Assessing the effects of whale-based tourism in Vava'u, Kingdom of Tonga:

Behavioural responses of humpback whales to vessel and swimmer approaches

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Abbreviated terms

AGL	Above Ground Level
AIC	Akaike Information Criterion
ASL	Above Sea Level
AT	Approach Type
AUT	Auckland University of Technology
B	Behaviour at the time of the approach
BS	Breeding Stock
BSS	Beaufort Sea State
BVLOS	Beyond Visual Line Of Sight
C	Calf presence
CASA	Civil Aviation Safety Authority (Australia)
CI	Confidence Interval
CoA	Certificate of Authorization
DD	Distance at Drop (swimmers)
DI	Distance (vessel)
DP	Depth
FA	Feeding Area
FAA	Federal Aviation Authority (United States)
FOV	Field of View
Fps	frames per second
GCS	Ground Control Station
GSD	Ground Sample Distance
GLM	Generalized Linear Model
ICAO	International Civil Aviation Organization
IWC	International Whaling Commission
LALE	Low Altitude Long Endurance

LASE	Low Altitude Short Endurance
LM	Linear Model
N	Nurturing
NFZ	No Fly Zone
NOAA	National Oceanic and Atmospheric Administration
P	P value
Ppi	pixels per inch
R	Resting
RPA	Remotely Piloted Aircraft
S	Socialising
SA	Surface-Active
SD	Standard Deviation
SE	Standard Error
SP	Swimmer Placement
T	Traveling
V	Vessel
VLOS	Visual Line Of Sight
VTOL	Vertical Take-Off and Landing
UAS	Unmanned Aerial System
UAV	Unmanned Aerial Vehicle

Attestation of authorship

I hereby declare that this submission is my work and that, to the best of my knowledge and belief, it contains no material previously written or published by another person, nor material that to a substantial extent has been submitted for the award of any other degree or diploma of a university or other institute of higher learning.

Lorenzo Fiori

19th August 2019

Co-authored works

Chapters 2.2, 3, 4 and 5 of this thesis represent a technical note and three separate original studies that have been published on peer-reviewed journals. All the co-authors have approved the inclusion of the joint work in this doctoral thesis.

Technical Note

The use of Unmanned Aerial Systems (UAS) in marine mammal research (Chapter 2.2).

Lorenzo Fiori conceived and wrote the paper (92%); Emmanuelle Martinez (5%) edited the manuscript; Ashray Doshi (1%) and Barbara Bollard (1%) reviewed the technical data presented in the manuscript; Mark B. Orams (1%) reviewed the manuscript.

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Mark B. Orams

Study I

Insights into the use of an unmanned aerial vehicle (UAV) to investigate the behaviour of humpback whales (Chapter 3).

Lorenzo Fiori conceived the survey design, conducted the data collection, analysed the data and wrote the paper (88%); Emmanuelle Martinez (5%) helped conceived the survey design and edited the manuscript; Martin K.-F. Bader assisted with the data analysis process and provided statistical advise (5%); Mark B. Orams (1%) and Barbara Bollard (1%) provided feedback on the survey design and reviewed the manuscript.

Emmanuelle Martinez	Martin K.-F. Bader
Barbara Bollard	Mark B. Orams

Study II

Effects of whale-based tourism in Vava'u, Kingdom of Tonga: Behavioural responses of humpback whales to vessel and swimming tourism activities (Chapter 4)

Lorenzo Fiori conceived the survey design, conducted the data collection, analysed the data and wrote the paper (94%); Emmanuelle Martinez (4%) helped conceive the survey design and edited the manuscript; Mark B. Orams (1%) and Barbara Bollard (1%) helped conceive and plan the research design and they each edited the manuscript.

Emmanuelle Martinez Barbara Bollard Mark B. Orams

Study III

Using unmanned aerial vehicles (UAVs) to assess humpback whale behavioural responses to swim-with interactions in Vava'u, Kingdom of Tonga (Chapter 5).

Lorenzo Fiori conceived the survey design, conducted the data collection, analysed the data and wrote the paper (94%); Emmanuelle Martinez (4%) helped conceived the survey design and edited the manuscript; Mark B. Orams (1%) and Barbara Bollard (1%) helped conceive and plan the research design and they each edited the manuscript.

