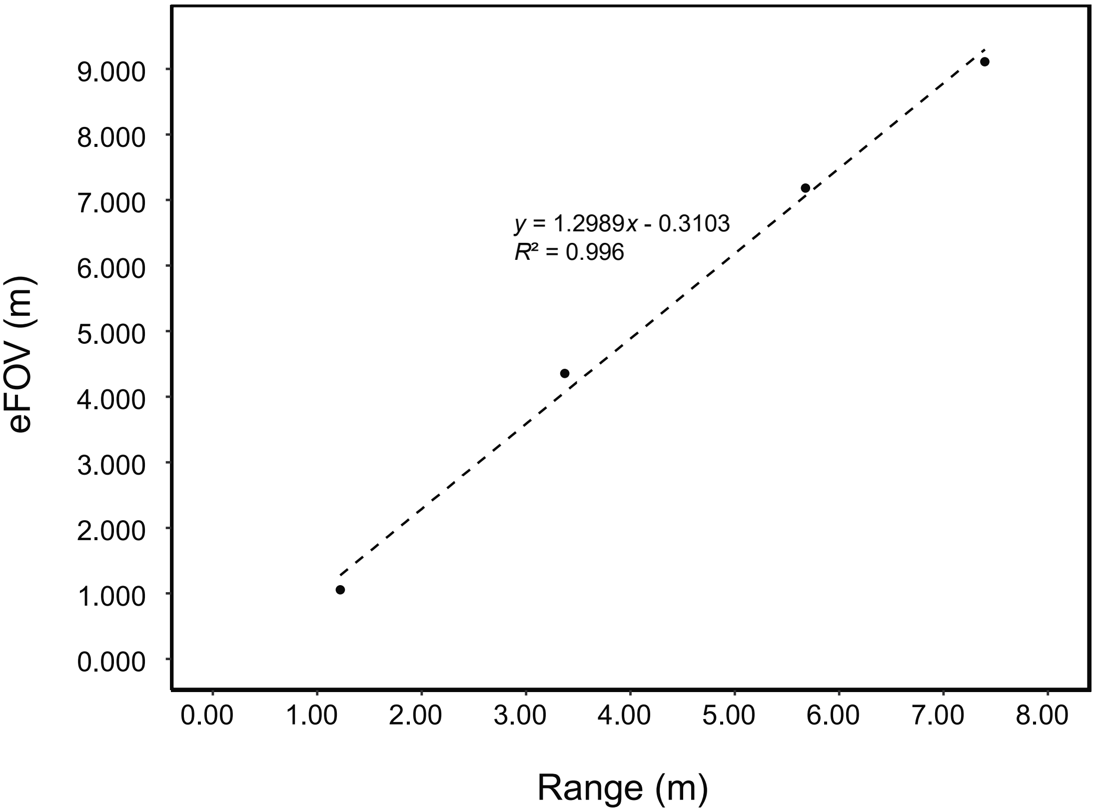


Figure 3.2. Minimum distance range (m) required for length measurements of large object sizes (1-10 m long) using the effective field-of-view (eFOV) of paired stereo-video cameras (i.e., the horizontal width of the overlapping FOV between cameras). Equation indicates line-of-best-fit for extrapolation of minimum distance range (y) required to measure a given object size (x), as constructed with a linear regression.

3.3.1.3 Replicates

As expected, both the precision and accuracy of measurements for a control target, in a clear water pool environment, improved with increased replication (Fig. 3.3). This effect was more pronounced as range increased (i.e., the further away the measurement was made, the more valuable additional replicates were). Accuracy and precision remained relatively stable for all measurements made at a close range (6 m) regardless of replicates. These trends were expected as accuracy and precision both characteristically decrease as range increases. Overall, the greatest improvement in accuracy occurred when increasing replicates from one to two, and in precision from two to three replicates. Decreasing the range from 12 to nine metres also greatly enhanced both measurement accuracy and precision.

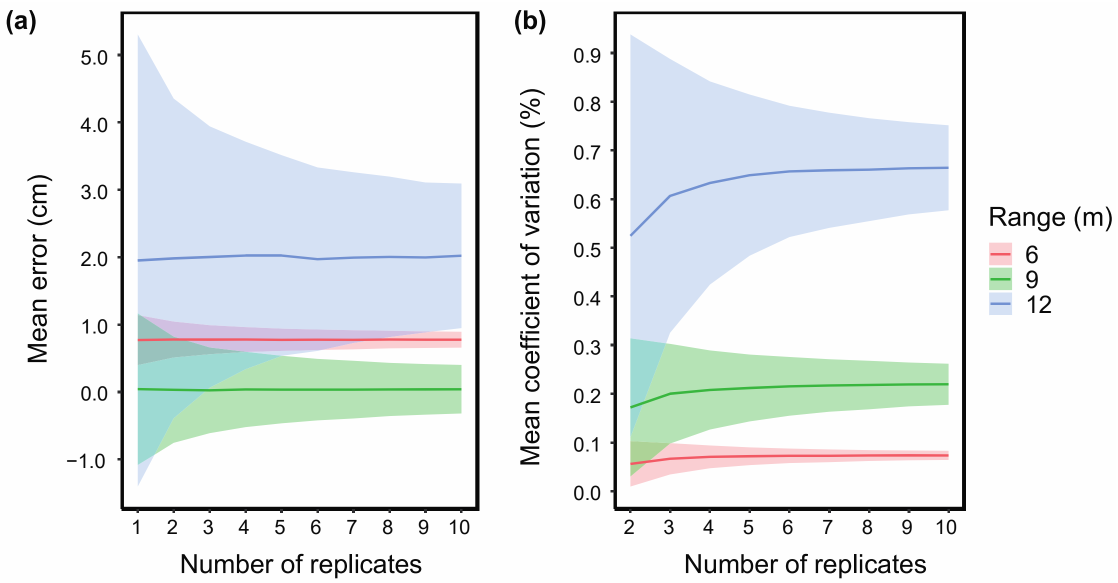


Figure 3.3. (a) accuracy (as mean error) and (b) precision (as coefficient of variation) of replicate 5 m PVC pipe measurements at three approach distances (i.e., ranges): 'close' (6 m), 'medium' (9 m), and 'distant' (12 m). Means (lines) ± SD (shaded regions) were drawn from simulated data created using a resampled bias-corrected bootstrap method (10,000 iterations) on n = 5 replicate measures for each range category.

3.3.2 Single-camera vs. stereo-image techniques

3.3.2.1 Accuracy and precision

Accuracy and precision were assessed using control measurements. Both the single-camera and SDOV methods produced highly accurate measurements (Table 3.4), with an overall mean error of -0.03% and 0.07%, respectively. There was no significant difference in accuracy of measurements between techniques ($T_{188} = 1.973$, $p = 0.496$). Both methods also produced highly precise replicate measurements, with an overall mean precision (as *CV*) of 1.12% (single-camera) and 0.64% (SDOV). However, the replicated SDOV measurements were 42.9% more precise than the single-camera measurements, and this difference was statistically significant ($T_{220} = 1.971$, $p < 0.001$).

Table 3.4: Comparative accuracy and precision of control measurements using single-camera videogrammetry and stereo-videogrammetry.

Single-camera system (Sobtzick, 2010)				
True length (m)	***n***	**Mean measured length ±** ***SD*** (m)	**Mean error** (%)	**Coefficient of Variation** (*CV*) (%)
1.00	*21*	1.009 ± *0.016*	-0.84	*1.54*
2.00	*21*	1.984 ± *0.020*	0.84	*1.02*
3.00	*21*	2.997 ± *0.038*	0.11	*1.27*
4.00	*18*	4.013 ± *0.046*	-0.31	*1.15*
5.00	*15*	5.024 ± *0.035*	-0.48	*0.70*
6.00	*24*	5.968 ± *0.059*	0.54	*0.99*
		Overall mean	-0.03	*1.12*
Stereo-image system				
True length (m)	***n***	**Mean adjusted length ±** ***SD*** (m)	**Mean error** (%)	**Coefficient of variation** (*CV*) (%)
1.00	*20*	1.000 ± *0.009*	-0.03	*0.90*
2.00	*20*	1.999 ± *0.011*	0.04	*0.53*
3.00	*19*	3.000 ± *0.011*	-0.01	*0.37*
4.00	*20*	4.006 ± *0.016*	-0.15	*0.39*
5.00	*16*	4.997 ± *0.055*	0.08	*1.10*
6.00	*13*	6.024 ± *0.036*	-0.39	*0.60*
		Overall mean	-0.07	*0.64*

Note. Single-camera videogrammetry range = 4 – 14 m. Stereo-videogrammetry range: 3.5 m – 14.5 m.

3.3.2.2 Whale measurements

Precision was again assessed for in situ whale measurements when replicates of individual whales were achieved. Replicate measurements were obtained for 97 and 22 whales using single-camera (n = 2-18) and SDOV (n = 2-8) videogrammetry, respectively (Appendix C: whale measurements). The stereo system achieved more precise replicate measurements of in situ whale TBL measurements than the single-camera system (i.e., smaller coefficient of variation; Table 3.5). Overall, replicate TBL measurements from SDOV were 68.8% more precise than those made using single-camera videogrammetry, and this was statistically significant ($T_{45} = 2.014$, $p < 0.001$). The precision of replicate SDOV TBL measurements ranged from a coefficient of variation (*CV*) of 0.12% to 2.69% with a mean *CV* of 1.12%. Single-camera videogrammetry whale measurement precision ranged from 0.0% *CV* to 5.20% *CV*, with an overall mean *CV* of 1.89%.

Table 3.5: Whale measurement summaries from single-camera and stereo-image methods.

Videogrammetry method	n_{whales}, n_{reps}	**mean TBL (m)**	**mean *SD* (m)**	**mean *SE***	**mean *CV* (%)**
Single-camera (Sobtzick, 2010)	*97, 4.71*	5.707	*0.106*	*0.053*	*1.86*
SDOV (this study, 2017)	*22, 3.64*	6.193	*0.069*	*0.037*	*1.12*

Note. Total body length (TBL) measurements of whales shown with number of whales (n_{whales}) and mean number of replicate measurements per whale (n_{reps}), *SD* = standard deviation, *SE* = standard error, *CV* = coefficient of variation.

Measures of the four morphometric body features (

Table 3.1) were all achieved with stereo-image methods, but measurability depended on the behaviour of individual whales and the characteristics of their passes (e.g., distance to the cameras, active swimming vs. gliding, water visibility, orientation to the sun). Snout-to-dorsal-fin length (SDF) was the most measurable morphometric feature, attained from 51.5% of identified whales. This was followed by total body length (TBL: 41.4%), fluke width (FW: 29.3%), and body width (BW: 15.2%). TBL was able to be measured during 20.4% (65) of identified passes (passes during which the whale was individually identified). SDF was measured during 25.8% (82) of passes. SDF was more achievable than TBL due to two main factors: 1) several passes occurred too close for the full body to be measured (i.e., within a few meters), and 2) the anterior dorsal fin insertion was more visible than the caudal notch, particularly at greater ranges and/or when the whale passed at the same vertical depth as the videographer. In perpendicular lateral views, the notch was obscured by the fluke. Fluke width was measured during 15.5% (n = 49) of identified passes. Width at the widest point was achieved during 2.8% (n = 9) of identified passes (see Appendix D). Width measurements were difficult due to a lack of identifiable reference points in this area of the body, and so were only achievable at close ranges when image clarity was sufficient to see subtle markings to assist with reference point identification.

3.4 Discussion

This study demonstrates that stereo-videogrammetry using a diver-operated stereo-video system (SDOV) is a reliable technique for obtaining morphometric measurements of small- to medium-sized cetaceans. Control trial measurements achieved very high precision and accuracy (less than 0.5% error and 1.5% variation) for objects up to 8 m in length at distances greater than 10 m. In open ocean conditions, similar precision was achieved for total body length measurements of dwarf minke whales (1.12% mean variation of whales

5.00-7.38 m in length) up to approximately 10 m range, beyond which precision began to decrease. When compared to single-camera videogrammetry methods as used by Dunstan et al. (2008) and Sobtzick (2010), the stereo-image method produced similar accuracy of control measurements, but 68.8% more precise measurements of dwarf minke whale body length. We establish that the optimal distance range for total body length measurements is usually less than 9 m with at least three replicate passes in which the whale has minimal dorso-ventral body flexure. Body width and tail fluke width were also achievable with stereo methods. This stereo approach therefore provides sufficiently high sensitivity for detecting growth and changes in body condition over time when repeated measures of the same individuals can be attained. Indeed, with a stereo-video precision of 2.6% at worst, the change in an individual whale's TBL would be detectable if it changed across years by 3% or more, equivalent to growth of 19 cm for a typical whale (mean length in this study was 6.25 m).

Precision of replicate control measurements was better than that of replicate whale measurements made in open ocean conditions, as might be expected. Additional error is introduced in situ, as compared to the pool trials, including shakier video from rough ocean surface conditions, poorer water clarity, and undetected dorso-ventral body flexure of the whales. While attempts to minimize these errors were made (i.e., choosing relatively smooth sections of video to make measurements, and rejecting passes with noticeable flexure), the results suggest that they were not entirely eliminated. However, the additional impact of these errors on precision was minimal, as variation remained below 1.5% for replicate whale TBL measurements. Thus, given very good conditions (i.e., calm seas, high water clarity, and slow-moving animals), robust measurements may be possible beyond the maximum suggested 9 m limit, and so this is an optimal range suggestion, not an absolute limit.

Not every pass of a whale is suitable for making an identification and/or a morphometric measurement. Over 80% of passes resulted in an individual identification;

however, only around 20% of identifiable passes resulted in a TBL measurement. This can be attributed to both the ability to identify the reference points required for a morphometric measurement and the behavioural characteristics of that pass. For example, if the whale was actively swimming throughout the entirety of a pass, without pausing to glide, the continuous dorso-ventral body flexure made it difficult or impossible to make a TBL measurement. However, this behaviour did not impact the ability to identify a single reference point to make an approach distance measurement. Only rarely was a visible pass unable to be identified (<20%), and this was generally due to distance, water visibility and/or poor lighting (i.e., backlighting from facing into the sun). Even at distances of 15-20 m, 50% of passes were identifiable, and whales were identified at distances up to 25.1 m. Conversely, the greatest distance at which a whale was measured for TBL was 10.85 m. Thus, when multiple whales are passing at once, the closer whale should be prioritised for filming, as it is more likely that the closer whale will be a) identifiable, and b) measurable. However, for useful ID and behavioural data (i.e., approach distance) as many as passes as possible could be filmed. Therefore, we recommend a simultaneous tracking protocol whereby the videographer visually tracks as many whales as possible and pans the cameras to the closest point of each pass, where possible.

Stereo-photogrammetry has been described as likely approaching the most accurate measurements possible for open ocean conditions, when known biases are corrected for (Dawson et al., 1995). Here, after correcting for the systematic distance range effect, control (calibrated pool testing) and field (whale) measurements were among the most accurate and precise reported in related literature (e.g., Dunbrack, 2006b; Shortis & Harvey, 1998; Spitz et al., 2000). Under both controlled and field conditions, the SDOV system outperformed the single-camera system in precision by 42.9% and 68.8%, respectively, and achieved comparable accuracy (under 0.5% mean error for control measurements). The significantly higher level of precision achieved by the stereo method means that it is more capable of detecting change in cetaceans' body sizes over time. Thus, for measuring morphometrics, growth, body condition, and population trends, the increased precision of the stereo system confers a clear advantage over the single-camera system.

The distance range effect appeared to be the most influential factor on measurement quality. While the correction factor improved accuracy, the precision of replicate control and field measurements began to decline quickly beyond approximately 12 m distance. Therefore, the most important factor determining the suitability of this method for application to other species and/or locations is likely to be how closely the target animals can be approached (or how close they are willing to approach the videographer). Approaches to within this distance are known to occur in Argentina with southern right whales (*Eubalaena australis*) (Lundquist et al., 2013) and publicly available images from other swim-with programs suggest this approach distance occurs in other locations as well, e.g., humpback whales (Tonga Tourism Authority, 2014), beluga whales (*Delphinapterus leucas*; Sea North Tours 2018), and sperm whales (*Physeter macrocephalus*; Discover Dominica Authority 2019). To ensure the distance range bias is consistently corrected for, we recommend that a correction factor is calculated for each calibration of the SDOV system, as it may differ slightly with each calibration.

Water visibility is also likely to impact this critical range point, as well as the orientation to the sun (i.e., due to backlighting impeding the ability to make a positive identification). For the case study herein, visibility was typically 20-25 m. In addition, the definition itself of "unacceptable" measurement quality will be conditional according to the desired measurement outcomes or sensitivity. For example, if an aim is simply to establish the age class of a large cetacean (e.g., juvenile vs. adult), the precision required would be much lower than if assessing and monitoring body condition of a smaller cetacean. The distance range limit also has implications for the maximum measurable animal size that can be achieved with stereo-video methods. By extrapolating the effective field-of-view size, animals up to approximately 11.5 m long should be measurable within the optimal measurement range of 9 m with this SDOV system. SDOV systems with a greater base separation may be explored to film and measure larger cetaceans.

The largest source of error in measuring whales with this technique is expected to arise from body flexure. This may result in an underestimated TBL of up to 5% for dwarf minke whales (Dunstan et al., 2008). This error is not confined to either single-camera or stereo videogrammetry; as such it should impact measurements made by both techniques equally. While more advanced technological procedures would be required to eliminate this error, it can be minimised with careful reviewing of imagery and rejection of images with detectable flexure, as demonstrated here. When dwarf minke whales approach swimmers in the GBR, they most often slow down and glide, and thus very few passes necessitated rejection due to dorso-ventral body flexure. Further, since most replicate TBL measurements had less than 2% variation, we were likely successful in reducing this error.

3.4.1 Recommended protocols for SDOV filming of dwarf minke whales

Based on our field testing and comparison of the SDOV and single-camera systems, we propose the following key videography protocols for using stereo-videogrammetry techniques to reliably assess and monitor individual whale morphometrics over time:

1. *An attempt should be made to film at least three passes of each animal to ensure at least two replicates.* Precision and accuracy of stereo length measurements increases with increasing replicates. This was expected, as Harvey et al. (2002) found both accuracy and precision of stereo measurements increased significantly up to three replicates for reef-fish targets (<1 m in length). Since the greatest increase in precision and accuracy occurred at 2-3 replicates, this would be the ideal minimum target for replicates. However, as this method

involves filming wild animals, the number of replicates (i.e., passes) of each animal cannot be guaranteed, nor can the ability to make a quality length measurement from each pass (e.g., if the whale is actively swimming and thus dorso-ventrally flexed). The measurement software program used in this study produces a unique precision estimate for each length measurement. This estimate is generated based on how closely the user has identified the same reference points in the paired stereo images for each measurement. Therefore, in the absence of replicates, this software precision estimate can be used to estimate a confidence level for single measurements.

2. *Generally, when multiple whales are present, the animal passing by closest to the videographer should be prioritized for filming.* Range was the most important factor to impact the accuracy and precision of measurements. The closer the pass, the more likely the whale was to be identified, and the better the quality of measurements. However, a pass that is too close may inhibit the ability to make certain morphometric measurements. Based on extrapolation of the effective field-of-view size, a 4 m animal would require a minimum approach distance of slightly over 3 m, and a 7 m animal would require a minimum approach distance of approximately 5.5 m. These minimum distance requirements were met for most passes by dwarf minke whales (over 99% of passes were sufficiently distant to measure a 4 m animal, and almost 90% for a 7 m animal). Thus, the animal passing the closest can be safely prioritized to generate the highest quality measurements, with minimal risk that the effective FOV will be too small. The passing behaviour of target animals will be species- and location-specific; however, dwarf minke whales are well-documented for approaching swimmers very closely, so this minimum distance requirement is likely to be less relevant to other cetaceans.

3. *Approach distance (i.e., closest whale) should be prioritized over orientation.* Measurement quality progressively decreases as range increases; however, trade-offs exist between different orientations for making morphometric measurements. For example, while

the reference points for measuring total body length are most clearly visible from above (i.e., when the whale passes directly below the videographer), dorso-ventral body flexure is more difficult to detect in this orientation. In contrast, body flexure is clear at perpendicular lateral views; however, the caudal notch (i.e., reference point for TBL measurement) can be obscured by the fluke from this perspective. Due to similar body structure among cetaceans, this is likely to affect other cetaceans equally to dwarf minke whales, so it is a potential source of error that all field studies should consider. While reliable morphometric measurements clearly cannot be made at great distances (15 m+), whales can still be identified and approach distances can still be measured, which can be used as a proxy for inquisitive or risk-taking behaviour in the presence of humans (Mangott, 2010; Mangott et al., 2011). Approach distance measurement quality remained acceptable at these greater distances because they were single-point measurements rather than two-point measurements; as a result, they are inherently less error-prone. Since water visibility rarely exceeds this identifiability range (up to 25 m), almost every pass can potentially be useful for an approach distance measurement (given the appropriate orientation for identification). However, since closer passes enable additional measurements to be made (i.e., morphometrics), distant passes should be lower order priority whenever prioritization is required (i.e., when more than one whale is present).

4. *Reference points should be standardized and as visible as possible.* Discrete physical boundaries are preferred when available, such as the tail fluke notch, tip of the snout, or fin insertion point. Reference points for other morphometric measurements, such as width, can be more difficult to establish due to lack of discrete, obvious, or consistent features.

3.4.2 Detecting change over time (growth and body condition)

The stereo-videogrammetry method achieved a mean *CV* of 1.24% for whales with replicate TBL measurements, and a maximum *CV* of 2.70%. Given the mean TBL measurement of 5.92 m, the average variation of an average size whale is 7.3 cm, and the maximum variation is 16.0 cm. Thus, any inter-annual change in TBL greater than 16.0 cm is likely to represent true growth.

Dwarf minke whales are thought to be born at approximately 2 m in length (Arnold, 1997; Best, 1985). Growth rates for this subspecies are not well documented, but may be up to 2 m within the first year, considering the smallest whales measured (excluding calves) were greater than 4 m. Thus, this technique is likely to detect growth during at least the first several years of life. As inter-annual growth slows with age (with body length as a proxy), the ability to detect change will diminish. So, while this technique is probably sensitive enough to detect growth in TBL, the extent of its usefulness for this beyond the first few years may not be known until dwarf minke whale growth rates are better described.

Total body length has been measured in-situ for several other cetaceans. Measurements for sperm whales have been obtained via boat-based photogrammetry, with precision of repeat measurements ranging from 1.3% *CV* (Jaquet, 2006), 4.4% (S. Dawson et al., 1995) to 5.1% (Gordon, 1990). The technique developed in this chapter provides improvement on most of these precision measures. Furthermore, these studies used allometric extrapolation of different morphometric features to generate an estimate of total body length (blow-hole to dorsal fin distance and tail fluke width). Thus, an additional error exists in these studies. A similar case is seen with measuring killer whales using extrapolation of dorsal fin height to total body length (Durban & Parsons, 2006). Both species are now targets of commercial swim-with industries, providing a potential opportunity for research, and specifically to utilize SDOV for in situ measurements. This would eliminate the error associated with allometric extrapolation, as well as the parallax error when single-camera techniques were employed.

Only a small number of whales were able to be measured for body width (BW, N = 6), which is a measurement often used as a proxy for body condition (e.g., thickness of fat stores). Difficulties in identifying reference points in this area of the body, and strict orientation requirements, precluded making such measurements during most passes of dwarf minke whales. As a result, variation in replicate measurements of BW of up to 6.92% was observed for individual whales (see Appendix D), and with a mean BW of 1.018 m, this represents a variation of up to 7.1 cm. If the issues with identifying reference points in this area can be resolved (e.g., software program modifications), the low variation achieved for replicate TBL measurements (1-2%) suggests that small 1-2 cm changes in width would be detectable and thus useful for assessing body condition of dwarf minke whales and other cetaceans. Alternatively, further processing of suitable frames through an additional program that automatically calculates width at select intervals along the body (e.g., Bierlich et al., 2021; Christiansen et al., 2020; Torres & Bierlich, 2020) may provide a solution to the issue of manually identifying reference points inherent to the image processing software used herein.

A final species-specific consideration must be made when selecting an appropriate SDOV system. As base separation (the distance between cameras) increases, so does the ability to measure larger objects at greater distances. However, greater base separation also introduces challenges in system calibration and field deployment due to size, revealing a trade-off between measurement accuracy and practical feasibility. In this study, an SDOV system with an 80 cm base separation was used. A larger, above-water system was tested by Growcott et al., (2012) for measuring sperm whales, and their selected base separation of 256 cm was sufficient to accurately measure objects up to 12 m in length at ranges of up to 70 m.

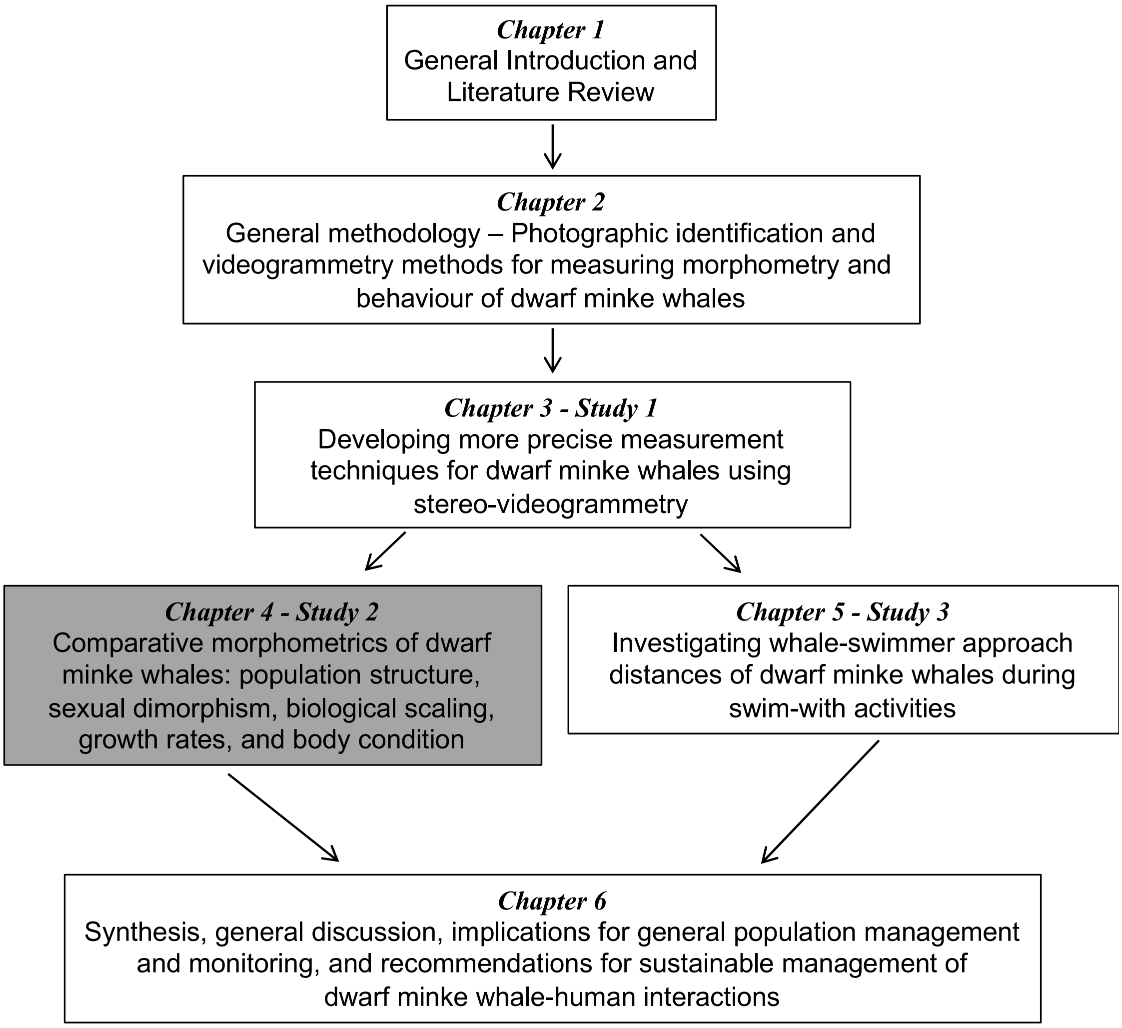
While this system was not constrained by underwater visibility, its principles could readily be adapted for underwater measurements of larger cetaceans (provided sufficient water clarity). Selecting the appropriate base separation is therefore essential for ensuring accurate and feasible measurements across different species and study conditions.

3.4.3 Conclusion

This chapter has demonstrated that it is possible to obtain high quality morphometric measurements of dwarf minke whales using in-water stereo-image techniques, with the potential for application to other medium-sized cetaceans under appropriate conditions (and inferred application to smaller species). I have also demonstrated that in-water stereo-videogrammetry is preferable over single-camera techniques, providing similar accuracy but significantly enhanced precision. Given sufficient replicates (i.e., two or more per individual), these results suggest that this method should be sufficiently sensitive to detect growth in total body length. With some software modifications and at least three replicates, this technique may potentially be useful for monitoring other biologically and/or ecologically significant changes in cetacean morphometrics, such as body condition. Thus, in-water stereo-videogrammetry may present a valuable opportunity for improving population and health monitoring of dwarf minke whales and other similarly-sized cetaceans.

4 CHAPTER 4:

COMPARATIVE MORPHOMETRICS



4.1 Introduction

4.1.1 Morphometry applications

Width- or girth-to-body-length relationships are commonly used as a proxy for body condition on live cetaceans, where energy reserves (i.e., blubber) cannot be directly measured (Best & Rüther, 1992; Christiansen et al., 2014, 2020; Gray et al., 2019; Torres et al., 2022; Vermeulen et al., 2023). Body condition measures represent the relative size of a cetacean's energy reserves, and thus enables one to infer their ability to fulfil critical life history roles such as courtship and mating, reproduction (Lockyer, 2007), lactation and parental care (Christiansen et al., 2014), and migration (Castrillon & Bengtson Nash, 2020). Further, temporal and spatial patterns of body condition and population demographics can identify responses to environmental impacts such as anthropogenic climate change and other threatening processes (Christiansen et al., 2020). This biological information can have wide-ranging practical applications for conservation and/or management purposes.

For example, Bradford et al. (2012) found that body condition of western gray whales (*Eschrichtius robustus*) varies significantly across demographics, with lactating mothers generally exhibiting the most depleted energy reserves. This may have negative consequences on calf growth rates and female calving intervals. Christiansen et al. (2020) found that North Atlantic right whales (*Eubalaena glacialis*) were in poorer health than southern right whales (*Eubalaena australis*) by comparing body condition between population stocks. North Atlantic right whales migrate through heavily developed coastal areas where ship strikes and entanglements occur regularly, while southern right whales inhabit relatively remote and unimpacted environments. Indeed, close to 90% of North Atlantic right whales exhibit entanglement scars, and entanglements occur in over 15% of the population each year. This higher incidence of sub-lethal entanglement and the resultant stress of such events are hypothesized to be the main contributing factors to the poorer body condition of the North

Atlantic population. This knowledge has led several government agencies to implement dedicated anti-entanglement initiatives to reduce these interactions for North Atlantic right whales (Department of Climate Change, 2021; Fisheries and Oceans Canada, 2022; National Marine Fisheries Service, 2008). This case demonstrates how body condition can be a useful measure to inform conservation and management practices for cetacean populations.

Biological scaling can also be investigated from morphological measurements. This can facilitate the development of growth curves and provide useful proxies for important features that may be difficult to measure directly, such as total body length (TBL). These relationships can be particularly useful for cetacean research, because direct TBL measurements are often unfeasible due to the research platform and/or the species' behaviour (e.g., vessel-based surveys or travelling animals). In several cetacean species, the proportional relationship between body length and caudal fluke width or blowholes-to-dorsal-fin length has enabled researchers to estimate total body length without imagery of the full animal (Castelblanco-Martínez et al., 2014; Clark & Odell, 1999; Dawson et al., 1995; Gordon, 1990; Jaquet, 2006; Ortega-Ortiz et al., 2022; Ramos et al., 2022; Scott & Winn, 1980). Similarly, dorsal fin heights have been used to approximate total body length of orcas (Durban and Parsons, 2006).

Sexual dimorphism can also be examined via biological scaling. The utility of photo-identification as a tool for cetacean research is enhanced when the sex of individuals is known (Augusto et al., 2013). Sexual dimorphism of external features is often subtle in cetaceans (Brown et al., 2016), and sex determination is generally rare in photo-identification databases (van Aswegen et al., 2019; Yahn et al., 2023), including for dwarf minke whales (Daley, 2019; Dunstan et al., 2008; Sobtzick, 2010). However, in some cases, sexual dimorphic differences have been used to increase the sample size of sexed individuals (Brown et al., 2016; Caspar & Begall, 2022; Yahn et al., 2023). Differential body proportions have been observed in Antarctic minke (*Balaenoptera bonaerensis*) and sei (*Balaenoptera borealis*) whales, wherein females have larger heads, proportionately, than male conspecifics (Kawamura, 1969; Ohsumi et al., 1970; Omura, 1957). Males of many cetacean species, particularly within the Odontocetes, exhibit longer dorsal fins proportional to their body length (Betty et al., 2022; Brown et al., 2016; Caspar & Begall, 2022; Clark & Odell, 1999; Yahn et al., 2023). Each of these applications can provide important biological and ecological information that can directly inform and contribute to conservation management strategies.

Further, body length measurements can directly contribute to the establishment of species growth curves (Bertalanffy, 1938). Establishing a species growth curve can facilitate age estimations of individual animals and provide important insights into demographic population structure (Dunstan et al., 2008; Sobtzick, 2010; Whitehead & Payne, 1978). This may be particularly useful for cetaceans for two reasons. First, for many species, no non-lethal age estimation methodologies have been established. Second, existing methods such as telomere length generally lack the precision required to establish a growth curve (Dunshea et al., 2011). Indeed, age estimation has proven sufficiently difficult for cetaceans that it has remained as one of the primary rationales from the Government of Japan to allow the continuation of their long-running scientific whaling program in the North Pacific and Antarctic oceans despite widespread criticism and condemnation of the program (Clapham et al., 2003; Clapham et al., 2007; Hofman, 2019; Peace, 2010).

4.1.2 Knowledge gaps for dwarf minke whales

Very little external morphometric data have been published for dwarf minke whales, particularly live animals. Most morphometric data have come from strandings (Best, 1985; Dawson & Slooten, 1990; Paterson et al., 2000; Zerbini et al., 1997), and non-target incidental take from whaling (Kato et al., 2022; Kato & Fujise, 2000). Of live dwarf minke whales, only total body length has been previously measured, on 140 individuals in the Great

Barrier Reef, Australia (Dunstan et al., 2008; Sobtzick, 2010). General morphological differences across the minke whale species complex have been investigated (Kato et al., 2022; Kato & Fujise, 2000); however, ontogenic allometry (i.e., changes in body proportions with age) within the dwarf minke whale subspecies is poorly known. Some population demographics have been identified, such as the size and general age class structure at the seasonal aggregation in the Great Barrier Reef, Australia. Dunstan et al. (2008) found that approximately two-thirds of the interacting population were immature in 2003 and 2004, and one-third were "mature/potentially mature", suggesting that this may represent an open population structure with a high level of recruitment of young individuals into the population. However, population structure has only been investigated across these two consecutive sampling periods, and any longer-term temporal changes remain unknown. Monitoring these trends over time is critical, as shifts in population demographics can provide insight into broader ecological changes and potential conservation concerns. For example, baleen whales that feed in polar regions are increasingly vulnerable to climate change, and changes in demographics may be one of the first signs of these impacts, making the monitoring of such trends particularly useful for future conservation and management efforts (Flores et al., 2012; Nicol et al., 2008; Simmonds & Isaac, 2007; van Weelden et al., 2021).

4.1.3 Objective and research questions

To address these gaps, the objective of this chapter was to gather and assess morphometric measurements of dwarf minke whales within the interacting population that aggregates in the northern Great Barrier Reef. From these measurements I then investigated temporal patterns of allometric growth, which allowed me to answer the following research questions:

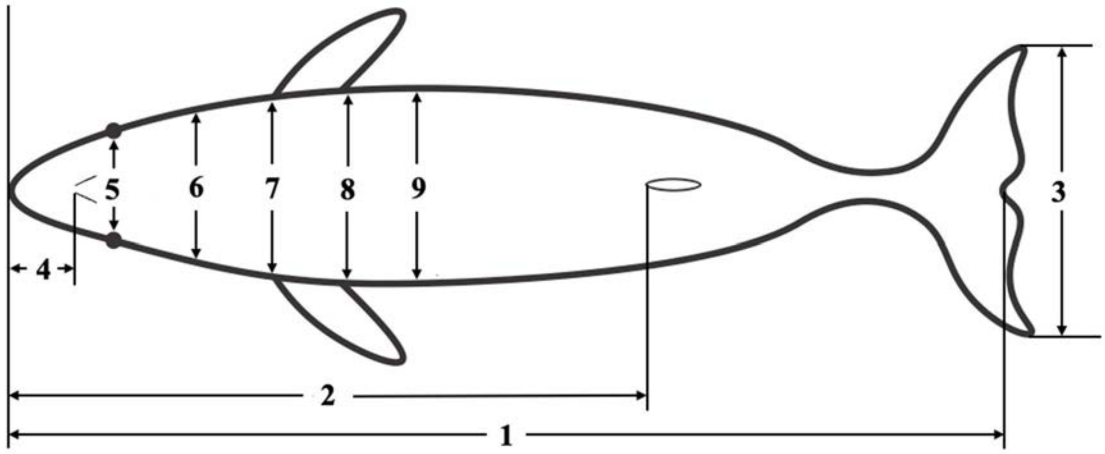
1) How do external features grow in relation to total body length?
2) Are there any measurable external features that can be used as a reliable proxy for total body length?
3) How can this filming methodology be used to investigate growth and body condition?
    a) What measurements represent the best indicator of body condition?
    b) How can these measurements be made from this footage (considering filming and analytical constraints such as body position/flexure and availability of reference points)?
4) Has the structure of the interacting population changed in the 10 to 11 years since an earlier study was conducted in 2006-2007 (Sobtzick, 2010)? If so, how? What implications or concerns does this raise?

4.2 Methods

4.2.1 Overview

In-water access to dwarf minke whales is available in the GBR via a long-running liveaboard dive tourism industry out of Cairns and Port Douglas, underwater visibility is generally good (15-25 m or more), and whale-swimmer approach distances are some of the closest recorded in tourism interactions. As such, underwater photogrammetry is a viable option for these conditions (see Chapter 3 section 3.1.3) and thus was used to obtain measurements of morphological features of interacting individuals. I filmed twenty-one (21) encounters with dwarf minke whale whales with a diver-operated stereo-video (SDOV) system in 2017, seventeen (17) encounters in 2018, and twenty-one (21) encounters in 2019, resulting in a total of 59 encounters. For this I followed the filming protocols developed in Chapter 3. Supplementary imagery of these encounters was also collected from passengers, crew, and additional researchers for photographic-identification (photo-ID) purposes. From the 2017 footage (SDOV + supplementary imagery), 106 complete IDs, 37 left-only IDs, and 31 right-only IDs were made, representing a range of 146 (minimum) to 174 (maximum possible) unique animals.

Nine morphologic features were selected for measurement purposes (Fig. 4.1) based on a qualitative assessment of usefulness and measurability (see Chapter 2 Table 2.2). Of the 146-183 individual whales identified in the 2017 footage, 93 were adequately filmed to measure at least one of the nine selected features. Measurement science computer program EventMeasure^{TM} was used for this, following the SeaGIS user guide (Seager, 2016d) and additional analytical protocols developed in Chapter 3 (see Chapter 3 section 3.4.1). Photo-ID was completed for all encounters in 2018 and 2019 as well; however, due to time constraints, not all SDOV footage could be analysed. Instead, from the photo-ID process, 16 multi-year resights were identified, which were whales that were filmed in more than one of the sampling years (i.e., 2017 – 2019). From these 16 animals, 10 were able to be measured to investigate inter-annual growth. All other analyses used 2017 data only. Next, I explored the relationships between body measurements on individual whales, establishing the allometric (i.e., proportional) relationships between features and exploring whether any can be used as a reliable proxy for total body length or body condition. Finally, general population demographics such as maturity status were inferred and compared to previously collected data to investigate temporal trends.



1. *Total body length (TBL)*: from tip of snout to caudal notch
2. *Snout-to-dorsal-fin (SDF)*: from tip of snout to the dorsal fin anterior insertion point
3. *Fluke width (FW)*: distal tips of caudal flukes
4. *Snout-to-blowhole (SBH)*: tip of snout to anterior terminus of left blowhole crease
5. *Width at eyes (WE)*: lateral margin of each eye at middle/widest point
6. *Width behind eyes (WBE)*: halfway between WE and WAP
7. *Width at pectoral fin anterior insertion point (WAP)*: pectoral fin anterior insertion points
8. *Width at pectoral fin posterior insertion point (WPP)*: pectoral fin posterior insertion points
9. *Width at widest point (WWP)*: visual estimation of widest point, at approximately mid-body

Figure 4.1. Schematic of a dwarf minke whale (dorsal view) with the nine morphological features selected for measurement.

4.2.2 Field site & data collection

A detailed description of the study species, field site, and data collection procedures can be found in Chapter 2 (sections 2.1 – 2.3). Dwarf minke whales were filmed in-water by researchers, passengers, and crew during trips on live-aboard dive tourism vessels and privately chartered research expeditions in June and July of 2017, 2018, and 2019. I collected continuous video footage of encounters with a diver-operated stereo-video (SDOV) system, and all other individuals captured regular still and video imagery from personal underwater cameras. Most vessels were considered 'platforms of opportunity', not dedicated research vessels; therefore, the study-specific limitations identified in Chapter 2 also apply here (section 2.2.2.4).

4.2.3 Data pre-processing: photo-identification

A detailed description of the general photo-identification (photo-ID) process can be found in Chapter 2 (section 2.3.1). To minimize the risk of erroneous re-sampling of partially identified whales (see Chapter 2 section 2.3.1), right-only partial IDs were excluded in all morphometric summaries and reports except for analyses by sex. For analyses by sex, left-only partial IDs were excluded rather than right-only partial IDs. This allowed an increased sample size for these analyses.