Emmanuelle Martinez Barbara Bollard Mark B. Orams

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Finally, I wish to thank the people of Vava'u, Kingdom of Tonga.

Malo 'aupito, this work is dedicated to you and to the whales of Tonga.

Ofa atu, alu'a!

Ethic statement

The animal ethic assessment took place in the preliminary phases of this study. Auckland University of Technology refers to the Animal Ethic Committee of University of Auckland. A detailed outline of the study was provided and animal ethics were not deemed necessary by the Committee as the aim of this research was to conduct an observational study. The swim-with interactions observed were conducted by licensed Tongan tour operators and the researcher/s did not enter the water in presence of the whales at any time during the data collection process. Moreover, the Unmanned Aerial Vehicles (UAVs) used to observe whales' behaviour were flown at an altitude of 30 metres above sea level at all times with no intent to further approach the whales. Potential disturbance to the whales was also assessed by this study and the results were compatible with no effects on whales' behaviour.

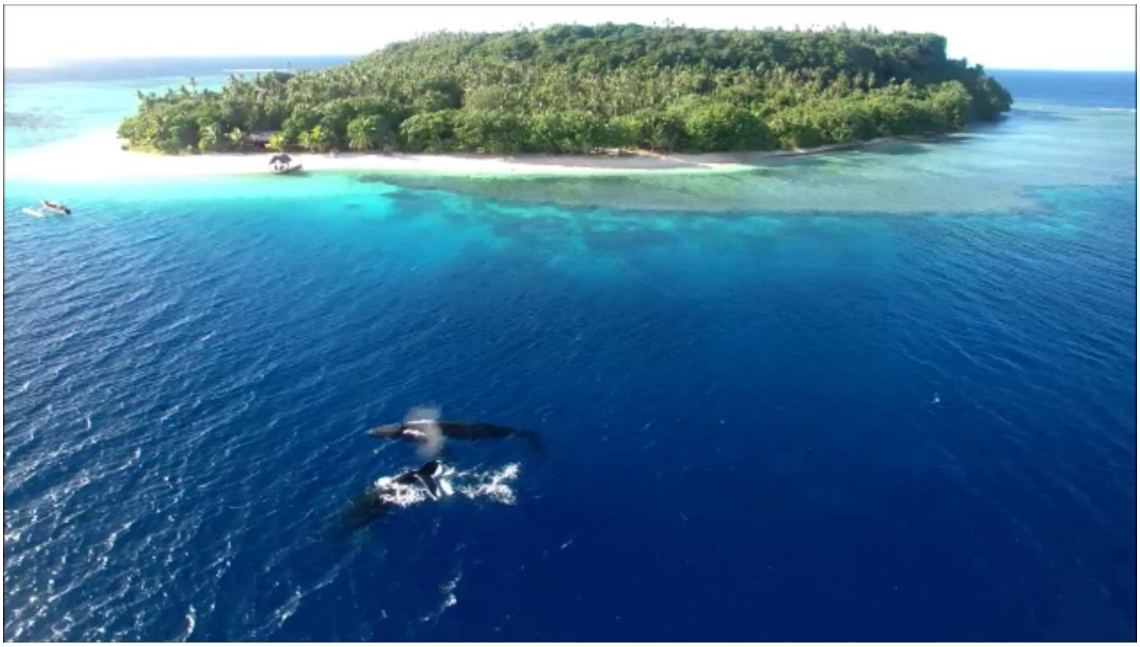
Abstract

Vava'u, Kingdom of Tonga, is a well-established whale-watching destination in the South Pacific. Between July and October, the waters around the archipelago represent one of the major breeding grounds for Oceania humpback whales (*Megaptera novaeangliae*). The Tongan government allows in-water interactions with whales and tour operators strongly promote the practice of swimming with whales, targeting mother-calf pairs in particular. However, there is increasing evidence, derived from empirical research on swim-with-cetaceans tourism, that this kind of interaction affects cetacean behaviour and can have negative effects on the cetaceans involved. This study represents the first empirical assessment of humpback whales' behavioural responses to the approach of vessels and swimmers in Vava'u. A large part of the data collection has been conducted using a lightweight Unmanned Aerial Vehicle (UAV) to observe interactions from an aerial perspective. Fifty-six surveys took place during the 2016 and 2017 whale breeding seasons aboard dedicated research and swim-with-whales vessels. Specifically, data collected included whales' dive time, number of reorientation events, and respiration rates in the absence and in the presence of boats and swimmers. Additionally, aerial videos of whales' behaviour and interactions with swimmers were recorded with the use of a Vertical Take-Off and Landing (VTOL) UAV flown at 30 metres altitude. Vessel approach type and swimmer distance to whales were also noted.