4.2.4 Data processing: extracting morphometric values

A detailed description of the measurement procedures can be found in Chapter 2 (section 2.3.2). 1,118 unique morphometric measurements of acceptable quality (see Chapter 2 section 2.5.3 and Chapter 3 section 3.2.5.1) were made on 94 dwarf minke whales from the 2017 SDOV footage. These measured whales represent 54.0-65.7% of all identified whales in this sampling period. A minimum of 3 replicates per measurement was achieved for greater than 90% of measurements. This ensured sufficient precision for each measurement (see Chapter 3 section 3.2.6). Measurements were extracted Animals identified in 2017 that were re-sighted in 2018 and/or 2019 were also measured to investigate multi-year growth (see Chapter 2 section 2.5). For demographic analyses, animals 6.00 m in length and over were considered maturing/mature and animals less than 6.00 m in length were considered immature (Dunstan et al., 2008; Kato et al., 2022; Kato & Fujise, 2000; Sobtzick, 2010). Cow and calf pairs were identified when a smaller whale was observed closely associated with a larger whale and was less than half of the length of the larger whale (Dunstan et al., 2008).

4.2.5 Data analysis

4.2.5.1 Ontogenic growth and allometric scaling

Simple linear regression was used to explore the relationship between TBL and five body measurements across measured whales from the 2017 season. Features used to investigate this scaling were snout-to-dorsal-fin length (SDF), fluke width (FW), snout-to-blowholes (SBH), width at eyes (WE), and width at pectoral fin posterior insertion point (WPP) (Fig. 4.1). SDF, FW, SBH, and WE were chosen as they are not known or suspected locations of blubber accumulation, and should therefore be a more reliable representation of true (i.e., skeletal) body growth, rather than body condition. WPP was selected despite being a potential indicator of body condition (i.e., a possible location of blubber accumulation) as this measurement demonstrated the least variation across the measured population (i.e., one would expect measurements with the greatest variation between individuals to represent body condition rather than true skeletal growth; see section 4.2.5.2). Data included in each regression were subsetted from the original 2017 data set, consisting of only those individuals who were measured for both TBL and each additional morphologic feature ($N_{TBL + SDF} = 71$, $N_{TBL + FW} = 44$, $N_{TBL + SBH} = 25$, $N_{TBL + WE} = 23$, $N_{TBL + WPP} = 16$). Measurement means (derived from replicate measurements of individual whales) for all features were log transformed and fitted to a linear regression against TBL, as per allometric scaling convention (Huxley, 1932; Huxley & Teissier, 1936; West et al., 1997). Significance was determined at $p < 0.05$. Features found to have the strongest predictive relationship to TBL were considered as possible candidates to be used as a proxy for TBL (i.e., narrowest 95% confidence interval).

4.2.5.1.1 Sexual dimorphism

To determine whether sexual dimorphism exists amongst morphometric features, 18 sexed dwarf minke whales were assessed for SDF as a proportion of TBL and 14 sexed whales were assessed for FW as a proportion of TBL. Other features were not investigated due to small sample sizes. Reductions in sample sizes occurred because only 11% of identified whales were able to be sexed (see Chapter 2 section 2.4.1) and not every sexed whale was able to be measured. To be eligible for this analysis, whales had to meet all of the following criteria: 1) known sex, 2) measured for TBL, and 3) measured for an additional morphometric feature. As a result, the only features that achieved a sample size greater than 10 were SDF and FW ($N_{SDF:TBL} = 18$, $N_{FW:TBL} = 14$). Welch's t-tests were conducted to investigate differences by sex for true SDF, proportional SDF and proportional FW (as a percent of TBL). T-test assumptions were tested using the Kolmogorov-Smirnov test for normality of residuals and the Bartlett's Test for homogeneity of variances (significance was determined at $p < 0.05$). No transformations of data were required. Data for true FW did not meet the T-test assumption of normality of residuals; therefore, these data were tested using the Wilcox rank sum exact test, with significance determined at $p < 0.05$).

4.2.5.2 Body condition

To determine which feature(s) may be best for monitoring body condition, similar width measurements were identified and their spread and precision were compared. Since blubber accumulation may occur behind the eyes, variance of per-whale mean width at eyes (WE) length and per-whale mean width behind eyes (WBE) length were compared using an F Test. I predicted that WBE measurements would have a greater variance than WE measurements, as blubber accumulation is thought to occur behind the eyes, while width at eyes should better represent true (i.e., skeletal) growth. To investigate differences in precision, the coefficient of variation (CV) WE and WBE replicates were compared using Welch's T-test. I predicted that WE measurements would be more precise than WBE measurements due to the availability of discrete reference points for width at eyes. Significance for both F Test and Welch's T-Test was determined at $p < 0.05$. Assumption of normality for the F Test was tested using the Shapiro-Wilk test, with significance determined at $p < 0.05$. No transformation was required. Assumptions of the Welch's T-Test were tested using the Kolmogorov-Smirnov test of normality of residuals and the Bartlett's test for homogeneity of variances, with significance for both determined at $p < 0.05$. Data were log transformed to meet these assumptions.

Next, precision and spread of width at anterior pectoral fin insertion (WAP), width at posterior pectoral fin insertion (WPP), and width at widest point (WWP) were compared to each other. Variance of these measurements were compared using the Bartlett's Test for homogeneity of variances, with significance determined at $p < 0.05$. The assumption of normality was tested using the Shapiro-Wilk test, with significance determined at $p < 0.05$. No data transformation was required for this analysis. It was predicted that variance would be greatest for WWP measurements. Precision was investigated by comparing the coefficient of variation of per-whale replicates using a one-way ANOVA. ANOVA assumptions were tested using the Kolmogorov-Smirnov test for normality of residuals and the Bartlett's Test for homogeneity of variances, with significance for both determined at $p < 0.05$. Data were log transformed to meet these assumptions. A Tukey's HSD test was done post-hoc to identify which measurements were significantly different, with significance determined at $p < 0.05$. I predicted that precision would be poorest for WWP measurements due to the lack of discrete reference points in this location, and that WAP and WPP precision would be similar.

4.2.5.3 Growth

A total of 17 identified whales were re-sighted in multiple sampling years. This enabled an investigation of longer-term growth of these individuals. Ten of these animals were able to be measured for TBL and SDF across multiple years. Four animals were measured in 2017 and again in 2019, representing approximately two years of growth. The remaining six whales were either measured in 2017 and again in 2018, or 2018 and again in 2019, thus representing approximately one year of growth. The small sample size of whales measured for multi-year growth precluded significance testing ($N_{TBL} = 10$, $N_{SDF} = 10$, $N_{FW} = 7$, $N_{SBH} = 3$, $N_{widths} = 1$).

4.2.5.4 Long-term demographic trends

To determine if long-term population structure changes have occurred, TBL measurements collected during the 2017 sampling period were compared to historical TBL measurements collected in 2006 and 2007 by Sobtzick (2010) in the same sampling area. Due to the similarities in data collection protocols and measurement accuracy between the previous study and this thesis (see Chapter 3 section 3.3.2), data were considered comparable across these studies. First, a one-way ANOVA was conducted to compare TBL measurement means across sampling years ($n_{2006} = 52$, $n_{2007} = 77$, $n_{2017} = 73$). Significance was determined at $p < 0.05$. ANOVA assumptions were tested using the Kolmogorov-Smirnov test for normality of residuals and the Bartlett's Test for homogeneity of variances. No transformations were required. A Pearson's Chi-squared test was also conducted using TBL measurements grouped by maturity status to determine if size class distribution differed across sampling years. Significance was determined at $p < 0.05$. Finally, a post-hoc Bonferroni test was conducted to determine which sampling years were different. As per the Bonferroni correction method, significance was determined at 0.017.

4.3 Results

4.3.1 Photo-identification and sex

Photo-identification analysis was completed for 21 dwarf minke whale encounters from June-July 2017. Within these encounters, 106 complete whale identifications were made (i.e., adequate imagery of both the left- and right-sides), with an additional 37 left-only partial identifications and 31 right-only partial identifications. Following the Minke Whale Project established photo-ID convention (see Chapter 2 section 2.3.1 and Sobtzick, 2010), this sample consists of a minimum of 143 unique animals (i.e., 106 complete IDs + 37 left-only IDs) with a potential maximum of 174 individuals (106 complete IDs + 37 left-only IDs + 31 right-only IDs). Sex was determined for 26 of these identified whales: 18 females (17 complete IDs and 1 right-only partial ID) and 8 males (6 complete IDs and 2 right-only partial IDs).

4.3.2 Descriptive morphometrics and allometry

4.3.2.1 Measurement summaries

A total of 1327 unique morphometric measurements were made across 104 individual dwarf minke whales. Mean precision of per-whale replicates ranged from below 1% CV for total body length (TBL) to 3.54% error for width at widest point (WWP) (Table 4.1). Replicate measurements of longitudinal features - TBL, snout-to-dorsal-fin (SDF), and snout-to-blowholes (SBH) - were generally more precise than of width measurements - width behind eyes (WBE), width at pectoral fin anterior insertion point (WAP), and fluke width (FW) - except width at eyes (WE) and width at pectoral fin posterior insertion point (WPP), which were more precise than SBH. The most achievable/measurable measurement types were the longitudinal length measurements SDF (56% of identified whales) and TBL (52% of identified whales). Fluke width (FW) was also highly achievable (32% of identified whales were able to be measured for FW). The least achievable measurement types were body width measurements (12-17% of identified whales), in particular width at widest point (WWP; 12% of identified whales).

4.3.2.2 Total body length (TBL)

Total body length (TBL) was measured for 74 unique whales in 2017 (Fig. 4.2). This represents 52.8% of all identified whales, based on the minimum estimate of 143 unique individuals. A minimum of three replicates were achieved on 93.2% of the measured population (N = 69). The mean overall TBL was 6.17 ± 0.69 SD (m), and individual whale TBL ranged from 3.34 m (n = 1, a calf) to a mean of 7.43 m (n = 3), with the smallest non-calf whale measuring 5.01 m in length. Most measured whales (59.5%, n = 44) were 6.00 m in length or longer. Over a third of measured whales (40.5%, n = 30) were 6.50 m or longer. Dwarf minke whales 6.00 m or longer are considered likely to be maturing or mature (Kato & Fujise, 2000), and those 6.50 m or longer are considered mature (Dunstan et al., 2008; Sobtzick, 2010).

Table 4.1. Morphometric measurement summaries by measurement type.

Morphological feature	**n whales measured**	**Mean length ± SD (m)**	**Mean relative length (as % of TBL)**	**Per-whale measurement range (m)**	**Mean precision of replicates (% error, represented by CV)**
1 *Total body length* (TBL)	74	6.19 ± 0.70	100%	3.34 - 7.43	0.77%
2 *Snout-to-dorsal-fin* (SDF)	80	4.02 ± 0.48	64.9%	1.74 - 4.88	1.07%
3 *Fluke width* (FW)	49	1.75 ± 0.20	28.3%	1.38 - 2.18	2.06%
4 *Snout-to-blowholes* (SBH)	28	0.89 ± 0.11	14.3%	0.71 - 1.07	1.45%
5 *Width at eyes* (WE)	24	0.82 ± 0.08	13.5%	0.66 - 0.97	1.37%
6 *Width behind eyes* (WBE)	21	0.87 ± 0.09	14.1%	0.67 - 1.01	2.54%
7 *Width at pectoral fin anterior insertion point* (WAP)	21	0.93 ± 0.10	15.0%	0.73 - 1.13	1.97%
8 *Width at pectoral fin posterior insertion point* (WPP)	18	0.97 ± 0.11	15.7%	0.74 - 1.18	1.18%
9 *Width at widest point* (WWP)	17	1.00 ± 0.12	16.2%	0.74 - 1.24	3.54%

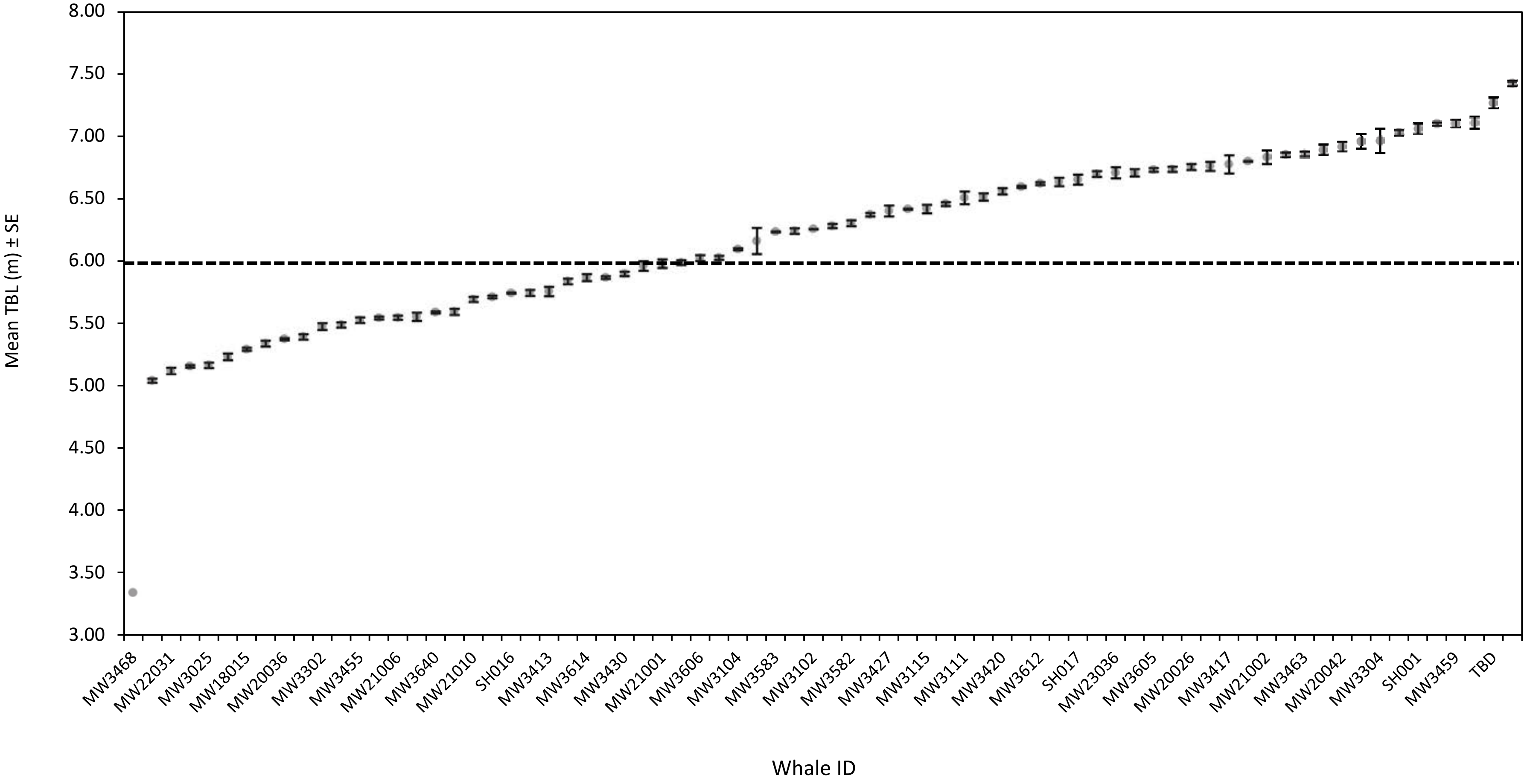


Figure 4.2. Mean total body length (TBL) of SDOV-measured whales, 2017. Error bars represent *SE* of replicates. n = 74 whales. Dashed line represents break between immature and maturing/mature whales.

4.3.3 Ontogenic growth and allometric scaling

All morphometric features tested exhibited an allometric relationship to total body length (TBL), increasing in size logarithmically with TBL (Table 4.2, Fig. 4.3). The allometric coefficient (α) was below 1 for all features tested against TBL, indicating that TBL is hypoallometric (i.e., TBL increases proportionately slower) to these features (Huxley, 1932). This ranged from a slight hypoallometric relationship with snout-to-dorsal-fin length (SDF) ($\alpha = 0.983$) to a strong hypoallometric relationship with width at pectoral fin posterior insertion point (WPP) ($\alpha = 0.680$). All features measured were also significantly strong predictors of TBL. Prediction intervals widened considerably as the size of features increased, from 0.19 m for the smallest SDF samples to 1.93 m for the largest WPP samples. Of all features tests, SDF showed the best fit with TBL, as expected, with the narrowest prediction margin and the ability to predict TBL with 95% confidence to within +/- 0.09 – 0.26 m, depending on the SDF length.

Table 4.2. Prediction equations of five morphometric features for total body length (TBL) and their corresponding 95% prediction intervals. SDF = snout-to-dorsal-fin length, FW = fluke width, SBH = snout-to-blowholes length, WE = width at eyes, WPP = width at pectoral fin posterior insertion point.

Morphometric feature, n	**Prediction equation ($y = bx^{\alpha}$)**	**TBL prediction interval (as ± per cent of x)**	**True prediction interval range (m)**
SDF, n = 71	$TBL = 0.228 \times SDF^{0.983}$	± 5.41% of SDF	± 0.094 – 0.264 m
FW, n = 44	$TBL = 2.586 \times FWF^{0.834}$	± 29.72% of FW	± 0.410 – 0.648 m
SBH, n = 25	$TBL = 1.206 \times SBH^{0.815}$	± 57.3% of SBH	± 0.407 – 0.613 m
WE, n = 23	$TBL = 1.072 \times WE^{0.898}$	± 62.6% of WE	± 0.413 – 0.607 m
WPP, n = 16	$TBL = 1.438 \times WPP^{0.680}$	± 78.3% of WPP	± 0.579 – 0.924 m

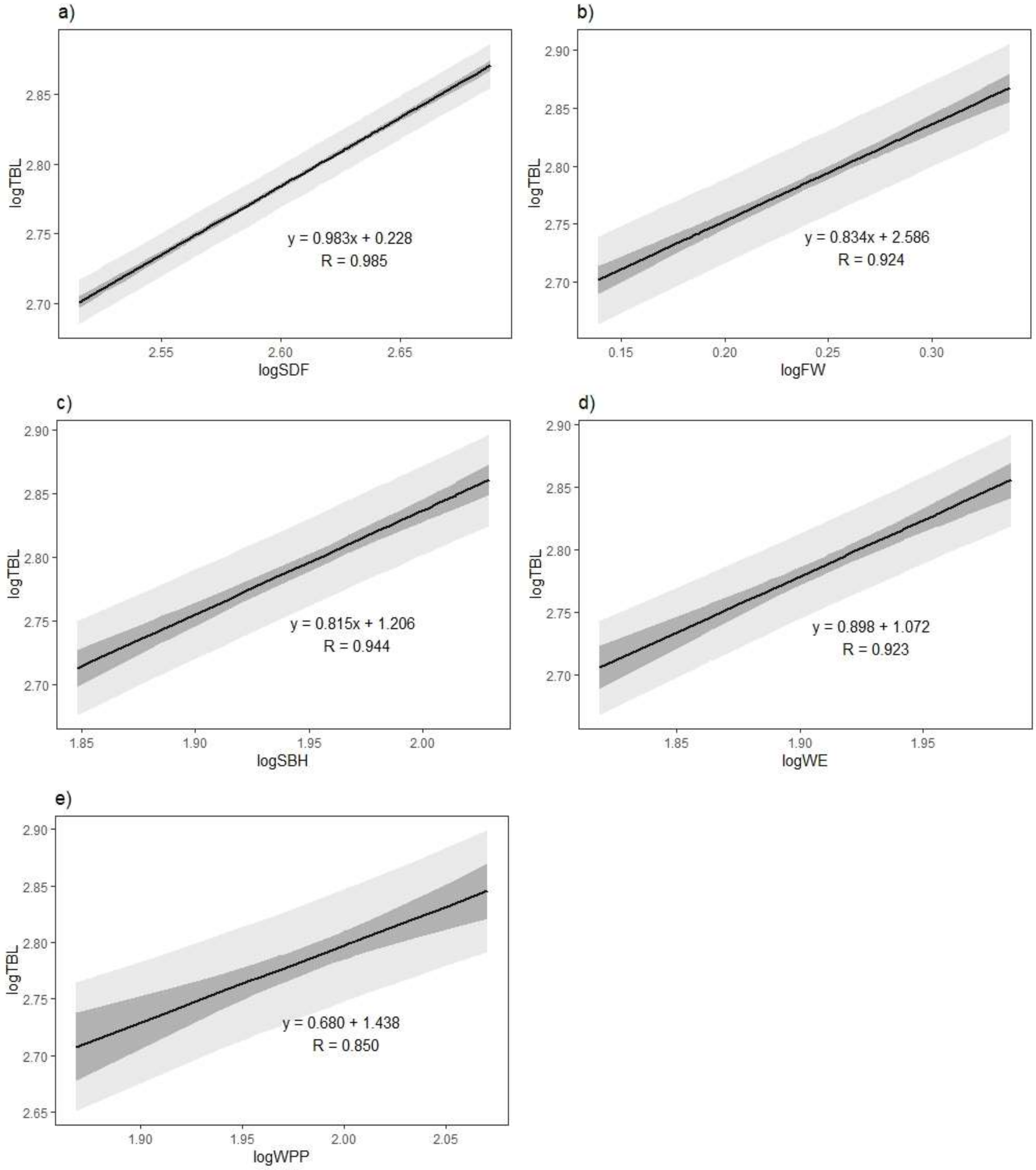


Figure 4.3. Simple linear regression of total body length (TBL) and **(a) snout-to-dorsal-fin length (SDF),** $R^2 = 0.971$, $F(1, 69) = 2301.7$, $p < 0.0001$; **(b) caudal fluke width (FW),** $R^2 = 0.853$, $F(1, 42) = 243.4$, $p < 0.001$; **(c) snout-to-blowholes length (SBH),** $R^2 = 0.891$, $F(1, 23) = 187.1$, $p < 0.001$; **(d) width at eyes (WE),** $R^2 = 0.852$, $F(1, 21) = 120.7$, $p < 0.001$; and **(e) width at widest point (WWP),** $R^2 = 0.722$, $F(1, 14) = 36.4$, $p < 0.001$. Solid line represents regression equation, dark grey area represents 95% confidence interval, and light grey area represents 95% prediction interval.

4.3.3.1 Sexual dimorphism

Mean snout-to-dorsal-fin length (SDF) was 0.19 m larger in female dwarf minke whales than males (Table 4.3). However, this difference was not significant, *t*(15.914) = 1.096, *p* = 0.289. Relative SDF (as a proportion of TBL) ranged from 64.0% - 67.4% of TBL for males and 64.3% - 66.7% of TBL for males. It was not significantly different between sexes, *t*(8.339) = -0.126, *p* = 0.903. Mean fluke width (FW) was 0.08 m larger in females than males, but this difference was not significant, *t*(11.977) = 0.87522, *p* = 0.3987. However, relative FW (as a proportion of TBL) was 2.1% greater in females than in males, and this difference was significant, *t*(10.12) = 3.394, *p* = 0.007 (Fig. 4.4). Relative FW ranged from 26.3% - 28.7% for males and from 28.1% - 32.1% for females.

Table 4.3: SDF and FW measurements relative to TBL, by sex.

	n_{SDF}	**Mean true SDF (m)** ± SE	**Mean relative SDF** (as % of TBL) ± SE	n_{FW}	**Mean true FW (m)** ± SE	**Mean relative FW** (as % of TBL) ± SE
Females	11	4.03 m ± 0.13	65.4% ± 0.22	8	1.73 m ± 0.072	29.5% ± 0.42*
Males	7	3.84 m ± 0.11	65.5% ± 0.50	6	1.65 m ± 0.058	27.4% ± 0.43*

*denotes statistical significance ($p < 0.05$)

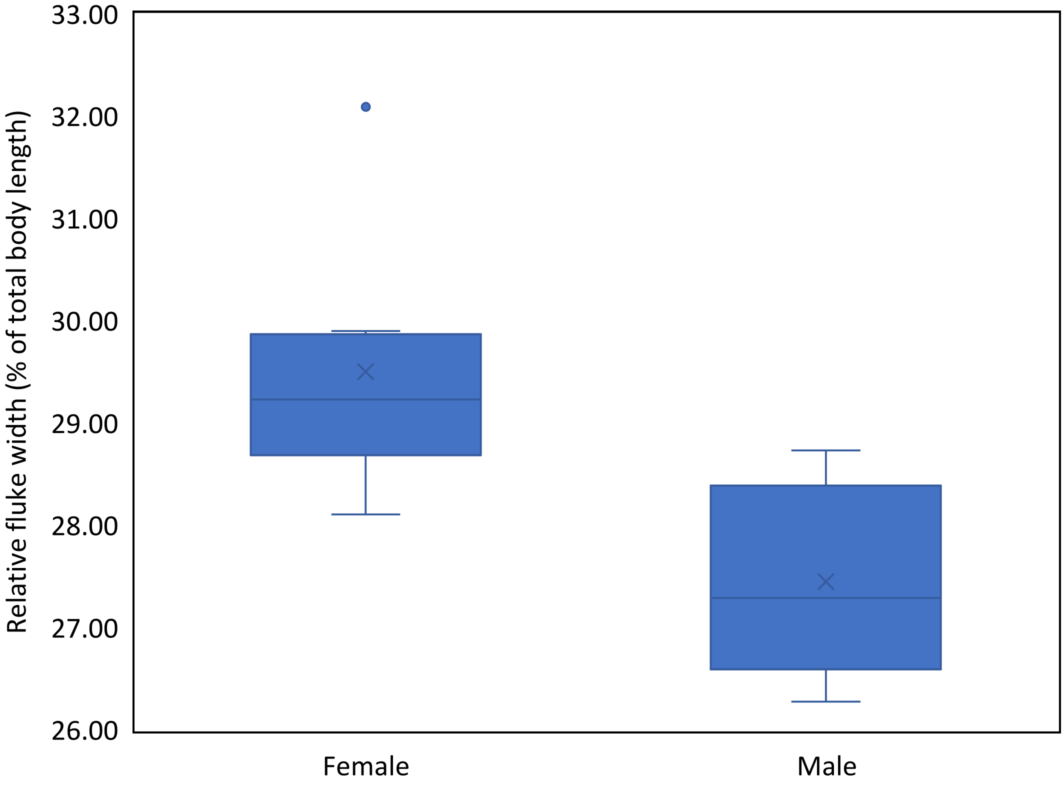


Figure 4.4. Median ± 25% inter-quartile ranges of relative caudal fluke width (FW) as a per cent of total body length (TBL) by sex for dwarf minke whales with both FW and TBL measurements. n_{male} = 5, n_{female} = 8. Whiskers extend to 1.5 times the inter-quartile range. Outliers are included. X = mean value.

4.3.3.2 Calf measurements

Shepherding and screening behaviours by dwarf minke whale mothers and accompanying whales can prevent calves being filmed. Measurements can also be difficult to obtain due to their erratic swimming behaviour, during which dorso-ventral flexion is prevalent. A single calf was able to be measured from the 2017 sampling period (Table 4.4). The sex of this individual was not determined.

Table 4.4: Measurements of a calf from the 2017 sampling period.

Whale ID	**TBL (m)**	**SDF (m)**
MW3468	3.34, n = 1	1.74, n = 1

4.3.4 Body condition

Of all width measurements (i.e., all possible body condition indices), width at eyes (WE) was the most measurable (i.e., was able to make more WE measurements than other width features), with 23 animals measured (Table 4.5). Width behind eyes (WBE) was almost as measurable, with 21 animals measured. These anterior width measurements did not differ significantly in range/variance, $F(20, 25) = 1.288$, $p = 0.543$ (Fig. 4.5). However, WE replicates were significantly more precise than WBE replicates, $t(41) = 2.973$, $p = 0.005$. Width at anterior pectoral fin insertion (WAP) was the most measurable mid-body width feature, with 21 animals measured. Width at widest point (WWP) was the least measurable width feature, with 17 animals measured. Width of mid-body measurements (WAP, WPP, and WWP) did not differ significantly in range/variance, $K^2(2) = 0.295$, $p = 0.863$. However, significant differences in precision of replicates were found across mid-body measurements, $F(2, 46) = 8.428$, $p < 0.001$. Tukey’s HSD test found that WWP replicates were significantly poorer than both WAP ($p = 0.024$, 95% C.I. = 0.078, 1.320) and WPP ($p < 0.001$, C.I. = 0.441, 1.753).

Table 4.5. Relative width measurements of dwarf minke whales, standardized by total body length (TBL), and the variability of each measurement type across individuals. WE = width at eyes, WBE = width behind eyes, WAP = with at pectoral fin anterior insertion point, WPP = width at pectoral fin posterior insertion point, WWP = width at widest point, n = number of whales measured.

Morpho-logical feature	n	Mean % of TBL ± SD	Min % of TBL	Max % of TBL	% of TBL range (max-min)	Mean precision of per-whale replicates (CV%)
WE	23	13.28 ± 0.50	12.25	14.25	2.00	1.37
WBE	21	14.08 ± 0.70	12.60	15.19	2.58	2.54
WAP	21	15.08 ± 0.68	14.08	16.07	1.99	1.97
WPP	18	15.78 ± 0.96	13.64	16.90	3.26	1.19
WWP	17	15.96 ± 1.04	13.52	17.66	4.14	3.54

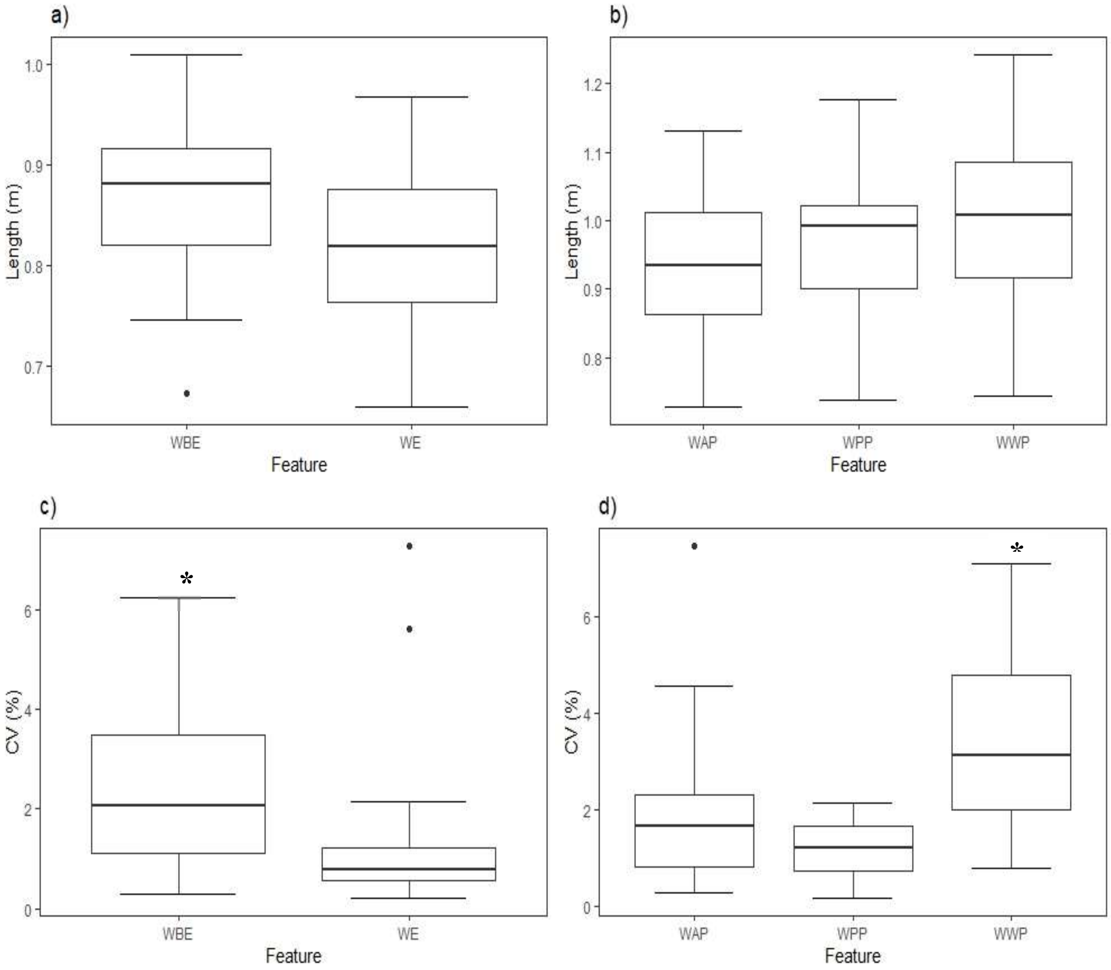


Figure 4.5. Median ± 25% inter-quartile ranges of measurements of a) width behind eyes (WBE) and width at eyes (WE); b) width at pectoral fin anterior insertion point (WAP), width at pectoral fin posterior insertion point (WPP), and width at widest point (WWP); c) coefficient of variation of replicate WBE and WE measurements; and d) coefficient of variation of replicate WAP, WPP, and WWP measurements. Whiskers extend to 1.5 times the inter-quartile range. Outliers are included. Asterisks denote statistical significance.

4.3.5 Growth

Ten (10) whales were re-sighted in multiple sampling periods and were measured during each sampling period (i.e., multi-year growth) (Table 4.6). Due to viewing constraints and/or video quality, not all body features were able to be measured on every whale (see Chapter 3 section 3.3.1). All 10 of these whales were able to be measured for TBL (Appendix E). All whales displayed positive TBL growth when measured across years (i.e., no whales shrank in length). Absolute growth per year ranged from 0.065-0.468 m, representing relative growth of 0.95% - 7.72% of prior TBL. Two-year growth ranged from 0.474 - 0.662 m, representing relative growth of 8.47% - 11.92% of prior TBL across two years. Growth appeared to differ across annual time periods; mean TBL growth from 2017-2018 was 4.575% ± 1.566 *SE* (n = 4), while mean TBL growth from 2018-2019 was 2.522% ± 0.233 *SE* (n = 2). However, the sample size of animals with single-year growth measurements was too small to conduct significance testing (n = 6).

Snout-to-dorsal-fin length (SDF) of individual whales increased over 4% per year, on average (Table 4.6). However, when measured as a proportion of TBL, relative SDF slightly decreased. Fluke width (FW) increased across all metrics, as did snout-to-blowholes length (SBH). Conversely, width at eyes (WE), width behind eyes (WBE), and width at pectoral fin anterior insertion point (WAP) all increased in true size but decreased in relation to TBL. Width at pectoral fin posterior insertion point (WPP) increased both in true size and in relation to TBL.

Table 4.6: Growth of features on whales measured across multiple years. TBL = total body length, SDF = snout-to-dorsal-fin length, FW = fluke width, SBH = snout-to-blowholes length, WE = width at eyes, WBE = width behind eyes, WAP = width at pectoral fin anterior insertion point, WPP = width at pectoral fin posterior insertion point, n = number of whales measured.

Morphological feature	**n**	**Mean* true growth per year (m)**	**Mean* relative growth per year (%)**	**Mean* growth relative to TBL per year (%)**
TBL	10	0.262	4.299	4.299
Immature (<6.00 m)	3	0.324	5.970	5.970
Maturing or mature (≥6.00 m)	7	0.235	3.582	3.582
SDF	10	0.154	4.095	-0.346**
FW	7	0.087	5.313	1.152
SBH	3	0.038	4.342	0.214
WE	1	0.014	1.497	-2.704
WBE	1	0.017	1.684	-2.540
WAP	1	0.017	1.624	-2.594
WPP	1	0.065	5.956	1.383

*Note that WE, WBE, WAP, and WPP were all made on a single whale (MW3416).
**One whale measured for SDF was not measured for TBL, thus was excluded from this calculation.

Relative yearly TBL growth appeared to vary inversely with TBL (Fig. 4.6). As the size (and, presumably, age) of a whale increased, relative growth per year generally decreased. However, considerable variation was found among individuals. The fastest growing whale (7.72% annual TBL growth) was indeed the smallest (5.234 m). On the other hand, the largest whale measured for growth (MW3465) demonstrated the second largest annual growth rate (6.59%). This whale was measured at 7.102 m TBL (± 0.014 *SE*, n = 3) in 2017 and re-measured at 7.570 m TBL (± 0.003 *SE*, n = 3) one year later in 2018. This 2018 mean TBL represents the largest length measurement in this study and the largest measured dwarf minke whale in the Great Barrier Reef to date.

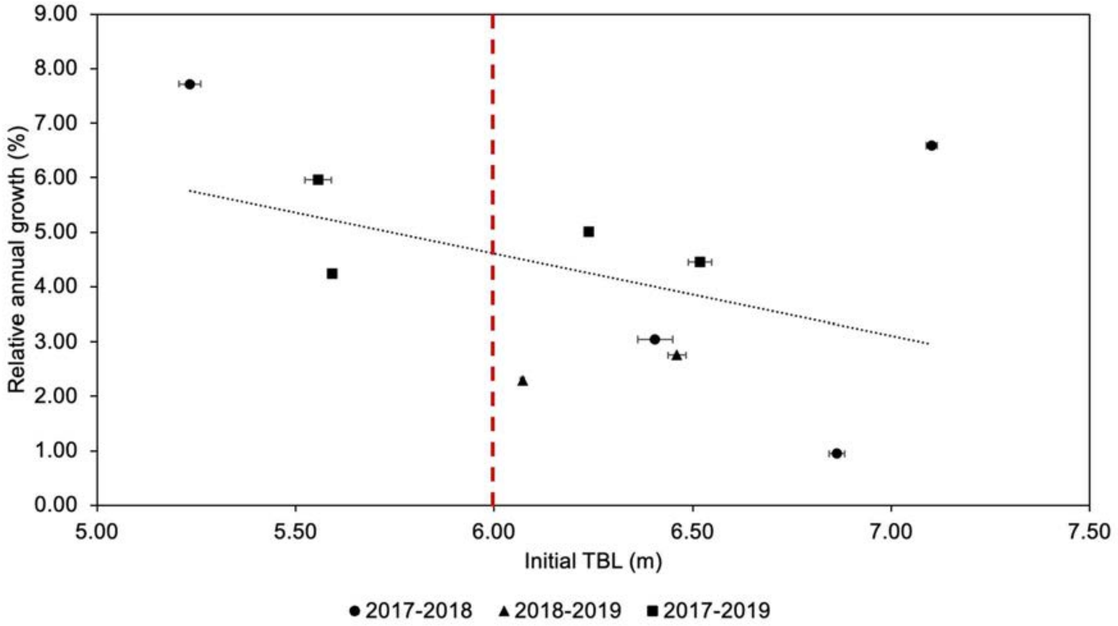


Figure 4.6. Annual relative total body length (TBL) growth of individual whales as a function of initial body length (m). Error bars represent *SE* of replicate TBL measurements. Vertical dotted line represents size distinction between juvenile whales and maturing & mature whales (i.e., 6.00 m TBL).

4.3.6 Long-term demographic trends

Over 50 dwarf minke whales were measured for total body length (TBL) in each of the 2006, 2007, and 2017 sampling periods (Table 4.7). Individuals measured ranged in size/age from a calf in 2007 (3.35 m) and 2017 (3.34 m) to mature whales over 7.00 m in length. TBL varied significantly between years, $F(1, 200) = 28.49$, $p < 0.001$]. Specifically, post-hoc comparisons using the Tukey HSD test indicated that TBL in 2017 was significantly larger than in both 2006 and 2007 by 0.5 m. TBL measurements from the 2006 and 2007 sampling periods were not significantly different from each other.

Table 4.7: Size range of measured whales (total body length, TBL) from previously collected data (2006 and 2007, Sobtzick, 2010) and 2017 (this study).

	2006	**2007**	**2017**
Mean TBL ± SE	5.68 m +/- 0.10	5.71 m +/- 0.08	6.23 m +/- 0.004
TBL_{min}, TBL_{max} (range)	4.03 m - 7.08 m (3.05 m)	3.35 m – 7.18 m (3.83 m)	3.34 m – 7.42 m (4.08 m)
n (% of identified whales)	52 (34.4%)	76 (53.1%)	73 (51.0%)
% Immature (< 6 m TBL)	63%	65%	39.7%
% Maturing or mature (≥ 6 m TBL)	37%	35%	60.3%

In 2017, a bimodal size class distribution was observed, with peaks in the 5.50 – 5.99 m and 6.50 – 6.99 m size classes (Fig. 4.7). The most common size encountered was whales in the 6.50 – 6.99 m range, representing over 30% of measured whales in 2017. In contrast, both 2006 and 2007 size class distributions were unimodal with peaks in 5.00 – 5.49 m and 5.50 – 5.99 m ranges. A Chi-square test of independence indicated that sampling year and size class distribution were significantly associated, $\chi 2 = 36.32$, df = NA, $p < 0.001$. Post-hoc comparisons by year revealed that the proportion of mature whales in 2017 was significantly greater than in 2006 and 2007.

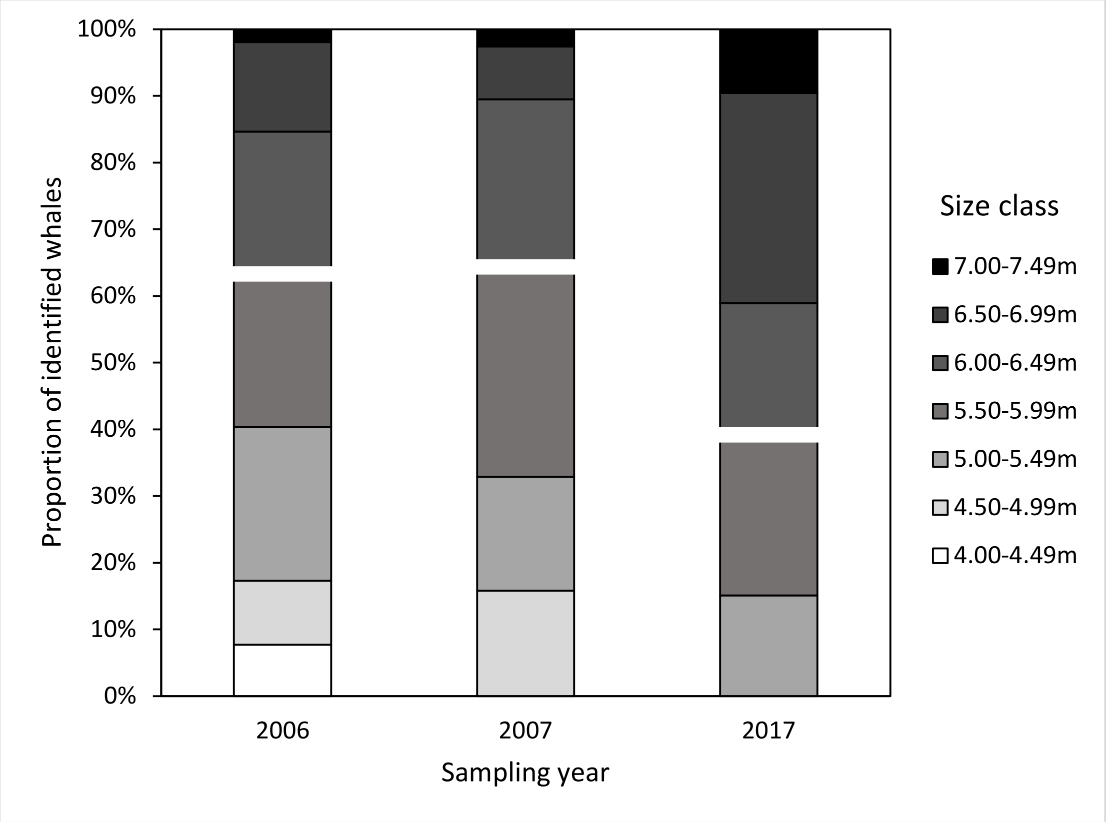


Figure 4.7. Percentage of measured dwarf minke whales in 0.5 m length classes by sampling year. White horizontal lines indicate break between immature and maturing/mature whales.

4.4 Discussion

4.4.1 Chapter summary

Prior to this study, very little morphometric data existed for dwarf minke whales, particularly live animals. Only 140 live, free-ranging individuals had been measured previously, and only total body length (TBL) was measured (Sobtzick, 2010). Due to this lack of data, important biological and ecological characteristics of this subspecies remain poorly described and unmonitored, including growth rates, population demographics and structure, and body condition. This chapter demonstrated that robust morphometric measurements of live dwarf minke whales can be obtained in the Great Barrier Reef aggregation area, which can be used to begin filling these knowledge gaps for this undescribed subspecies. Over 1,300 measurements were obtained on over 100 whales and were utilised to investigate several important biological characteristics of the Great Barrier Reef population including demographic structure, allometric scaling, sexual dimorphism, ontogenic growth, and long-term population trends. Two useful length proxies for dwarf minke whales were established, where total body length can be estimated from fluke width (FW) or snout-to-dorsal-fin (SDF) length. This is useful as TBL cannot always be measured directly but is an important indicator of age. Finally, I established a baseline range of body width measurements and identified the most useful width measurements to enable future monitoring of body condition for dwarf minke whales. These measurements represent the first ever morphological features measured on free-ranging dwarf minke whales beyond TBL.

Individual animals measured in this study ranged from the smallest to largest measured dwarf minke whales in the Great Barrier Reef, from a calf of 3.34 m in length to a (presumably) mature female re-measured in 2018 at 7.57 m TBL. The size ranges of total body length and other morphological features measured in this study generally agree with the limited data available in the literature for dwarf minke whales (Dunstan et al., 2008; Kato et al., 2022; Kato & Fujise, 2000; Sobtzick, 2010). Measured females were larger than measured males, which is also supported by existing literature for dwarf minke whales and other Mysticetes. Further, the findings herein regarding calf size may help to refine understanding of dwarf minke whale calf development, data that are particularly limited in the literature. Previously, a 3.43 m long dwarf minke was documented from a stranding in Brazil, where the whale’s stomach was “almost full” of krill, suggesting that this animal had finished weaning (Secchi et al., 2003). More recently, two calves approaching this size have been observed closely associated with their mothers in the Great Barrier Reef: the 3.34 m and 3.35 m calves measured here in 2017 and by Sobtzick (2010) in 2007, respectively. These findings suggest rapid growth of suckling calves in the first few months of life and that weaning may occur shortly after departing from the Great Barrier Reef aggregation area.

4.4.2 Ontogenic allometry

Total body length (TBL) was hypoallometric compared to other morphological features tested. This means that TBL increased proportionately slower than other body measurements. In other words, dwarf minke whales are relatively ‘long and skinny’ when they are young and gain more girth relative to length as they age. Though limited data are available for the smallest dwarf minke whales (i.e., under 5.00 m TBL), the single calf measured in 2017 exhibited the shortest relative SDF of all individuals, at 52% of TBL compared to 63-69% of TBL in sub-adult and adult dwarf minke whales. This indicates that the calf’s tail region (i.e., the longitudinal length not captured in an SDF measurement) was larger relative to its total length than for older whales. This may be indicative of a general trend observed in baleen whales, wherein the head region is hyperallometric (i.e., proportionately smallest amongst calves) due to ontogenic adaptations related to shifting feeding strategies (i.e., transitioning from nursing to independent foraging) (Goldbogen et al., 2010; Kahane-Rapport & Goldbogen, 2018; Lanzetti et al., 2023). Additionally, a relatively larger tail region may also help to ensure that a small calf can “keep up” with its significantly larger mother while migrating. This may be particularly imperative as dwarf minke whales likely travel as far as the Antarctic after leaving the Great Barrier Reef (Andrews et al., 2015). While the calf measurements in this chapter only represent a single whale under 5.00 m in length, this finding agrees with data from larger whales in this study and data for other baleen whales (Goldbogen et al., 2010; Kahane-Rapport & Goldbogen, 2018; Mackintosh & Wheeler, 1929).

Female dwarf minke whales exhibited significantly wider tails relative to their body length than males (section 4.3.3.1). A possible functional explanation for this observation is that females will have greater propulsion requirements than males due to the increased body mass and resultant drag of pregnancy. However, while absolute sexual size dimorphism is common amongst baleen whales (i.e., females are generally larger than males), relative sexual size dimorphism is not commonly observed except for the length of the genital slit (Mesnick and Ralls, 2018). Males of several odontocete species, such as long-finned pilot whales (*Globicephala melas edwardii*) have relatively wider tails and longer pectoral fins than females (Betty et al., 2022; Clark & Odell, 1999), though odontocetes demonstrate the opposite sex-biased size dimorphism to baleen whales (i.e., males are larger than females). While sample size was small (8 females and 5 males), this study found minimal overlap in the ranges of relative caudal fluke width (FW) between male and female dwarf minke whales. The largest relative FW measured on a male was 28.7%, while the majority of relative FWs of females were greater than 29%. Therefore, with additional data to increase sample size, FW could potentially serve as a diagnostic tool for sex in dwarf minke whales in a certain subset of individuals. For example, it may be possible to determine that animals with a FW smaller than *xx*% of TBL are likely to be male, and animals with a FW larger than *yy*% of TBL and/or longer than *z.z* m are likely to be female. This could help to increase sample size of sexed whales in future studies, which is a limitation of the in-water observational methodologies used in this study.

4.4.3 Predictors of total body length

All morphological features tested demonstrated strong predictive relationships with total body length (TBL). This was expected, as ontogenic growth occurs across all three physical dimensions. However, the size of the prediction intervals varied widely across features, from 0.18 m for whales with small snout-to-dorsal-fin length (SDF) to 1.93 m for whales with large width at pectoral fin posterior insertion point (WPP). Further, the "measurability" of each feature varies as well (see section 4.3.2.1). Therefore, the usefulness of each length proxy for practical application also varies.

For example, SDF was the best predictor of TBL as it generated the most precise prediction interval (± 5.41% SDF, or ± 0.09 - 0.26 m based on the size ranges measured in this study). Suppose a study sought to obtain TBL measurements on as many dwarf minke whales as possible. Using the methodology presented here, SDF is approximately 10% more "measurable" than TBL, so for every 100 whales able to be measured for TBL, 110 whales should be able to be measured for SDF. The length proxy equation calculated in section 4.3.3 ($\log_{TBL} = 0.9832\log_{SDF} + 0.2276$, ± 5.41% SDF) could then be used to estimate the TBL of the 10 whales that were able to be measured for SDF but not TBL, thus increasing the sample size of TBL measurements by 10%.

Suppose the same study also sought to determine the maturity status of these whales. The likelihood of each SDF-measured whale having a TBL either smaller *or* greater than 6.00 m would need to be calculated (see section 4.3.2.2). To determine this with 95% certainty from the SDF-generated estimates, the resultant TBL prediction interval for each whale must not overlap 6.00 m (i.e., must not contain values both above and below 6.00 m). Rather, the entire TBL prediction interval must either be completely above or below this threshold. Thus, using the SDF prediction equation, the maturity status can be confidently estimated for dwarf minke whales with an SDF less than 3.80 m *or* greater than 4.07 m. Individuals with SDF lengths between these values will result in a TBL prediction interval that includes values both above *and* below 6.00 m, and thus maturity status cannot be confidently inferred. In the 2017 measured population, approximately 18% of dwarf minke whales fell inside these values. Therefore, the maturity status of 82% of this dataset could be estimated, with 95% confidence, by using SDF in the absence of TBL measurements. Fluke width (FW) could also be used in this manner; using the length proxy equation for FW, maturity status could be inferred for whales with fluke widths either less than 1.54 m or greater than 1.87 m. However, FW may not be as useful as SDF since a) FW is a less achievable measurement, with only 31.0% of whales measured for FW in 2017 as compared to 56% of whales measured for SDF; and b) the wider prediction interval means that only 47.7% of the 2017 measured population would meet the prediction interval criteria for assessing maturity status.

4.4.4 Body condition

Unexpectedly, the areas of suspected blubber accumulation - width behind eyes (WBE) and width at pectoral fin posterior insertion point (WPP) - did not exhibit greater variance across the sampled population than other similar features. However, when investigated for sensitivity (i.e., precision of replicates), width at eyes (WE), width at pectoral fin anterior insertion point (WAP), and width at pectoral fin posterior insertion point (WPP) conferred a significant advantage. This is likely due to the availability of discrete reference points in these areas. Additionally, since these features have similar distribution across the population to the areas that are suspected to represent body condition (i.e., WE and WWP), then these features may be used as a proxy for body condition and population means can likely be compared on a long-term (i.e., yearly) basis. However, the high time and cost investments required for such data analysis likely preclude the use of this methodology for regular monitoring of body condition of dwarf minke whales.

Alternatively, newer methodologies have been developed in recent years to extract more accurate body condition measurements of cetaceans. These approaches use custom-written graphical user interfaces (GUIs) (Christiansen et al., 2020; Dawson et al., 2017; Gray et al., 2019; Torres & Bierlich, 2020) or *R* scripts (Arranz et al., 2022; Christiansen et al., 2019) to estimate 2- and 3- dimensional “volume” of cetaceans from UAV imagery. To achieve this, a specific fixed camera positioning is required that is strictly perpendicular to a 'flat' animal. Typically, this is done by hovering a UAV quadcopter above an animal that is either resting at the surface or surfacing in calm waters with minimal dorso-ventral body flexure (Fig. 4.7). Unfortunately, the surfacing behaviour and prevailing weather conditions at the dwarf minke whale aggregation area in the Great Barrier Reef (e.g., brief breaths with notable body flexure, no known logging at the surface, and frequent trade winds exceeding 20 knots with rough sea states) are likely to limit the effectiveness of such methodologies for dwarf minke whales in the GBR aggregation area (see Chapter 3 section 3.1.3).

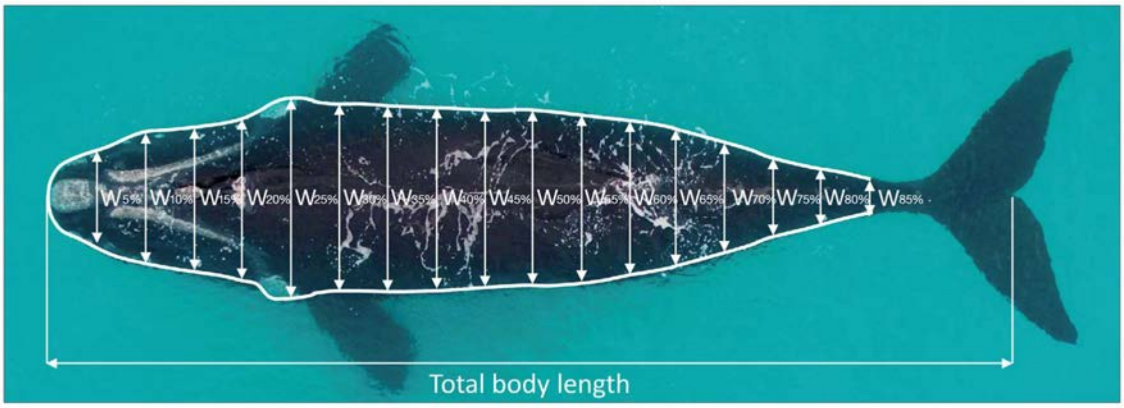


Figure 4.8. Example aerial photograph for measuring body condition of a right whale using a custom-written GUI in MATLAB. Width measurements represent 5% TBL increments from 5-85% TBL. Reprinted from Christiansen et al. (2020).

Future research may instead involve AI-assisted photo-identification techniques and the creation of 3D models of cetaceans. 3D modelling would be a significant improvement on length-girth indices and 2D "volume" estimates (Hirtle et al., 2022). These types of models are well established for other organisms but current methods for cetaceans are not well developed (Irschick et al., 2021). Nonetheless, the Great Barrier Reef dwarf minke whale population may be a promising candidate for the development of such technology. Due to the three-dimensional nature of the swim-with interactions (i.e., the *whales* approach the swimmers), video footage from multiple angles and directions is often collected, which is a requirement for the development of 3D models (Hirtle et al., 2022). Pursuit of this 3D modelling is recommended for monitoring of dwarf minke whale populations as this emerging technology may provide significantly more accurate and precise estimates of body condition and more time-effective analysis. The baseline width measurements and continuous video footage collected in this chapter may be useful for the development of these methodologies for dwarf minke whales.

4.4.5 Growth

All whales measured for multi-year growth displayed positive *total body length* (TBL) growth, although, considerable variation was seen amongst individual whales. Relative TBL growth per year of immature whales was nearly twice that of maturing/mature whales. This finding is supported by the literature describing the general pattern of postnatal ontogenic growth across most fauna, where growth is fastest in neonates and sub-adults and slows near sexual maturity (Bertalanffy, 1938). However, the small sample size here (i.e., limited number of immature whales sampled) precluded significance testing, and more data are needed to support these results.

Unexpectedly, one of the fastest growth rates observed in this study was of a mature whale. MW3465, a 7.102 m (initial sighting TBL) female whale, grew nearly 0.5 m from 2017 to 2018. This was the second fastest annual growth rate measured. Some of this apparent growth may be attributed to the small systematic bias identified in the 2017 season control trial (Chapter 3 section 3.3.1.1), whereby measurements made at a greater distance were slightly overestimated. Indeed, the 2018 measurements of this whale were made at a distance of over 14 m - the most distant TBL measurements made in this study - compared to a distance of approx. 7 m in 2017. However, the potential overestimation cannot be accurately quantified as there is no available correction factor for measurements made in the 2018 season. If the correction factor calculated for the 2017 season measurements was applied here, the adjusted mean TBL of MW3465 would be 7.385 m, reducing the apparent growth from 0.047 m to 0.029 m. But again, it is unknown if the SDOV configuration in 2018 exhibited a similar systematic bias to that found in 2017.

Further, annual growth between 2017 and 2018 was almost double that of 2018-2019. Three-quarters of relative TBL growth measurements across the 2017-2018 period were greater than 3%. Conversely, no TBL growth faster than 3% was observed across the 2018-2019 sampling year. While the sample size remains small and more data are needed to investigate these trends further, this could represent fluctuating environmental conditions such as food availability. It is currently unknown whether food availability directly influences longitudinal growth in adult whales. However, common minke whale (*Balaenoptera acutorostrata*) and southern right whale (*Eubalaena australis*) cows with poorer body condition during lactation are known to produce calves with shorter total body length (Christiansen et al., 2014, 2018). Therefore, it is possible that food availability can influence longitudinal growth throughout later life history stages as well.

Only one whale measured in 2017 was smaller than 5 m in length, a calf measuring 3.34 m TBL. Dwarf minke whales are born at approximately 2 m TBL (Best, 1985). Therefore, the cohort of animals between 2 and 5 m in length appears to be under-represented here. Based on a limited growth curve generated by Kato and Fujise (2000) from a small number of landed animals, this could represent individuals of up to several years of age mostly unseen in this study. Alternatively, it is possible that rapid growth in the first year of life results in dwarf minke whales measuring 5 m in length when they return to the aggregation area the following year. The refugia hypothesis supports rapid early growth as, during this life history stage, individuals are at their smallest size and therefore most vulnerable to predation (Branch & Williams, 2012; Robles, 2008). Antarctic minke whales are known to double in length in the first six months of life (Williamson, 1975). If similar growth occurs in dwarf minke whales, animals would reach 4 m in length by approximately six months of age. Thus, even if growth during the following six months decreased by 50%, animals would still reach 5 m in length by one year of age. The calves measured in 2007 (at 3.35 m) by Sobtzick (2010) and in this thesis (3.34 m) support this hypothesis of rapid early growth, likely demonstrating more than 1 m growth in as little as two to three months.

Lethal age sampling has demonstrated conflicting results. Counting of earplug growth layers indicated that two dwarf minke whales (3.53 m and 3.85 m) of similar length to the aforementioned calves were one year old, while a 4.29 m whale was estimated to be three years old (Kato et al., 2022). These data suggest considerably slower growth rates than those presented in this study. However, a variety of issues with this age estimation technique have been identified (Read et al., 2018), including significant variation amongst age-readers (Kitakado et al., 2013) and poor earplug layer formation in the closely related ordinary minke whale (*Balaenoptera acutorostrata*) (Maeda et al., 2013). Thus, considering a) the limitations of lethal sampling techniques, b) the length estimates of known calves from this study, and c) the poor quality of whaling length estimates (Best, 1984; Clapham & Ivashchenko, 2009, 2016; Ivashchenko & Clapham, 2015; Yablokov, 1994), we can reasonably infer that data presented in this study and by Sobtzick (2010) are substantially more reliable than those obtained via other techniques. Therefore, it is plausible that whales under 5 m in length are not actually under-represented at this study site, but that early growth rates are sufficiently fast that calves depart the aggregation area at approximately 3 – 3.5 m in length and return the following season around 5 m.

Conversely, over 15% of whales measured in 2006 and 2007 (Sobtzick, 2010) were under 5 m in length. Chapter 3 identified the poorer precision of single-camera measurements from Sobtzick (2010) as compared to the stereo-image measurements made in this study. However, there was no indication of a systematic bias that could result in an under-estimation of size of a magnitude that could explain this difference in size distribution. Raw measurements from 2017 were slightly over-estimated, but a correction factor was applied and adjusted measurements were used (see section 4.4.5 and Chapter 3 section 3.3.1.1). It is possible that some individuals from this population migrate to other areas of the south Pacific, as a small number of dwarf minke whales have been sighted in New Zealand (Dawson & Slooten, 1990), New Caledonia (Borsa, 2006), and Tonga (Acevedo et al., 2011) waters. However, connectivity and use of these areas is not known, and sightings are rare. Therefore, it is unknown why a proportion of whales between 4 and 5 m in length were observed in 2006 and 2007 and not in 2017.

4.4.6 Long-term demographic trends

Across all measured whales, mean total body length (TBL) was over 0.5 m smaller in 2006-2007, than in 2017. In both 2006 and 2007, there were approximately twice as many immature as maturing/mature whales, as we found in this study in 2017. This size distribution was almost reversed in 2017, when the majority of measured whales were maturing/mature. Some of this variation may be attributable to methodological differences. Single-camera photogrammetry systems are known to systematically underestimate length due to parallax error (Harvey et al., 2002). However, with careful review of footage, angles as small as 10° off-perpendicular are detectable, and thus the effect size is estimated to be, at most, -1.5% (Dunstan et al., 2008). This would result in a maximum underestimation of TBL of 0.09 m for a 6 m whale. Thus, parallax error should not account for the entire observed difference in mean TBL between sampling periods.

Several questions arise from these findings. Why were dwarf minke whales significantly larger in 2017 than a decade earlier? Is there a declining recruitment of juveniles into this population? Is survivorship of younger whales declining? If so, why? Is food availability declining? Studies have identified that climate change is decreasing productivity in the Southern Ocean (Barnes & Tarling, 2017; Clarke & Harris, 2003; Flores et al., 2012; Rogers et al., 2020), where dwarf minke whales feed (Acevedo et al., 2011; Kasamatsu et al., 1993; Kato & Fujise, 2000; Pastene et al., 2010). Such changes are predicted to significantly impact marine mammal populations (Nicol et al., 2008; Simmonds & Isaac, 2007). Further, cetaceans have been proposed as sentinel species, potentially serving as early warning signals of ecosystem changes (Bossart, 2011; Hazen et al., 2019; Williamson et al., 2021). Thus, declining numbers of juvenile dwarf minke whales at this study site may be a consequence of such ecosystem changes and could potentially indicate approaching migratory mammal population collapse.

Alternatively, habituation and/or desensitization could be occurring amongst the interacting population in the Great Barrier Reef, such that older whales that have had more exposure to human interaction may be becoming less avoidant of vessels (Mangott et al., 2011). Behaviour change in response to tourism activities is well documented amongst cetaceans (Fiori et al., 2019; Stack et al., 2021); however, avoidance is more common than habituation or de-sensitization in the absence of provisioning (Machernis et al., 2018). Previous research on whale-swimmer approach distance during in-water tourism interactions with dwarf minke whales has found that some whales approach swimmers closer both over the course of a single interaction and during subsequent interactions in the same season (Mangott, 2010; Mangott et al., 2011). These observations suggest that de-sensitisation does occur, at least in the short-term. It is unknown whether this trend of closer approaches persists across subsequent seasons, though individual dwarf minke whales are often re-sighted across multiple years (Sobtzick, 2010). Whale-swimmer approach distances are investigated in Chapter 5. Moreover, complete processing of the Minke Whale Project's existing long-term photo-identification database could provide further insight into the interaction history of the 2017 cohort. Of particular interest would be the sightings histories of the larger (and, presumably, older) whales identified in 2017, to determine whether they do in fact have a substantial history of exposure to human interaction.

4.4.7 Limitations

Assumption of independence of samples was not strictly met throughout the study; i.e., sampling effort was not systematised spatially or temporally. "Platforms of opportunity", i.e., dive tourism vessels, were used for data collection, and as a result, sampling distribution of the aggregation area was spatially biased by such factors as vessel itinerary and proximity to reef dive sites. Spatial distribution of dwarf minke whales and habitat use within the aggregation area are unknown, thus the effect of non-random spatial sampling cannot be quantified. Additionally, the availability of individual dwarf minke whales to be filmed and measured was dependent on their willingness to voluntarily approach myself in the water. Thus, there also exists a potential for behavioural biases skewing the sample of measured whales, and it is not known how strong this potential might be. However, the majority of dwarf minke whale sightings, even at a distance, turn into interactions (Mangott et al., 2011). Whales also tend to aggregate specifically around swimmers during these interactions (Mangott, 2010). Further, most size classes of dwarf minke whales are represented herein, from calves to the largest measured dwarf minke whale recorded in the Great Barrier Reef. These observations suggest a minimal, if any, tendency of animals to avoid human interactions at this study site. Finally, explicit protocols were developed and followed during the video footage collection process to capture footage of as many whales as possible, rather than, for example, focusing only on the closest of approaches (see Chapter 3 section 3.4.1). Thus, the risk of oversampling more interactive whales (i.e., whales approaching the closest) or missing entire cohorts/demographics is assumed to be low.

4.4.8 Conclusion and future research directions

This chapter has provided important baseline data on the morphometric characteristics of a dwarf minke whale population, offering valuable insights for monitoring and conservation. While this study identified potential long-term trends, such as changes in population demographics and baseline body condition indices, these findings underscore the need for continued, systematic monitoring to address increasing threats such as climate change. Preliminary evidence of sexual dimorphism presents an opportunity to improve sex determination in future studies and within the long-term photo-ID database maintained by the Minke Whale Project. Additionally, the identification of caudal fluke width and snout-to-dorsal-fin length as proxies for total body length provides tools to enhance morphometric sample sizes and facilitate assessments of population size and health.

Looking forward, these findings highlight several key areas for future research and conservation efforts. Validating the identified length proxies and sexual dimorphism across a larger dataset and over multiple seasons will be crucial for confirming their reliability and applicability. These tools, integrated into long-term monitoring programs, could significantly improve the ability to track population-level health indicators and detect ecosystem changes, such as those caused by climate-driven shifts in prey availability in the Southern Ocean.

Such research/monitoring projects have been repeatedly recommended by researchers (Birtles et al., 2014; Department of Climate Change, Energy, the Environment and Water, 2021; Curnock et al., 2019; Great Barrier Reef Marine Park Authority, 2014). Many of these proposed research priorities have been endorsed by the Australian government (e.g., the Great

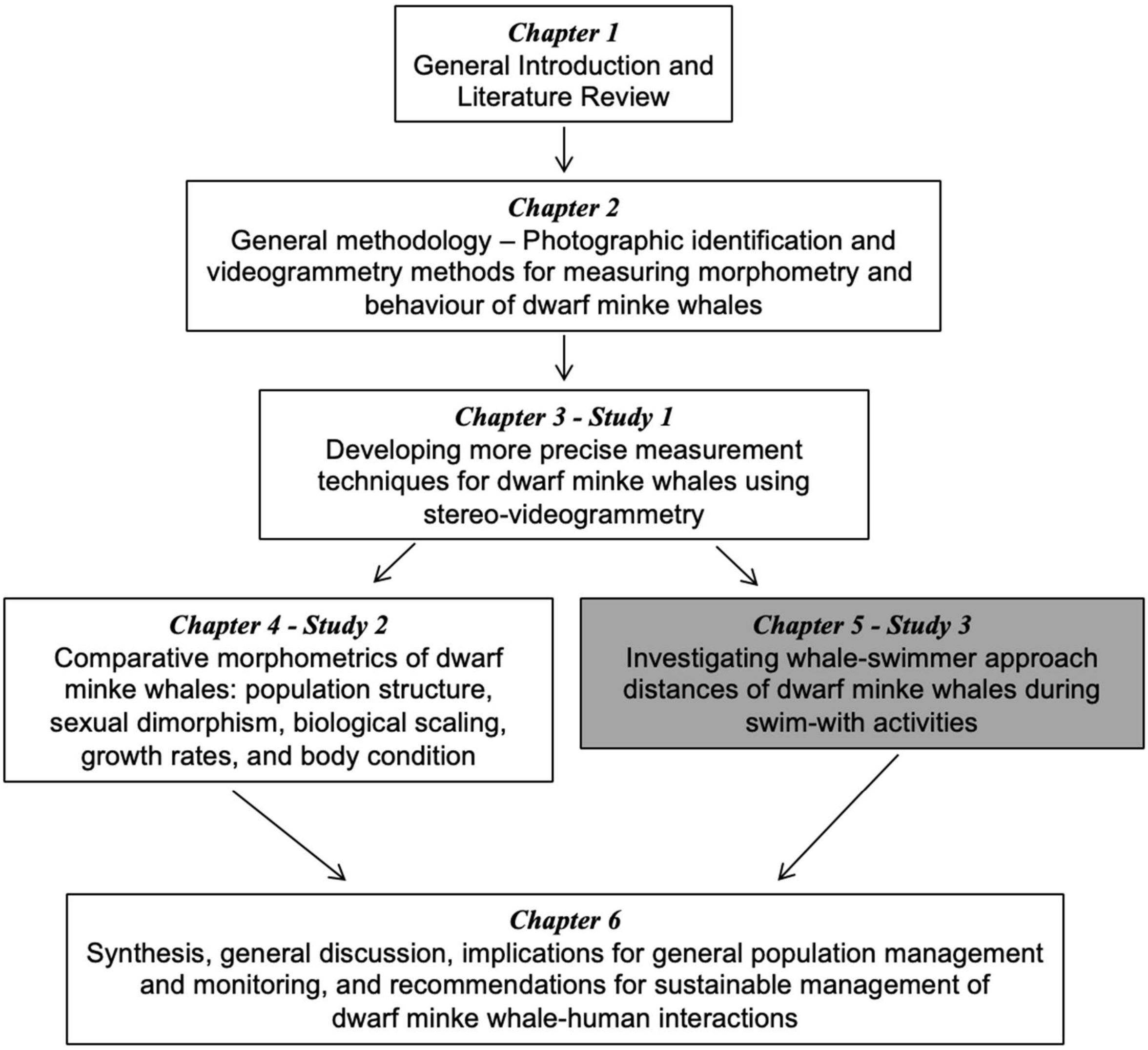
Barrier Reef Marine Park Authority, GBRMPA), as they would directly contribute to some of the government's existing research and monitoring objectives (Birtles et al., 2014; Department of Climate Change, Energy, the Environment and Water, 2021; Curnock et al., 2019). Nevertheless, only limited funding for such research has been provided to date.

The limited funding allocated towards dwarf minke whale research and monitoring may be at least in part due to the significant knowledge gaps that still exist for this "Data Deficient" subspecies (IUCN Red List of Threatened Species). Addressing the problem of data deficiency is considered a fundamental step for planning conservation strategies (Bland & Collen, 2016). The baseline data collected in this chapter, along with future research, can help to fill some of the remaining knowledge gaps that contribute to the dwarf minke whale's Data Deficient status. This will assist in developing a deeper understanding of the threats and extinction risks to this undescribed subspecies, to more adequately inform future monitoring and conservation strategies.

However, achieving these goals will require increased investment in research and monitoring initiatives. Continued collaboration between government agencies, research institutions, and conservation organisations will be essential to ensure that the findings presented here contribute meaningfully to policy development and management strategies. Thus, while this chapter has made significant strides in addressing the lack of baseline data for dwarf minke whales, its broader impact will depend on future research and conservation efforts that build on these findings.

5 CHAPTER 5:

INVESTIGATING INTERACTIVE BEHAVIOUR BY DWARF MINKE WHALES DURING SWIM-WITH ACTIVITIES IN THE GREAT BARRIER REEF



5.1 Introduction

5.1.1 Animal behaviour

Understanding animal behaviour is a key challenge in ecological research (Ford et al., 2012). If heterogeneity in capture probability, as a consequence of among-individual variation, is not accounted for, abundance estimates can be significantly biased (Seber, 1982; Whitehead, 2001). This can significantly affect population and species management (Hammond et al., 1990), as biases in abundance estimates can inhibit the ability to detect important trends such as changes in population structure and survival (Hagihara et al., 2014).

Variation in behaviour can result in differential responses to disturbances, which can then negatively impact individuals and populations (Foroughirad & Mann, 2013; Mann et al., 2021; Senigaglia et al., 2019; Williams et al., 2002). For example, provisioning of bottlenose dolphins (*Tursiops truncatus*) for tourism purposes in Shark Bay, Western Australia resulted in decreased maternal care and increased calf mortality in the local population (Mann et al., 2000). Inconsistent daily feeding times resulted in mothers spending extended periods of time in the provisioning area anticipating the next feed, leaving their calves unattended and vulnerable to predation by sharks. As a result, provisioning times were reduced and standardised, and calf survivorship then increased (Senigaglia et al., 2019). Furthermore, individual life-history characteristics, such as sex, and species differences, can also impact responses to tourism and other disturbances. For example, male and female bottlenose dolphins and killer whales (*Orcinus orca*) respond differently to approaching whale-watch vessels, resulting in differential energetic consequences in response to the same disturbance stimuli (Lusseau, 2003b; Stockin et al., 2008; Williams et al., 2002, 2009). Thus, understanding variation in behaviour is important across a variety of research needs and can guide the development of effective conservation and management strategies.

5.1.2 Measuring behavioural responses of animals to human presence

A commonly used method of assessing the behavioural responses of animals to human presence is to measure threshold distances (Blumstein, 2016). Often referred to as “flight initiation distance” (FID), threshold distance refers to the distance at which an animal will initiate a disturbance behaviour (i.e., fleeing) in response to an approaching human or a potential threat (i.e., a predator). A decrease in FID over time is considered an indicator of de-sensitisation or habituation (Allan et al., 2020). Historically, behavioural ecologists assumed that these behavioural responses were “equal” within a population or species; that is, individuals would all respond in a similar manner (Weston et al., 2012). Recent research, however, has challenged this assumption, finding significant variation in FID between conspecifics in response to the same human stimulus (Allan et al., 2020; Beale & Monaghan, 2004; Bejder et al., 2009; Dissegna et al., 2022; Hanson & Riley, 2018). This has been observed across a wide range of taxa including birds (Stalmaster & Newman, 1978), reptiles (Carter et al., 2012), amphibians (Rodríguez-Prieto & Fernández-Juricic, 2005), and mammals (Williams et al., 2002).

Several factors have been identified as drivers of individual variation in behavioural responses to humans. Such characteristics include age (Constantine, 2001; Stalmaster & Newman, 1978), sex (Lusseau, 2003b; Williams et al., 2002), body size (Dissegna et al., 2022), reproductive condition (Parent & Weatherhead, 2000), nutritional condition (Doenier, 1997; Seltmann et al., 2012), prior experience (Bejder et al., 2006; Frost et al., 2007; Gayford et al., 2023), and personality traits such as boldness (Allan et al., 2020; Carter et al., 2012; Petelle et al., 2013; Strong et al., 2017). In baleen whales, known drivers of variation in interactive behaviour are generally related to age and sex demographics. Specifically, humpback whale (*Megaptera novaeangliae*) calves show increased curiosity and play (Clark & Garland, 2022), particularly male calves (Zoidis et al., 2014), while mothers with calves maintain greater distances from other whales (Smultea, 1994). Studies investigating variation in behavioural responses of baleen whales to humans have generally focused on group-level trends, such as differences between calf and non-calf groups (e.g., Stack et al., 2021; Sullivan & Torres, 2018). This may be due in part to the difficulty of obtaining more detailed demographic data (e.g., sex, age) on free-ranging animals. More thorough investigations have been recommended for a more comprehensive understanding of the impacts of human disturbance to baleen whales, particularly with respect to whale-watching tourism (Christiansen et al., 2015; Sullivan & Torres, 2018).

5.1.3 Behaviour of dwarf minke whales

As described in Chapter 2, a small, vessel-based tourism industry conducting swims with dwarf minke whales exists in the northern Great Barrier Reef. During swim-with activities, dwarf minke whales appear particularly interested in humans, aggregating specifically around swimmers compared to other objects, such as vessels and buoys (Mangott, 2010). Encounters typically end when the vessel itinerary dictates a move to another location or swimmers are instructed out of the water (e.g., for meal times or when dusk falls), rather than because the whales voluntarily depart. Dwarf minke whales have also been observed following tourism vessels on departure from a dive site and arriving at the vessel's next location shortly after (pers. obs.), although the frequency of this behaviour has not been determined. This level of inquisitiveness and voluntary interaction is unusual for wildlife, particularly in the absence of food provisioning (Kerlinger et al., 2013).

The absence of avoidance and aggressive behaviour during swim-with dwarf minke whales activities suggests that these interactions are not stressful to the whales (Constantine, 2001; Constantine et al., 2004; Hosey, 2000; Samuels et al., 2003). However, the highly interactive behaviour of the whales raises alternative concerns for both whales and human participants. The high levels of inquisitiveness and regular occurrence of investigative behaviours (Mangott, 2010) may increase the risk of accidental injuries to both people and the whales (Birtles et al., 2014; Curnock, Birtles, Valentine, et al., 2013). Extensive effort has been made to identify the short- and long-term risks of swimming with dwarf minke whales (Birtles, Arnold, et al., 2002; Birtles et al., 2001, 2014; Curnock, 2010; Curnock, Birtles, & Valentine, 2013; Curnock et al., 2019; Mangott et al., 2011; Sobtzick, 2010), and numerous risk reduction and mitigation strategies have been identified and implemented (Birtles et al., 2008, 2014; Curnock, Birtles, Valentine, et al., 2013). However, while the behaviour of swimmers can be strictly managed, the behaviour of the whales cannot, and close approaches remain a common occurrence (Mangott, 2010). Furthermore, the inquisitive nature of dwarf minke whales may put them at an increased risk of habituation to human presence (Birtles et al., 2001; Curnock, Birtles, & Valentine, 2013; Mangott, 2010; Mangott et al., 2011; Sobtzick, 2010). Some identified whales are commonly re-sighted both in the short-term (i.e., within a single season) and long-term (i.e., across multiple seasons), further substantiating concerns about the cumulative impacts of multiple interactions (Birtles et al., 2014; Dunstan et al., 2008; Hutchings et al., 2023; Mangott et al., 2011; Sobtzick, 2010). Thus, an understanding of dwarf minke whale behaviour during in-water interactions is crucial to address concerns around these tourism activities.

5.1.4 Whale-swimmer approach distances

For swim-with dwarf minke whales activities, a close approximation of FID is whale-swimmer approach distance. These two concepts differ slightly in that FID measures how close an animal allows a human to approach, while interactions with dwarf minke whales are characterised by the whales approaching the swimmer. Despite this difference, FID and whale-swimmer approach distance can be considered functionally equivalent for the purpose of assessing interactivity and/or habituation as they both reflect a threshold approach distance of interactions with humans. Whale-swimmer approach distances have been used to investigate exploratory behaviour in killer whales in Norway (Chanvallon et al., 2017) and dwarf minke whales in the Great Barrier Reef (Mangott, 2010; Mangott et al., 2011).

Several aspects of dwarf minke whale exploratory behaviour have been examined through whale-swimmer approach distances (Mangott, 2010; Mangott et al., 2011). Whales decreased their approach distances across time, both during a single interaction and during subsequent interactions when individual animals were re-sighted, and re-sighted individuals also increased their interaction duration when re-sighted (Mangott, 2010). These changes in behaviour over time are suggestive of habituation or de-sensitisation (see section 5.1.2), although do not strictly fit the criteria due to the whales approaching the humans (not *vice versa*). Thus, Mangott (2010) proposed that this phenomenon be termed “habituation type II” or “increased attraction”. Whale group size was also found to influence approach distance, with approach distances decreasing as whale group size increased (Mangott, 2010). Other external factors examined, such as wind speed and vessel status (i.e., drifting or stationary), did not influence approach distances (Mangott, 2010).

A risk assessment also found that the potential for harm to both swimmers and whales increased with decreasing approach distance (Mangott, 2010). For example, a distant breach posed no risk to a vessel or swimmers, whereas a close breach (i.e., within a few metres from a swimmer), could result in serious injury or death to the swimmer(s) and/or injury to the whale (i.e., due to an increased likelihood of collision with the vessel or entanglement in mooring lines or other ropes). As a result, approaches and behaviours performed closer than 3 m to swimmers were deemed “behaviours of concern” (Mangott, 2010). Recommendations were made that crew monitoring these interactions should take the occurrences of behaviours of concern as early warning signals of increased risk. This foundational research on dwarf minke whale behaviour exemplifies the critical role of behavioural studies for understanding both the impacts and risks associated with swimming-with-whales tourism activities.

5.1.5 Knowledge gaps

Whale-swimmer approach distances have only been investigated during the first 90 min of interactions with dwarf minke whales (Mangott, 2010). However, the mean duration of in-water interactions is two hours, with encounters up to 11 hours recorded (Curnock, Birtles, & Valentine, 2013). Thus, a substantial portion of encounters last longer than what has been investigated in previous studies, and behaviours across a wider range of expected interaction durations remain to be quantified. In particular, if dwarf minke whales continue to approach more closely beyond 90 min, modelling longer encounters will provide useful information for higher-risk scenarios.

In addition, Mangott (2010) grouped dwarf minke whale interactions by whale group size, using the categories “1 – 3 whales”, “4 – 6 whales”, and “greater than 6 whales”. While this approach provided a broad understanding of how group size influences approach distance, it lacks detail of finer-scale variations. The largest category could represent a wide range of interaction sizes, from groups of 7 whales up to 25 whales, the largest recorded group size (Curnock, Birtles, & Valentine, 2013). Since whale group size influences approach distance, the potential for considerably closer approaches, and thus higher risk of harm with increasing group numbers, has not been adequately quantified. In addition, to reduce confounding effects from other identified variables (i.e., encounter length and whale group size), Mangott (2011) investigated the effect of prior experience (i.e., re-sightings) on approach distance for five whales only, from encounters with similar characteristics (i.e. similar duration and whale group size). Thus, it is unclear whether the influence of prior experience on whale-swimmer interactions persists across a broader range of individuals and interactions, and whether this effect persists over the long term (i.e., across multiple seasons).

Finally, there may be other variables that influence approach distance that have not been identified. For example, ecological or environmental characteristics, such as weather, location, or site-specific characteristics, and individual-specific traits, such as sex, age, or body size, may affect approach distances. Knowledge of the effect of these factors on whale-swimmer approach distances, and how these might change under particular conditions, can help to better understand the mechanisms underlying the highly inquisitive behaviour of dwarf minke whales. In addition, the increased risk of harm associated with these factors could be more clearly quantified. If predictors of approach distance are identified and able to be monitored, tourism operators could undertake real-time, adaptive monitoring and management of risks associated with close approaches during swim-with activities and adjust their operations to better minimise these risks to both swimmers and animals.

5.1.6 Identifying potential predictors of whale-swimmer approach distance

5.1.6.1 Environmental conditions

Environmental factors may play a role in shaping the behaviour of dwarf minke whales. High winds can alter the diving behaviour of beluga whales (Stafford et al., 2016), and similar impacts on whale behaviour may occur with other species. Although previous research suggests that wind speed does not directly influence whale-swimmer approach distances of dwarf minke whales (Mangott, 2010), the proximity of many dive sites to large barrier reefs often results in relatively calm surface conditions, even during high winds (pers. obs.). Therefore, wind speed alone may not be a reliable indicator of surface conditions. Instead, wave height and/or Beaufort sea state might provide a more accurate measure of surface conditions, with calmer conditions (e.g., low wave height) potentially encouraging closer approaches by dwarf minke whales to swimmers.

Bathymetric features may also influence dwarf minke whale behaviour. Many species aggregate around seamounts, including humpback whales (Bestley et al., 2019; Garrigue et al., 2015), blue whales (*Balaenoptera musculus*; Fiedler et al., 1998), and sperm whales (*Physeter macrocephalus*; Hann et al., 2016; Wong & Whitehead, 2014). Additionally, stress in response to spatial restriction is well documented in captive animals (Beerda et al., 1999; Morgan & Tromborg, 2007; Oliveira et al., 2016; Pearce & Paterson, 1993). Thus, whales may be more confident to explore their environment, including approaching humans, at sites with bathymetry that allows freer movement, such as coral pinnacle sites in deep water rather than shallower reef wall sites.

Seasonal timing may also influence dwarf minke whale interactivity. Sightings in the northern Great Barrier Reef follow a roughly normal distribution, with a consistent peak from late June through early July (Birtles et al., 2014). Box (2022) standardized these sightings, demonstrating that this peak is not due to increased vessel search effort but likely reflects the natural progression of migratory animals arriving and departing the aggregation area. As whale group size can influence whale-swimmer approach distance (Mangott, 2010), approach distances may vary similarly across the seasonal aggregation period, corresponding with local whale abundance.