The comparison between UAV data collection methods and standard boat-based observation highlights how the aerial perspective provided by the UAV allows for a more precise assessment of whales' behavioural state. In particular, important intraspecific interactions, such as nurturing and socialising, were detected more frequently and accurately via UAV than by boat-based observations. Furthermore, the data collected showed no signs of behavioural responses from the whales to the UAV flying at an altitude of 30 metres.

With regard to whales' responses to vessels and swimmers, results indicate that the proportion of time spent diving in the presence of in-water tourism activities increased significantly for mother-calf pairs. While the average mother dive time increased three-fold in presence of swimmers, the calf dive time did not differ from control data when there were no swimmers in the water. That is, calves spent a significantly higher proportion of time at the surface than their mothers during in-water tourism activities. The data also indicated that calves significantly reduced their number of respirations. Avoidance responses and significant changes in time spent in different behavioural states were recorded as a response to the vessels and swimmers. For instance, mother-calf pairs had a decreased proportion of time spent nurturing while the time spent travelling increased when approached by swimmers. Other observations of the whales included an increase of agonistic behaviours directed towards swimmers, putting swimmers at risk of injury. Finally, extremely low levels of compliance to existing Tongan swim-with-whales regulations were documented. That is, the minimum resting period between interactions was frequently disregarded and consecutive swims from different tour operators (also referred to as queueing) was regularly observed. These findings should be carefully considered by Tongan stakeholders and other governments of countries that allow in-water interactions between tourists and whales. Measures to reduce the risk of negative impacts on the targeted cetaceans, and the potential for life-threatening injuries to tourists, should be implemented.

Chapter - 1 - Introduction



Chapter 1 cover picture. A couple of adult humpback whales (*Megaptera novaeangliae*) dives in front of Eueiki Island (18°45′ S, 174°01′ E), Vava’u, Kingdom of Tonga. Frame extracted from the aerial videos recorded by the UAV during this study.

Cetaceans have been captivating human interest worldwide throughout the ages for commercial, social, and scientific reasons (Orams, 2002). Whaling was an important economic resource for coastal communities, until the collapse of whale stocks forced the International Whaling Commission (IWC) to ban the intentional harvesting of whales in 1986. Since then, tourism based on whale-watching has grown on a global scale (O'Connor, Campbell, Cortez, & Knowels, 2009). Amongst the many cetacean species focus of whale-watching activities, humpback whales (*Megaptera novaeangliae*) and their complex repertoire of aerial behaviours, such as breaches, peduncle slaps, pectoral and fluke slaps, are the most popular (Clapham, 2008). Their predictable coastal migratory routes also make humpback whales an ideal focus for the whale-based commercial tourism industry. These factors, as well as their global distribution, have contributed to making humpback whales the most frequently targeted species for whale-watching (O'Connor et al., 2009) and swim-with-whales (Hendrix & Rose, 2014) tourism operations worldwide.

The end of commercial whaling has resulted in a population recovery for some species of baleen whales, including humpback whales (Magera, Flemming, Kaschner, Christensen, & Lotze, 2013). However, concerns have been raised regarding the effect the growing demand for tourist interactions with free-ranging cetaceans has on wild populations over a long-term timeframe (Higham & Bejder, 2008). In the last three decades a number of researchers have investigated cetacean reactions to tourism activities (refer to section 2.2, p. 21, for a comprehensive literature review) but have been mostly limited to the observation of behavioural changes induced by vessel and human (i.e., swimmer) approaches. In contrast, some studies on land mammals have assessed both physiological (i.e., heart rate) and behavioural predator responses (i.e., alert/flight response) to anthropogenic stimuli and have found that changes at the physiological level do not necessarily correspond to behavioural clues (e.g., MacArthur, Geist, & Johnston, 1982; Ditmer et al., 2015). While the study of physiological responses in wild cetaceans exposed to human activities might be possible in the future, the technological advancement of non-invasive research methodologies such as unmanned aerial vehicles can improve our understanding of cetacean behaviour (Nowacek et al., 2016). This might help providing important information for the management of whale-watching and swim-with-whale tourism activities and mitigating potential long-term consequences for the species focus of this growing industry.

1.1 Rationale and significance of the study

Vava'u, a northern archipelago of the Kingdom of Tonga, is an important breeding ground for the endangered Oceania humpback whales (Childerhouse et al., 2008). From July to October, the sheltered waters between the islands of Vava'u represent a major calving site for the Tongan sub-population of the South Pacific humpbacks (Baker et al., 1998). Humpback whales frequently show inquisitive behaviour when in the presence of boats, and the opportunity for close encounters has supported the growth of the Vava'u whale-watching industry (O'Connor et al., 2009). Moreover, the Kingdom of Tonga is one of the few countries worldwide that permits people to swim with humpback whales for recreational purposes (Hendrix & Rose, 2014). The opportunity to approach the whales in the water is one of the key aspects that draws whale-watchers and tourists to Vava'u (Orams, 2002).

Between 1998 and 2006, the annual number of whale-watchers visiting Tonga has increased five-fold, reaching up to 10,000 participants and contributing around 15% of the total Tongan foreign income (O'Connor et al., 2009). Following the growing demand for in-water interaction with whales, the number of tour operators in Tonga has dramatically increased. In 1993, there was only one licensed boat in Vava'u (Kessler, Harcourt, & Heller, 2013), and by 2017 the island group had 20 tour operators holding permits to conduct in-water cetacean-based interactive activities (Tongan Ministry of Tourism, personal communication, 8 October, 2017). With a permit, each whale tour operator can utilise up to two boats simultaneously, every day, during whale season. Activities and especially interactions with whales are controlled by the *Tonga Whale Watching and Swimming Regulations 2013* (2013).

Despite attempts to manage the potential negative effects of whale-based tourism in Tonga through these regulations, Walker & Moscardo (2011) documented low levels of compliance with both the official regulations and guidelines by Vava'u tour operators. Along with a low compliance with regulations, tour operators often focus on whale mother-calf pairs, a scenario which some authors have identified is more likely to disrupt important parental behaviours and activities (e.g., Kessler et al., 2013; Mangott, Birtles, & Marsh, 2011). In the growing peer-reviewed research literature on swim-with-cetacean tourism there is increasing evidence that such activities are not benign (e.g., Constantine, 2001; Filby, Stockin, & Scarpaci, 2014; Fumagalli et al., 2018; Lundquist et al., 2013; Martinez, Orams, & Stockin, 2010; Peters, Parra, Skuza, & Möller, 2012). That is, these activities affect cetacean behaviour and could be detrimental to the species which are targeted by tour operators (Orams, Forestell, & Springs, 2014). Because of the potential negative consequences of in-water cetacean-human interactions, some countries have banned such tourism, particularly for the larger cetacean species of baleen whales (e.g., USA, UK) (Carlson, 2013).

The growth of in-water tourism activities targeting humpback whales in countries such as Tonga (and also more recently in Australia) is occurring without any empirical data on the effects of these interactions (Hendrix & Rose, 2014). This lack of knowledge about the effects of swim-with-humpback whales tourism contrasts with the wider literature reporting on short-term changes in behaviour in humpback whales subjected to boat-based whale-watching tourism (Avila, Correa, & Parsons, 2015; Baker & Herman, 1989; Corkeron, 1995; Schaffar, Madon, Garrigue, & Constantine, 2010; Scheidat, Castro, Gonzalez, & Williams, 2004; Sousa-Lima, Morete, Fortes, Freitas, & Engel, 2002; Stamation, Croft, Shaughnessy, Waples, & Briggs, 2010). There are also a range of studies which report on the behavioural effects of whale-watching and swim-with-dolphins tourism on other cetacean species (Arias et al., 2018; Cecchetti, Stockin, Gordon, & Azevedo, 2017; Christiansen, Lusseau, Stensland, & Berggren, 2010; Constantine, 2001; Lundquist, Gemmell, & Würsig, 2012; Lusseau, 2003; Lusseau, Bain, Williams, & Smith, 2009; Neumann & Orams, 2005; Pirotta, Merchant, Thompson, Barton, & Lusseau, 2015; Scarpaci, Bigger, Corkeron, & Nugegoda, 2000; Stockin, Lusseau, Binedell, Wiseman, & Orams, 2008; Tyne, Christiansen, Heenehan, Johnston, & Bejder, 2018; Williams, Trites, & Bain, 2002).