Whales may also approach swimmers more closely as a season progresses, due to the accumulation of re-sightings. Approximately one-third of identified whales are re-sighted within a season, with up to eight encounters recorded per animal (Sobtzick, 2010). As these re-sightings increase, whales gain more experience interacting with humans, which may lead to closer approaches and longer interactions (Mangott, 2010, see section 5.1.4). Rather than an either/or effect, local whale abundance and re-sightings are likely to exert concurrent influences on approach distances. Therefore, it is reasonable to expect closer approaches during the mid-peak and end of the season compared to the beginning, considering whale group size/abundance, re-sightings history, and encounter duration.

5.1.6.2 Biological characteristics

Biological characteristics may also influence the interactivity levels of dwarf minke whales. Sex influences the behavioural response of individuals to approaching whale-watching vessels in several odontocete species (see section 5.1.1). Approximately one-third of photo-identified dwarf minke whales in the GBR can be sexed. Of these, approximately three-quarters are female (Hutchings et al., 2023; Sobtzick, 2010). It is unclear if this indicates a true female-biased sex ratio in the population or, alternatively, females are more interactive, resulting in increased opportunities for researchers to sight the genital slits. Anecdotal evidence suggests that female dwarf minke whales may exhibit more social behaviours, such as belly presentations, during swim-with encounters (A. Birtles, personal communication, multiple dates between 2016 and 2023), which suggests a potential for greater female interactivity, and thus possibly closer approach distances.

Body size may also serve as a predictor for whale-swimmer approach distances. Juveniles of many cetacean species are more interactive with humans than older conspecifics (Constantine, 2001; Samuels et al., 2003). Thus, it is reasonable to expect that younger, and by proxy, smaller, whales may approach humans closer than older individuals. However, older, and by proxy, larger, whales may approach closer due to a higher likelihood of habituation or de-sensitisation simply from to a longer-term interaction history than younger (i.e., smaller) whales. Short-term habituation type II or “increased attraction” has been documented in a small number of dwarf minke whales (see section 5.1.4), whereby five whales that were re-sighted within a season decreased their approach distance in subsequent sightings (Mangott, 2010). If this increased attraction persists in the longer term (i.e., across multiple years), and occurs on a larger scale (i.e., more than five whales), then the older, larger, whales should have a higher likelihood of having experienced swim-with activities, and thus might approach swimmers more closely than “naïve” (i.e., younger and smaller) whales.

Finally, whale-swimmer approach distances may vary as a function of personality or other individual characteristics. Personality traits, such as boldness, can significantly influence animal behaviour, affecting how individuals interact with their environment and other species (Allan et al., 2020; White et al., 2013; Wilson et al., 1994). Boldness is often assessed by measuring FID and has been studied in various species to understand its impact on their responses to potential threats or novel stimuli (Carter et al., 2012; Petelle et al., 2013; Strong et al., 2017). For dwarf minke whales, this personality trait could play an important role in determining their interactivity with swimmers. Whales exhibiting higher boldness may approach swimmers more closely and engage more readily than more cautious individuals. Since boldness is not a directly measurable variable, it may be indirectly inferred from the remaining variation in approach distance between individual whales that cannot be explained by other measurable variables such as environmental conditions, prior experience, demographic factors such as age and/or sex.

5.1.6.3 Encounter parameters

Numerous differences have been identified in encounter characteristics across the various sites visited by the tourism industry. Number of encounters, encounter duration, mean number of whales per encounter, and cumulative time spent interacting with whales all vary significantly between dive sites where swim-with activities occur (Table 5.1; Curnock, Birtles, & Valentine, 2013; Sobtzick, 2010), even when standardised for search effort (Box, 2022). As some of these same parameters have been found to influence approach distance (e.g., whale group size and encounter length), it is likely that whale-swimmer approach distance could differ considerably across these dive sites/locations.

Table 5.1: Encounter statistics for the top five dwarf minke whale encounter locations in the Great Barrier Reef. Data aggregated from 2003 – 2008.

Reef site	Number of encounters	Mean encounter duration (min)	Mean number of whales per encounter
Lighthouse Bommie (Ribbon Reef 10)	266	170	4.74
Steve's Bommie (Ribbon Reef 3)	122	103	2.28
Challenger Bay (Ribbon Reef 10)	69	77	2.59
Pixie Pinnacle (Ribbon Reef 10)	65	69	2.22
Flare Point (Ribbon Reef 3)	57	53	2.14

Note. Adapted from Curnock, Birtles, & Valentine (2013).

Approximately two-thirds of permitted tourism interactions with dwarf minke whales occur in the direct vicinity around Ribbon Reef Nos. 9 and 10 in the Great Barrier Reef (Curnock, Birtles, & Valentine, 2013). As a result, this area is colloquially referred to by researchers and tour operators as the "hotspot" of the aggregation area. Researchers have previously recommended that the area around Ribbon Reefs Nos. 9 and 10 be declared a Special Management Area for better monitoring and regulation of swim-with activities by the Great Barrier Reef Marine Park Authority (Birtles et al., 2014). Encounters in this location are also generally longer, with larger whale group sizes than in other areas of the Great

Barrier Reef (Sobtzick, 2010). Thus, encounters occurring in this localised region of the aggregation area may potentially have significantly closer whale-swimmer approach distances than encounters occurring outside this region.

Some vessels conduct “drift encounters” with dwarf minke whales, where the vessel is not at anchor or attached to a mooring and instead drifts in the wind. These encounters generally result in larger whale group sizes (Box, 2022), possibly because the vessel acts as an aggregation device and attracts or “picks up” new whales as it drifts through the area (Mangott, 2010; Sobtzick, 2010). Thus, drift encounters may also have the potential for significantly closer whale-swimmer approach distances than stationary (i.e., anchored or moored) encounters.

5.1.7 Aims

The aim of this chapter is to develop a more detailed understanding of the highly interactive behaviour of dwarf minke whales during swim-with interactions in the Great Barrier Reef. I have two specific objectives for this chapter:

(1) To identify additional predictors of interactive behaviour by dwarf minke whales at both the group (i.e., encounter) and individual level; and

(2) To quantify the effects of these variables on whale-swimmer approach distances.

Whale-swimmer approach distance was used as a proxy for interactive behaviour and was chosen for several reasons. Firstly, whale-swimmer approach distance is a quantifiable measurement that can be tracked over time or compared between individual whales to evaluate the sustainability of swim-with activities in relation to the potential for behavioural changes to occur (i.e., habituation type II or increased attraction). Second, it is also relevant to tourism management in relation to the increased risk of harm to both the whales and swimmers associated with close approaches. Thirdly, stereo-videogrammetry technology provides the opportunity to obtain more precise measurements of whale-swimmer approach distance during swim-with interactions than have previously been collected, and specific methodologies have been developed for such purposes (see Chapter 3).

5.2 Methods

Generalised linear mixed effects models (GLMMs or GLM models) and regression techniques were used to quantify the variation in whale-swimmer approach distances across 21 encounters with dwarf minke whales in the Great Barrier Reef across the 2017 season. Mixed-effects models are considered robust methodology for investigating both between-individual and within-individual variation in behaviour of animals (Dingemanse & Dochtermann, 2013). They have been widely used to model FIDs across a variety of wildlife species (e.g., Beale & Monaghan, 2004; Dumont et al., 2012; Rodríguez-Prieto & Fernández-Juricic, 2005; Seltmann et al., 2012; Strong et al., 2017). Ten variables were selected for their potential to influence or predict whale-swimmer approach distances (see section 5.2.3). These variables consisted of a variety of contextual factors including environmental conditions (e.g., wind speed and wave height), encounter parameters (e.g., location and vessel ID), and demographic variables (e.g., whale sex and total body length) that may potentially influence or predict whale-swimmer approach distance at both the collective (i.e., encounter) and individual levels.

5.2.1 Study site and data collection

Dwarf minke whales were filmed in-water by researchers, passengers, and crew during trips on live-aboard dive tourism vessels and privately chartered research expeditions in June and July 2017. When whales were sighted, environmental and encounter data were recorded including time, location, wind speed, wave height, vessel status, and an initial estimate of whale group size (see Appendix A: Whale Sighting Sheet). I entered the water as soon as possible with a diver-operated stereo-video (SDOV) system and collected continuous video footage of the encounter. This footage was multipurpose. It was used for photo-identification, whale body measurements, and approach distance measurements. Many other swimmers (e.g., passengers, vessel crew, and additional researchers) also captured regular still and video imagery with personal underwater cameras, and most donated copies of their imagery for photo-identification of individual animals and, where possible, to identify the sex of a whale. Most vessels used for data collection were tourism vessels and thus considered 'platforms of opportunity' (i.e., not dedicated research vessels). Therefore, the study-specific limitations identified in Chapter 2 also apply here. Detailed calibration and filming methodologies can be found in Chapter 3.

5.2.2 Data pre-processing

5.2.2.1 Photo-identification

A detailed description of the photo-identification process can be found in (Chapter 2, section 2.3.1). Imagery collected by passengers, crew, additional researchers (when present), and myself (via stereo-video recording) were used to identify individual whales present in each encounter and to document their sightings history across multiple encounters within the season (i.e., to determine if individual whales were re-sighted).

5.2.2.2 Stereo-video imagery processing

A full description of the sex-identification and body measurement processes can be found in Chapter 2. Briefly, a whale's ventral side must be seen to identify its sex. Sex is identified by the relative positioning of the genital and anal slits (i.e., very close together in females and distinctly separated in males). The ventral surface of a dwarf minke whale is most often observed during a “belly presentation” behaviour, and less commonly during a “barrel roll” or other similar behaviour (Mangott, 2010). The total body length (TBL) of a whale could be determined if the following footage was collected: 1) adequate imagery to make a positive identification of the animal; and 2) adequate SDOV footage that allowed for measurement from the tip of the animal’s snout to its caudal notch. In this study, sex was determined for 17% of photo-identified whales (n = 24) and TBL was measured for 52.1% of identified whales (n = 73). Both sex and TBL were determined for 10.7% of identified whales (n = 15, N = 140).

Approach distances were determined by measuring the closest point of each pass/approach of a whale available in the SDOV footage using the computer software program EventMeasure (see Chapter 2 section 2.3.2.4). This distance was used as an approximation of how close the whales approach swimmers in the water. I chose the same position in the water during each encounter, which was usually the farthest available point on the surface rope from the vessel. This was done to standardise the filming conditions and prevent any potential behavioural differences in the whales due to varying filming positions. For example, whales may be less likely to interact with swimmers near the start of the rope, as it is closer to the vessel’s hull. To determine the closest point of a pass/approach, an entire pass was viewed at 0.5x speed and then the video was back-tracked to the estimated closest approach of the whale. The paired stereo-videos were paused at this point and a single-point observation was marked by selecting a reference point on the whale that was visible in both videos. This observation was coded with the individual whale photo-ID number, and the distance from the camera to the reference point on the whale was automatically calculated by the software program. This procedure was repeated several times around this estimated closest point. The observation that returned the closest distance output was retained and all other measurements for that pass were deleted. When a whale passed by side-on (lateral view), the reference point used was generally a region on the shoulder with a distinctly visible pattern or area of high contrast. When a whale passed underneath (dorsal view), either the anterior dorsal fin insertion point was used or a clearly visible pattern or scar on the dorsal surface.

5.2.3 Variable selection and categorisation

Ten explanatory variables were selected to investigate their potential influence on whale-swimmer approach distances (Table 5.2): time in encounter (TIE), whale group size (NUM), day of season (DOS), vessel status (VS), nearest site (SITE), inside or outside aggregation area ‘hotspot’ (AA), encounter type (ET), wave height (WH), sex (SEX), and total body length (TBL). These variables were selected for the possibility that they may influence or predict exploratory behaviour of dwarf minke whales and, if so, could be used to predict whale-swimmer approach distances (see section 5.1.6). Environmental and encounter variables were categorised as group variables as they exert an influence evenly across all individuals in an encounter (i.e., at the group level). Individual variables represent characteristics specific to individual animals.

Table 5.2: Description and categorisation of independent variables modelled.

Variable	**Description and categorisation**
Environmental (group) variables	
Wave height (WH)	Wave height in immediate vicinity, to nearest 0.5 m Recorded at beginning of encounter
Encounter type (ET)	Restricted or open Restricted: reef wall sites Open: coral pinnacle sites OR drift encounters
Day of season (DOS)	Day 1 = 1st June 2017; Day 2 = 2nd June…Day 61 = 31st July
Group size (NUM)	Maximum number of whales seen at once; represents a confirmed minimum number of whales present
Encounter (group) variables	
Nearest dive site (SITE)	Name of site where encounter occurred, or closest site if drifting
Proximity to aggregation area 'hostpot' (AA)	Inside or outside Inside: within immediate vicinity of Ribbon Reef Nos. 9 & 10 Outside: not within immediate vicinity of Ribbon Reef Nos. 9 & 10
Time in encounter (TIE)	Time of approach in hh:mm:ss after the start of the encounter Calculated individually for each approach distance measurement
Vessel status (VS)	Anchored, moored, or drifting Anchored: at anchor Moored: attached at an existing dive site mooring Drifting: drift encounter
Individual variables	
Sex	Male, female, or unknown
Total body length (TBL)	Length of whale to nearest 0.01 m, from tip of snout to caudal notch
Encounter number (ENC)	Encounters across the sampling period were ranked chronologically when whales were sighted in multiple encounters (e.g., #1, #2, #3 …) Calculated individually for each whale ID and applied to all approach measurements within each whale-encounter

5.2.4 Data analysis

From the SDOV footage obtained during the 2017 season, 1,118 suitable whale-swimmer passes were measured for approach distance (see section Chapter 2 section 2.3.2.4 and section 5.2.2.4). Approach distance measurements were obtained for 121 identified whales, representing 61% – 85% of all identified whales in the 2017 sampling period (see Chapter 4 section 4.3.1).

5.2.4.1 Close approaches

Passes were defined as "close approaches" if a whale approached a swimmer within 3 m or less, as per Mangott (2010). A total of 63 close approaches were recorded, made by 25 individual whales (see Appendix F: close approaches). Whales that made at least one close approach were categorised as "close approachers", and their mean approach distances were compared to "non-close approachers" using a Welch's T-test. Approach distances by "non-close approachers" were randomly subsampled to ensure an equal number of observations between groups (n = 365 passes per group). Welch's T-test was chosen as data were approximately normal but variances were slightly non-homogenous.

5.2.4.2 Repeat passes

To investigate the effect of repeat passes on approach distance, two separate linear regressions were performed. First, I modelled the relationship between total number of passes per whale and mean approach distance per whale. Second, I modelled total number of passes per whale and the closest approach distance per whale ($N_{\text{whales}} = 121$, $N_{\text{passes}} = 1{,}118$). Number of passes (NUM) was investigated this way as it was rejected from inclusion in GLM modelling due to collinearity with the variable TIE. Approach distances and number of passes were log transformed to meet the assumptions of normality. Significance was determined at $p < 0.05$. The Gini coefficient was calculated to assess inequality (i.e., variability) in the number of passes made by individual whales across the sample population.

5.2.4.3 Group variables: generalised linear mixed models

Group variables (environmental and encounter variables) were assessed for their potential influence on whale-swimmer approach distance using Generalised Linear Mixed Models (GLMMs or GLM models). Separate model selection procedures were conducted for group and individual variables. This was done to preserve the largest sample size possible, as group variables were available for every whale and pass, while demographic data (i.e., individual variables) were only available for subsets of identified whales that could be measured for total body length or sex-ID (see section 5.2.2). Encounter-level re-sighting histories were also modelled separately due to the small sample size of re-sighted whales ($n = 11$).

5.2.4.3.1 Model construction, selection, and evaluation

Variables were checked for collinearity using pairs plots and ensuring variance inflation factors of less than three (Zuur et al., 2009). Approach distances were approximately normally distributed with a slight right skew and bounded from 0 to infinity; therefore, a Gamma distribution with log-link function was used for all GLM models. This distribution improved normality and homogeneity of variances in model residuals relative to the Gaussian distribution with identity link. To account for the nested structure of the data, whereby repeat measurements were obtained within encounters and individuals (i.e., multiple passes), whale ID and encounter ID were included as random effects factors.

Group variables (e.g., location, vessel status, time in encounter) were available for every pass, thus all 1,118 passes were included in this analysis. Group variables were modelled as fixed effects factors and approach distance as the response variable. One-, two-, and three-fixed effects models predicting approach distance were constructed using the R package glmmTMB (Brooks et al., 2017). To allow for comparison of models with varying fixed effects, models were initially fit using maximum likelihood (ML) estimation (Zuur et al., 2009). A forward model selection approach was used wherein the one-variable model with the minimum AICc score (and any additional models within 2.0 AICc units of the optimal model, i.e., ΔAICc) were used as the base of the two-variable model, and so on (Anderson & Burnham, 2002; Burnham & Anderson, 1998). This process was discontinued once additional variables showed no sign of improving model fit. The overall best fitting model was then selected by choosing the most parsimonious model (i.e., the one with the fewest predictor variables) amongst the highest-ranking models (i.e., all models within 2.0 ΔAICc). This model construction, selection, and evaluation process was repeated for all GLM models in this chapter.

Significance of random effects (whale ID and encounter ID) was assessed in the best fitting model using Likelihood Ratio Tests (LRTs). The LRTs were performed by comparing the full model, which included both random effects, with two reduced models, each excluding one random effect. These tests revealed that whale ID was a significant random effect (LRT, $\chi^2 = 46.71$, df = 1, $p < 0.001$) but encounter ID was not a significant random effect (LRT, $\chi^2 = 0.25$, df = 1, $p = 0.616$). As a result, encounter ID was removed and the model evaluation procedure was re-run without that variable. Significance of fixed effects was determined for the best fitting model and all other models within 2.0 ΔAICc using Wald tests. Lastly, the final model was re-fitted using restricted maximum likelihood (REML) to obtain the most accurate (i.e., unbiased) estimates of the variance components (Zuur et al., 2009).

5.2.4.3.2 Post-model fitting and visualisation procedures

Adequacy of the most parsimonious model was assessed by evaluating the normality and homogeneity of variances of the model residuals using the R package DHARMa (Hartig, 2022). Visual inspection of the simulated residuals showed no apparent patterns or trends, indicating that the model adequately captured the variability in the data. The quantile-quantile (QQ) plot of the residuals showed good agreement with the expected quantiles, suggesting that the assumption of normally distributed residuals was met. A Kolmogorov-Smirnov (KS) test ($p = 0.357$) supported the adequacy of the model. No significant deviation from normality was detected, and residual variance was homogenous. The final model equation was used to visualise predicted approach distances within the parameter ranges of the original data and extrapolated beyond (i.e., longer encounter durations and larger whale group sizes) to model the full extent of relevant parameter ranges for swim-with encounters.

5.2.4.4 Individual variables

5.2.4.4.1 Total body length (TBL)

To determine the effect of body size on approach distance, 73 whales were measured for TBL during the 2017 season. This represents 52.1% of identified whales from this sampling period. From this subset of whales, 915 passes were measured for approach distance. Two GLM models were constructed using TBL as a predictor of passing distance: one consisting of TBL as the only fixed effect, and one also including any significant variables identified from the group variable models (i.e., to account for significant variables identified from the larger, non-subsetted data set; see section 5.2.4.3.1). The AICc scores of these two models were compared to a null model that consisted of only the significant group variables. The best-fitting model was determined and evaluated as previously described (see section 5.2.4.3.1).

5.2.4.4.2 Sex

The sex of 24 whales was identified in the 2017 sampling period: 16 females and eight males. To determine whether sex was a significant predictor for approach distance, 362 passes from this subset of known-sex whales were measured for approach distance. Construction, analysis, and significance testing of these GLM models were completed as for TBL above, whereby sex was modelled alone and with significant group variables and then compared to a null model of only significant group variables. The best-fitting model was determined as previously (see section 5.2.4.3.1).

5.2.4.4.3 Re-sighted whales

Encounter number (ENC) was modelled separately to other variables due to a small number of re-sighted whales across encounters. These data consisted of 138 individual approach distance measurements made by 11 whales. Of these, eight whales were sighted twice and three whales were sighted three times. GLM model construction and selection were completed as for other individual variables above, whereby encounter number was modelled alone and with significant group variables and then compared to a null model of only significant group variables. The best-fitting model was determined as previously (see section 5.2.4.3.1).

5.3 Results

5.3.1 Approach distance and encounter overview

Overall mean whale-swimmer approach distance during the 2017 sampling period was 8.02 m ± 0.11 *SE* (n = 1,118). This ranged from the closest pass of 0.94 m to the farthest identifiable pass of 25.12 m (Fig. 5.1). Mean interaction duration was 225 min (3.75 h) with a range from 10 min to 540 min (9 h). Mean whale group size across these encounters was 5.6 whales and ranged from 1 whale to 20 whales.

5.3.2 Close approaches

A total of 63 close approaches were recorded by 25 whales, representing 5.6% of all measured passes (n = 1,118). Two approaches of less than 1 m to a swimmer (the videographer) were documented. The mean approach distance by "close approachers" (6.08 m ± 0.147 *SE*) was over 2.5 m closer than that for "non-close approachers" (8.81 m ± 0.190 *SE*), and this difference was significant ($t_{720.8} = 10.641$, $p < 0.001$; Figure 5.2).

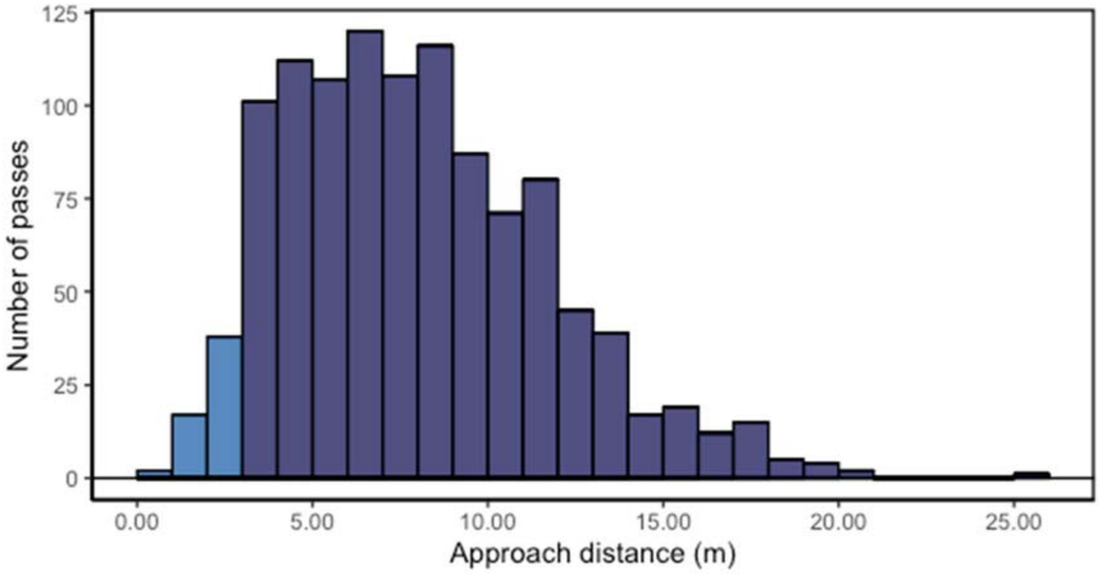


Figure 5.1. Distribution of whale-swimmer approach distances (m) of all measured passes in 2017 (n = 1118 passes by 121 whales). Light blue bins represent "close approaches" (< 3.00m).

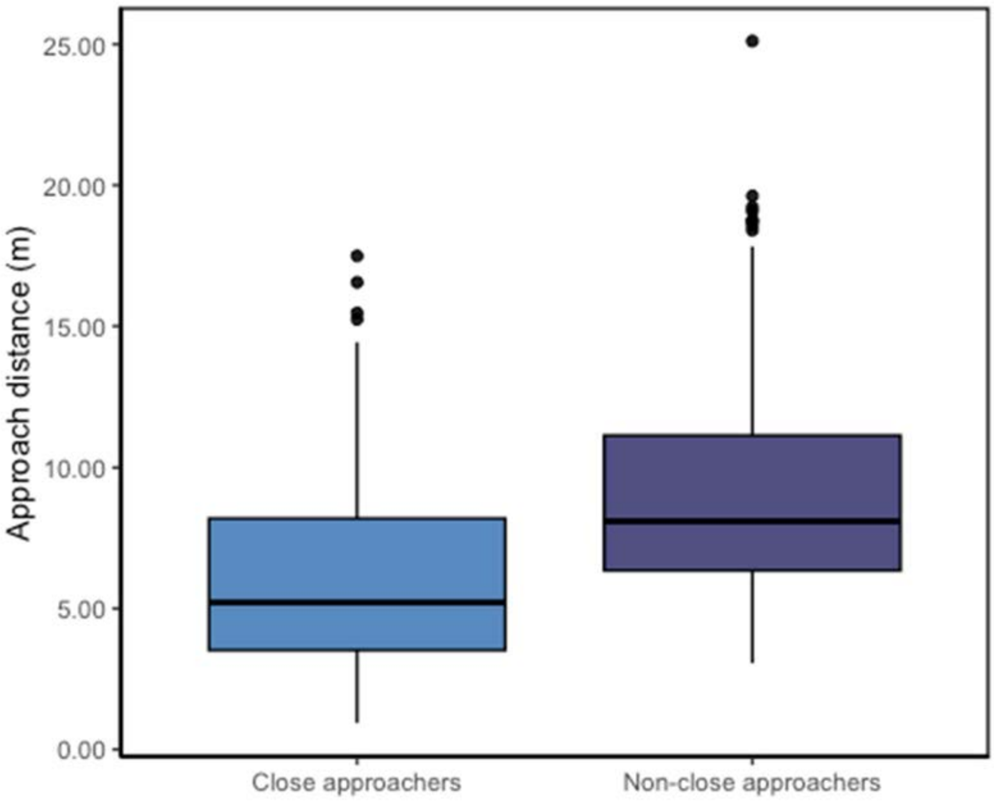


Figure 5.2. Median ± 25% inter-quartile ranges of approach distances (m) by "close approachers" (≤ 3 m, n = 365 passes) and "non-close approachers" (> 3 m, n = 753 passes). Whiskers extend to 1.5 times the inter-quartile range. Outliers are included.

5.3.3 Repeat passes

The number of passes measured per whale ranged from 1 to 46 (Fig. 5.3). Mean number of passes was 9.24 ± 0.81 *SE* and the median number of passes was six, demonstrating a strong right skew. The calculated Gini coefficient for the distribution of measurements was 0.493, indicating moderate inequality (i.e., variability) in the number of passes made between individual whales. Nine of the 63 close approaches (14.2%) were made by MW21010, an immature male. This whale made the most passes of any animal in this sampling period, with 46 passes measured in a single encounter. The whale with the second highest number of passes made 35 passes in one encounter (MW3430).

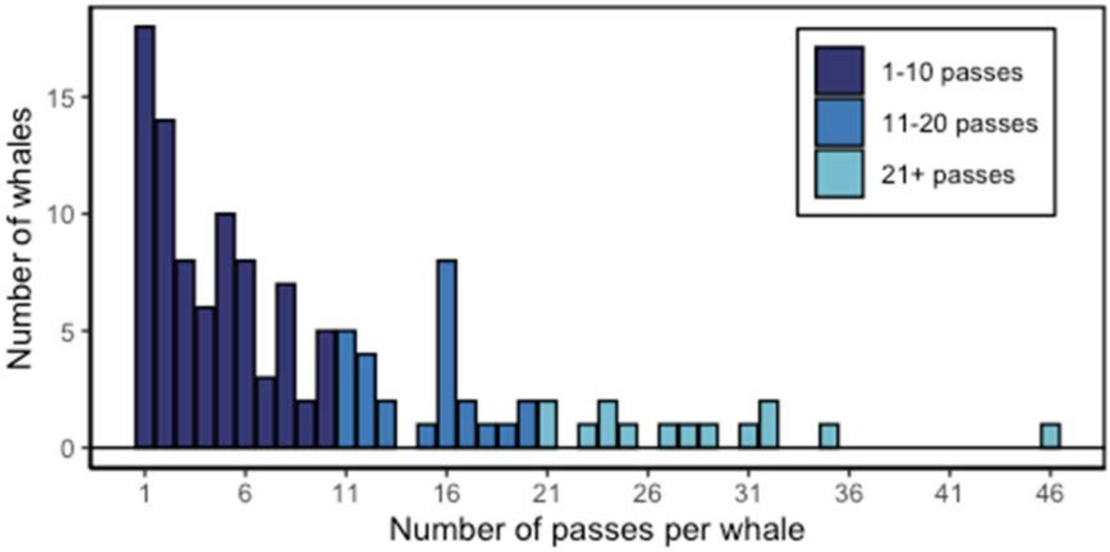


Figure 5.3. Number of measured passes per whale across 21 encounters in 2017 (N = 121).

A slight negative correlation was identified between the total number of passes and mean approach distance per whale (β = -0.04, R^2 = 0.015; Figure 5.4a). This indicates that, the more passes a whale made, the closer they would approach overall. However, the low R^2 value indicates that this effect was small, and the relationship was not statistically significant ($F_{1, 119}$ = 1.856, p = 0.176). Therefore, number of passes did not have a significant effect on overall approach distance. In contrast, a strong negative correlation was found between the total number of passes and the minimum approach distance of each whale (β = -0.39, R^2 = 0.372; Figure 5.4b), indicating that the number of passes a whale made was a significant predictor of a whale's minimum approach distance ($F_{1,119}$ = 70.56, p < 0.001).

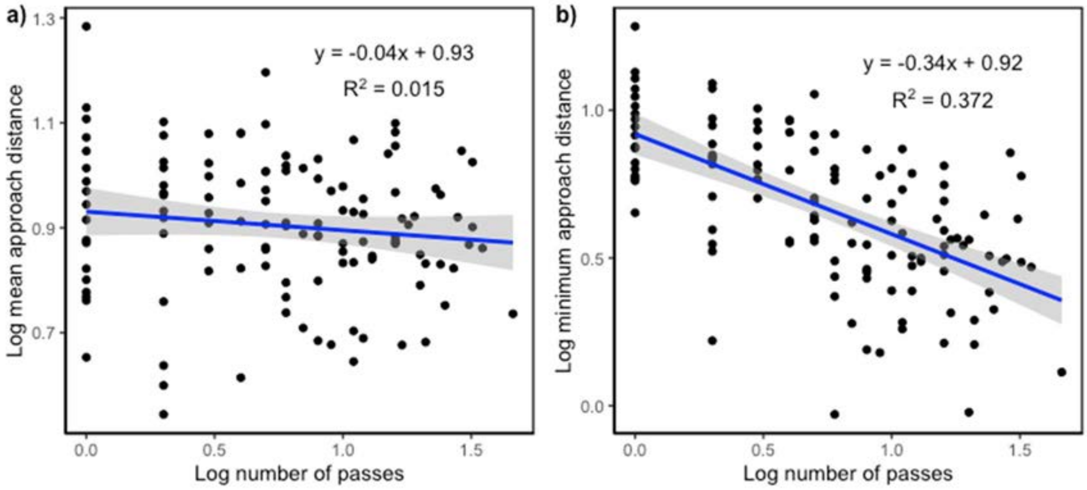


Figure 5.4. a) Log mean approach distance (m) per whale by log number of passes per whale; and b) Log minimum approach distance (m) per whale by log number of passes per whale, across all encounters in 2017.

5.3.4 Group variables

Two group variable models achieved either the lowest AICc score (AICc$_{min}$) or were within 2.0 ΔAICc: 1) group size (NUM), time in encounter (TIE), and wave height (WH); and 2) NUM and TIE only (Table 5.3). The most parsimonious model of external predictors was the two-fixed effects model consisting of NUM and TIE. Significance testing showed that NUM and TIE were both significant predictors of approach distance, such that as NUM and TIE increased, approach distance decreased (z_{NUM}_1 = -4.44, $p_{NUM} < 0.001$; z_{TIE}_1 = -3.43, $p_{TIE} = 0.001$). While a marginally higher AICc score was achieved for the model containing WH, model assessment showed that WH was not a statistically significant predictor of approach distance in this model (z_{WH}_1 = -1.20, $p_{WH} = 0.230$). Evaluation of residuals in the most parsimonious model (NUM + TIE) showed adequate fit with no major departures from model assumptions. No other group variables were significant predictors of whale-swimmer approach distance~~.~~

Table 5.3: Second-order Corrected Akaike Information Criterion (AICc) scores of 1-, 2-, and 3-fixed effect(s) Generalised Linear Mixed Models assessing the effect of external variables on whale-swimmer approach distance.

1-var model	AICc	2-var model	AICc	3-var model	AICc
TIE	16759.29	**NUM* + TIE***	**16751.45**	**NUM* + TIE* + WH**	**16751.01**
NUM	16761.15	NUM + WH	16758.17	NUM + TIE + DOS	16753.39
VS	16770.22	TIE + VS	16758.74	NUM + TIE + AA	16753.48
AA	16770.78	TIE + AA	16759.95	NUM + TIE + ET	16753.73
NULL	16771.42	TIE + WH	16760.91	NUM + TIE + VS	16755.36
WH	16772.35	TIE + DOS	16761.15	NUM + TIE + SITE	16756.91
DOS	16773.44	NUM + DOS	16762.25		
ET	16775.25	NUM + ET	16762.36		
DOS	16788.62	NUM + AA	16762.88		
SITE	16775.64	TIE + ET	16763.34		
		NUM + VS	16763.42		
		TIE + SITE	16764.12		
		NUM + SITE	16767.68		

Note. Random effects = whale ID*. Bolded text represents the highest-ranking model (i.e., $AICc_{min}$) and other models within 2.0 ΔAICc. * indicates statistical significance ($p > 0.05$). NUM = group size, TIE = time in encounter, VS = vessel status, AA = inside/outside aggregation hotspot, DOS = day of season, WH = wave height, ET = encounter type, SITE = nearest site.

5.3.5 Individual variables

5.3.5.1 Total body length (TBL)

TBL of the 73 measured whales ranged from 5.04 m to 7.43 m, with a mean of 6.23 m ± 0.004 SE. From this subset of measured whales, 915 passes were measured for approach distance (Fig. 5.4).

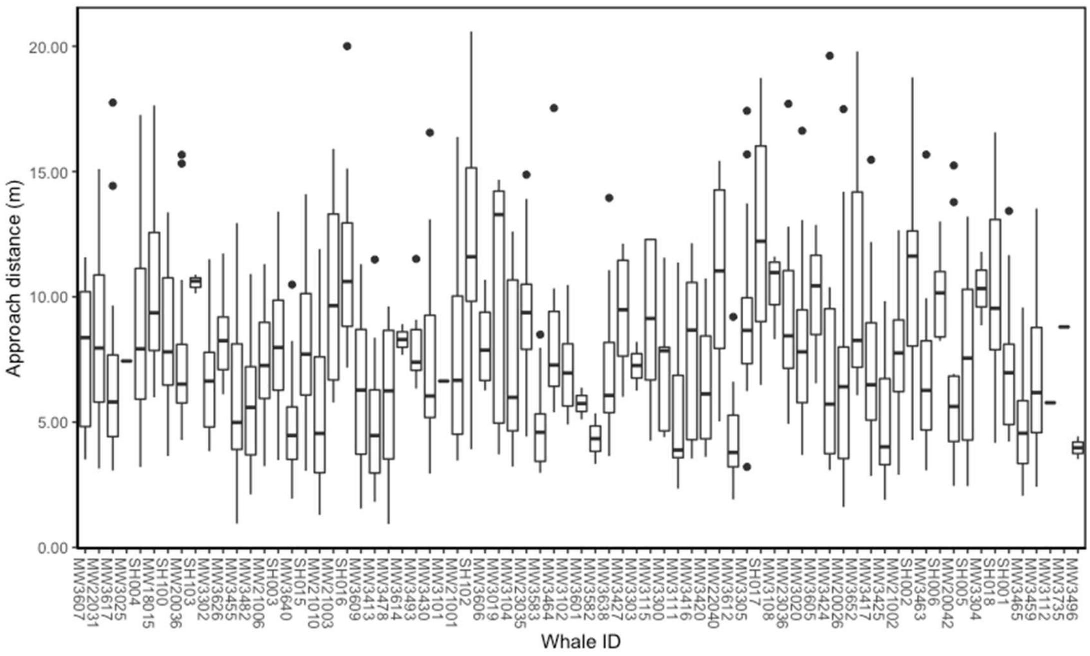


Figure 5.4. Median ± 25% inter-quartile ranges of approach distances (m) of whales measured for TBL (n = 73). Identified whales (i.e., x-axis) are arranged from smallest to largest by mean measured TBL (5.04 m to 7.43 m). Whiskers extend to 1.5 times the inter-quartile range. Outliers are included.

TBL was not a significant predictor of approach distance (Table 5.4). The most parsimonious and best-fitting model was M_0, containing the variables NUM and TIE only. Neither model containing TBL scored within 2.0 ΔAICc. Both NUM and TIE were found to be significant predictors of approach distance in M_0 ($z_{NUM}\_1 = -5.25$, $p_{NUM} < 0.001$; $z_{TIE}\_1 = -3.45$, $p_{TIE} = 0.001$) and M_1 ($z_{NUM}\_1 = -5.17$, $p_{NUM} < 0.001$; $z_{TIE}\_1 = -3.58$, $p_{TIE} < 0.001$. TBL was not significant in M_1 ($z_{TBL}\_1 = 34.17$, $p_{TBL} = 0.88$).

Table 5.4: Second-order Akaike's Information Criterion (AICc) scores of Generalised Linear Mixed Models (GLMMs) assessing the effect of TBL on whale-swimmer approach distance.

Independent variables	**AICc**
M_0: NUM* + TIE*	**16786.56**
M_1: NUM + TIE + TBL	17342.85
M_2: TBL	17364.00

Note. Random effects = whale ID. Bolded text represents the highest-ranking model (i.e., $AICc_{min}$) and other models within 2.0 $AICc_{min}$. * indicates statistical significance. NUM = whale group size, TIE = time in encounter, TBL = total body length.

5.3.5.2 Sex

Sex was not a significant predictor of approach distance (Table 5.5). The highest-ranking model was M_0, with independent variables NUM and TIE only. M_1, with NUM, TIE, and Sex, scored within 2.0 ΔAICc and was also assessed. Both NUM and TIE were significant predictors of approach distance in M_0 (z_{NUM}_1 = -2.60, p_{NUM} = 0.009; z_{TIE}_1 = -2.21, p_{TIE} = 0.027) and M_1 (z_{NUM}_1 = -2.62, p = 0.009; z_{TIE}_1 = -2.30, p_{TIE} = 0.021). Sex was not significant in M_1 (z_{TBL}_1 = -1.08, p_{TBL} = 0.281). Therefore, the most parsimonious and best-fitting model was M_0, which consisted of the independent variables NUM and TIE only.

Table 5.5: Second-order Akaike's Information Criterion (AICc) scores of Generalised Linear Mixed Models (GLMMs) assessing the effect of sex on whale-swimmer approach distance.

Independent variables	**AICc**
M_0: NUM* + TIE*	**6844.30**
M_1: NUM* + TIE* + SEX	**6845.24**
M_2: SEX	6855.48

Note. Random effects = whale ID. Bolded text represents the highest-ranking model (i.e., AICc_{min}) and other models within 2.0 ΔAICc. * indicates statistical significance. NUM = group size, TIE = time in encounter, SEX = sex ID (male or female).

5.3.5.3 Re-sighted whales

Encounter number (ENC) was not a significant predictor of approach distance (Table 5.6) While the model containing ENC achieved the highest-ranking AICc score, ENC was not statistically significant ($z_{ENC}\_1 = 0.48$, $p_{ENC} = 0.628$). Thus, the next highest scoring model was assessed, the null model containing only the independent variables NUM and TIE.

Table 5.6: Second-order Akaike's Information Criterion (AICc) scores of Generalised Linear Mixed Models (GLMMs) assessing the effect of sex on whale-swimmer approach distance.

Independent variables	**AICc**
M_2: ENC	**2641.70**
M_0: NUM + TIE	2663.39
M_1: NUM + TIE + ENC	2669.16

Note. Random effectss = whale ID. Bolded text represents the highest-ranking model (i.e., AICc_{min}) and other models within 2.0 ΔAICc. NUM = group size, TIE = time in encounter, SEX = sex ID (male or female).

The most parsimonious model for approach distance included only NUM and TIE as fixed effects and whale ID as a random effect. The final model represented as an equation was:

$$AD = exp(9.255 - 0.02136 \bullet NUM - 0.00002014 \bullet TIE),$$

where AD = approach distance, NUM = whale group size, and TIE = time in encounter

Since whale ID was a random effect, it cannot be explicitly represented in the model equation; however, it was a significant random effect in the final model, representing individual variability, and its inclusion in the model ensured that the fixed effects estimates were not biased by this variability. This model equation shows that for every additional five whales present in an encounter, mean whale-swimmer approach distance decreased by approximately 0.5 m (Fig. 5.5). Across an encounter of approximately eight hours, mean approach distance decreased by approximately 50% for all group sizes. After a 12-hour encounter duration, mean approach distance for all group sizes was predicted to be less than 5 m.

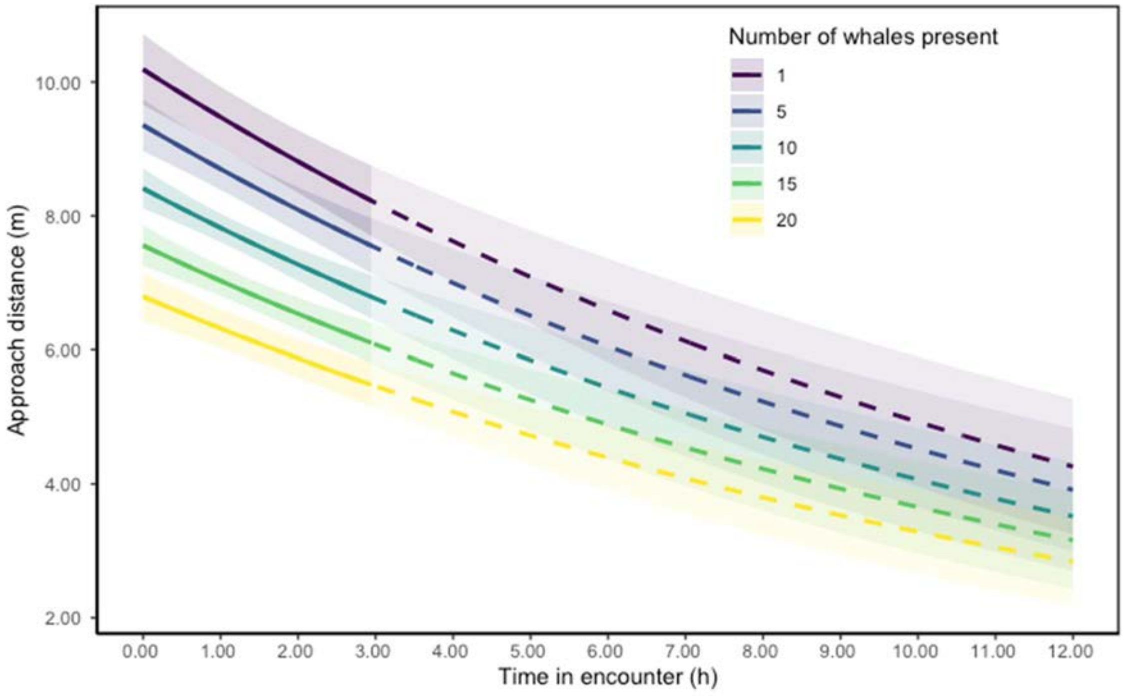


Figure 5.5. Modelled relationship (mean ± 95% CI) of mean whale-swimmer approach distance (m) by time in encounter across five theoretical encounters of differing group sizes. Solid lines represent modelling of actual data (i.e., up to approx. 3h into an encounter).

5.4 Discussion

5.4.1 Chapter overview

The overall aim of this chapter was to develop a more detailed understanding of the highly interactive behaviour of dwarf minke whales during swim-with interactions in the Great Barrier Reef. Specifically, I aimed to: (1) identify predictors of interactive behaviour at both the group (i.e., encounter) and individual levels; and (2) to quantify the effects of these variables on whale-swimmer approach distances. Approach distances were highly variable both within and between individual whales, ranging from the closest pass of 0.94 m to the farthest identifiable pass of over 25 m. Most group-level factors such as weather conditions (i.e., WH), location (i.e., SITE, AA), time of year (i.e., DOS), WS, and ET) did not influence whale-swimmer approach distance. Similarly, individual characteristics such as sex and body size (TBL) did not influence whale-swimmer approach distances. Rather, whale-swimmer approach distance decreased as a) encounters progressed, b) whale group size increased, and c) individual per-whale passes increased. These findings agree with previous studies showing that whale group size and encounter duration influence dwarf minke whale interactivity (Mangott, 2010; Mangott et al., 2011), and provide a more detailed understanding of how these factors affect interactive behaviour across a wider range of expected encounter conditions. Further, after accounting for these variables, significant variation remained across individual whales (i.e., the random effect of whale ID), indicating that individual differences among whales contribute to their approach behaviour, beyond what can be explained by the fixed effects alone.

5.4.2 Repeat passes and closer approaches

An unequal distribution of passes amongst whales was found, whereby some whales made disproportionately more passes than others. This suggests considerable diversity between whales in the level of engagement with swimmers during swim-with activities. The majority of whales (63%) made less than 10 passes, suggesting limited interactivity, whereas one young male whale was involved in nine of the closest 20 passes recorded, and made the most passes of any whale recorded in the season (n = 46). Additionally, while over half of whales only made one pass, nearly 85% of the closest approaches were by whales making multiple passes. The whales making more passes also tended to approach more closely than whales making fewer passes, independent of the number of encounters they were sighted in. Mean approach distance per whale was only slightly correlated with the number of passes made by that whale; however, the closest approach made by a whale was highly correlated with the number of passes it made. This observed correlation demonstrates a potential behavioural pattern where repeat passes serve as a meaningful indicator of the likelihood of closer approaches. These results suggest that individual variation, wherein a small number of whales are more interactive and more likely to make more passes and closer approaches. Mangott (2010) suggested that particularly inquisitive individuals become familiar with the stimuli through repeated interactions. However, encounter number did not influence approach distance in my study, suggesting that familiarity is likely only one of multiple drivers of this variation in behaviour.

5.4.3 Repeat encounters vs repeat passes

While some findings in this study were consistent with previous research (e.g., Mangott, 2010; Mangott 2011), others were not. While overall mean approach distance was similar between my study (8.02 m ± 0.11 *SE*) and Mangott's (2010) study (7.08 m ± 0.09 *SE*), Mangott (2010) found that some whales decreased their approach distances when they were re-sighted in subsequent encounters, where I found that re-sightings at the encounter level did not influence approach distance. Instead, I found that whales approached closer with repeated passes independent of whether it was a repeat encounter or not. While the number of encounter sightings is roughly correlated with number of passes (i.e., if a whale was sighted in multiple encounters then it has necessarily made multiple passes, at minimum one pass per encounter), some whales only made a single pass within an encounter, whereas others made many (up to 46 in this study). Thus, encounter-level re-sightings histories do not capture finer-scale behavioural differences between individuals (i.e., number of passes). My findings demonstrate the importance of investigating behaviour at both the group and individual levels to best reflect the complexities of dwarf minke whale behaviour.

5.4.4 Potential drivers of individual variation

Tolerance to human presence is not static or uniform across a species (Beale & Monaghan, 2004; Blumstein, 2016; Hanson & Riley, 2018). Allan et al. (2020) argue that overlooking individual variation in tolerance can substantially affect behavioural research by missing a key driver of behavioural patterns. Overlooking individual variation in tolerance may result in missing a crucial factor influencing behavioural patterns, which may have substantial implications for behavioural research (Allan et al., 2020). My findings indicate that whale-swimmer approach distances were highly variable between individuals, and this variation persisted even after accounting for known external drivers, such as whale group size and number of passes/encounter progression.

Multiple drivers of individual variation in flight initiation distance have been identified in other species. These include age (Constantine, 2001), sex (Lusseau 2003a), body size (Dissegna et al., 2022), reproductive condition (Parent & Weatherhead, 2000), nutritional condition (Doenier, 1997; Seltmann et al., 2012), prior experience (Bejder, Samuels, Whitehead, & Gales, 2006; Gayford et al., 2023), and personality traits such as boldness (Petelle et al., 2013; Strong et al., 2017). I found that sex and age (by proxy of body size, TBL) are not likely to be consistent drivers of individual variation in dwarf minke whales, as neither sex nor TBL were significant predictors of whale-swimmer approach distance. While age was not directly measured here, in general, the longer the whale, the older it was likely to be, at least during the significant growing years, which may be up to the first 10 years of life for dwarf minke whales (Kato & Fujise, 2000).

The results presented here suggest that prior experience (at the level of individual passes) and personality may be potential drivers of individual variation in dwarf minke whale behaviour. As encounters progressed and dwarf minke whales made more passes, they tended to decrease their approach distance, demonstrating that prior experience influences – or at least predicts - future behaviour in the short-term. Mangott (2010) also found that this trend persisted across multiple encounters, providing further evidence that prior experience is important and may also influence behaviour in the medium-term. However, individual differences in behaviour persisted that could not be explained by prior experience, whale group size, or demographic factors, suggesting an internal characteristic or personality trait may be driving these differences. Indeed, individual variation in flight initiation distance has been used as a direct measure of the personality trait boldness (Carter et al., 2012; Hall et al., 2020; Petelle et al., 2013; Weston et al., 2012). Thus, some of the unexplained variation in behaviour observed in this study may represent individual differences in personality traits, such as boldness.

5.4.5 Non-significant variables

While group size, time in encounter, and number of passes per whale were the only variables identified to directly influence approach distance. However, other variables investigated are not necessarily irrelevant. Previous studies have found that mean group size and encounter duration may be significantly different across dive sites/locations frequented by permitted operators (Curnock, Birtles, & Valentine, 2013). I found that both group size and time in encounter influence passing distance (and thus encounter duration by proxy of time in encounter). As such, nearest dive site/location can be considered an indirect predictor of approach distance. For example, encounters at Lighthouse Bommie, near Ribbon Reef no. 10, are generally larger and longer than those at other sites (Curnock, Birtles, & Valentine, 2013). I hypothesise that approach distances at this site will generally be closer than at other locations because of encounter duration and group sizes. Day of season may be similarly relevant, as mean whale group size is larger during the peak of the season in late June and early July (Box, 2022).

5.4.6 Significance of closer approaches and increased attraction

While this study demonstrates that dwarf minke whales change their behaviour over the short-term, the consequences or impacts of these changes remain unknown. Behavioural changes can negatively impact the health of an animal or population by reducing the time available for essential activities (Carzon et al., 2023; Lusseau 2004). Since the northern Great Barrier Reef aggregation area is thought to serve as a mating ground for dwarf minke whales (Birtles, Arnold, et al., 2002), the increased attraction to swimmers could disturb this essential life function, resulting in decreased reproduction, similar to the impacts of tourism on bottlenose dolphins in Shark Bay, Western Australia (see section 5.1.1 and Mann et al., 2000). However, connecting short-term behaviour changes to long-term effects is notoriously challenging (Bejder, 2005; Christiansen et al., 2015). Statistically significant changes in behaviour are not always biologically significant (New et al., 2013), as compensation can occur without affecting overall energy budgets (Lusseau, 2004). On the other hand, disturbance can have hidden costs not accounted for (New et al., 2013). The behaviour of dwarf minke whales when not in contact with vessels in the Great Barrier Reef is unknown and, as such, the extent that these tourism interactions may be disrupting critical activities like mating – and the resultant costs – are also unknown.

Whales and dolphins that become de-sensitised or habituated towards human presence may also be at a greater risk of experiencing harassment (Samuels et al., 2003; Samuels & Bejder, 2004), collisions with vessels (Bejder & Samuels, 2003), and entanglement in fishing gear or marine debris (Knowlton et al., 2012; Lien, 2009). Thus, the progressively increasing attraction to humans observed in this study could expose this population, or particularly susceptible individuals, to elevated risks of negative consequences due to cumulative impacts. However, dwarf minke whales are not known for their highly inquisitive behaviour outside of their seasonal aggregation in the Great Barrier Reef. Elsewhere, dwarf minke whales are generally considered solitary animals (Birtles & Mangott, 2011). However, even solitary animals have a requirement to seek out conspecifics to reproduce. In capital breeding cetaceans, the seasonal mating period follows a rise in testosterone and other androgen concentrations in both sexes (Atkinson et al., 2023; Cates et al., 2019; Dalle Luche et al., 2020; Schroeder & Keller, 1989). This endocrine signalling not only prepares the animals for mating physiologically (e.g., sperm production in males), it also enhances mating and courtship behaviours (Balthazart, 1983; Melica, Atkinson, Calambokidis, et al., 2021; Melica, Atkinson, Gendron, et al., 2021; Wingfield et al., 1990). If the northern Great Barrier Reef indeed serves as a mating ground for dwarf minke whales, then these behavioural changes, with the purpose of seeking out a mate, may also increase their exploratory drive towards other stimuli in their environment, including vessels and humans. As such, their high interactivity may be a locally confined phenomenon associated with the social and reproductive functions that this aggregation likely serves, and not translate to increased risks elsewhere in their range.

5.4.7 Implications for tourism management

Previous studies have identified that closeness of approach, total number of whales seen, and total time spent with whales are important factors for visitor satisfaction during whale-watching activities (Muloin, 1998; Orams, 2000). Similar results have also been found for swim-with dwarf minke whales activities in the Great Barrier Reef (Birtles, Valentine, et al., 2002; Valentine et al., 2004). However, these same characteristics that contribute to participant satisfaction may also increase the risk of harm due to closer whale-swimmer/vessel approach distances. This trade-off between risk and satisfaction presents a substantial management challenge for tourism operators, as there is a clear incentive to allow closer and longer encounters, yet these factors also likely increase the risk of harm due to closeness of approach. My study found a decrease in mean approach distance both as whale group size and encounter duration increased, providing predictable behavioural patterns of increased interactivity and, consequently, a likely resultant increased risk of harm.

A plausible management recommendation may be to introduce time limits associated with whale-swimmer interactions. Time limits have not been established for the swim-with dwarf minke whale industry, despite their prevalence in swim-with industries elsewhere (Gero et al., 2016). However, it would be challenging to impose such limits without restricting all in-water activities, as encounters with dwarf minke whales involve the whales approaching the swimmers. Furthermore, enforcing time limits may also lead to a decrease in passenger satisfaction (Mangott, 2010). Thus, time limits are unlikely to be voluntarily adopted by tourism operators. Instead, further stakeholder consultation is recommended to determine whether the behavioural patterns identified in this study are of sufficient concern for management intervention, and what operational strategies may be suitable to employ.

5.4.8 Limitations

A limitation to this study lies in the lack of SDOV coverage across longer encounters and multiple years. While the mean encounter length observed in this study was 3.75 hours (n = 17), many lasted for four or more hours (42.8%), with the longest encounter lasting over nine hours. Due to the physical limitations of the SDOV camera system (i.e., inability to swap out batteries), a maximum of approximately three hours of video footage was collected during each encounter before the batteries required charging. Thus, it is unknown how well the extrapolation of the approach distance model developed here represents true whale behaviour during longer encounters. Nevertheless, I identified a clear pattern that dwarf minke whales approach swimmers more closely both as an encounter progresses and as whale group size increases, over at least the first three hours of an encounter. Further research would be useful to determine if this pattern remains consistent as encounters progress beyond three hours, an encounter duration that frequently occurs in the Great Barrier Reef.

5.4.9 Unresolved questions and further research recommendations

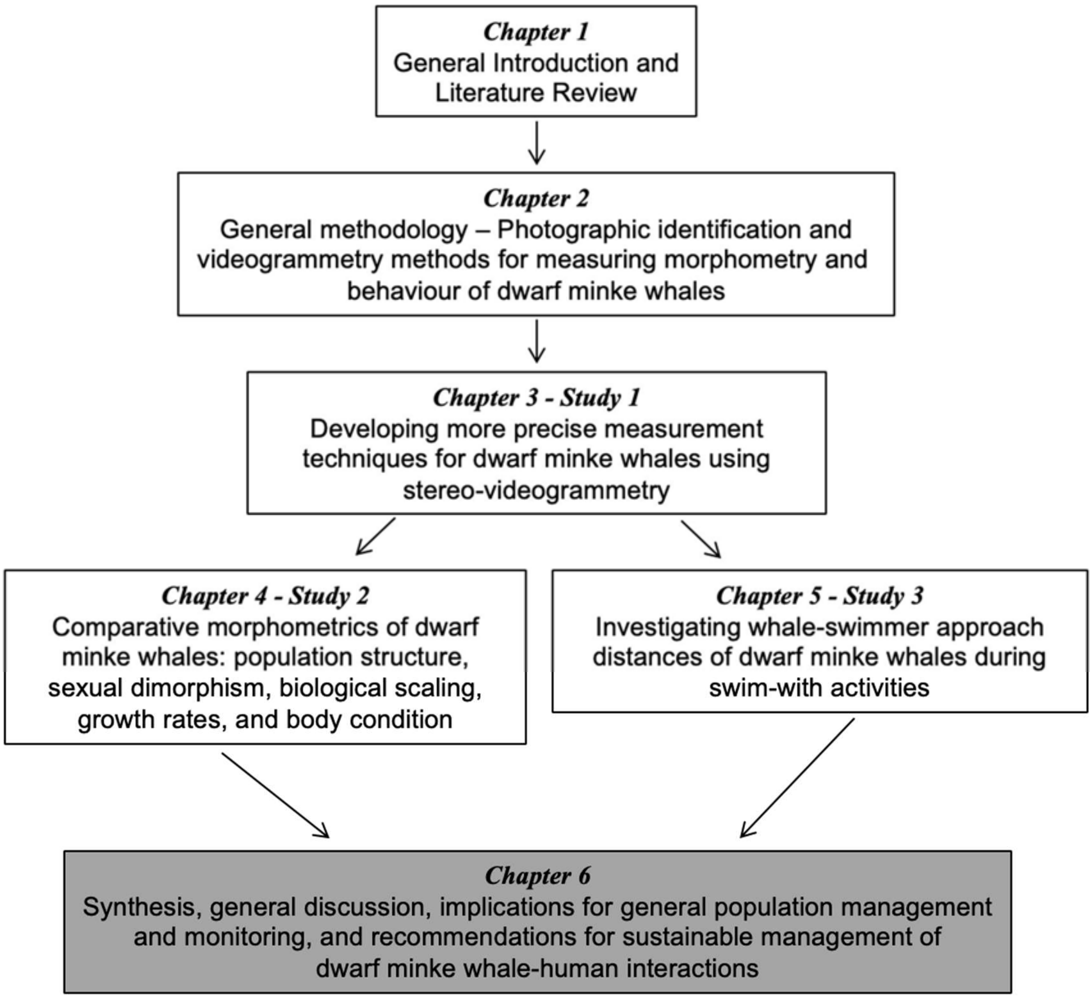
Investigating long-term sighting histories of individual dwarf minke whales may provide additional insights into individual variation observed in dwarf minke whale behaviour. For example, have whales making repeat passes and close approaches had extensive exposure to swim-with activities in previous years? Are short-term behaviour changes persistent over the longer term (i.e., across multiple seasons)? Approximately 25% of whales are re-sighted across multiple years, and the potential thus exists for cumulative impacts of repeated interactions over many years (Sobtzick, 2010). Due to gaps in the availability of long-term (i.e., multi-year) photo-identification data, the interaction history of the whales identified in this study in the years prior to this study was not investigated. This research is recommended both for the possibility of identifying highly interactive individuals that may increase the risk of harm during swim-with encounters and to identify if longer-term habituation may be occurring due to these tourism activities.

5.4.10 Conclusion

This study has provided a deeper understanding of dwarf minke whale behaviour during swim-with interactions in the Great Barrier Reef, particularly regarding highly inquisitive behaviour that can increase the risk of harm to both the swimmers and the whales. I found that the factors influencing whale-swimmer approach distance are multifaceted and complex, and suggest that both external and internal factors contribute to interactive behaviour in dwarf minke whales. As encounters with whales become longer and involve larger groups, the chances of close approaches and potential harm to both the whales and swimmers increase. Individual differences in whale behaviour persist, however, and close whale-swimmer approaches can occur at any time. Nevertheless, it is important for researchers and tourism managers/operators to be aware of the patterns identified in this chapter and ensure that their management strategies take into consideration the concerns raised here. The results of this study may also contribute to future revisions of existing management protocols for the permitted industry.

6 CHAPTER 6

GENERAL DISCUSSION



6.1 Introduction

The swim-with dwarf minke whales tourism industry in the Great Barrier Reef is a lucrative industry that also provides a fruitful avenue for studying the biology and behaviour of these cetaceans. Prior to the discovery of the aggregation area in the northern Great Barrier Reef, there was a substantial lack of research on dwarf minke whales, with scant information available on their social structures, migratory patterns, and interactions with humans. The identification of this seasonal aggregation and the whales' frequent interactions with tourism vessels marked a pivotal advancement in research, allowing dedicated research on dwarf minke whales. While significant advancements have been made in understanding their biology and behaviour, persistent knowledge gaps remain. The underlying mechanisms driving their aggregation, the specific behavioural responses to vessels and swimmers, and the potential implications for their conservation status remain areas of active investigation. My thesis sought to address some of these knowledge deficits, focusing on morphometric and behavioural parameters that appear to be unique to this population, thereby contributing to the broader understanding of dwarf minke whale ecology.

6.2 Thesis summary

The overall purpose of this thesis was to increase knowledge of basic dwarf minke whale biology and to better understand dwarf minke whale behaviour during tourism interactions in the Great Barrier Reef, Australia. Recent advances in stereo-videogrammetry technology have allowed more accurate and precise measurement estimates than have previously been available. In-water videogrammetry imagery can be used for a variety of applications, facilitating both biological and behavioural research through the ability to measure morphometric features and whale-swimmer approach distances. This thesis had two overarching aims (see Chapter 1):

(3) **To increase the quality and quantity of morphometric measurements of dwarf minke whales.**

(4) **Increase understanding of dwarf minke whale biology and behaviour using these improved measurement techniques.**

To achieve these aims, I specified three objectives for my study, each corresponding to its own data chapter:

Objective 1: To develop more precise measurement techniques for dwarf minke whales (Chapter 3).

Objective 2: Investigate the external morphometry of dwarf minke whales in the Great Barrier Reef (Chapter 4).

Objective 3: Explore the potential drivers of differences in whale-swimmer approach distance across individual whales and encounters (Chapter 5).

Objective 1 relates directly to thesis aim 1, and objectives 2 and 3 relates directly to thesis aim 2.

6.2.1 Study 1 summary: Developing protocols for in-water stereo-videogrammetry data collection

Chapter 3 addressed thesis objective 1, to develop more precise measurement techniques for dwarf minke whales. First, I improved upon previous videogrammetry methods for filming dwarf minke whales by employing a stereo-videogrammetry system rather than a single-camera system. This method provided significantly more precise measurements than have been previously collected. Next I developed an in-water methodological protocol that prioritizes a) the best opportunities to make robust body measurements, and b) the best opportunities to capture behaviour to allow post-field video measurements of whale-swimmer approach distances. Finally, I developed specific analytical protocols to maximise reliability of measurements (e.g., identified minimum replicate aims) while remaining mindful of time constraints for analysis. This chapter successfully developed a methodological protocol to increase quality (i.e., precision) and quantity of body measurements of dwarf minke whales, which were employed in Chapters 4 and 5. These methods may be applicable to other marine megafauna species where more efficient emerging methodologies (i.e., drone-based techniques) are similarly unsuitable and access under similar conditions is available.

6.2.2 Study 2 summary: Comparative morphometrics of dwarf minke whales

Chapter 4 addressed thesis objective 2, to investigate the external morphometry of dwarf minke whales. Using the improved stereo-videogrammetry measurement techniques developed in Chapter 3, I measured a suite of nine morphological features of dwarf minke whales and used these measurements to investigate several aspects of morphometry, including allometric and ontogenic growth patterns and potential sexual dimorphism. I also identified useful proxies for total body length (TBL) for when TBL measurements are unavailable, provided baseline measurements that could be used in future assessments of body condition, and identified a long-term shift in population structure, with a decreased proportion of juvenile dwarf minke whales and a significant increase in mean TBL from measurements made a decade earlier.

6.2.3 Study 3 summary: Drivers of interactive behaviour of dwarf minke whales

Chapter 5 addressed thesis objective 3, to explore a range of potential drivers of interactive behaviour of dwarf minke whales during swim-with tourism encounters. Using the improved measurement techniques I developed in Chapter 3, I measured whale-swimmer approach distances across 21 swim-with encounters in 2017 and used generalized linear mixed models (GLMMs) and regression techniques to investigate potential drivers of variation at both the group level (i.e., external variables such as encounter location and weather conditions) and individual level (i.e., demographic characteristics of individual whales). I found that as whale group size and encounter duration increased, mean whale-swimmer approach distance decreased. After accounting for these external drivers, significant variation in whale-swimmer approach distance and number of passes persisted between individual whales that could not be explained by demographic factors such as age (by proxy of total body length) or sex. It is unclear what is driving this remaining variation in both frequency and closeness of approach. Possible contributing factors could include longer-term exposure to human interaction (i.e., over multiple years) or individual differences in personality traits.

6.3 Long-term demographic changes

Chapter 4 revealed a long-term change in the observed population structure of dwarf minke whales interacting with vessels in the Great Barrier Reef. In 2006/2007, approximately two-thirds of measured individuals were likely juveniles and one-third were likely maturing or mature individuals (Sobtzick, 2010). Conversely, measurements presented in Chapter 4 of this thesis showed that approximately two-thirds of measured whales were maturing/mature and one-third were juveniles. The mean length of dwarf minke whales in 2017 was also 0.5 m longer than in 2006/2007. Although different methodologies were used between these studies, there is no evidence of systematic biases of sufficient magnitude to cause these differences, such as measurement error or sampling bias. Thus, they are likely to represent true changes; however, the underlying reasons for these changes remain unclear.

6.3.1 Behavioural change: desensitisation to human interactions?

The observed shift in population structure could represent long-term habituation of individual dwarf minke whales to swim-with activities in the Great Barrier Reef, such that whales who have experienced human interaction in the past demonstrate an increased attraction to humans in the future. This would result in an increased proportion of older (and, by proxy, larger) whales interacting in 2017 than in previous years. I found in Chapter 5 that as individual whales make more approaches/passes to swimmers in the water, and as encounters progress, the whales tend to decrease their approach distances. This demonstrates evidence of short-term habituation, on the scale of minutes to hours. Similar results have been found in other studies (Mangott, 2010; Mangott et al., 2011). Further, these studies also found that whales re-sighted within the same seasons tend to decrease their approach distance in subsequent encounters. This demonstrates evidence of more medium-term habituation, on the scale of days to weeks. While this medium-term habituation was not found in Chapter 5 of this thesis, this trend may have been present but obscured due to the over-representation of whales sighted only once across the season (see Chapter 5 section 5.4.1).

Possible drivers of this differential behaviour may be longer-term prior experience (i.e., across multiple years) (Mangott, 2010; Mangott et al., 2011; Sobtzick, 2010) or personality traits such as boldness (see Chapter 5 sections 5.1.6 and 5.4.2). This phenomenon of individual dwarf minke whales exhibiting highly interactive behaviour has been documented previously. Mangott (2010) found that over 20% of the instances where a whale made physical contact with an object (e.g., a boat, rope, or swimmer) were caused by a single whale that had been re-sighted multiple times (Mangott, 2010). Sobtzick (2010) sighted one individual seven times within one season, during which it spent over 33 hours interacting with vessels and swimmers. The long-term photo-identification database of dwarf minke whales in the Great Barrier Reef has identified that approximately one-third of identified whales are re-sighted within the same season and one-quarter are re-sighted in the following season (Sobtzick 2010). Thus, with a substantial portion of whales exhibiting both medium- and long-term re-engagement with swimmers, the potential exists for long-term desensitisation, resulting in increasingly close approaches by re-sighted whales.

Historical whaling records indicate that it could take up to 10 years for dwarf minke whales to reach 6 m in length (Kato et al., 2022; Kato & Fujise, 2000). The time period between population structure estimates (2006/2007 – 2017) aligns with this proposed maturation period. If a cohort of whales across all life-history stages became habituated to humans throughout the early years of this tourism activity in the GBR (e.g., 2000 – 2010), this could explain why the whales measured in 2017 were significantly larger than the whales measured previously. Thus, the combined evidence of short- and medium-term habituation, along with the increased size and proportion of adult whales in the interacting population, suggests that longer-term desensitisation over multiple years could be influencing the observed population dynamics.

6.3.2 Environmental/ecological stressors

Alternatively, instead of representing a change in behaviour of the interacting population, the observed shift in demographic ratios could represent a true change in the overall population structure of dwarf minke whales in the Great Barrier Reef. Large-scale oceanographic changes are occurring due to climate change and overfishing that may impact baleen whales (Agrelo et al., 2021; Cabrera et al., 2022; Flores et al., 2012; Joyce et al., 2023; Nicol et al., 2008; Smetacek & Nicol, 2005). These include decreased prey availability (Atkinson et al., 2004; Hofman, 2019), increased algal blooms and disease outbreaks (Burns, 2002; Sanderson & Alexander, 2020), retreating sea ice decreasing suitable feeding habitat (Friedlaender et al., 2006; Smetacek & Nicol, 2005) and increasing migration distances

(Thomas et al., 2016). One of the first expected impacts of these processes on cetaceans is a decrease in reproductive success and calf survival (Kebke et al., 2022; Simmonds & Isaac, 2007; Tulloch et al., 2019). This would manifest as a shift in population structure with a decreased proportion of younger (i.e., shorter) individuals and a resultant increase in mean body length, similar to the trends identified in this thesis. These shifts in response to climate change-induced stressors have already been documented in several cetacean populations including humpback whales (Gabriele et al., 2022), bottlenose dolphins (Mann et al., 2021), right whales (Leaper et al., 2006), and gray whales (Perryman et al., 2021). This shift in population structure could alternatively represent positive changes, such as improved environmental conditions resulting in increased growth rates and decreased mortality of adults. However, when considering the broader ecological context, particularly the well-documented threats and impacts of the Anthropocene era, this is unlikely to be the cause of such trends.

6.3.3 Challenges in resolving these issues

The uncertainty in determining the underlying cause of the observed population dynamics in this study exemplifies a methodological limitation of using tourist vessels, and other platforms of opportunity, to conduct scientific research. Due to a) the non-systematic sampling of the study area, and b) the reliance on voluntary approaches by the whales, it is unknown how much of the overall dwarf minke whale population is represented by the ‘interacting population’ in the Great Barrier Reef (see Chapter 1 section 1.1.2 and Chapter 4 section 4.4.6). Thus, it is challenging to determine whether whales observed during swim-with interactions are a representative sample of the overall population in this area. As a result, careful contextualisation is required for interpreting these data and other data collected via platforms of opportunity.

The full extent of re-encounters in the GBR Reef is also unknown. Firstly, photo-ID data is not collected for every encounter on every vessel. If some encounters are missed, then some interacting whales will remain unidentified – both whales interacting for the first time and re-sightings of already identified whales. Secondly, non-endorsed encounters, from both private vessels and unpermitted tourism vessels, are known to occur, but their frequency is not known (Sobtzick, 2010; Birtles et al., 2014). Therefore, data regarding sightings histories and encounter durations represent *minimum* estimates of these values, and the true occurrence of repeated interaction by individual whales will almost certainly be higher than documented in this study and others (Sobtzick, 2010). Further, the absence of trained guides during wildlife encounters has the potential to increase the risk of injury, harassment, and disturbance to the target animals (Boren et al., 2008; Pagel et al., 2020; Reynolds & Braithwaite, 2001). Thus, when non-endorsed swims with dwarf minke whales occur without trained crew monitoring and managing encounters, the risk of harm to the swimmers almost certainly increases as well.

Finally, the longer-term sightings histories of identified whales has not been systematically studied (i.e., re-sightings of individual whales across multiple years). Over 20 years of interactions with dwarf minke whales in the Great Barrier Reef have been collated into a photo catalogue managed by James Cook University's Minke Whale Project. However, time and cost constraints have resulted in a significant backlog in the photo-identification process, and a large number of historical photos still require assessment. Completing the photo-identification in this long-term database may provide important re-sightings data to further contextualise variation in interactive behaviours. Since most individual whales were only encountered once in previous studies (and this thesis), it has been suggested that the potential for population-level impacts is low (Sobtzick, 2010; Mangott, 2010). Nevertheless, it is evident that some individual whales exhibit highly interactive behaviour, and it is thus prudent from both a sustainability and safety/risk management perspective to study this behaviour further and to continue monitoring the population structure changes identified in this thesis. However, given the methodological constraints and limitations of collecting data from platforms of opportunity, it may be challenging to thoroughly investigate these issues from tourist vessels alone. Therefore, dedicated research platforms could be necessary for future research.

6.4 Contribution to conservation and monitoring of dwarf minke whales

As the world's only known predictable aggregation of dwarf minke whales occurs in the Great Barrier Reef (GBR), the Australian government is largely responsible for the conservation and management of this undescribed subspecies. Governance of whales is complex, particularly for migratory species that cross multiple jurisdictional boundaries (Miller et al., 2018). As a result, the protection of dwarf minke whales occurs under several government departments (e.g., Queensland Parks and Wildlife, Great Barrier Reef Marine Park Authority or GBRMPA), operating under a framework of multiple plans (e.g., Department of Climate Change, Energy, the Environment and Water, 2021; Woinarski et al., 2014), acts (e.g., EPBC Act 1999), guidelines (e.g., Australian Government Department for the Environment and Energy, 2017), and international conventions (e.g., International Union for the Conservation of Nature, Convention on Migratory Species, The International Whaling Commission, etc.). Numerous scientific reports and publications have emphasised the need for ongoing research and monitoring of dwarf minke whales to fulfill conservation and sustainability obligations relating to the protection of whales and their habitat (Arnold & Birtles, 1999; Birtles et al., 2014, 2015; Curnock, Birtles, Valentine, et al., 2013; Mangott et al., 2011; Valentine et al., 2004). Most recently, a report from the GBRMPA deemed existing monitoring of dwarf minke whales in the GBR inadequate to achieve the agency's various policy objectives and requirements (Curnock et al., 2019). This report outlined key knowledge gaps, research needs, and priority monitoring indicators to address these needs and provided detailed recommendations for the development of a dedicated monitoring program to achieve the relevant management outcomes. Despite this, limited resources have been allocated towards such a program and implementation remains lacking. The following section will outline the main contributions of my thesis to addressing knowledge gaps and research needs relevant to the protection of dwarf minke whales in the Great Barrier Reef.

6.4.1 Increased accuracy and precision of measurements

Several of the key monitoring priorities identified for dwarf minke whales require obtaining morphometric measurements of individual whales. Priority monitoring indicators that involve population characteristics such as demography (e.g., age composition and sex ratios) and body condition require precise measurements of total body length (TBL) and other external features such as girth (Curnock et al., 2019; Sobtzick, 2010). Further, changes in observed population demographics and whale-swimmer approach distances might also be indicative of behavioural changes such as long-term habituation, which is a particular concern for the swim-with dwarf minke whale tourism industry in the Great Barrier Reef (Birtles et al., 2014; Curnock, Birtles, Valentine, et al., 2013; Curnock et al., 2019; Mangott, 2010; Mangott et al., 2011). The stereo-videogrammetry filming and analytical protocols developed in Chapter 3 have provided the ability to make more robust measurements than have been available previously, thus increasing reliability of the data obtained and subsequent interpretation of results. The filming protocols were developed to maximise the quality and quantity of data obtained during in-water interactions with dwarf minke whales, expanding research and monitoring capabilities from a platform of opportunity with inherent methodological limitations (see Chapter 4 section 4.4.7).

6.4.2 New methodologies to increase sample sizes

6.4.2.1 New element of sexual dimorphism in dwarf minke whales

Changes in sex ratios have been repeatedly identified as a monitoring priority for dwarf minke whales in the Great Barrier Reef (Curnock et al., 2019; Sobtzick, 2010), but the difficulties of determining sex from external characteristics limit the ability to monitor this characteristic. In Chapter 4 of this thesis I presented data indicating the presence of a previously undescribed element of sexual dimorphism in dwarf minke whales, whereby females had significantly wider tails (i.e., fluke width; FW) relative to total body length (TBL) than males. While the present sample size was too small to perform statistical analyses on these data ($n_M = 5$, $n_F = 8$), only a small portion of the observed ranges overlapped between males and females. With a larger sample size, Bayesian analysis could be used to determine a binary classification threshold for sex identification for some individuals using only measurements of FW and TBL. Thus, the potential for a novel sex determination method, as presented in this study, offers an avenue to overcome the common limitation of small sample sizes, thereby enhancing the capacity to monitor sex ratios of dwarf minke whales in the Great Barrier Reef.

6.4.2.2 Alternative morphometrics as a proxy for total body length

When total body length (TBL) cannot be directly measured, it can be possible to measure another feature and use this measurement as a proxy, provided the relationship between the features is well understood and both measurements are sufficiently correlated. Such relationships have proven useful across a wide range of cetacean research (see Chapter 4 section 4.1.1). Chapter 4 identified a very strong positive correlation between snout-to-dorsal-fin length (SDF) and TBL in dwarf minke whales, with a correlation coefficient above 97%. A logarithmic regression yielded a robust predictive model of TBL from SDF, with an

R^2 value of 0.971. As such, SDF may be used as a robust proxy for TBL when TBL is unable to be measured, thus increasing the ability to make TBL measurements. SDF was also able to be measured on more whales than TBL (see Chapter 4 section 4.4.3), meaning that this length proxy presents an opportunity to increase the sample size of TBL-measured whales. A larger sample size of measured whales will enhance the precision and reliability of data, which, in turn, will improve the quality and applicability of future research findings for conservation and management efforts.

6.4.3 Identified changes in dwarf minke whale population demographics

Population structure changes can be a sensitive indicator to detect large-scale impacts to whale populations before the onset of significantly mortality, and as such could represent an ‘early warning signal’ for large-scale impacts to the population (Clements et al., 2017). For dwarf minke whales in the Great Barrier Reef, such changes could also represent long-term behavioural impacts to the ‘interacting population’ from tourism activities (Curnock, 2010; Mangott et al., 2011; Sobtzick, 2010). As such, monitoring changes in population characteristics, including age composition and sex ratios, has emerged as a key priority indicator for dwarf minke whales in the Great Barrier Reef (Birtles et al., 2014; Curnock, 2010; Curnock et al., 2019). Chapter 4 of this thesis identified a relative decrease in juvenile dwarf minke whales between 2006/2007 and 2017, which may suggest that negative impacts are occurring to this population from a range of potential stressors (see section 6.3). Since a change in age composition is considered a priority indicator for impacts to dwarf minke whales, this finding may be sufficient to catalyse investment in dedicated monitoring of this population to assess long-term trends, and/or further research to determine the underlying cause(s) and consequences of such shifts.

6.5 Implications for swim-with dwarf minke whale tourism in the Great Barrier Reef

Understanding the behaviour of dwarf minke whales during swim-with activities in the Great Barrier Reef is important for assessing the sustainability of this tourism industry and mitigating potential harm to both humans and whales. Given the variability in animal responses to disturbance and the limited external validity of most behavioural response studies, generic management regimes are not advisable (Birtles et al., 2014; Orams, 2004). Instead, tailored management plans specific to the species, location, and type of tourism activity, couple with a precautionary approach considering the potential for long-term impacts, are recommended (Arnold & Birtles, 1999; Birtles et al., 2001; Curnock, Birtles, Valentine, et al., 2013; Higham et al., 2009; Orams, 2004; Valentine et al., 2004). Chapter 5 revealed clear trends of short-term behaviour change during swim-with interactions, indicating that whales approach swimmers more closely as encounter duration and group size increase. A previous risk assessment identified the lack of sufficient information to assess the cumulative impacts on dwarf minke whales from swim-with interactions, emphasizing the need for ongoing research (Curnock, Birtles, Valentine, et al., 2013). Therefore, it is recommended that a new risk assessment be conducted to comprehensively evaluate the implications of this thesis's findings, particularly those regarding population dynamics and the drivers of interactive behaviour, to better inform management strategies and ensure the safety of both whales and humans.

6.6 Future research recommendations resulting from this thesis

6.6.1 Developing automated methodologies for reducing analytical time costs

6.6.1.1 Photo-identification

Much of the challenge in applying the methodologies from this thesis for time-effective monitoring of dwarf minke whales stems from the associated time costs. Artificial intelligence (AI) and machine learning technology are developing rapidly, and the photo-identification process has been partially or fully automated for several cetacean species including right whales (Bogucki et al., 2019; Khan et al., 2022), Risso's dolphins (Maglietta et al., 2020), orcas (Bergler et al., 2021), blue whales (Ramos-Arredondo et al., 2020), and humpback whales (Cheeseman et al., 2022). Multi-species models have also been developed (Blount et al., 2022; Patton et al., 2023). The application of such technology appears promising for photo-ID of dwarf minke whales (Konovalov et al., 2020), but has not yet been fully developed. Consequently, every photo must be compared visually by a trained researcher; as a result, this process is extremely labour-intensive and requires extensive training and quality control checking (Sobtzick, 2010). The development of automated photo-ID technology for humpback whales reduced processing time by over 98% (Cheeseman et al., 2022), demonstrating the usefulness of automated identification techniques for cetacean research and potential monitoring applications. As such, developing similar techniques for dwarf minke whales is recommended as a top priority to enhance the research and monitoring capabilities for this undescribed subspecies.

6.6.1.2 Morphometry

The extensive time required to process stereo-videogrammetry footage via SeaGIS also limits this method's applications from a monitoring perspective. The only fully automated element of this methodology was the calculation of the two-dimensional distance between two points in the paired video imagery. The equipment calibration process, photo-ID matching, selection of appropriate frames for measurement, identifying reference points, and reviewing measurement quality were all completed manually for each measurement. As a result, processing the footage for a single season required approximately an entire year of full-time effort. Although the initial proposal for this thesis involved processing all footage collected during the 2017, 2018, and 2019 sampling periods, this significant time requirement allowed for a complete analysis of the 2017 season only, with a selective processing of the 2018 and 2019 sampling periods to extract growth measurements of multi-year re-sighted animals. Thus, while these methods were successful for a suite of other research objectives (see section 6.2), they are likely insufficient for continued cost- and time-effective monitoring purposes without some modifications.

Automation of the morphometric measurement process has advanced rapidly in recent years (Burnett et al., 2019; Lemos et al., 2022; Torres et al., 2022; Torres & Bierlich, 2020). Not only has machine learning enabled more efficient data processing, it has also facilitated more robust assessments of body condition via the ability to make 3-dimensional volumetric estimations (Bierlich et al., 2021; Burnett et al., 2019; Gray et al., 2019; Lemos et al., 2022; Torres & Bierlich, 2020). The first techniques to develop 3-dimensionsal volume estimations represented the body as a series of ellipses or frustrums (Christiansen et al., 2018, 2019; Krause et al., 2017). More recently, increasingly accurate models have been developed that integrate specific morphometric measurements of the target species (Arranz et al., 2022; Hirtle et al., 2022; Irschick et al., 2021; Zhang et al., 2023). From the video footage collected in this thesis (i.e., filming free-swimming animals from multiple angles) and the morphometric measurements obtained in Chapter 4, this study can provide baseline data for the development of such 3D models of dwarf minke whales. This could broaden researchers' study scope, enabling efficient population structure monitoring, improved body condition assessment, and advancements in sexual dimorphism research (see Chapter 4 section 4.4.3).

Developing more robust techniques for assessing and monitoring body condition would also help to resolve the questions posed in section 6.3 regarding the cause of the changing population structure of dwarf minke whales. Declines in body condition are likely to precede increased mortality in response to decreased food availability (Learmonth et al., 2006; Lockyer, 1986, 2007). Consequently, body condition may be a more sensitive indicator of impacts due to climate change than abundance or population structure (Kebke et al., 2022; Parmesan, 2006), particularly for migratory species where pressures may be occurring in distant parts of their range (Newson et al., 2009). Thus, detecting declines in health prior to the onset of significant mortality is crucial for conservation as it can potentially allow time for a management response to avert population decline. Long-term declines in body condition have already been observed across several baleen whale species (Akmajian et al., 2021; Bradford et al., 2012; George et al., 2015; Haug et al., 2002; Lockyer, 1986; Miller et al., 2012; Torres et al., 2022; Vermeulen et al., 2023). Therefore, improving these techniques to the point where they are sensitive enough to detect important changes (e.g., population structure and/or body condition) in a short period of time will allow these methodologies to be applied for conservation and monitoring of dwarf minke whales.