The lack of research into the effects of swim-with-humpback whales tourism occurs within the context of an Oceania humpback whale metapopulation (IWC breeding stocks E2, E3 and F), which has an estimated population of 4,329 individuals, of which the Tongan breeding sub-stock (E3) represents almost half (Constantine et al., 2012). This population is a small fraction of the pre-whaling numbers and despite the frequency of South Pacific humpback whale sightings in some island groups over the breeding season, the population shows little to no signs of recovery from the near population collapse caused by whaling (Constantine et al., 2012).

Given this background, this doctoral research project addresses the following important question: What are the effects of in-water tourism activities and vessel approaches on the behaviour of humpback whales in Vava'u, Kingdom of Tonga? The study seeks to answer this question and to consider the potential long-term consequences of these tourism interactions on the Tongan humpback whale population. In addition, the research presented in this thesis provides information for government conservation agencies which can help inform the development and implementation of management approaches for swim-with-whales tourism. Finally, a large part of the data collection for this doctoral research was performed using lightweight commercially available UAVs. The value of the use of this technology for cetacean behaviour research has been assessed as part of this study and thereby makes a valuable contribution to the development of new approaches to marine mammal behavioural studies.

1.2 Research question and objectives

This Doctoral thesis sought to address the following primary research question:

What are the effects of in-water tourism activities on humpback whales in Vava'u, Kingdom of Tonga?

The overall research objectives of the study were to:

I. Quantify the interaction levels between whales and swim-with-whales vessels.
II. Determine and quantify the short-term behavioural responses of humpback whales to swim-with-whales vessels and swimmer approaches.
III. Determine and quantify the potential changes in the proportion of time spent in each behavioural state by humpback whales during in-water tourism interactions.
IV. Quantify levels of industry compliance with whale-watching regulations and guidelines to determine the effectiveness of the current management regime.
V. Consider the potential implications for whale conservation as a result of the research findings.

The study also sought to investigate the following secondary research question:

What are the advantages of the use of VTOL UAV for humpback whale behavioural studies?

The secondary research objectives of the study were to:

VI. Compare humpback whale behaviour data collected using boat-based methods with humpback whale behaviour data collected using a UAV.

VII. Determine and quantify the potential behavioural responses of humpback whales to a UAV flying at 30 metres altitude above the whale/s.

1.3 Structure of the thesis

This thesis is organised into six chapters. Chapter 1 introduces the rationale and significance of the study and outlines the thesis research questions and objectives.

Chapter 2 presents a literature review and is organised in three sections. In the first section, background information regarding humpback whales and the study site of Vava'u, Kingdom of Tonga, is provided. The second and third parts establish the context of the research work on the effects of whale-based tourism on cetacean behaviour and the use of UAVs for marine mammal studies, respectively.

Chapters 3 to 5 are chapters which report on discrete aspects of the overall study and which have been developed into manuscripts which have been published (see p. xvi for details).

In Chapter 3, the advantages of UAV methods to collect humpback whale behavioural data are assessed. Moreover, the potential disturbance on whales exposed to the UAV presence is investigated (thesis objectives VI and VII).