6.7 Concluding remarks

Resources for monitoring and research are limited, and priorities are often set within the Great Barrier Reef based on risks to World Heritage Area (WHA) values (Department of Climate Change, Energy, the Environment and Water, 2021). While this often results in prioritising research issues such as coral reef health and climate change, it would be remiss to overlook the significance of dwarf minke whales within this ecological framework. Despite the absence of explicit alarms for this species, there are compelling reasons to allocate resources towards dwarf minke whales. Their unique interactions with humans, their potential as climate and ecosystem sentinels (Bossart, 2011; Hazen et al., 2019; Williamson et al., 2021) and the sustained public interest in whales all underscore their significance. These factors, combined with Australia’s international obligations, advocate for a dedicated focus on monitoring dwarf minke whales in the GBR. Recognising the constraints of limited funding, the argument for a cost-effective monitoring approach integrated into tourism activities is particularly robust in the present circumstances. Therefore, the future research directives proposed here, along with the baseline results achieved in this thesis, holds valuable promise in contributing meaningfully to the ongoing conservation and understanding of dwarf minke whales.

References

Acevedo, J., Olavarría, C., Plana, J., Aguayo-Lobo, A., Larrea, A., & Pastene, L. A. (2011). Occurrence of dwarf minke whales (*Balaenoptera acutorostrata* subsp.) around the Antarctic Peninsula. *Polar Biology*, *34*(2), 313–318. https://doi.org/10.1007/s00300-010-0884-y

Agrelo, M., Daura-Jorge, F. G., Rowntree, V. J., Sironi, M., Hammond, P. S., Ingram, S. N., Marón, C. F., Vilches, F. O., Seger, J., Payne, R., & Simões-Lopes, P. C. (2021). Ocean warming threatens southern right whale population recovery. *Science Advances 7*(42). https://doi.org/10.1126/sciadv.abh2823

Akmajian, A. M., Scordino, J. J., Gearin, P., & Gosho, M. (2021). Body condition of gray whales (*Eschrichtius robustus*) feeding on the Pacific Coast reflects local and basinwide environmental drivers and biological parameters. *Journal of Cetacean Resource Management 22,* 87–110. https://doi.org/10.47536/jcrm.v22i1.223

Allan, A. T. L., Bailey, A. L., & Hill, R. A. (2020). Habituation is not neutral or equal: Individual differences in tolerance suggest an overlooked personality trait. *Science Advances 6*(28), 870–878. https://doi.org/10.1126/sciadv.aaz0870

Anderson, D., & Burnham, K. (2002). Avoiding pitfalls when using information-theoretic methods. *The Journal of Wildlife Management*, *66*(3), 912–918. https://doi.org/10.2307/3803155

Andriolo, A., Rocha, J. M. da, Zerbini, A. N., Simões-Lopes, P. C., Moreno, I. B., Lucena, A., Danilewicz, D., & Bassoi, M. (2010). Distribution and relative abundance of large whales in a former whaling ground off eastern South America. *Zoologia (Curitiba)*, *27*(5), 741–750. https://doi.org/10.1590/S1984-46702010000500011

Aniceto, A. S., Carroll, J. L., Tetley, M. J., & van Oosterhout, C. (2016). Position, swimming direction and group size of fin whales (*Balaenoptera physalus*) in the presence of a fastferry in the Bay of Biscay. *Oceanologia*, *58*(3), 235–240. https://doi.org/10.1016/j.oceano.2016.02.002

Apprill, A., Miller, C. A., Moore, M. J., Durban, J. W., Fearnbach, H., & Barrett-Lennard, L. G. (2017). Extensive core microbiome in drone-captured whale blow supports a framework for health monitoring. *MSystems*, *2*(5). https://doi.org/10.1128/msystems.00119-17

Arnbom, T. (1987). Individual identification of sperm whales. Report of the International Whaling Commission, 37(20), 1–204.

Arnold, P. (1997). Occurrence of dwarf minke whales (Balaenoptera acutorostrata) on the Northern Great Barrier Reef, Australia. *Reports of the International Whaling Commission*, *48*, 419–424.

Arnold, P., & Birtles, A. (1999). Towards sustainable management of the developing dwarf minke whale tourism industry in northern Queensland. *CRC Reef Research Technical Report*.

Arnold, P., Birtles, R., Dunstan, A., Lukoschek, V., & Matthews, M. (2005). Colour patterns of the dwarf minke whale Balaenoptera acutorostrata sensu lato: description, cladistic analysis and taxonomic implications. *Memoirs of the Queensland Museum*, *51*(2), 277–307.

Arnold, P., Marsh, H., & Heinsohn, G. (1987). The occurrence of two forms of minke whales in east Australian waters with a description of external characters and skeleton of the diminutive or dwarf form. *Scientific Reports of the Whales Research Institute*, *38*, 1–46.

Arranz, P., Christiansen, F., Glarou, M., Gero, S., Visser, F., Oudejans, M. G., Aguilar de Soto, N., & Sprogis, K. R. (2022). Body condition and allometry of free-ranging short-finned pilot whales in the North Atlantic. *Sustainability*, *14*(22). https://doi.org/10.3390/su142214787

Atkinson, A., Siegel, V., Pakhomov, E., & Rothery, P. (2004). Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature*, *432*(7013), 100–103. https://doi.org/10.1038/nature02996

Atkinson, S., Melica, V., Teerlink, S., Mashburn, K., Moran, J., & Pearson, H. (2023). Use of hormones in assessing reproductive physiology of humpback whales (*Megaptera novaeangliae*) from Juneau, Alaska. *Theriogenology Wild*, *3*, 100050. https://doi.org/10.1016/j.therwi.2023.100050

Auger-Méthé, M., & Whitehead, H. (2007). The use of natural markings in studies of long-finned pilot whales (*Globicephala melas*). *Marine Mammal Science*, *23*(1), 77–93. https://doi.org/10.1111/j.1748-7692.2006.00090.x

Augusto, J. F., Frasier, T. R., & Whitehead, H. (2013). Using photography to determine sex in pilot whales (*Globicephala melas*) is not possible: Males and females have similar dorsal fins. *Marine Mammal Science*, *29*(1), 213–220. https://doi.org/10.1111/j.1748-7692.2011.00546.x

Australian Government Department of Agriculture, Water and the Environment. (2017). *National guidelines for whale and dolphin watching 2017*. https://www.environment.gov.au/marine/publications/national-guidelines-whale-and-dolphin-watching-2017.

Avila, I., Correa, L., & Parsons, E. (2015). Whale-watching activity in Bahía Málaga, on the Pacific coast of Colombia, and its effect on humpback whale (*Megaptera novaeangliae*) behaviour. *Tourism in Marine Environments*, *11*(1), 19–32. https://doi.org/10.3727/154427315X14398263718394

Bain, D., Trites, A., & Williams, R. (2002). *A model linking energetic effects of whale watching to killer whale (Orcinus orca) population dynamics*. Orca Relief. https://www.orcarelief.org/docs/bain_paper.pdf

Baker, C. S., Lento, G. M., Cipriano, F., Dalebout, M. L., & Palumbi, S. R. (2000). Scientific whaling: Source of illegal products for market? *Science*, *290*(5497), 1695–1696. https://doi.org/10.1126/SCIENCE.290.5497.1695B

Balthazart, J. (1983). Hormonal correlates of behavior. In D. S. Farner, J. R. King, & K. C. Parkes (Eds.), *Avian biology* (pp. 221–365). Academic Press. https://doi.org/10.1016/B978-0-12-249407-9.50013-2

Barnes, D. K. A., & Tarling, G. A. (2017). Polar oceans in a changing climate. *Current Biology, 27*(11) R454–R460. https://doi.org/10.1016/j.cub.2017.01.045

Barra, T., Bejder, L., Dalleau, M., Delaspre, S., Landes, A., Harvey, M., & Hoarau, L. (2020). Social media reveals high rates of agonistic behaviors of humpback whales in response to swim-with activities off Reunion Island. *Tourism in Marine Environments*, *15*, 191–209. https://doi.org/10.3727/154427320X15960647825531

Beale, C. M., & Monaghan, P. (2004). Behavioural responses to human disturbance: A matter of choice? *Animal Behaviour*, *68*(5), 1065–1069. https://doi.org/10.1016/j.anbehav.2004.07.002

Beerda, B., Schilder, M., Van Hooff, J., De Vries, H., & Mol, J. (1999). Chronic stress in dogs subjected to social and spatial restriction. I. Behavioral responses. *Physiology & Behaviour*, *66*(2), 233–242. https://doi.org/10.1016/S0031-9384(98)00289-3

Bejder, L. (2005). Linking short and long-term effects of nature-based tourism on cetaceans [PhD Thesis]. In *Department of Biology*. Dalhousie University.

Bejder, L., Dawson, S., & Harraway, J. (1999). Responses by Hector's dolphins to boats and swimmers in Porpoise Bay, New Zealand. *Marine Mammal Science*, *15*(3), 738–750. https://doi.org/10.1111/j.1748-7692.1999.tb00840.x

Bejder, L., & Samuels, A. (2003). Evaluating the effects of nature-based tourism on cetaceans. *Marine Mammals: Fisheries, Tourism and Management Issues, 1,* 229–256.

Bejder, L., Samuels, A., Whitehead, H., Finn, H., & Allen, S. (2009). Impact assessment research: Use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. *Marine Ecology Progress Series*, *395*, 177–185. https://doi.org/10.3354/meps07979

Bejder, L., Samuels, A., Whitehead, H., & Gales, N. (2006). Interpreting short-term behavioural responses to disturbance within a longitudinal perspective. *Animal Behaviour*, *72*, 1149–1158. https://doi.org/10.1016/j.anbehav.2006.04.003

Bejder, L., Samuels, A., Whitehead, H., Gales, N., Mann, J., Connor, R., Heithaus, M., Watson-Capps, J., Flaherty, C., & Krützen, M. (2006). Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. *Conservation Biology*, *20*(6), 1791–1798. https://doi.org/10.1111/j.1523-1739.2006.00540.x

Bergler, C., Gebhard, A., Towers, J. R., Butyrev, L., Sutton, G. J., Shaw, T. J. H., Maier, A., & Nöth, E. (2021). FIN-PRINT a fully-automated multi-stage deep-learning-based framework for the individual recognition of killer whales. *Scientific Reports*, *11*(1). https://doi.org/10.1038/s41598-021-02506-6

Berta, A., Sumich, J., & Kovacs, K. (2005). *Marine Mammals: Evolutionary Biology*. Elsevier.

Bertalanffy, L. (1938). A quantitative theory of organic growth. *Human Biology*, *10*(2), 181–213.

Best, P. (1984). Accuracy of shipboard estimates of the length of Antarctic minke whales. *Report of the International Whaling Commission*, *34*, 323–325.

Best, P. (1985). External characters of southern minke whales and the existence of a diminutive form. *Scientific Reports of the Whales Research Institute*, *36*, 1–33.

Best, P. B., & Rüther, H. (1992). Aerial photogrammetry of southern right whales, Eubalaena australis. *Journal of Zoology*, *228*(4), 595–614. https://doi.org/10.1111/j.1469-7998.1992.tb04458.x

Bestley, S., Andrews-Goff, V., van Wijk, E., Rintoul, S. R., Double, M. C., & How, J. (2019). New insights into prime Southern Ocean forage grounds for thriving Western Australian humpback whales. *Scientific Reports*, *9*(1). https://doi.org/10.1038/s41598-019-50497-2

Betty, E. L., Stockin, K. A., Hinton, B., Bollard, B. A., Smith, A. N. H., Orams, M. B., & Murphy, E. (2022). Age, growth, and sexual dimorphism of the Southern Hemisphere long-finned pilot whale (*Globicephala melas edwardii*). *Journal of Mammalogy*, *103*(3), 560–575. https://doi.org/10.1093/jmammal/gyab165

Bierlich, K. C., Hewitt, J., Bird, C. N., Schick, R. S., Friedlaender, A., Torres, L. G., Dale, J., Goldbogen, J., Read, A. J., Calambokidis, J., & Johnston, D. W. (2021). Comparing uncertainty associated with 1-, 2-, and 3D aerial photogrammetry-based body condition measurements of baleen whales. *Frontiers in Marine Science*, *8*, 749943. https://doi.org/10.3389/fmars.2021.749943

Bierlich, K. C., Kane, A., Hildebrand, L., Bird, C. N., Fernandez Ajo, A., Stewart, J. D., Hewitt, J., Hildebrand, I., Sumich, J., & Torres, L. G. (2023). Downsized: gray whales using an alternative foraging ground have smaller morphology. *Biology Letters*, *19*(8). https://doi.org/10.1098/rsbl.2023.0043

Birtles, A., Andrews, R., & Jenner, C. (2015). *Spatial ecology, migratory paths and critical areas of habitat use of Australia's dwarf minke whales. Preliminary Final Report*.

Birtles, A., Arnold, P., Curnock, M., Dunstan, A., & Valentine, P. (2001). Developing ecologically sustainable dwarf minke whale tourism (1999-2001). *Final Report to the Commonwealth Department of Environment and Heritage (Environment Australia)*.

Birtles, A., Arnold, P., Curnock, M., Salmon, S., Mangott, A., Sobtzick, S., & Valentine, P. (2008). *Code of practice for dwarf minke whale interactions in the Great Barrier Reef World Heritage Area*. Great Barrier Reef Marine Park Authority, Townsville, Australia.

Birtles, A., & Mangott, A. (2011). Highly interactive behaviour of inquisitive dwarf minke whales. In P. Brakes & M. Simmonds (Eds.), *Whales & Dolphins: cognition, culture, conservation and human perceptions*. Earthscan.

Birtles, A., Valentine, P., Curnock, M., Arnold, P., & Dunstan, A. (2002). Incorporating visitor experiences into ecologically sustainable dwarf minke whale tourism in the northern Great Barrier Reef. *CRC Reef Research Centre Technical Report, 42,* 1–65.

Birtles, A., Valentine, P., Curnock, M., Mangott, A., Sobtzick, S., & Marsh, H. (2014). *Report to the Great Barrier Reef Marine Park Authority on the dwarf minke whale tourism monitoring program (2003-2008)*. Great Barrier Reef Marine Park Authority.

Birtles, Arnold, P., & Dunstan, A. (2002). Commercial swim programs with dwarf minke whales on the northern Great Barrier Reef, Australia: Some characteristics of the encounters with management implications. *Australian Mammalogy*, *24*(1), 23–38. https://doi.org/10.1071/AM02023

Bland, L., & Collen, B. (2016). Species loss: lack of data leaves a gap. *Nature*, *537*, 488–488. https://doi.org/https://doi.org/10.1038/537488c

Blount, D., Gero, S., Van Oast, J., Parham, J., Kingen, C., Scheiner, B., Stere, T., Fisher, M., Minton, G., Khan, C., Dulau, V., Thompson, J., Moskvyak, O., Berger-Wolf, T., Stewart, C. V., Holmberg, J., & Levenson, J. J. (2022). Flukebook: an open-source AI platform for cetacean photo identification. *Mammalian Biology*, *102*(3), 1005–1023. https://doi.org/10.1007/s42991-021-00221-3

Blueweiss, L., Fox, H., Kudzma, V., Nakashima, D., Peters, R., & Sams, S. (1978). Relationships between body size and some life history parameters. *Oecologica*, *37*, 257–272. https://doi.org/10.1007/BF00344996

Blumstein, D. T. (2016). Habituation and sensitization: new thoughts about old ideas. *Animal Behaviour*, *120*, 255–262. https://doi.org/10.1016/j.anbehav.2016.05.012

Bogucki, R., Cygan, M., Khan, C. B., Klimek, M., Milczek, J. K., & Mucha, M. (2019). Applying deep learning to right whale photo identification. *Conservation Biology*, *33*(3), 676–684. https://doi.org/10.1111/cobi.13226

Boren, L. J., Gemmell, N., Barton, K., & Zealand, N. (2008). The role and presence of a guide: preliminary findings from swim with seal programs and land-based seal viewing in New Zealand. *Tourism in Marine Environments*, *5*(3), 187–199. https://doi.org/10.3727/154427308787716776

Borsa, P. (2006). Marine mammal strandings in the New Caledonia region, Southwest Pacific. *C. R. Biologies*, *329*(4), 277–288. https://doi.org/10.1016/j.crvi.2006.01.004

Bossart, G. D. (2011). Marine mammals as sentinel species for oceans and human health. *Veterinary Pathology*, *48*(3), 676–690. https://doi.org/10.1177/0300985810388525

Boutros, N., Shortis, M. R., & Harvey, E. S. (2015). A comparison of calibration methods and system configurations of underwater stereo-video systems for applications in marine ecology. *Limnology and Oceanography: Methods*, *13*(5), 224–236. https://doi.org/10.1002/lom3.10020

Box, C. (2022). *Patterns of relative abundance of dwarf minke whales during the austral winter season in the northern Great Barrier Reef* [Honours Thesis]. James Cook University.

Bradford, A. L., Weller, D. W., Punt, A. E., Ivashchenko, Y. V, Burdin, A. M., VanBlaricom, G. R., & Brownell, R. L. (2012). *Leaner leviathans: body condition variation in a critically endangered whale population*. *93*(1), 251–266. https://doi.org/10.1644/1

Bräger, S., Chong, A., Dawson, S., Slooten, E., & Würsig, B. (1999). A combined stereo-photogrammetry and underwater-video system to study group composition of dolphins. *Helgoland Marine Research*, *53*, 122–128. https://doi.org/10.1007/s101520050015

Branch, T., & Williams, T. (2012). Legacy of Industrial Whaling. In J. Estes (Ed.), *Whales, Whaling, and Ocean Ecosystems* (pp. 262–278). University of California Press. https://doi.org/10.1525/california/9780520248847.003.0020

Brooks, M., Kristensen, K., van Benthem, K., Magnusson, A., Berg, C., Nielsen, A., Skaug, H., Maechler, M., & Bolker, B. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, *9*(2), 378–400. https://doi.org/10.3929/ethz-b-000240890

Brown, A. M., Bejder, L., Parra, G. J., Cagnazzi, D., Hunt, T., Smith, J. L., & Allen, S. J. (2016). Sexual dimorphism and geographic variation in dorsal fin features of Australian humpback dolphins, *Sousa sahulensis*. In *Advances in Marine Biology* (Vol. 73, pp. 273–314). Academic Press. https://doi.org/10.1016/bs.amb.2015.08.002

Burnett, J. D., Lemos, L., Barlow, D., Wing, M. G., Chandler, T., & Torres, L. G. (2019). Estimating morphometric attributes of baleen whales with photogrammetry from small UASs: A case study with blue and gray whales. *Marine Mammal Science*, *35*(1), 108–139. https://doi.org/10.1111/mms.12527

Burnham, K., & Anderson, D. (1998). Practical use of the information-theoretic approach. In *Model selection and inference* (pp. 75–117). Springer New York. https://doi.org/10.1007/978-1-4757-2917-7_3

Burns, W. (2002). Climate change and the International Whaling Commission in the 21st century. In W. Burns & A. Gillespie (Eds.), *The future of cetaceans in a changing world* (pp. 339–379). Transnational Publishers. https://doi.org/10.1163/9789004480599_016

Cabrera, A. A., Schall, E., Bérubé, M., Anderwald, P., Bachmann, L., Berrow, S., Best, P. B., Clapham, P. J., Cunha, H. A., Dalla Rosa, L., Dias, C., Findlay, K. P., Haug, T., Heide-Jørgensen, M. P., Hoelzel, A. R., Kovacs, K. M., Landry, S., Larsen, F., Lopes, X. M., Palsbøll, P. J. (2022). Strong and lasting impacts of past global warming on baleen whales and their prey. *Global Change Biology*, *28*(8), 2657–2677. https://doi.org/10.1111/gcb.16085

Calambokidis, J., & Barlow, J. (2004). Abundance of blue and humpback whales in the eastern north pacific estimated by capture-recapture and line-transect methods. In *Marine Mammal Science* (Vol. 20, Issue 1, pp. 63–85). Society for Marine Mammology. https://doi.org/10.1111/j.1748-7692.2004.tb01141.x

Carlson, C. (2011). *A Review of Whale Watch Guidelines and Regulations Around the World: Version 2011*. Cambridge, UK: International Whaling Commission.

Carter, A. J., Heinsohn, R., Goldizen, A. W., & Biro, P. A. (2012). Boldness, trappability and sampling bias in wild lizards. *Animal Behaviour*, *83*(4), 1051–1058. https://doi.org/10.1016/j.anbehav.2012.01.033

Carzon, P., Clua, É., Dudzinski, K. M., & Delfour, F. (2023). Deleterious behaviors and risks related to close interactions between humans and free-ranging dolphins: A review. *Biological Conservation*, *279*. https://doi.org/10.1016/j.biocon.2023.109948

Caspar, K. R., & Begall, S. (2022). Sexual dimorphism in toothed whales (Odontoceti) follows Rensch's rule. *Mammalian Biology*, *102*(2), 523–529. https://doi.org/10.1007/s42991-022-00239-1

Castelblanco-Martínez, D. N., Morales-Vela, B., & Padilla-Saldívar, J. A. (2014). Using craniometrical predictors to infer body size of Antillean manatees. *Mammalia*, *78*(1), 109–115. https://doi.org/10.1515/mammalia-2012-0136

Castrillon, J., & Bengtson Nash, S. (2020). Evaluating cetacean body condition; a review of traditional approaches and new developments. *Ecology and Evolution*, *10*(12), 6144–6162. https://doi.org/10.1002/ece3.6301

Cates, K. A., Atkinson, S., Gabriele, C. M., Pack, A. A., Straley, J. M., & Yin, S. (2019). Testosterone trends within and across seasons in male humpback whales (Megaptera novaeangliae) from Hawaii and Alaska. *General and Comparative Endocrinology*, *279*, 164–173. https://doi.org/10.1016/J.YGCEN.2019.03.013

Caughley, G. (1966). Mortality patterns in mammals. *Ecology*, *47*(6), 906–918. https://doi.org/10.2307/1935638

Chanvallon, S., Blois-Heulin, C., Robert De Latour, P., & Lemasson, A. (2017). Spontaneous approaches of divers by free-ranging orcas (*Orcinus orca*): Age- and sex-differences in exploratory behaviours and visual laterality. *Scientific Reports*, *7*(1). https://doi.org/10.1038/s41598-017-11488-3

Cheeseman, T., Southerland, K., Park, J., Olio, M., Flynn, K., Calambokidis, J., Jones, L., Garrigue, C., Frisch Jordán, A., Howard, A., Reade, W., Neilson, J., Gabriele, C., & Clapham, P. (2022). Advanced image recognition: a fully automated, high-accuracy photo-identification matching system for humpback whales. *Mammalian Biology*, *102*(3), 915–929. https://doi.org/10.1007/s42991-021-00180-9

Chion, C., Cantin, G., Dionne, S., Dubeau, B., Lamontagne, P., Landry, J. A., Marceau, D., Martins, C. C. A., Ménard, N., Michaud, R., Parrott, L., & Turgeon, S. (2013). Spatiotemporal modelling for policy analysis: Application to sustainable management of whale-watching activities. *Marine Policy*, *38*, 151–162. https://doi.org/10.1016/j.marpol.2012.05.031

Christiansen, F., Bertulli, C. G., Rasmussen, M. H., & Lusseau, D. (2015). Estimating cumulative exposure of wildlife to non-lethal disturbance using spatially explicit capture-recapture models. *Journal of Wildlife Management*, *79*(2), 311–324. https://doi.org/10.1002/jwmg.836

Christiansen, F., Dawson, S., Durban, J., Fearnbach, H., Miller, C., Bejder, L., Uhart, M., Sironi, M., Corkeron, P., Rayment, W., Leunissen, E., Haria, E., Ward, R., Warick, H., Kerr, I., Lynn, M., Pettis, H., & Moore, M. (2020). Population comparison of right whale body condition reveals poor state of the North Atlantic right whale. *Marine Ecology Progress Series*, *640*, 1–16. https://doi.org/10.3354/meps13299

Christiansen, F., Dujon, A. M., Sprogis, K. R., Arnould, J. P. Y., & Bejder, L. (2016). Noninvasive unmanned aerial vehicle provides estimates of the energetic cost of reproduction in humpback whales. *Ecosphere*, *7*(10), 1–18. https://doi.org/10.1002/ecs2.1468

Christiansen, F., Sironi, M., Moore, M. J., Di Martino, M., Ricciardi, M., Warick, H. A., Irschick, D. J., Gutierrez, R., & Uhart, M. M. (2019). Estimating body mass of free-living whales using aerial photogrammetry and 3D volumetrics. *Methods in Ecology and Evolution*, *10*(12), 2034–2044. https://doi.org/10.1111/2041-210X.13298

Christiansen, F., Tervo, O. M., Heide-Jørgensen, M. P., & Teilmann, J. (2023). Prey consumption of bowhead whales in West Greenland estimated from drone measurements of body size and condition. *Polar Biology*. https://doi.org/10.1007/s00300-023-03207-8

Christiansen, F., Víkingsson, G. A., Rasmussen, M. H., & Lusseau, D. (2014). Female body condition affects foetal growth in a capital breeding mysticete. *Functional Ecology*, *28*(3), 579–588. https://doi.org/10.1111/1365-2435.12200

Christiansen, F., Vivier, F., Charlton, C., Ward, R., Amerson, A., Burnell, S., & Bejder, L. (2018). Maternal body size and condition determine calf growth rates in southern right whales. *Marine Ecology Progress Series*, *592*, 267–282. https://doi.org/10.3354/meps12522

Cisneros-Montemayor, A. M., Sumaila, U. R., Kaschner, K., & Pauly, D. (2010). The global potential for whale watching. *Marine Policy*, *34*(6), 1273–1278. https://doi.org/10.1016/j.marpol.2010.05.005

Clapham, P., Berggren, P., Childerhouse, S., Friday, N., Kasuya, T., Kell, L., Kock, K., Manzanilla-Naim, S., Notabartolo Di Sciara, G., Perrin, W., Read, A., Reeves, R., Rogan, E., Rojas-Bracho, L., Smith, T., Stachowitsch, M., Taylor, B., Thiele, D., Wade, P., & Brownell, R. (2003). Whaling as Science. *BioScience*, *53*(3), 210–212. https://doi.org/10.1641/0006-3568(2003)053[0210:WAS]2.0.CO;2

Clapham, P., & Ivashchenko, Y. (2009). A whale of a deception. *Marine Fisheries Review*, *71*, 44–52. https://doi.org/10.1038/nbt0409-342

Clapham, P., & Ivashchenko, Y. (2016). Stretching the truth: length data highlight falsification of Japanese sperm whale catch statistics in the southern hemisphere. *Royal Society Open Science*, *3*(9), 160506. https://doi.org/10.1098/rsos.160506

Clapham, P. J. (2016). Managing leviathan: conservation challenges for the great whales in a post-whaling world. *Oceanography*, *29*(3), 214–225. https://www.jstor.org/stable/24862723

Clapham, P. J., Childerhouse, S., Gales, N. J., Rojas-Bracho, L., Tillman, M. F., & Brownell, R. L. (2007). The whaling issue: conservation, confusion, and casuistry. *Marine Policy*, *31*(3), 314–319. https://doi.org/10.1016/j.marpol.2006.09.004

Clark, C., & Garland, E. (2022). *Ethology and behavioral ecology of mysticetes* (B. Würsig, Ed.). Springer Nature Switzerland. https://doi.org/10.1007/978-3-030-98449-6

Clark, S. T., & Odell, D. K. (1999). Allometric relationships and sexual dimorphism in captive killer whales (*Orcinus orca*). *Journal of Mammalogy*, *80*(3), 777–785. https://doi.org/10.2307/1383247

Clarke, A., & Harris, C. M. (2003). Polar marine ecosystems: major threats and future change. *Environmental Conservation*, *30*(01), 1–25. https://doi.org/10.1017/S0376892903000018

Clarke, T. A., & Fryer, J. F. (1998). The development of camera calibration methods and models. *Photogrammetric Record*, *16*(91), 51–66. https://doi.org/10.1111/0031-868X.00113

Clements, C. F., Blanchard, J. L., Nash, K. L., Hindell, M. A., & Ozgul, A. (2017). Body size shifts and early warning signals precede the historic collapse of whale stocks. *Nature Ecology and Evolution*, *1*(7). https://doi.org/10.1038/s41559-017-0188

Connor, R., & Smolker, R. (1985). Habituated dolphins (*Tursiops* sp.) in Western Australia. *Journal of Mammalogy*, *66*(2), 398–400. https://doi.org/10.2307/1381260

Constantine, R. (2001). Increased avoidance of swimmers by wild bottlenose dolphins (*Tursiops truncatus*) due to long-term exposure to swim-with-dolphin tourism. *Marine Mammal Science*, *17*(4), 689–702. https://doi.org/10.1111/j.1748-7692.2001.tb01293.x

Constantine, R., Brunton, D., & Dennis, T. (2004). Dolphin-watching tour boats change bottlenose dolphin (*Tursiops truncatus*) behaviour. *Biological Conservation*, *117*(3), 299–307. https://doi.org/10.1016/j.biocon.2003.12.009

Corkeron, P. J. (2004). Whale watching, iconography, and marine conservation. *Conservation Biology*, *18*(3), 847–849. https://www.jstor.org/stable/3589096

Cox, T. M., Read, A. J., Swanner, D., Urian, K., & Waples, D. (2003). Behavioral responses of bottlenose dolphins, *Tursiops truncatus*, to gillnets and acoustic alarms. *Biological Conservation*, *115*(2), 203–212. https://doi.org/10.1016/S0006-3207(03)00108-3

Cubbage, J. C., & Calambokidis, J. (1987). Size-class segregation of bowhead whales discerned through aerial stereophotogrammetry. *Marine Mammal Science*, *3*(2), 179–185. https://doi.org/10.1111/j.1748-7692.1987.tb00160.x

Curnock, M. (2010). *Mechanisms for assessing the sustainability of swimming-with-whales tourism in the Great Barrier Reef* [PhD Thesis]. James Cook University.

Curnock, M., Birtles, A., & Valentine, P. (2013). Increased use levels, effort, and spatial distribution of tourists swimming with dwarf minke whales at the Great Barrier Reef. *Tourism in Marine Environments*, *9*(12), 5–17. https://doi.org/10.3727/154427313X13659574649867

Curnock, M., Birtles, A., Valentine, P., Prideaux, B., Li, S., Sobtzick, S., & Schmidt-Roach, A. (2013). *Implementing sustainable and World's Best Practice swim-with-whales tourism in Tropical North Queensland.* Final Project Report for the Commonwealth Department of Resources, Energy and Tourism, T-QUAL Grants-Tourism Quality Projects.

Curnock, M., Williams, G., Noad, M., Smith, J., West, L., Birtles, A., Hillcoat, S., McCauley, R., Meager, J., Brooks, L., Paton, D., Blayden, P., Sobtzick, S., & Marsh, H. (2019). *Monitoring whales within the Reef 2050 Integrated Monitoring and Reporting Program: Final Report of the Whales Team in the Megafauna Expert Group*. Great Barrier Reef Marine Park Authority, Townsville. https://core.ac.uk/download/pdf/322826579.pdf

Dahlheim, M. E., Schulman-Janiger, A., Black, N., Ternullo, R., Ellifrit, D., & Balcomb, K. C. (2008). Eastern temperate north Pacific offshore killer whales (*Orcinus orca*): occurrence, movements, and insights into feeding ecology. *Marine Mammal Science*, *24*(3), 719–729. https://doi.org/10.1111/j.1748-7692.2008.00206.x

Daley, E. (2019). *Dwarf minke whales in the northern Great Barrier Reef: a population-based cohort study of the world's only known aggregation* [Master's thesis]. James Cook University.

Dalle Luche, G., Boggs, A. S. P., Kucklick, J. R., Groß, J., Hawker, D. W., & Bengtson Nash, S. (2020). Androstenedione and testosterone but not progesterone are potential biomarkers of pregnancy in Humpback Whales (*Megaptera novaeangliae*) approaching parturition. *Scientific Reports*, *10*(1). https://doi.org/10.1038/s41598-020-58933-4

Dawson, S., Chessum, C., Hunt, P., & Slooten, E. (1995). An inexpensive, stereophotographic technique to measure sperm whales from small boats. *Report of the International Whaling Commission*, *45*(43), 1–436.

Dawson, S. M., Bowman, M. H., Leunissen, E., & Sirguey, P. (2017). Inexpensive aerial photogrammetry for studies of whales and large marine animals. *Frontiers in Marine Science*, *4*, 1–7. https://doi.org/10.3389/fmars.2017.00366

Dawson, S. M., & Slooten, E. (1990). Stranding of a dwarf minke whale at Banks Peninsula New Zealand. *New Zealand Natural Sciences*, *17*, 89–94.

Deakos, M. H. (2010). Paired-laser photogrammetry as a simple and accurate system for measuring the body size of free-ranging manta rays (*Manta alfredi*). *Aquatic Biology*, *10*(1), 1–10. https://doi.org/10.3354/ab00258

Department of Climate Change, Energy, the Environment and Water. (2021, October 3). *Entanglements*. Australian Government. https://www.dcceew.gov.au/environment/marine/marine-species/cetaceans/entanglements

Department of Climate Change, Energy, the Environment and Water. (2021). *Reef 2050 long-term sustainability plan 2021-2025.* Australian Government.

https://www.dcceew.gov.au/parks-heritage/great-barrier-reef/publications/reef-2050-long-term-sustainability-plan-2021-25

Di Beneditto, A. P. M., Oliveira, L. R. de, Ott, P. H., Machado, R., Sucunza, F., Santos, R. A. dos, Milmann, L., Rezende, C. E. de, & Baumgarten, J. (2018). New trophic link and potential feeding area of dwarf minke whale (*Balaenoptera acutorostrata* subsp.) in mid latitude waters of the southwestern Atlantic Ocean. *Mammalia*, *83*(1), 49–52. https://doi.org/10.1515/mammalia-2017-0127

Dingemanse, N. J., & Dochtermann, N. A. (2013). Quantifying individual variation in behaviour: Mixed-effect modelling approaches. *Journal of Animal Ecology*, *82*(1), 39–54. https://doi.org/10.1111/1365-2656.12013

Discover Dominica Authority. (2019). *Whale watching*. http://www.discoverdominica.com

Dissegna, A., Grassi, M., & Chiandetti, C. (2022). Individual differences in habituation: Innate covariation between habituation, exploration, and body size in naïve chicks (*Gallus gallus*). *Behavioural Processes*, *200*, 104705. https://doi.org/10.1016/j.beproc.2022.104705

Djiba, A., Bamy, I., Samba Ould Balil, A., & van Waerebeek, K. (2015). Biodiversity of cetaceans in coastal waters of northwest Africa: new insights through platform-of-opportunity visual surveying in 2011-2013. *Oceanographic and Biological Features in the Canary Current Large Marine Ecosystem. IOC Technical Series*, *115*, 283–297. http://hdl.handle.net/1834/9195

Doenier, P. (1997). Effects of winter supplemental feeding on browse consumption by white-tailed deer. *Wildlife Society Bulletin*, *25*, 235–243. https://www.cabidigitallibrary.org/doi/full/10.5555/19980701512

Duffy, J. P., Cunliffe, A. M., DeBell, L., Sandbrook, C., Wich, S. A., Shutler, J. D., Myers-Smith, I. H., Varela, M. R., & Anderson, K. (2018). Location, location, location:

considerations when using lightweight drones in challenging environments. *Remote Sensing in Ecology and Conservation*, *4*(1), 7–19. https://doi.org/10.1002/rse2.58

Dumont, F., Pasquaretta, C., Réale, D., Bogliani, G., & von Hardenberg, A. (2012). Flight initiation distance and starting distance: biological effect or mathematical artefact? *Ethology*, *118*(11), 1051–1062. https://doi.org/10.1111/eth.12006

Dunbrack, R. L. (2006a). In situ measurement of fish body length using perspective-based remote stereo-video. *Fisheries Research*, *82*(1–3), 327–331. https://doi.org/10.1016/j.fishres.2006.08.017

Dunbrack, R. L. (2006b). In situ measurement of fish body length using perspective-based remote stereo-video. *Fisheries Research*, *82*(1–3), 327–331. https://doi.org/10.1016/j.fishres.2006.08.017

Dunshea, G., Duffield, D., Gales, N., Hindell, M., Wells, R. S., & Jarman, S. N. (2011). Telomeres as age markers in vertebrate molecular ecology. In *Molecular Ecology Resources* (Vol. 11, Issue 2, pp. 225–235). https://doi.org/10.1111/j.1755-0998.2010.02976.x

Dunstan, A., Sobtzick, S., Birtles, A., & Arnold, P. (2008). Use of videogrammetry to estimate length to provide population demographics of dwarf minke whales in the northern Great Barrier Reef. *Journal of Cetacean Resource Management*, *9*(3), 49–57. https://researchonline.jcu.edu.au/10509/

Durban, J. W., & Parsons, K. M. (2006). Laser-metrics of free-ranging killer whales. *Marine Mammal Science*, *22*(3), 735–743. https://doi.org/10.1111/j.1748-7692.2006.00068.x

Evans, P. (1996). Human disturbance of cetaceans. In V. J. Taylor & N. Dunstone (Eds.), *The exploitation of mammal populations* (pp. 376–394). Springer.

Fabry, V. J., McClintock, J., Mathis, J. T., & Grebmeier, J. (2009). Ocean acidification at high latitudes: the bellwether. *Oceanography*, *22*(4), 160–171. https://doi.org/10.5670/oceanog.2009.105

Fettermann, T., Fiori, L., Gillman, L., Stockin, K. A., & Bollard, B. (2022). Drone surveys are more accurate than boat-based surveys of bottlenose dolphins (*Tursiops truncatus*). *Drones*, *6*(4). https://doi.org/10.3390/drones6040082

Fiedler, P. C., Reilly, S. B., Hewitt, R. P., Demer, D., Philbrick, V. A., Smith, S., Armstrong, W., Croll, D. A., Tershy, B. R., & Mate, B. R. (1998). Blue whale habitat and prey in the California Channel Islands. In *Deep-Sea Research II* (Vol. 45). https://doi.org/10.1016/S0967-0645(98)80017-9

Finkler, W., & Higham, J. E. S. (2020). Stakeholder perspectives on sustainable whale watching: a science communication approach. *Journal of Sustainable Tourism*, *28*(4), 535–549. https://doi.org/10.1080/09669582.2019.1684930

Fiori, L., Martinez, E., Orams, M. B., & Bollard, B. (2019). Effects of whale-based tourism in Vava'u, Kingdom of Tonga: Behavioural responses of humpback whales to vessel and swimming tourism activities. *PLoS ONE*, *14*(7). https://doi.org/10.1371/journal.pone.0219364

Fiori, L., Martinez, E., Orams, M. B., & Bollard, B. (2020). Using Unmanned Aerial Vehicles (UAVs) to assess humpback whale behavioral responses to swim-with interactions in Vava'u, Kingdom of Tonga. *Journal of Sustainable Tourism*, *28*(11), 1743–1761. https://doi.org/10.1080/09669582.2020.1758706

Fisheries and Oceans Canada. (2022, April 5). *North Atlantic right whale*. Government of Canada. https://www.dfo-mpo.gc.ca/fisheries-peches/commercial-commerciale/atl-arc/narw-bnan/2022/right-whale-baleine-noires-0405-eng.html

Flores, H., Atkinson, A., Kawaguchi, S., Krafft, B. A., Milinevsky, G., Nicol, S., Reiss, C., Tarling, G. A., Werner, R., Bravo Rebolledo, E., Cirelli, V., Cuzin-Roudy, J., Fielding, S., Groeneveld, J. J., Haraldsson, M., Lombana, A., Marschoff, E., Meyer, B., Pakhomov, E. A., Werner, T. (2012). Impact of climate change on Antarctic krill. *Marine Ecology Progress Series*, *458*, 1–19. https://doi.org/10.3354/meps09831

Ford, J. H., Bravington, M. V., & Robbins, J. (2012). Incorporating individual variability into mark-recapture models. *Methods in Ecology and Evolution*, *3*(6), 1047–1054. https://doi.org/10.1111/j.2041-210X.2012.00243.x

Foroughirad, V., & Mann, J. (2013). Long-term impacts of fish provisioning on the behavior and survival of wild bottlenose dolphins. In *Biological Conservation* (Vol. 160, pp. 242–249). https://doi.org/10.1016/j.biocon.2013.01.001

Fortune, S. M. E., Trites, A. W., Perryman, W. L., Moore, M. J., Pettis, H. M., & Lynn, M. S. (2012). Growth and rapid early development of North Atlantic right whales (*Eubalaena glacialis*). *Journal of Mammalogy*, *93*(5), 1342–1354. https://doi.org/10.1644/11-MAMM-A-297.1

Franklin, T., Franklin, W., Brooks, L., Harrison, P., Burns, D., Holmberg, J., & Calambokidis, J. (2020). Photo-identification of individual humpback whales (*Megaptera novaeangliae*) using all available natural marks: Implications for misidentification and automated algorithm matching technology. *Journal of Cetacean Research and Management*, *21*(1), 71–83. https://doi.org/10.47536/JCRM.V21I1.186

Friedlaender, A. S., Halpin, P. N., Qian, S. S., Lawson, G. L., Wiebe, P. H., Thiele, D., & Read, A. J. (2006). Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the Western Antarctic Peninsula. *Marine Ecology-Progress Series*, *317*, 297–310. https://doi.org/10.3354/meps317297

Frohoff, T. (2004). Stress in dolphins. In Bekoff M (Ed.), *Encyclopedia of Animal Behavior* (Vol. 3).

Frost, A. J., Winrow-Giffen, A., Ashley, P. J., & Sneddon, L. U. (2007). Plasticity in animal personality traits: Does prior experience alter the degree of boldness? *Proceedings of the Royal Society B: Biological Sciences*, *274*(1608), 333–339. https://doi.org/10.1098/rspb.2006.3751

Fujiwara, M., & Caswell, H. (2001). Demography of the endangered North Atlantic right whale. *Nature*, *414*(6863), 537–541. https://doi.org/10.1038/35107054

Gabriele, C. M., Amundson, C. L., Neilson, J. L., Straley, J. M., Baker, C. S., & Danielson, S. L. (2022). Sharp decline in humpback whale (*Megaptera novaeangliae*) survival and reproductive success in southeastern Alaska during and after the 2014–2016 Northeast Pacific marine heatwave. *Mammalian Biology*, *102*(4), 1113–1131. https://doi.org/10.1007/s42991-021-00187-2

Gao, M., Hugenholtz, C. H., Fox, T. A., Kucharczyk, M., Barchyn, T. E., & Nesbit, P. R. (2021). Weather constraints on global drone flyability. *Scientific Reports*, *11*(1). https://doi.org/10.1038/s41598-021-91325-w

Garrigue, C., Clapham, P. J., Geyer, Y., Kennedy, A. S., & Zerbini, A. N. (2015). Satellite tracking reveals novel migratory patterns and the importance of seamounts for endangered south Pacific humpback whales. *Royal Society Open Science*, *2*(11). https://doi.org/10.1098/rsos.150489

Gayford, J. H., Pearse, W. D., De La Parra Venegas, R., & Whitehead, D. A. (2023). Quantifying the behavioural consequences of shark ecotourism. *Scientific Reports*, *13*(1). https://doi.org/10.1038/s41598-023-39560-1

Gedamke, J. (2004). *Minke whale song, spacing, and acoustic communication on the Great Barrier Reef, Australia* [PhD Thesis]. James Cook University.

George, J. C., Druckenmiller, M. L., Laidre, K. L., Suydam, R., & Person, B. (2015). Bowhead whale body condition and links to summer sea ice and upwelling in the Beaufort Sea. *Progress in Oceanography*, *136*, 250–262. https://doi.org/10.1016/j.pocean.2015.05.001

Gero, S., Pace, S., Kaufman, G., Parsons, E. C. M., Ritter, F., Sironi, M., & Rose, N. A. (2016). Initial survey of global commercial swim-with-whale operations. *Journal of Cetacean Resource Management, SC/66b/WW/02*.

Gibson, R., Atkinson, R., & Gordon, J. (2016). A review of underwater stereo-image measurement for marine biology and ecology applications. *Oceanography and Marine Biology: An Annual Review*, *47*, 257–292.

Goebel, M. E., Perryman, W. L., Hinke, J. T., Krause, D. J., Hann, N. A., Gardner, S., & LeRoi, D. J. (2015). A small unmanned aerial system for estimating abundance and size of Antarctic predators. *Polar Biology*. https://doi.org/10.1007/s00300-014-1625-4

Goldbogen, J. A., Potvin, J., & Shadwick, R. E. (2010). Skull and buccal cavity allometry increase mass-specific engulfment capacity in fin whales. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1683), 861–868. https://doi.org/10.1098/rspb.2009.1680

Gordon, J. (1990). A simple photographic technique for measuring the length of whales from boats at sea. *Report of the International Whaling Commission*, *40*, 581–588.

Gowans, S., & Whitehead, H. (2001). Photographic identification of northern bottlenose whales (*Hyperoodon ampullatus*): Sources of heterogeneity from natural marks. *Marine Mammal Science*, *17*(1), 76–93. https://doi.org/10.1111/j.1748-7692.2001.tb00981.x

Gray, P. C., Bierlich, K. C., Mantell, S. A., Friedlaender, A. S., Goldbogen, J. A., & Johnston, D. W. (2019). Drones and convolutional neural networks facilitate automated and accurate cetacean species identification and photogrammetry. *Methods in Ecology and Evolution*, *10*(9), 1490–1500. https://doi.org/10.1111/2041-210X.13246

Great Barrier Reef Marine Park Authority. (2014). *A vulnerability assessment for the Great Barrier Reef: Dwarf minke whales*. *October*, 1–41.

Growcott, A., Sirguey, P., & Dawson, S. M. (2012). Development and assessment of a digital stereo photogrammetric system to measure cetaceans at sea. *Photogrammetric Engineering & Remote Sensing*, *78*(3), 237–246. https://doi.org/10.14358/PERS.78.3.237

Hagihara, R., Jones, R. E., Grech, A., Lanyon, J. M., Sheppard, J. K., & Marsh, H. (2014). Improving population estimates by quantifying diving and surfacing patterns: a dugong example. *Marine Mammal Science*, *30*(1), 348–366. https://doi.org/10.1111/mms.12041

Hall, M. J., Burns, A. L., Martin, J. M., & Hochuli, D. F. (2020). Flight initiation distance changes across landscapes and habitats in a successful urban coloniser. *Urban Ecosystems*, *23*(4), 785–791. https://doi.org/10.1007/s11252-020-00969-5

Hammond, P. S. (1990). Capturing whales on film–estimating cetacean population parameters from individual recognition data. *Mammal Review*, *20*(1), 17–22. https://doi.org/10.1111/j.1365-2907.1990.tb00099.x

Hammond, P. S., Mizroch, S. A., & Donovan, G. P. (1990). Heterogeneity in the Gulf of Maine? Estimating humpback whale population size when capture probabilities are not equal. *Report of the International Whaling Commission, 12*, 135-139.

Hann, C. H., Smith, T. D., & Torres, L. G. (2016). A sperm whale's perspective: The importance of seasonality and seamount depth. In *Marine Mammal Science* (Vol. 32, Issue 4, pp. 1470–1481). Blackwell Publishing Inc. https://doi.org/10.1111/mms.12320

Hanson, K. T., & Riley, E. P. (2018). Beyond neutrality: the human–primate interface during the habituation process. *International Journal of Primatology*, *39*(5), 852–877. https://doi.org/10.1007/s10764-017-0009-3

Hartig, F. (2022). DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models. In *R package version 0.4.5, <https://CRAN.R-project.org/package=DHARMa>*.

Harvey, E., Shortis, M., Stadler, M., & Cappo, M. (2002). A comparison of the accuracy and precision of measurements from single and stereo-video systems. *Marine Technology Society Journal*, *36*(2), 38–49. https://doi.org/10.4031/002533202787914106

Hassel, L. B., Venturotti, A., Magalhaes, F. A., Cuenca, S., Siciliano, S., & Marques, F. F. C. (2003). Summer sightings of dwarf minke whales (*Balaenoptera acutorostrata*) off the eastern coast of Rio de Janeiro State, Brazil. *Latin American Journal of Aquatic Mammals*, *2*(1), 47–50. https://doi.org/10.5597/lajam00030

Haug, T., Lindstrøm, U., Nilssen, K. T., Lindstrom, U., & Nilssen, K. T. (2002). Variations in minke whale (*Balaenoptera acutorostrata*) diet and body condition in response to ecosystem changes in the Barents Sea. *Sarsia*, *87*(6), 409–422. https://doi.org/10.1080/0036482021000155715

Hazen, E. L., Abrahms, B., Brodie, S., Carroll, G., Jacox, M. G., Savoca, M. S., Scales, K. L., Sydeman, W. J., & Bograd, S. J. (2019). Marine top predators as climate and ecosystem sentinels. In *Frontiers in Ecology and the Environment* (Vol. 17, Issue 10, pp. 565–574). Wiley Blackwell. https://doi.org/10.1002/fee.2125

Higham, J., Bejder, L., & Lusseau, D. (2009). An integrated and adaptive management model to address the long-term sustainability of tourist interactions with cetaceans. *Environmental Conservation 35*(4), 294–302. https://doi.org/10.1017/S0376892908005249

Hirtle, N. O., Stepanuk, J. E. F., Heywood, E. I., Christiansen, F., & Thorne, L. H. (2022). Integrating 3D models with morphometric measurements to improve volumetric estimates in marine mammals. *Methods in Ecology and Evolution*, *13*(11), 2478–2490. https://doi.org/10.1111/2041-210X.13962

Hoarau, L., Dalleau, M., Delaspre, S., Barra, T., & Landes, A. Emmanuelle. (2020). Assessing and mitigating humpback whale (*Megaptera novaeangliae*) disturbance of whale-watching activities in Reunion Island. *Tourism in Marine Environments*, *15*, 173–189. https://doi.org/10.3727/154427320X15943326793398

Hoelzel, A. (1998). Genetic structure of cetacean populations in sympatry, parapatry, and mixed assemblages: implications for conservation policy. *Journal of Heredity*, *89*(5), 451–458. https://doi.org/10.1093/jhered/89.5.451

Hofman, R. J. (2019). Stopping overexploitation of living resources on the high seas. *Marine Policy*, *103*, 91–100. https://doi.org/10.1016/j.marpol.2019.02.037

Hosey, G. (2000). Zoo animals and their human audiences: what is the visitor effect? *Animal Welfare*, *9*(4), 343–357. https://doi.org/10.1017/S0962728600022946

Hoyt, E. (2001). Whale-Watching 2001: Worldwide tourism numbers, expenditures, and expanding socioeconomic benefits. In *International Fund for Animal Welfare, Yarmouth Ports, MA, USA*. https://doi.org/10.2307/4444572

Hoyt, E. (2018). Tourism. In B. Würsig, J. Thewissen, & K. Kovacs (Eds.), *Encyclopedia of marine mammals* (3rd ed., pp. 1010–1014). Academic Press.

Hutchings, M., Hamann, M., Smithers, S., Daley, E., & Birtles, R. (2023). Color pattern complexity in dwarf minke whales (*Balaenoptera acutorostrata*) of the northern Great Barrier Reef of Australia. *Marine Mammal Science*, *39*(3), 780–793. https://doi.org/10.1111/mms.13013

Huxley, T. (1932). *Problems of relative growth*. Dial Press.

Huxley, T., & Teissier, G. (1936). Terminology of relative growth. *Nature*, *137*, 780–781.

International Whaling Commission (IWC). (2000). *Report of the Scientific Committee, 52nd meeting of the International Whaling Commission*.

International Whaling Commission (IWC). (2001). *Report of the Workshop on the Comprehensive Assessment of Right Whales: A Worldwide Comparison*.

International Whaling Commission (IWC). (2013). Annex M: Report of the Sub-Committee on Whalewatching. *Journal of Cetacean Resource Management*, *14*, 318–329.

International Whaling Commission (IWC). (2014). Report of the Scientific Committee, 65th meeting of the International Whaling Commission. In *65th meeting of the International Whaling Commission*.

International Whaling Commission (IWC). (2015). *Report of the Scientific Committee, 66th meeting of the International Whaling Commission*.

Irschick, D. J., Martin, J., Siebert, U., Kristensen, J. H., Madsen, P. T., & Christiansen, F. (2021). Creation of accurate 3D models of harbor porpoises (*Phocoena phocoena*) using 3D photogrammetry. *Marine Mammal Science*, *37*(2), 482–491. https://doi.org/10.1111/mms.12759

Ivashchenko, Y., & Clapham, P. (2015). What's the catch? Validity of whaling data for Japanese catches of sperm whales in the north Pacific. *Royal Society Open Science*, *2*(150177), 0–7. https://doi.org/10.1098/rsos.150177

Jaquet, N. (2006). A simple photogrammetric technique to measure sperm whales at sea. *Marine Mammal Science*, *22*(4), 862–879. https://doi.org/10.1111/j.1748-7692.2006.00060.x

Jones, E. (1971). *Isistizcs brasiliensis*, a squaloid shark, the probable cause of crater wounds on fishes and cetaceans. *Fishery Bulletin*, *69*(4), 791.

Joyce, T., Ferguson, M., Berchok, C., Wright, D., Crance, J., Braen, E., Eguchi, T., Perryman, W., & Weller, D. (2023). The role of sea ice in the distribution, habitat use, and phenology of eastern north Pacific gray whales. *Marine Ecology Progress Series*, *709*, 141–158. https://doi.org/10.3354/meps14271

Kahane-Rapport, S. R., & Goldbogen, J. A. (2018). Allometric scaling of morphology and engulfment capacity in rorqual whales. *Journal of Morphology*, *279*(9), 1256–1268. https://doi.org/10.1002/jmor.20846

Kasamatsu, F., Yamamoto, Y., Zenitani, R., Ishikawa, H., Ishibashi, T., Sato, H., Takashima, K., & Tanifuji, S. (1993). Report of the 1990-1991 southern minke whale research cruise under scientific permit in Area V. *Reports of the International Whaling Commission*, *43*, 505–522.

Kato, H., & Fujise, Y. (2000). *Dwarf minke whales: morphology, growth and life history with some analyses on morphometric variation among the different forms and regions*. Impington: Internatinoal Whaling Commission.

Kato, H., Fujise, Y., Nakamura, G., Hakamada, T., Pastene, L. A., & Best, P. B. (2022). Dwarf minke whales: Morphology, growth and life history based on samples collected from the higher latitudes in the southern hemisphere. *Cetacean Population Studies*, *3*, 93–128. https://doi.org/10.34331/cpops.2020F008

Katona, S., Baxter, B., Brazier, O., Kraus, S., Perkins, J., & Whitehead, H. (1979). Identification of humpback whales by fluke photographs. In H. E. Winn & B. L. Olla (Eds.), *Behavior of marine animals: current perspectives in research* (pp. 33–44). Springer US. https://doi.org/10.1007/978-1-4684-2985-5_2

Kawamura, A. (1969). Some consideration on the stock unit of sei whales by the aspect of ectoparasitic organisms on the body. *Bulletin of the Japanese Society of Fisheries Oceanography*, *14*, 38–43.

Kebke, A., Samarra, F., & Derous, D. (2022). Climate change and cetacean health: impacts and future directions. In *Philosophical transactions of the Royal Society b: biological sciences* (Vol. 377, Issue 1854). Royal Society Publishing. https://doi.org/10.1098/rstb.2021.0249

Kerlinger, P., Burger, J., Cordell, H., Decker, D., & Cole, D. (2013). *Wildlife and recreationists: coexistence through management and research*. Island Press.

Kessler, M., & Harcourt, R. (2012). Management implications for the changing interactions between people and whales in Ha'apai, Tonga. *Marine Policy*, *36*(2), 440–445. https://doi.org/10.1016/j.marpol.2011.08.004

Kessler, M., & Harcourt, R. (2013). Whale watching regulation compliance trends and the implications for management off Sydney, Australia. *Marine Policy*, *42*, 14–19. https://doi.org/10.1016/J.MARPOL.2013.01.016

Khan, C., Blount, D., Parham, J., Holmberg, J., Hamilton, P., Charlton, C., Christiansen, F., Johnston, D., Rayment, W., Dawson, S., Vermeulen, E., Rowntree, V., Groch, K., Levenson, J. J., & Bogucki, R. (2022). Artificial intelligence for right whale photo identification: from data science competition to worldwide collaboration. *Mammalian Biology*, *102*(3), 1025–1042. https://doi.org/10.1007/s42991-022-00253-3

Kiszka, J., Macleod, K., van Canneyt, O., Walker, D., & Ridoux, V. (2007). Distribution, encounter rates, and habitat characteristics of toothed cetaceans in the Bay of Biscay and adjacent waters from platform-of-opportunity data. *ICES Journal of Marine Science*, *64*(5), 1033–1043. https://doi.org/10.1093/icesjms/fsm067

Kitakado, T., Lockyer, C., & Punt, A. E. (2013). A statistical model for quantifying age-reading errors and its application to the Antarctic minke whales. *Journal of Cetacean Resource Management*, *13*(3), 181–190. https://doi.org/10.47536/jcrm.v13i3.534

Klimley, A., & Brown, S. (1983). Stereophotography for the field biologist: measurement of lengths and three-dimensional positions of free-swimming sharks. *Marine Biology*, *74*(2), 175–185. https://doi.org/10.1007/BF00413921

Knowlton, A. R., Hamilton, P. K., Marx, M. K., Pettis, H. M., & Kraus, S. D. (2012). Monitoring North Atlantic right whale Eubalaena glacialis entanglement rates: a 30 yr retrospective. *Marine Ecology Progress Series*, *466*, 293–302. https://doi.org/10.3354/meps09923

Konishi, K. (2006). Characteristics of blubber distribution and body condition indicators for Antarctic minke whales (*Balaenoptera bonaerensis*). *Mammal Study*, *31*, 15–22. https://doi.org/10.3106/1348-6160(2006)31[15:COBDAB]2.0.CO;2

Konishi, K., Hakamada, T., Kiwada, H., Kitakado, T., & Walløe, L. (2013). Decrease in stomach contents in the Antarctic minke whale (*Balaenoptera bonaerensis*) in the southern ocean. *Polar Biology*, *37*, 205–215. https://doi.org/10.1007/s00300-013-1424-3

Konishi, K., Tamura, T., Zenitani, R., Bando, T., Kato, H., & Walløe, L. (2008). Decline in energy storage in the Antarctic minke whale (*Balaenoptera bonaerensis*) in the Southern Ocean. *Polar Biology*, *31*(12), 1509–1520. https://doi.org/10.1007/s00300-008-0491-3

Konovalov, D. A. D. A., Swinhoe, N., Efremova, D. B. D. B., Birtles, R. A., Kusetic, M., Hillcoat, S., Curnock, M. I. M. I., Williams, G., & Sheaves, M. (2020). Automatic sorting of dwarf minke whale underwater images. *Information (Switzerland)*, *11*(4), 1–17. https://doi.org/10.3390/info11040200

Koopmans, M., & Wijffels, R. H. (2008). Seasonal growth rate of the sponge *Haliclona oculata* (Demospongiae: Haplosclerida). *Marine Biotechnology*, *10*(5), 502–510. https://doi.org/10.1007/s10126-008-9086-9

Krause, D. J., Hinke, J. T., Perryman, W. L., Goebel, M. E., & LeRoi, D. J. (2017). An accurate and adaptable photogrammetric approach for estimating the mass and body condition of pinnipeds using an unmanned aerial system. *PLoS ONE*, *12*(11), 1–20. https://doi.org/10.1371/journal.pone.0187465

Lanzetti, A., Portela-Miguez, R., Fernandez, V., & Goswami, A. (2023). Testing heterochrony: connecting skull shape ontogeny and evolution of feeding adaptations in baleen whales. *Evolution & Development*. https://doi.org/10.1111/ede.12447

Leaper, R., Cooke, J., Trathan, P., Reid, K., Rowntree, V., & Payne, R. (2006). Global climate drives southern right whale (*Eubalaena australis*) population dynamics. *Biology Letters*, *2*(2), 289–292. https://doi.org/10.1098/rsbl.2005.0431

Learmonth, J. A., Macleod, C. D., Santos, M. B., Pierce, G. J., Crick, H. Q. P., & Robinson, R. A. (2006). Potential effects of climate change on marine mammals. In *Oceanography and Marine Biology* (Vol. 44, pp. 431–464). Taylor and Francis Ltd. https://doi.org/10.1201/9781420006391.ch8

Lemos, L. S., Olsen, A., Smith, A., Burnett, J. D., Chandler, T. E., Larson, S., Hunt, K. E., & Torres, L. G. (2022). Stressed and slim or relaxed and chubby? A simultaneous assessment of gray whale body condition and hormone variability. *Marine Mammal Science*, *38*(2), 1–11. https://doi.org/10.1111/mms.12877

Leslie, M. S., Perkins-Taylor, C. M., Durban, J. W., Moore, M. J., Miller, C. A., Chanarat, P., Bahamonde, P., Chiang, G., & Apprill, A. (2020). Body size data collected non-invasively from drone images indicate a morphologically distinct Chilean blue whale (*Balaenoptera musculus*) taxon. *Endangered Species Research*, *43*, 291–304. https://doi.org/10.3354/esr01066

Lien, J. (2009). Entrapment and entanglement. In *Encyclopedia of Marine Mammals* (pp. 391–392). Academic Press. https://doi.org/10.1016/B978-0-12-373553-9.00092-4

Lockyer, C. (1986). Body fat condition in northeast Atlantic fin whales, Balaenoptera physalus, and its relationship with reproduction and food resource. *Canadian Journal of Fisheries and Aquatic Sciences*, *43*(1), 142–147. https://doi.org/10.1139/f86-015

Lockyer, C. (2007). All creatures great and smaller: a study in cetacean life history energetics. *Journal of the Marine Biological Association of the UK*, *87*(04), 1035. https://doi.org/10.1017/S0025315407054720

Lundquist, D., Sironi, M., Würsig, B., Rowntree, V., Martino, J., & Lundquist, L. (2013). Response of southern right whales to simulated swim-with-whale tourism at Península Valdés, Argentina. *Marine Mammal Science*, *29*(2), 24–45. https://doi.org/10.1111/j.1748-7692.2012.00583.x

Lusseau, D. (2003a). Effects of tour boats on the behavior of bottlenose dolphins: using Markov chains to model anthropogenic impacts. *Conservation Biology*, *17*(6), 1785–1793. https://doi.org/10.1111/j.1523-1739.2003.00054.x

Lusseau, D. (2003b). Male and female bottlenose dolphins *Tursiops* spp. have different strategies to avoid interactions with tour boats in Doubtful Sound, New Zealand. *Marine Ecology Progress Series*, *257*, 267–274. https://doi.org/10.3354/meps257267

Lusseau, D. (2004). The hidden cost of tourism: detecting long-term effects of tourism using behavioral information. *Ecology and Society*, *9*(1). https://www.jstor.org/stable/26267644

Machernis, A. F., Powell, J. R., Engleby, L., & Spradlin, T. R. (2018). An updated literature review examining the impacts of tourism on marine mammals over the last fifteen years (2000-2015) to inform research and management programs. *NOAA Technical Memorandum*, *NMFS-SER-7*(July), 1–66. https://doi.org/10.7289/V5/TM-NMFS-SER-7

Mackintosh, N. A., & Wheeler, J. (1929). *Southern blue and fin whales*. Cambridge University Press.

Maeda, H., Kawamoto, T., & Kato, H. (2013). A study on the improvement of age estimation in common minke whales using the method of gelatinized extraction of earplug. *NAMMCO Scientific Publications*, *10*. https://doi.org/10.7557/3.2609

Magalhães, S., Ui Prieto, R., ónica, M., Silva, A., Oão Gonçalves, J., Afonso-Dias, M., & Santos, R. (2002). Short-term reactions of sperm whales (*Physeter macrocephalus*) to whale-watching vessels in the Azores. *Aquatic Mammals*, *283*, 267–274.

Maglietta, R., Reno, V., Caccioppoli, R., Seller, E., Bellomo, S., Santacesaria, F. C., Colella, R., Cipriano, G., Stella, E., Hartman, K., Fanizza, C., Dimauro, G., & Carlucci, R. (2020). Convolutional Neural Networks for Risso's dolphins identification. *IEEE Access*, *8*, 80195–80206. https://doi.org/10.1109/ACCESS.2020.2990427

Mallard, G. (2019). Regulating whale watching: A common agency analysis. *Annals of Tourism Research*, *76*, 191–199. https://doi.org/10.1016/J.ANNALS.2019.04.011

Mangott, A. (2010). *Behaviour of dwarf minke whales (Balaenoptera acutorostrata subsp.) associated with a swim-with industry in the northern Great Barrier Reef* [PhD Thesis]. James Cook University.

Mangott, A., Birtles, R. A., & Marsh, H. (2011). Attraction of dwarf minke whales Balaenoptera acutorostrata to vessels and swimmers in the Great Barrier Reef World Heritage Area - the management challenges of an inquisitive whale. *Journal of Ecotourism*, *10*(1), 64–76. https://doi.org/10.1080/14724041003690468

Mann, J. (1999). Behavioral sampling methods for cetaceans: a review and critique. *Marine Mammal Science*, *15*(1), 102–122. https://doi.org/10.1111/j.1748-7692.1999.tb00784.x

Mann, J., Connor, R. C., Barre, L. M., & Heithaus, M. R. (2000). Female reproductive success in bottlenose dolphins (*Tursiops* sp.): life history, habitat, provisioning, and group-size effects. *Behavioral Ecology*, *11*(2), 210–219. https://doi.org/10.1093/beheco/11.2.210

Mann, J., Foroughirad, V., McEntee, M. H. F., Miketa, M. L., Evans, T. C., Karniski, C., Krzyszczyk, E., Patterson, E. M., Strohman, J. C., & Wallen, M. M. (2021). Elevated calf mortality and long-term responses of wild bottlenose dolphins to extreme climate events: impacts of foraging specialization and provisioning. *Frontiers in Marine Science*, *8*. https://doi.org/10.3389/fmars.2021.617550

Mead, J. G., & Payne, R. S. (1975). A specimen of the tasman beaked whale, *Tasmacetus shepherdi*, from Argentina. In *Source: Journal of Mammalogy* (Vol. 56, Issue 1).

Melica, V., Atkinson, S., Calambokidis, J., Lang, A., Scordino, J., & Mueter, F. (2021). Application of endocrine biomarkers to update information on reproductive physiology in gray whale (*Eschrichtius robustus*). *PLoS ONE*, *16*(8). https://doi.org/10.1371/journal.pone.0255368

Melica, V., Atkinson, S., Gendron, D., Calambokidis, J., & Mueter, F. (2021). Blubber endocrine profiles provide insights into reproductive biology in blue whales from the eastern north Pacific Ocean. *General and Comparative Endocrinology*, *310*. https://doi.org/10.1016/j.ygcen.2021.113830

Miller, C. A., Best, P. B., Perryman, W. L., Baumgartner, M. F., & Moore, M. J. (2012). Body shape changes associated with reproductive status, nutritive condition and growth in right whales *Eubalaena glacialis* and *E. australis*. *Marine Ecology Progress Series*, *459*, 135–156. https://doi.org/10.3354/meps09675

Miller, R. L., Marsh, H., Cottrell, A., & Hamann, M. (2018). Protecting migratory species in the Australian marine environment: A cross-jurisdictional analysis of policy and management plans. *Frontiers in Marine Science*, *5*. https://doi.org/10.3389/fmars.2018.00229

Milmann, L., Cardoso, J., Francisco, A., Santos, F. P., Seminara, C., Abras, D. R., Marques, M. L., Hille, D. A., Lemos, L. S., Ruenes, G. F., Hauser-Davis, R. A., & Siciliano, S.

(2023). Dwarf minke whale (*Balaenoptera acutorostrata* subsp.) interactions with vessels off the coast of Brazil. *Cetacean Population Studies*, *4*, 1–7. https://doi.org/10.34331/cpops.2022S002

Milmann, L., Taguchi, M., Siciliano, S., Baumgarten, J. E., Oliveira, L. R., Valiati, V. H., Goto, M., Ott, P. H., & Pastene, L. A. (2021). New genetic evidences for distinct populations of the common minke whale (*Balaenoptera acutorostrata*) in the southern hemisphere. *Polar Biology*, *0123456789*. https://doi.org/10.1007/s00300-021-02897-2

Morgan, K., & Tromborg, C. (2007). Sources of stress in captivity. *Applied Animal Behaviour Science*, *102*(3–4), 262–302. https://doi.org/10.1016/j.applanim.2006.05.032

Muloin, S. (1998). Wildlife tourism: the psychological benefits of whale watching. *Pacific Tourism Review*, *2*(3–4), 199–213.

National Academies of Sciences, E. and M. (2017). Approaches to understanding the cumulative effects of stressors on marine mammals. In *Approaches to Understanding the Cumulative Effects of Stressors on Marine Mammals*. National Academies Press. https://doi.org/10.17226/23479

National Marine Fisheries Service. (2008). *Improvements are needed in the federal process used to protect marine mammals from commercial fishing*. https://www.gao.gov/products/gao-09-78

Natural Resource Management Ministerial Council. (2005). *Australian National Guidelines for Whale and Dolphin Watching*. 1–19.

New, L. F., Harwood, J., Thomas, L., Donovan, C., Clark, J. S., Hastie, G., Thompson, P. M., Cheney, B., Scott-Hayward, L., & Lusseau, D. (2013). Modelling the biological significance of behavioural change in coastal bottlenose dolphins in response to disturbance. *Functional Ecology*, *27*(2), 314–322. https://doi.org/10.1111/1365-2435.12052

Newson, S. E., Mendes, S., Crick, H. Q. P., Dulvy, N. K., Houghton, J. D. R., Hays, G. C., Hutson, A. M., MacLeod, C. D., Pierce, G. J., & Robinson, R. A. (2009). Indicators of the impact of climate change on migratory species. *Endangered Species Research*, *7*(2), 101–113. https://doi.org/10.3354/esr00162

Nicol, S., Worby, A., & Leaper, R. (2008). Changes in the Antarctic sea ice ecosystem: potential effects on krill and baleen whales. *Marine and Freshwater Research*, *59*(5), 361–382. https://doi.org/10.1071/MF07161

Nisbet, I. C. T. (2000). Disturbance, habituation, and management of waterbird colonies. *Waterbirds: The International Journal of Waterbird Biology*, *23*(2), 312–332. https://www.jstor.org/stable/4641163

Nowacek, D. P., Thorne, L. H., Johnston, D. W., & Tyack, P. L. (2007). Responses of cetaceans to anthropogenic noise. *Mammal Review*, *37*(2), 81–115. https://doi.org/10.1111/j.1365-2907.2007.00104.x

O'Connor, S., Campbell, R., Knowles, T., Cortez, H., & Grey, F. (2009). Whale watching worldwide: Tourism numbers, expenditures and economic benefits - a special report from the International Fund for Animal Welfare. *International Fund for Animal Welfare*.

Ohsumi, S., Masaki, Y., & Kawamura, A. (1970). Stock of the Antarctic minke whale. *Scientific Reports of the Whales Research Institute*, *22*, 75–125.

Oliveira, F., Nogueira-Filho, S., Sousa, M., Dias, C., Mendl, M., & Nogueira, S. (2016). Measurement of cognitive bias and cortisol levels to evaluate the effects of space restriction on captive collared peccary (Mammalia, Tayassuidae). *Applied Animal Behaviour Science*, *181*, 76–82. https://doi.org/10.1016/j.applanim.2016.05.021

Omura, H. (1957). Osteological study of the little piked whale from the coast of Japan. *Scientific Reports of the Whales Research Institute*, *12*, 1–21.

Orams, M. (2004). Why dolphins may get ulcers: considering the impacts of cetacean-based tourism in New Zealand. *Tourism in Marine Environments*, *1*(1), 17–28. https://doi.org/10.3727/154427304774865878

Orams, M. B. (2000). Tourists getting close to whales, is it what whale-watching is all about? *Tourism Management*, *21*(6), 561–569. https://doi.org/10.1016/S0261-5177(00)00006-6

Orbach, D. N., Eaton, J., Fiori, L., Piwetz, S., Weir, J. S., Würsig, M., & Würsig, B. (2020). Mating patterns of dusky dolphins (*Lagenorhynchus obscurus*) explored using an unmanned aerial vehicle. *Marine Mammal Science*, *36*(4), 1097–1110. https://doi.org/10.1111/mms.12695

Ortega-Ortiz, C. D., Mata Cruz, R. M., Gerrodette, T., & Gendron, D. (2022). A photogrammetric method to estimate total length of the largest mammal, the blue whale (*Balaenoptera musculus*). *Mammalian Biology*, *102*(3), 629–643. https://doi.org/10.1007/s42991-022-00307-6

Pagel, C. D., Orams, M. B., & Lück, M. (2020). #Biteme: considering the potential influence of social media on in-water encounters with marine wildlife. *Tourism in Marine Environments*, *15*, 249–258. https://doi.org/10.3727/154427320X15754936027058

Parent, C., & Weatherhead, P. (2000). Behavioral and life history responses of eastern massasauga rattlesnakes (*Sistrurus catenatus catenatus*) to human disturbance. *Oecologia*, *125*, 170–178. https://doi.org/10.1007/s004420000442

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. In *Annual Review of Ecology, Evolution, and Systematics* (Vol. 37, pp. 637–669). https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Parsons, E., & Brown, D. (2017). Recent advances in whale watching research: 2000-2015. *Tourism in Marine Environments*, *12*(2), 125–137. https://doi.org/10.3727/154427317X694728

Parsons, E. C. M. (2012). The negative impacts of whale-watching. *Journal of Marine Biology*, *2012*, 1–9. https://doi.org/10.1155/2012/807294

Pastene, L. A., Acevedo, J., Goto, M., Zerbini, A. N., Acuña, P., & Aguayo-Lobo, A. (2010). Population structure and possible migratory links of common minke whales, *Balaenoptera acutorostrata*, in the southern hemisphere. *Conservation Genetics 11, 1553–1558*. https://doi.org/10.1007/s10592-009-9944-7

Paterson, R., Cato, D. H., Janetski, H., & Williams, S. (2000). An adult dwarf minke whale *Balaenoptera acutorostrata* Lacépède, 1840 from Fraser Island, Queensland. *Memoirs of the Queensland Museum*, *45*, 557–568.

Patton, P. T., Cheeseman, T., Abe, K., Yamaguchi, T., Reade, W., Southerland, K., Howard, A., Oleson, E. M., Allen, J. B., Ashe, E., Athayde, A., Baird, R. W., Basran, C., Cabrera, E., Calambokidis, J., Cardoso, J., Carroll, E. L., Cesario, A., Cheney, B. J., Bejder, L. (2023). A deep learning approach to photo–identification demonstrates high performance on two dozen cetacean species. *Methods in Ecology and Evolution*, *14*(10), 2611–2625. https://doi.org/10.1111/2041-210X.14167

Peace, A. (2010). The whaling war: conflicting cultural perspectives. *Anthropology Today*, *26*(3), 5–9. https://doi.org/10.1111/j.1467-8322.2010.00734.x

Pearce, G., & Paterson, A. (1993). The effect of space restriction and provision of toys during rearing on the behaviour, productivity and physiology of male pigs. *Applied Animal Behaviour Science*, *36*(1), 11–28. https://doi.org/10.1016/0168-1591(93)90095-7

Perryman, W. L., Joyce, T., Weller, D. W., & Durban, J. W. (2021). Environmental factors influencing eastern north Pacific gray whale calf production 1994–2016. *Marine Mammal Science*, *37*(2), 448–462. https://doi.org/10.1111/mms.12755

Perryman, W. L., & Lynn, M. S. (1993). Identification of geographic forms of common dolphin (*Delphinus delphis*) from aerial photogrammetry. *Marine Mammal Science*, *9*(2), 119–137. https://doi.org/10.1111/j.1748-7692.1993.tb00438.x

Perryman, W. L., & Westlake, R. L. (1998). A new geographic form of the spinner dolphin, *Stenella longirostris*, detected with aerial photogrammetry. *Marine Mammal Science*, *14*(1), 38–50. https://doi.org/10.1111/j.1748-7692.1998.tb00689.x

Petelle, M. B., McCoy, D. E., Alejandro, V., Martin, J. G. A., & Blumstein, D. T. (2013). Development of boldness and docility in yellow-bellied marmots. *Animal Behaviour*, *86*(6), 1147–1154. https://doi.org/10.1016/j.anbehav.2013.09.016

Peters, R. H. (1986). *The ecological implications of body size.* (Vol. 2). Cambridge University Press.

Phillips, K., Rodriguez, V. B., Harvey, E., Ellis, D., Seager, J., Begg, G., & Hender, J. (2008). Assessing the operational feasibility of stereo-video and evaluating monitoring options for the Southern Bluefin Tuna Fishery ranch sector. *Fisheries Research and Development Corporation report, 44(2009)*, 46.

Pirotta, E., Booth, C. G., Costa, D. P., Fleishman, E., Kraus, S. D., Lusseau, D., Moretti, D., New, L. F., Schick, R. S., Schwarz, L. K., Simmons, S. E., Thomas, L., Tyack, P. L., Weise, M. J., Wells, R. S., & Harwood, J. (2018). Understanding the population consequences of disturbance. *Ecology and Evolution*, *8*(19), 9934–9946. https://doi.org/10.1002/ece3.4458

Pirotta, V., Smith, A., Ostrowski, M., Russell, D., Jonsen, I. D., Grech, A., & Harcourt, R. (2017). An economical custom-built drone for assessing whale health. *Frontiers in Marine Science*, *4*, 425. https://doi.org/10.3389/fmars.2017.00425

Pittenger, J. B. (1990). Body proportions as information for age and cuteness: animals in illustrated children's books. *Perception & Psychophysics*, *48*(2), 124–130. https://doi.org/10.3758/BF03207078

Ramirez-Flores, O., Birtles, A., Pazmino, D., Zenger, K. R., & Van-Herwerden, L. (2019). Dwarf minke whales from the south Pacific share a matrilineal lineage distinct from *Balaenoptera acutorostrata acutorostrata* and *B. a. scammoni*. *Australian Mammalogy*, *41*(2), 231–240. https://doi.org/10.1071/AM18015

Ramos, E. A., Landeo-Yauri, S., Castelblanco-Martínez, N., Arreola, M. R., Quade, A. H., & Rieucau, G. (2022). Drone-based photogrammetry assessments of body size and body condition of Antillean manatees. *Mammalian Biology*, *102*(3), 765–779. https://doi.org/10.1007/s42991-022-00228-4

Ramos-Arredondo, R. I., Carvajal-Gámez, B. E., Gendron, D., Gallegos-Funes, F. J., Mújica-Vargas, D., & Rosas-Fernández, J. B. (2020). PhotoId-Whale: blue whale dorsal fin classification for mobile devices. *PLoS ONE*, *15*(10 October 2020). https://doi.org/10.1371/journal.pone.0237570

Ramp, C., Gaspard, D., Gavrilchuk, K., Unger, M., Schleimer, A., Delarue, J., Landry, S., & Sears, R. (2021). Up in the air: drone images reveal underestimation of entanglement rates in large rorqual whales. *Endangered Species Research*, *44*, 33–44. https://doi.org/10.3354/esr01084

Ranquist, E., Steiner, M., & Argrow, B. (2017). Exploring the range of weather impacts on UAS operations. *18th Conference on Aviation, Range, and Aerospace Meteorology*, Seattle, WA.

Ratnaswamy, M. J., & Winn, H. E. (1993). Photogrammetric estimates of allometry and calf production in fin whales, *Balaenoptera physalus*. *Journal of Mammalogy*, *74*(2), 323–330. https://doi.org/10.2307/1382387

Ratsimbazafindranahaka, M. N., Razafimahatratra, E., Mathevet, R., Adam, O., Huetz, C., Charrier, I., & Saloma, A. (2021). Morphometric study of humpback whale mother-calf pairs in the Sainte Marie channel, Madagascar, using a simple drone-based photogrammetric method. *Western Indian Ocean Journal of Marine Science*, *20*(2), 95–107. https://doi.org/10.4314/wiojms.v20i2.8

Read, F. L., Hohn, A. A., & Lockyer, C. H. (2018). A review of age estimation methods in marine mammals with special reference to monodontids. *NAMMCO Scientific Publications*, *10*. https://doi.org/10.7557/3.4474

Reynolds, P. C., & Braithwaite, D. (2001). Towards a conceptual framework for wildlife tourism. *Tourism Management*, *22*(1), 31–42. https://doi.org/10.1016/S0261-5177(00)00018-2

Rice, C. (1998). Marine mammals of the world: systematics and distribution. *Society for Marine Mammalogy Special Publications*, *4*, 1–231.

Robles, C. (2008). Intertidal Zonation. In S. Jørgensen & B. Fath (Eds.), *Encyclopedia of Ecology* (pp. 2003–2010). Academic Press.

Rodríguez-Prieto, I., & Fernández-Juricic, E. (2005). Effects of direct human disturbance on the endemic Iberian frog Rana iberica at individual and population levels. *Biological Conservation*, *123*(1), 1–9. https://doi.org/10.1016/j.biocon.2004.10.003

Rogers, A. D., Frinault, B. A. V, Barnes, D. K. A., Bindoff, N. L., Downie, R., Ducklow, H. W., Friedlaender, A. S., Hart, T., Hill, S. L., Hofmann, E. E., Linse, K., Mcmahon, C. R., Murphy, E. J., Pakhomov, E. A., Reygondeau, G., Staniland, I. J., Wolf-Gladrow, D. A., & Wright, R. M. (2020). Antarctic futures: an assessment of climate-driven changes in ecosystem structure, function, and service provisioning in the southern ocean. *Annual Review of Marine Science*, *12*, 87–120. https://doi.org/10.1146/annurev-marine-010419

Rohner, C. A., Richardson, A. J., Marshall, A. D., Weeks, S. J., & Pierce, S. J. (2011). How large is the world's largest fish? Measuring whale sharks Rhincodon typus with laser photogrammetry. *Journal of Fish Biology*, *78*(1), 378–385. https://doi.org/10.1111/j.1095-8649.2010.02861.x

Samuels, A., & Bejder, L. (2004). Chronic interaction between humans and free-ranging bottlenose dolphins near Panama City Beach, Florida USA. *Journal of Cetacean Research and Management*, *6*(1), 69–77. https://doi.org/10.47536/jcrm.v6i1.792

Samuels, A., Bejder, L., Constantine, R., & Heinrich, S. (2003). Swimming with wild cetaceans in the southern hemisphere. In N. Gales, M. Hindell, & R. Kirkwood (Eds.), *Marine Mammals: Fisheries, Tourism and Management Issues*. CSIRO Publishing.

Samuels, A., Bejder, L., & Heinrich, S. (2000). *A review of the literature pertaining to swimming with wild dolphins* (p. 57). Bethesda, Maryland, US: Marine Mammal Commission.

Sanderson, C. E., & Alexander, K. A. (2020). Unchartered waters: climate change likely to intensify infectious disease outbreaks causing mass mortality events in marine mammals. *Global Change Biology*, *26*(8), 4284–4301. https://doi.org/10.1111/gcb.15163

Schmidt-Nielsen, K. (1984). *Scaling: why is animal size so important?* Cambridge University Press.

Schroeder, J. P., & Keller, K. V. (1989). Seasonality of serum testosterone levels and sperm density in *Tursiops truncatus*. *Journal of Experimental Zoology*, *249*(3), 316–321. https://doi.org/10.1002/jez.1402490310

Scott, G., & Winn, H. (1980). *Comparative evaluation of aerial and shipboard sampling techniques for estimating the abundance of humpback whales (Megaptera novaeangliae).* Contract report to US Marine Mammal Commission.

Sea North Tours. (2018). *Zodiac beluga whale watching*. http://www.seanorthtours.com

Seager, J. (2016a). *CAL. Computer program v. 2.30.* (2.30). SeaGIS.

Seager, J. (2016b). *CAL: User Guide v. 2.30.*

Seager, J. (2016c). *EventMeasure. Computer program v. 4.44.* (4.44). SeaGIS.

Seager, J. (2016d). *EventMeasure: User Guide v. 4.44.*

Sears, R., Williamson, J, M., Wenzel, F., Bérubé, M., Gendron, D., & Jones, P. (1990). Photographic identification of the blue whale (*Balaenoptera musculus*) in the Gulf of St. Lawrence, Canada. *Report of the International Whaling Commission Special Issue*, *12*, 335–342.

Seber, G. A. F. (1982). *The estimation of animal abundance and related parameters* (Vol. 8). Blackburn Press.

Secchi, E. R., Barcellos, L., Zerbini, A. N., & Rosa, L. D. (2003). Biological observations on a dwarf minke whale, *Balaenoptera acutorostrata*, caught in southern Brazilian waters, with a new record of prey for the species. *Latin American Journal of Aquatic Mammals*, *2*(2), 109–115. https://doi.org/10.5597/lajam00039

Seltmann, M. W., Öst, M., Jaatinen, K., Atkinson, S., Mashburn, K., & Hollmén, T. (2012). Stress responsiveness, age and body condition interactively affect flight initiation distance in breeding female eiders. *Animal Behaviour*, *84*(4), 889–896. https://doi.org/10.1016/j.anbehav.2012.07.012

Senigaglia, V., Christiansen, F., Sprogis, K. R., Symons, J., & Bejder, L. (2019). Food-provisioning negatively affects calf survival and female reproductive success in bottlenose dolphins. *Scientific Reports*, *9*(1). https://doi.org/10.1038/s41598-019-45395-6

Shane, S., Wells, R., & Wursig, B. (1986). Ecology, behavior and social organization of the bottlenose dolphin: a review. *Marine Mammal Science*, *2*(1), 34–63. https://doi.org/10.1111/j.1748-7692.1986.tb00026.x

Shortis, M. (2015). Calibration techniques for accurate measurements by underwater camera systems. *Sensors*, *15*(12), 30810–30827. https://doi.org/10.3390/s151229831

Shortis, M. R., & Harvey, E. S. (1998). Design and calibration of an underwater stereo-video system for the monitoring of marine fauna populations. *International Archives of Photogrammetry and Remote Sensing*, *32*(5), 792–799.

Simmonds, M. P., & Isaac, S. J. (2007). The impacts of climate change on marine mammals: early signs of significant problems. *Oryx*, *41*(01), 19–26. https://doi.org/10.1017/S0030605307001524

Sitar, A., May-Collado, L. J., Wright, A. J., Peters-Burton, E., Rockwood, L., & Parsons, E. C. M. (2016). Boat operators in Bocas del Toro, Panama display low levels of compliance with national whale-watching regulations. *Marine Policy*, *68*, 221–228. https://doi.org/10.1016/J.MARPOL.2016.03.011

Smetacek, V., & Nicol, S. (2005). Polar ocean ecosystems in a changing world. *Nature*, *437*(7057), 362–368. https://doi.org/10.1038/nature04161

Smith, K. R., Scarpaci, C., Louden, B. M., & Otway, N. M. (2015). Behaviour of aggregated grey nurse sharks Carcharias taurus off eastern Australia: similarities and differences among life-history stages and sites. *Endangered Species Research*, *27*(1), 69–85. https://doi.org/10.3354/esr00652

Smultea, M. (1994). Segregation by humpback whale (Megaptera novaeangliae) cows with a calf in coastal habitat near the island of Hawaii. *Canadian Journal of Mammalogy*, *72*, 805–811. https://doi.org/10.1139/z94-109

Sobtzick, S. (2010). *Dwarf minke whales in the northern Great Barrier Reef and implications for the sustainable management of the swim-with whales industry* [PhD Thesis]. James Cook University.

Sousa-Lima, R. S., & Groch, K. R. (2010). Correlation between body length and fluke width in humpback whales, *Megaptera novaeangliae*. *Marine Mammal Science*, *26*(4), 977–981. https://doi.org/10.1111/j.1748-7692.2010.00373.x

Spitz, S., Herman, L. M., Pack, A. A., & Deakos, M. H. (2002). The relation of body size of male humpback whales to their social roles on the Hawaiian winter grounds. *Canadian Journal of Zoology*, *80*(11), 1938–1947. https://doi.org/10.1139/z02-177

Spitz, S., Herman, L., & Peck, A. (2000). Measuring sizes of humpback whales (*Megaptera novaeangliae*) by underwater videogrammetry. *Marine Mammal Science*, *16*(3), 839–846. https://doi.org/10.1111/j.1748-7692.2000.tb00962.x

Sprogis, K. R., Bejder, L., & Christiansen, F. (2017). Swim-with-whale tourism trial in the Ningaloo Marine Park, Western Australia. *Report to the Department of Parks and Wildlife, Western Australia. Murdoch University, Murdoch, WA. 49pp.*

Sprogis, K. R., Bejder, L., Hanf, D., & Christiansen, F. (2020). Behavioural responses of migrating humpback whales to swim-with-whale activities in the Ningaloo Marine Park, Western Australia. *Journal of Experimental Marine Biology and Ecology*, *522*, 151–254. https://doi.org/10.1016/j.jembe.2019.151254

Stack, S., & Currie, J. (2022). Realising the potential of platforms of opportunity: rethinking scientific data collection. In M. Lück & B. Porter (Eds.), *Advancing Public and Industry Participation in Coastal and Marine Sciences* (pp. 43–57). Cambridge Scholars Publishing.

Stack, S., Sprogis, K. R., Olson, G., Sullivan, F., Machernis, A., & Currie, J. (2021). The behavioural impacts of commercial swimming with whale tours on humpback whales (*Megaptera novaeangliae*) in Hervey Bay. *Frontiers in Marine Science*, 1112. https://doi.org/10.3389/fmars.2021.696136

Stafford, K., Citta, J., Okkonen, S., & Suydam, R. (2016). Wind-dependent beluga whale dive behavior in Barrow Canyon, Alaska. *Deep Sea Research Part I: Oceanographic Research Papers*, *118*, 57–65. https://doi.org/10.1016/J.DSR.2016.10.006

Stalmaster, M., & Newman, J. (1978). Behavioral responses of wintering bald eagles to human activity. *The Journal of Wildlife Management*, 506–513. https://doi.org/10.2307/3800811

Steckenreuter, A., Möller, L., & Harcourt, R. (2012). How does Australia's largest dolphin-watching industry affect the behaviour of a small and resident population of Indo-Pacific bottlenose dolphins? *Journal of Environmental Management*, *97*(1), 14–21. https://doi.org/10.1016/j.jenvman.2011.11.002

Stedman, B. (1990). The International Whaling Commission and negotiation for a global moratorium on whaling. *Nine Case Studies in International Environmental Negotiation*, 151–175.

Stevick, P. T., Allen, J., Clapham, P. J., Katona, S. K., Larsen, F., Lien, J., Mattila, D. K., Palsbøll, P. J., Sears, R., Sigurjónsson, J., Smith, T. D., Vikingsson, G., Øien, N., & Hammond, P. S. (2006). Population spatial structuring on the feeding grounds in north Atlantic humpback whales (*Megaptera novaeangliae*). *Journal of Zoology*, *270*(2), 244–255. https://doi.org/10.1111/j.1469-7998.2006.00128.x

Stewart, J. D., Durban, J. W., Knowlton, A. R., Lynn, M. S., Fearnbach, H., Barbaro, J., Perryman, W. L., Miller, C. A., & Moore, M. J. (2021). Decreasing body lengths in north Atlantic right whales. *Current Biology*, *31*(14), 3174-3179.e3. https://doi.org/10.1016/j.cub.2021.04.067

Stockin, K. A., Lusseau, D., Binedell, V., Wiseman, N., & Orams, M. B. (2008). Tourism affects the behavioural budget of the common dolphin *Delphinus* sp. in the Hauraki

Gulf, New Zealand. *Marine Ecology Progress Series*, *355*, 287–295. https://doi.org/10.3354/meps07386

Stower, W., Davies, D., & Jones, I. (1960). Morphometric studies of the desert locust, *Schistocerca gregaria* (Forsk.). *The Journal of Animal Ecology*, *29*(2), 309–339. https://doi.org/10.2307/2206

Strong, J. S., Weladji, R. B., Holand, Ø., Røed, K. H., & Nieminen, M. (2017). Personality and fitness consequences of flight initiation distance and mating behavior in subdominant male reindeer (*Rangifer tarandus*). *Ethology*, *123*(6–7), 484–492. https://doi.org/10.1111/eth.12619

Sullivan, F. A., & Torres, L. G. (2018). Assessment of vessel disturbance to gray whales to inform sustainable ecotourism. *Journal of Wildlife Management*, *82*(5), 896–905. https://doi.org/10.1002/jwmg.21462

Technavio. (2022). *Sustainable Tourism Market 2023-2027.*

Thomas, P. O., Reeves, R. R., & Brownell, R. L. (2016). Status of the world's baleen whales. *Marine Mammal Science*, *32*(2), 682–734. https://doi.org/10.1111/mms.12281

Thorpe, W. (1963). *Learning and instinct in animals* (2nd ed.). Methuen.

Tomilin, A. G. (1967). Mammals of the USSR and adjacent countries. vol. 9, Cetacea. *Israel Program Sci. Transl*, 1124.

Tonga Tourism Authority. (2014). *Swim with whales; swim with the whales in Tonga.* Retrieved from http://www.tongaholiday.com

Torres, L. G., Barlow, D. R., Chandler, T. E., & Burnett, J. D. (2020). Insight into the kinematics of blue whale surface foraging through drone observations and prey data. *PeerJ*, *2020*(4). https://doi.org/10.7717/peerj.8906

Torres, L. G., Bird, C. N., Rodríguez-González, F., Christiansen, F., Bejder, L., Lemos, L., Urban R, J., Swartz, S., Willoughby, A., Hewitt, J., & Bierlich, KC. (2022). Range-wide comparison of gray whale body condition reveals contrasting sub-population health characteristics and vulnerability to environmental change. *Frontiers in Marine Science*, *9*. https://doi.org/10.3389/fmars.2022.867258

Torres, W., & Bierlich, K. (2020). MorphoMetriX: a photogrammetric measurement GUI for morphometric analysis of megafauna. *Journal of Open Source Software*, *5*(45), 1825. https://doi.org/10.21105/joss.01825

Tseng, Y. P., Huang, Y. C., Kyle, G. T., & Yang, M. C. (2011). Modeling the impacts of cetacean-focused tourism in Taiwan: Observations from cetacean-watching boats: 2002-2005. *Environmental Management*, *47*(1), 56–66. https://doi.org/10.1007/s00267-010-9567-2

Tulloch, V. J., Plagányi, É., Brown, C., Richardson, A., & Matear, R. (2019). Future recovery of baleen whales is imperiled by climate change. *Global Change Biology*, 1–19. https://doi.org/10.1111/GCB.14573

Urian, K., Gorgone, A., Read, A., Balmer, B., Wells, R. S., Berggren, P., Durban, J., Eguchi, T., Rayment, W., & Hammond, P. S. (2015). Recommendations for photo-identification methods used in capture-recapture models with cetaceans. *Marine Mammal Science*, *31*(1), 298–321. https://doi.org/10.1111/mms.12141

Valentine, P., Birtles, A., Curnock, M., Arnold, P., & Dunstan, A. (2004). Getting closer to whales - passenger expectations and experiences, and the management of swim with dwarf minke whale interactions in the Great Barrier Reef. *Tourism Management*, *25*, 647–655. https://doi.org/10.1016/j.tourman.2003.09.001

Valenzuela, L. O., Sironi, M., Rowntree, V. J., & Seger, J. (2009). Isotopic and genetic evidence for culturally inherited site fidelity to feeding grounds in southern right whales (*Eubalaena australis*). *Molecular Ecology*, *18*(5), 782–791. https://doi.org/10.1111/j.1365-294X.2008.04069.x van Aswegen, M., Christiansen, F., Symons, J., Mann, J., Nicholson, K., Sprogis, K. R., & Bejder, L. (2019). Morphological differences between coastal bottlenose dolphin (*Tursiops aduncus*) populations identified using non-invasive stereo-laser photogrammetry. *Scientific Reports*, *9*(1). https://doi.org/10.1038/s41598-019-48419-3

van Weelden, C., Towers, J. R., & Bosker, T. (2021). Impacts of climate change on cetacean distribution, habitat and migration. *Climate Change Ecology*, *1*(April), 100009. https://doi.org/10.1016/j.ecochg.2021.100009

Vermeulen, E., Cammareri, A., & Holsbeek, L. (2012). Alteration of southern right whale (*Eubalaena australis*) behaviour by human-induced disturbance in Bahía San Antonio, Patagonia, Argentina. *Aquatic Mammals*, *38*(1), 56–64. https://doi.org/10.1578/AM.38.1.2012.56

Vermeulen, E., Thavar, T., Glarou, M., Ganswindt, A., & Christiansen, F. (2023). Decadal decline in maternal body condition of a southern ocean capital breeder. *Scientific Reports*, *13*(1), 3228. https://doi.org/10.1038/s41598-023-30238-2

West, G. B., Brown, J. H., & Enquist, B. J. (1997). A general model for the origin of allometric scaling laws in biology. *Science*, *276*(5309), 122–126. https://doi.org/10.1126/science.276.5309.122

Weston, M. A., Mcleod, E. M., Blumstein, D. T., & Guay, P. J. (2012). A review of flight-initiation distances and their application to managing disturbance to Australian birds. *Emu*, *112*(4), 269–286. https://doi.org/10.1071/MU12026

White, J. R., Meekan, M. G., McCormick, M. I., & Ferrari, M. C. O. (2013). A comparison of measures of boldness and their relationships to survival in young fish. *PLoS ONE*, *8*(7). https://doi.org/10.1371/journal.pone.0068900

Whitehead, H. (2001). Direct estimation of within-group heterogeneity in photo-identification of sperm whales. *Marine Mammal Science*, *17*(4), 718–728. https://doi.org/10.1111/j.1748-7692.2001.tb01295.x

Whitehead, H., & Payne, R. (1978). New techniques for assessing populations of right whales without killing them. *Mammals in the Seas: Report*, *3*(5), 189.

Williams, R., Bain, D. E., Smith, J. C., & Lusseau, D. (2009). Effects of vessel on behaviour patterns of individual southern resident killer whales *Orcinus orca*. *Endangered Species Research*, *6*(3), 199–209. https://doi.org/10.3354/esr00150

Williams, R., Hedley, S. L., & Hammond, P. S. (2006). Modeling distribution and abundance of Antarctic baleen whales using ships of opportunity. *Ecology and Society*, *11*(1). https://doi.org/10.5751/ES-01534-110101

Williams, R., Trites, A., & Bain, D. (2002). Behavioural responses of killer whales (*Orcinus orca*) to whale-watching boats: opportunistic observations and experimental approaches. *Journal of Zoology*, *256*, 255–270. https://doi.org/10.1017/S0952836902000298

Williamson, G. R. (1975). Minke whales off Brazil. *Scientific Reports of the Whales Research Institute*, *27*, 37–59.

Williamson, M. J., ten Doeschate, M. T. I., Deaville, R., Brownlow, A. C., & Taylor, N. L. (2021). Cetaceans as sentinels for informing climate change policy in UK waters. *Marine Policy*, *131*, 104634. https://doi.org/10.1016/J.MARPOL.2021.104634

Wilson, D. S., Clark, A. B., Coleman, K., & Dearstyne, T. (1994). Shyness and boldness in humans and other animals. *Trends in Ecology & Ecolution*, *9*(11), 442–446. https://doi.org/10.1016/0169-5347(94)90134-1

Wingfield, J. C., Hegner, R. E., & Dufty, A. M. (1990). The “challenge hypothesis”: theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. In *Ball Source: The American Naturalist* (Vol. 136, Issue 6). https://doi.org/10.1086/285134

Woinarski, J., Burbidge, A., Harrison, P., & Milne, D. (2014). *The Action Plan for Australian Mammals 2012*.

Wong, J. B., & Auger-Méthé, M. (2018). Using laser photogrammetry to measure long-finned pilot whales (*Globicephala melas*). *Proceedings of the Nova Scotian Institute of Science*, *49*(2), 269–291. https://doi.org/10.15273/pnsis.v49i2.8164

Wong, S. N. P., & Whitehead, H. (2014). Seasonal occurrence of sperm whales (Physeter macrocephalus) around Kelvin Seamount in the Sargasso Sea in relation to oceanographic processes. *Deep-Sea Research Part I: Oceanographic Research Papers*, *91*, 10–16. https://doi.org/10.1016/j.dsr.2014.05.001

Woodward, B. L., Winn, J. P., & Fish, F. E. (2006). Morphological specializations of baleen whales associated with hydrodynamic performance and ecological niche. *Journal of Morphology*, *267*, 1284–1294. https://doi.org/10.1002/jmor

Würsig, B., & Würsig, M. (1977). The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). *Science*, *4318*, 755–756. https://doi.org/10.1126/science.198.4318.755

Yablokov, A. V. (1994). Validity of whaling data. *Nature*, *367*, 108. https://doi.org/10.1038/367108a0

Yahn, S. N., Baird, R. W., Mahaffy, S. D., & Robertson, K. M. (2023). Sexually dimorphic characteristics of short-finned pilot whales, false killer whales, pygmy killer whales, and melon-headed whales assessed using fin and body morphometrics from photographs taken at sea. *Marine Mammal Science*, *39*(1), 98–113. https://doi.org/10.1111/mms.12963

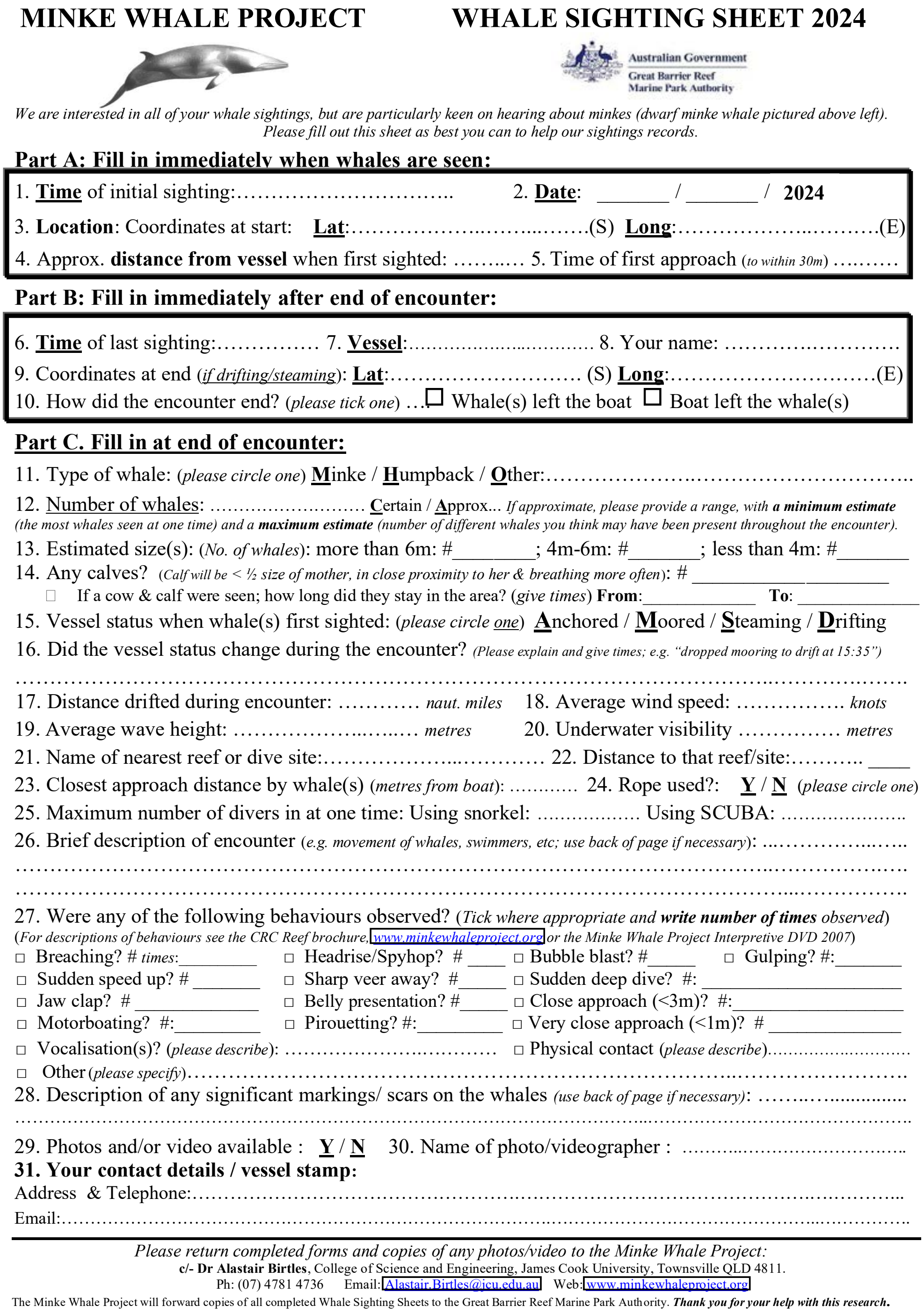
Zerbini, A., Secchi, E., Siciliano, S., & Simoes-Lopes, P. (1997). A review of the occurrence and distribution of whales of the genus *Balaenoptera* along the Brazilian coast. *Reports of the International Whaling Commission*, *47*, 407–417.

Zhang, C., Zhou, H., Christiansen, F., Hao, Y., Wang, K., Kou, Z., Chen, R., Min, J., Davis, R., & Wang, D. (2023). Marine mammal morphometrics: 3D modeling and estimation validation. *Frontiers in Marine Science*, *10*. https://doi.org/10.3389/fmars.2023.1105629

Zoidis, A. M., Lomac-MacNair, K. S., Chomos-Betz, A. E., Day, A. J., & McFarland, A. S. (2014). Effects of sex, seasonal period, and sea state on calf behavior in Hawaiian humpback whales (*Megaptera novaeangliae*). *Aquatic Mammals*, *40*(1), 44–58. https://doi.org/10.1578/AM.40.1.2014.44

Zuur, A., Ieno, E., Walker, N., Saveliev, A., & Smith, G. (2009). *Mixed effects models and extensions in ecology with R* (Vol. 574). Springer New York. https://doi.org/10.1007/978-0-387-87458-6

Appendix A: Whale Sighting Sheet



MINKE WHALE PROJECT **WHALE SIGHTING SHEET 2024**

Australian Government
Great Barrier Reef
Marine Park Authority

We are interested in all of your whale sightings, but are particularly keen on hearing about minkes (dwarf minke whale pictured above left).
Please fill out this sheet as best you can to help our sightings records.

Part A: Fill in immediately when whales are seen:

1. **Time** of initial sighting:…………………………….. 2. **Date**: _______ / _______ / **2024**

3. **Location**: Coordinates at start: **Lat**:………………..……...…….(S) **Long**:………………..……….(E)

4. Approx. **distance from vessel** when first sighted: ……..… 5. Time of first approach (*to within 30m*) ….……

Part B: Fill in immediately after end of encounter:

6. **Time** of last sighting:…………… 7. **Vessel**:.................................. 8. Your name: ………….……………

9. Coordinates at end (*if drifting/steaming*): **Lat**:………………………. (S) **Long**:…………………………(E)

10. How did the encounter end? (*please tick one*) …☐ Whale(s) left the boat ☐ Boat left the whale(s)

Part C. Fill in at end of encounter:

11. Type of whale: (*please circle one*) **M**inke / **H**umpback / **O**ther:…………………….…………………………..

12. Number of whales: ……………….……… **C**ertain / **A**pprox... *If approximate, please provide a range, with* ***a minimum estimate*** *(the most whales seen at one time) and a* ***maximum estimate*** *(number of different whales you think may have been present throughout the encounter).*

13. Estimated size(s): (*No. of whales*): more than 6m: #________; 4m-6m: #_______; less than 4m: #_______

14. Any calves? (*Calf will be < ½ size of mother, in close proximity to her & breathing more often*): # ____________________

☐ If a cow & calf were seen; how long did they stay in the area? (*give times*) **From**:____________ **To**: _____________

15. Vessel status when whale(s) first sighted: (*please circle one*) **A**nchored / **M**oored / **S**teaming / **D**rifting

16. Did the vessel status change during the encounter? (*Please explain and give times; e.g. "dropped mooring to drift at 15:35"*)

……………………………………………………………………………………………………..……………….……

17. Distance drifted during encounter: ………… *naut. miles* 18. Average wind speed: ……………. *knots*

19. Average wave height: ………………..…..… *metres* 20. Underwater visibility …………… *metres*

21. Name of nearest reef or dive site:………………...………… 22. Distance to that reef/site:……….. ____

23. Closest approach distance by whale(s) (*metres from boat*): ………… 24. Rope used?: **Y** / **N** (*please circle one*)

25. Maximum number of divers in at one time: Using snorkel: ……………… Using SCUBA: …………………

26. Brief description of encounter (*e.g. movement of whales, swimmers, etc; use back of page if necessary*): ..……………..…..

……………………………………………………………………………………………………..………………..…

……………………………………………………………………………………………………...………………

27. Were any of the following behaviours observed? (*Tick where appropriate and* ***write number of times*** *observed*)
(*For descriptions of behaviours see the CRC Reef brochure,* *www.minkewhaleproject.org* *or the Minke Whale Project Interpretive DVD 2007*)

☐ Breaching? # *times*:________
☐ Sudden speed up? # _______
☐ Jaw clap? # _____________
☐ Motorboating? #:_________
☐ Headrise/Spyhop? # ____
☐ Sharp veer away? #_____
☐ Belly presentation? #_____
☐ Pirouetting? #:_________
☐ Bubble blast? #_____
☐ Sudden deep dive? #: ____________________
☐ Close approach (<3m)? #:_________________
☐ Very close approach (<1m)? # ______________
☐ Gulping? #:_______
☐ Vocalisation(s)? (*please describe*): ……………………..………
☐ Physical contact (*please describe*)...........................
☐ Other (*please specify*)…………………………………………………………………..……………………

28. Description of any significant markings/ scars on the whales (*use back of page if necessary*): ……..….................

……………………………………………………………………………………...……………………………….

29. Photos and/or video available : **Y** / **N** 30. Name of photo/videographer : ………..……………………..

31. Your contact details / vessel stamp:

Address & Telephone:…………………………………….……………………………………………….……………...

Email:………………………………………………………………..…………………………………...……………..

Please return completed forms and copies of any photos/video to the Minke Whale Project:
c/- **Dr Alastair Birtles**, College of Science and Engineering, James Cook University, Townsville QLD 4811.
Ph: (07) 4781 4736 Email: Alastair.Birtles@jcu.edu.au Web: www.minkewhaleproject.org

The Minke Whale Project will forward copies of all completed Whale Sighting Sheets to the Great Barrier Reef Marine Park Authority. ***Thank you for your help with this research.***

Figure A: Whale Sighting Sheet used to record basic encounter and environmental data for every permitted swim-with dwarf minke whale interaction in the Great Barrier Reef. Note the 2024 version of this data sheet is identical to the 2017, 2018, and 2019 versions used in this thesis.

Appendix B: Image grading for photo-identification of dwarf minke whales

Table B1: *Cumulative scoring scale to assess image quality for photo-identification of dwarf minke whales. Developed by Arnbom (1987), updated by Sobtzick (2010). Imagery achieving an overall score below Category 3 was rejected to reduce error.*

	5 points	**4 points**	**3 points**	**2 points**	**1 point**
Focus	In focus with clear grain	Good focus and grain with only minimal loss in quality	Fair focus and grain, some loss in ability to discern markings	Poor focus and grain with significant loss in clarity	Out of focus/grainy
Lighting/ exposure/ reflections	Excellent, no backlighting, over-exposure, or reflections	Good, very little backlighting, over-exposure, or reflections	Fair, some backlighting, over-exposure, or reflections	Poor, a lot of backlighting, over-exposure, or reflections	Very poor, strong backlighting, over-exposure, or reflections

Category 5:	**Excellent**	(10 points)
Category 4:	**Good**	(8 – 9 points)
Category 3:	**Moderate**	(6 – 7 points)
Category 2:	**Poor**	(4 – 5 points)
Category 1:	**Very poor**	(2 – 3 points)

Table B2: *Evaluation of the information content of imagery for photo-identification of dwarf minke whales. Developed by Arnbom (1987), updated by Sobtzick (2010).*

	Category 5	**Category 4**	**Category 3**	**Category 2**	**Category 1**
Photo-identification information content	Very much information, e.g., close-up of shoulder area or close-up of very distinct scar	Much information, e.g., close lateral shot of whale with multiple patterns or scars	Moderate information, e.g., distant shot of whole whale lateral view or top-side shot of whale	Little information, e.g., indistinct scar or pattern	No information, e.g., tail fluke without markings or scars

Appendix C: Total body length (TBL) measurements

Table C: *Summary of total body length (TBL) measurements for whales with replicate measurements.* SD = *standard deviation,* SE = *standard error,* CV = *coefficient of variation.*

Stereo-videogrammetry (2017)					
Whale ID	***n***	**Mean TBL (m)**	***SD* (m)**	***SE***	***CV* (%)**
MW3102	*2*	6.141	*0.166*	*0.117*	*2.70*
MW3104	*3*	6.098	*0.014*	*0.008*	*0.24*
MW3108	*3*	6.702	*0.041*	*0.024*	*0.61*
MW3302	*3*	5.478	*0.047*	*0.027*	*0.85*
MW3416	*2*	6.489	*0.008*	*0.006*	*0.13*
MW3417	*4*	6.780	*0.146*	*0.073*	*2.15*
MW3424	*3*	6.740	*0.036*	*0.021*	*0.54*
MW3430	*6*	5.893	*0.060*	*0.025*	*1.03*
MW3455	*4*	5.529	*0.046*	*0.023*	*0.83*
MW3459	*4*	7.105	*0.061*	*0.031*	*0.86*
MW3463	*2*	6.876	*0.036*	*0.026*	*0.53*
MW3493	*3*	5.915	*0.078*	*0.045*	*1.33*
MW3497	*2*	5.001	*0.052*	*0.037*	*1.04*
MW3498	*3*	7.169	*0.092*	*0.053*	*1.29*
SH001	*4*	7.021	*0.106*	*0.053*	*1.50*
SH002	*2*	6.868	*0.030*	*0.021*	*0.44*
SH003	*8*	5.560	*0.106*	*0.037*	*1.90*
SH004	*7*	5.305	*0.114*	*0.043*	*2.15*
SH005	*3*	6.961	*0.102*	*0.059*	*1.46*
SH015	*5*	5.535	*0.115*	*0.051*	*2.07*
SH016	*3*	5.746	*0.007*	*0.004*	*0.12*
SH100	*4*	5.341	*0.047*	*0.024*	*0.89*
					Overall mean *CV* ***1.12%***
Single-camera videogrammetry (Sobtzick, 2010)					
Whale ID (year measured if multiple years)	***n***	**Mean TBL (m)**	***SD* (m)**	***SE***	***CV* (%)**

3	*2*	5.36	*0.049*	*0.035*	*0.92*
4 (2006)	*6*	5.85	*0.122*	*0.05*	*2.09*
4 (2007)	*7*	6.43	*0.132*	*0.05*	*2.06*
5	*6*	6.51	*0.147*	*0.06*	*2.26*
8	*2*	5.59	*0.007*	*0.005*	*0.13*
11	*11*	4.68	*0.166*	*0.05*	*3.54*
17	*2*	5.15	*0.134*	*0.095*	*2.61*
18	*9*	7.12	*0.12*	*0.04*	*1.69*
19	*13*	5.53	*0.108*	*0.03*	*1.96*
23	*4*	4.4	*0.02*	*0.01*	*0.46*
24	*4*	4.57	*0.02*	*0.01*	*0.44*
25	*3*	5.8	*0.139*	*0.08*	*2.39*
27	*8*	5.65	*0.113*	*0.04*	*2.00*
34	*3*	6.21	*0.035*	*0.02*	*0.56*
42	*4*	5.56	*0.08*	*0.04*	*1.44*
46 (2004)	*3*	5.44	*0.156*	*0.09*	*2.87*
46 (2007)	*4*	6.01	*0.12*	*0.06*	*2.00*
48 (2006)	*3*	6.14	*0.208*	*0.12*	*3.39*
48 (2007)	*5*	6.33	*0.089*	*0.04*	*1.41*
51	*2*	5.18	*0.17*	*0.12*	*3.28*
54	*3*	6.7	*0.173*	*0.1*	*2.59*
55	*17*	6.04	*0.124*	*0.03*	*2.05*
56 (2006)	*18*	6.23	*0.127*	*0.03*	*2.04*
56 (2007)	*2*	6.64	*0.184*	*0.13*	*2.77*
57	*2*	6.66	*0.134*	*0.095*	*2.02*
58	*2*	6.69	*0.092*	*0.065*	*1.37*
59	*3*	5.41	*0.087*	*0.05*	*1.60*
62	*3*	4.79	*0.208*	*0.12*	*4.34*
65	*2*	5.76	*0.049*	*0.035*	*0.86*
68	*7*	4.03	*0.106*	*0.04*	*2.63*
71	*3*	7.08	*0.052*	*0.03*	*0.73*
72	*2*	5.09	*0.106*	*0.075*	*2.08*
73	*11*	5.14	*0.099*	*0.03*	*1.94*
76	*3*	6.05	*0.104*	*0.06*	*1.72*

82	*3*	5.22	*0.087*	*0.05*	*1.66*
84	*4*	6.09	*0.06*	*0.03*	*0.99*
90	*7*	5.75	*0.106*	*0.04*	*1.84*
92	*6*	5.41	*0.147*	*0.06*	*2.72*
93	*4*	5.44	*0.06*	*0.03*	*1.10*
94	*7*	5.9	*0.159*	*0.06*	*2.69*
99	*4*	5.79	*0.08*	*0.04*	*1.38*
106	*9*	7	*0.12*	*0.04*	*1.71*
108	*2*	4.54	*0.042*	*0.03*	*0.94*
113	*5*	4.34	*0.112*	*0.05*	*2.58*
117	*2*	5.85	*0.021*	*0.015*	*0.36*
118	*2*	6.94	*0.021*	*0.015*	*0.31*
119	*5*	5.78	*0.089*	*0.04*	*1.55*
125	*4*	5.49	*0.14*	*0.07*	*2.55*
130	*2*	6.58	*0.085*	*0.06*	*1.29*
141	*5*	6.62	*0.112*	*0.05*	*1.69*
143	*3*	5.01	*0.069*	*0.04*	*1.38*
146	*9*	5.71	*0.18*	*0.06*	*3.15*
147	*2*	6.47	*0.071*	*0.05*	*1.09*
156	*2*	5.45	*0.042*	*0.03*	*0.78*
157	*2*	5.26	*0.071*	*0.05*	*1.34*
162	*2*	5.58	*0.007*	*0.005*	*0.13*
163	*3*	5.19	*0.052*	*0.03*	*1.00*
172	*9*	6.18	*0.27*	*0.09*	*4.37*
174	*2*	6.14	*0.071*	*0.05*	*1.15*
183	*3*	6.11	*0.191*	*0.11*	*3.12*
185	*4*	5.37	*0.08*	*0.04*	*1.49*
187	*2*	5.98	*0.028*	*0.02*	*0.47*
188	*3*	6.14	*0.069*	*0.04*	*1.13*
190	*2*	5.51	*0.064*	*0.045*	*1.16*
191	*6*	5.67	*0.196*	*0.08*	*3.46*
192	*6*	4.86	*0.122*	*0.05*	*2.52*
193	*5*	6.05	*0.067*	*0.03*	*1.11*
194	*8*	6.77	*0.226*	*0.08*	*3.34*

195	*2*	5.53	*0.17*	*0.12*	*3.07*
197	*4*	5.87	*0.04*	*0.02*	*0.68*
199	*2*	5.91	*0.113*	*0.08*	*1.91*
200	*3*	4.67	*0.104*	*0.06*	*2.23*
206	*3*	4.8	*0.087*	*0.05*	*1.80*
210	*7*	6.3	*0.132*	*0.05*	*2.10*
211	*10*	6.35	*0.126*	*0.04*	*1.99*
214	*3*	5.42	*0.087*	*0.05*	*1.60*
215	*3*	5.63	*0.139*	*0.08*	*2.46*
216#	*5*	6.02	*0.313*	*0.14*	*5.20*
217	*3*	3.35	*0.087*	*0.05*	*2.59*
218	*3*	4.79	*0.104*	*0.06*	*2.17*
219	*4*	5.12	*0.06*	*0.03*	*1.17*
220	*2*	5.26	*0.042*	*0.03*	*0.81*
221	*2*	6.23	*0.049*	*0.035*	*0.80*
225 (2004)	*9*	6.13	*0.12*	*0.04*	*1.96*
224 (2005)	*2*	6.65	*0.247*	*0.175*	*3.72*
228	*3*	4.77	*0.087*	*0.05*	*1.82*
233	*2*	5.75	*0.163*	*0.115*	*2.83*
238	*4*	6.2	*0.1*	*0.05*	*1.61*
240	*5*	5.5	*0.134*	*0.06*	*2.44*
243	*2*	5.64	*0.021*	*0.015*	*0.38*
244	*6*	5.69	*0.171*	*0.07*	*3.01*
245	*4*	5.23	*0.08*	*0.04*	*1.53*
246	*2*	4.89	*0.035*	*0.025*	*0.72*
247	*3*	6.83	*0.121*	*0.07*	*1.78*
248	*6*	5.88	*0.098*	*0.04*	*1.67*
250	*2*	6.42	*0.177*	*0.125*	*2.75*
254	*34*	5.68	*0.233*	*0.04*	*4.11*
255	*8*	5.77	*0.17*	*0.06*	*2.94*
256	*3*	5.18	*0.017*	*0.01*	*0.33*
R2	*2*	6.77	*0*	*0*	*0.00*
TL3	*2*	4.61	*0.064*	*0.045*	*1.38*
TR14	*2*	5.29	*0.021*	*0.015*	*0.40*

Overall mean *CV*	***1.86%***

Appendix D: Width at widest point (WWP) measurements

Table D: *Summary of measurements of width at the widest point of the body.* SD = *standard deviation,* SE = *standard error,* CV = *coefficient of variation.*

Whale ID	*n*	Mean width (m)	*SD* (m)	*SE*	*CV* (%)
MW3111	*2*	1.006	*0.062*	*0.044*	*6.16%*
SH018	*2*	1.200	*0.014*	*0.010*	*1.12%*
MW3102	*2*	1.007	*0.070*	*0.050*	*6.92%*
MW3019	*1*	0.971	*n/a*	*n/a*	*n/a*
SH017	*1*	1.017	*n/a*	*n/a*	*n/a*
MW3302	*1*	0.906	*n/a*	*n/a*	*n/a*
	Overall	1.018			

Appendix E: Total body length (TBL) measurements of multi-year resighted whales

Appendix E: Total body length (TBL) measurements of all whales re-sighted and measured across multiple years, 2017 – 2019.

Whale ID	Year of first measurement *Mean TBL ± CV*	Year of re-measurement *Mean TBL (m) ± CV%*
MW17010	2018 *6.460 m ± 0.35%*	2019 *6.638 m ± 0.18%*
MW18075	2018 *6.071 m ± 0.08%*	2019 *6.210 m ± 0.42%*
MW3416	2017 *6.518 m ± 0.44%*	2019 *7.098 m ± 0.13%*
MW3427	2017 *6.405 m ± 0.69%*	2018 *6.600 m ± 0.45%*
MW3463	2017 *6.863 m ± 0.29%*	2018 *6.928 m ± 0.30%*
MW3465	2017 *7.102 m ± 0.20%*	2018 *7.570 m ± 0.04%*
MW3583	2017 *6.238 m ± 0.06%*	2019 *6.862 m ± 0.23%*
MW3640	2017 *5.591 m ± 0.16%*	2019 *6.065 m ± 0.07%*
SH003	2017 *5.556 m ± 0.59%*	2019 *6.218 m ± 0.16%*
SH004	2017 *5.234 m ± 0.52%*	2018 *5.638 m ± 0.05%*

Appendix F: Close approaches

Appendix F. All close approaches (i.e., all passes 3 m or less, ± precision, n = 63) measured in the 2017 sampling period. Close approaches per whale are ranked by distance. For sex, U = unknown, M = male, F = female. Shading is alternated by whale.

Approach distance (m)	**Whale ID (pass#/total)**	**Sex**	**Total body length (m)**
1.61	MW20026 (1/4)	F	6.759
2.40	MW20026 (2/4)	F	6.759
2.72	MW20026 (3/4)	F	6.759
2.94	MW20026 (4/4)	F	6.759
2.45	MW20042	U	6.919
2.90	MW21002	F	6.836
1.30	MW21010 (1/12)	M	5.696
1.37	MW21010 (2/12)	M	5.696
1.66	MW21010 (3/12)	M	5.696
1.70	MW21010 (4/12)	M	5.696
1.79	MW21010 (5/12)	M	5.696
1.90	MW21010 (6/12)	M	5.696
1.94	MW21010 (7/12)	M	5.696
2.26	MW21010 (8/12)	M	5.696
2.45	MW21010 (9/12)	M	5.696
2.53	MW21010 (10/12)	M	5.696
2.64	MW21010 (11/12)	M	5.696
2.91	MW21010 (12/12)	M	5.696
2.34	MW3111	U	6.511
2.84	MW3404	F	not measured
1.82	MW3413 (1/4)	M	5.759
2.32	MW3413 (2/4)	M	5.759
2.88	MW3413 (3/4)	M	5.759
3.05	MW3413 (4/4)	M	5.759
1.63	MW3415 (1/2)	F	not measured
2.23	MW3415 (2/2)	F	not measured
2.85	MW3417	U	6.78
1.66	MW3422	U	not measured
1.90	MW3425	U	6.804
2.95	MW3430 (1/2)	F	5.9
3.00	MW3430 (2/2)	F	5.9
0.95	MW3455 (1/3)	U	5.529
1.24	MW3455 (2/3)	U	5.529
3.00	MW3455 (3/3)	U	5.529
2.42	MW3459 (1/2)	U	7.105
2.96	MW3459 (2/2)	U	7.105

2.06	MW3465 (1/3)	F	7.102
2.39	MW3465 (2/3)	F	7.102
2.66	MW3465 (3/3)	F	7.102
0.93	MW3478 (1/2)	U	5.84
3.04	MW3478 (2/2)	U	5.84
2.12	MW3482 (1/3)	F	5.546
2.41	MW3482 (2/3)	F	5.546
2.67	MW3482 (3/3)	F	5.546
2.98	MW3583	F	6.238
1.55	MW3609 (1/2)	U	5.747
2.67	MW3609 (2/2)	U	5.747
1.92	MW3612 (1/3)	U	6.626
2.42	MW3612 (2/3)	U	6.626
2.99	MW3612 (3/3)	U	6.626
2.70	MW3613 (1/2)	U	not measured
3.03	MW3613 (2/2)	U	not measured
1.51	MW3616 (1/5)	M	not measured
2.38	MW3616 (2/5)	M	not measured
2.52	MW3616 (3/5)	M	not measured
2.62	MW3616 (4/5)	M	not measured
2.71	MW3616 (5/5)	M	not measured
1.95	MW3640 (1/4)	U	5.591
2.25	MW3640 (2/4)	U	5.591
2.27	MW3640 (3/4)	U	5.591
3.01	MW3640 (4/4)	U	5.591
2.45	SH005	U	6.961
2.74	SH101	F	not measured