Chapters 4 and 5 address the primary research question and focus on assessing the effects of humpback whale-based tourism in Vava'u. While Chapter 4 presents a more traditional boat-based observational study, Chapter 5 is focused on the first application of UAV technology in the assessment of the effects of tourism activity on cetacean behaviour. More specifically, the data presented in Chapter 4 were collected by a boat-based observer aboard dedicated research and opportunistic swim-with-whales vessels, while Chapter 5 presents behavioural data collected using a UAV platform. In addition to the use of different methods, the two chapters focus on different objectives of this thesis. Chapter 4 reports on the interaction levels between humpback whales and swim-with-whales vessels in Vava'u (thesis objective I) and quantifies the whale responses to vessel and swimmer approaches (thesis objective II). Chapter 4 also documents the levels of compliance to Tongan swim-with-whales regulations (thesis objective IV). Chapter 5 uses the construct of proportion of time spent in each behavioural state by whales to assess and quantify potential changes both in the absence of and during the presence of tourism interactions in Vava'u (thesis objective III). Finally, Chapter 5 also focuses on humpback whale calf behavioural responses to interactions with swimmers (thesis objective II).

Chapter 6 summarises and discusses the main findings of this thesis, highlights the contributions to knowledge and considers the limitations of this study. Finally, future research questions and recommendations for the management of swim-with-whales tourism in Tonga and other countries where these interactions are permitted are provided (thesis objective V).

Chapter - 2 - Literature review

Chapter 2 cover picture. Two humpback whales approach a whale-watching vessel in Platypus Bay (24°55′ S, 153°07′ E), Fraser Island, Queensland, Australia. Photo credit: Emmanuelle Martinez.

This literature review is organised in three main sections. The first part introduces humpback whale's life-history and distribution, in particular in the South Pacific and the Tongan breeding ground of Vava'u. The second section focuses on the whale-watching industry worldwide and reviews the past research that is relevant to the effects of whale-watching and swim-with-cetaceans tourism activities on the behaviour of cetaceans. The third and final section summarises the state of the art of UAV technology and applications to marine mammal research.

2.1 Humpback whales

2.1.1 Life-history and distribution

Humpback whales (*Megaptera novaeangliae*, Borowski, 1781) are the sole representatives of the genus *Megaptera*, but analysis of mitochondrial DNA sequences has proven that they are closely related to other balaenopterids, in particular fin whales (*Balaenoptera physalus*) (Sasaki et al., 2004). Humpback whales also share important anatomical characteristics with balaenopterids, such as the presence of a dorsal fin, and the ventral grooves that expand during feeding activities (Matthews, 1937). However, they can be easily distinguished from other baleen whales by their elongated pectoral fins that can reach up to one third of their total body length (Figure 1, p. 11). Another characteristic indicative of the species is the evident presence of knobs, called tubercles, on the rostrum (Clapham, 2008). Humpback whales can reach 17 metres in body length (Clapham & Mead, 1999) and are sexually dimorphic, with females generally larger than males (Chittleborough, 1958). Females are also distinctive with a hemispherical lobe of approximately 15 centimetres diameter in the genital region (Clapham & Mead, 1999).

Figure 1. Humpback whale (*Megaptera novaeangliae*). Source: NOAA Fisheries, West Coast Region, Marine Mammals, Humpback Whale Identification.

Similar to other baleen whales, humpback whales strongly differ from odontocetes for their lack of functional teeth. This difference is due to the fact that baleen whales forage by filtering the water through a series of corneous plates attached to the upper jaw, while odontocetes snatch and immobilise prey with their jaws (Bannister, 2008). Humpback whales in particular have been described as ‘gulp feeders’ and prey on small crustaceans (e.g., euphausiids) and schooling fish (e.g., Clupeidae) (Whitehead, 1981). Humpback whales often form large feeding aggregations (Dawbin, 1966) and co-operate creating a circular underwater curtain of bubbles around schools of prey (Figure 2, p. 12). This complex feeding strategy, commonly known as ‘bubble netting’, is believed to confound the preys, which remain trapped until the whales swallow it by lunging vertically through the water column (Hain, Carter, Kraus, Mayo, & Winn, 1982).

Figure 2. Humpback whales (*Megaptera novaeangliae*) ‘bubble netting’, a cooperative feeding strategy. Source: WHOI and Ingenious Bubble Net Fishing, Nature’s Great Events, BBC.

Humpback whales are a species present in all oceans from low to high latitudes, with the exception of closed basins such as the Mediterranean Sea and the Red Sea, where they are rarely spotted (Clapham, 2008). In late autumn, they migrate from the high latitude feeding grounds to tropical waters, where they breed and give birth (Chittleborough, 1965). Although humpback whales often form small, unstable groups, large groups can aggregate during the breeding season when males aggressively compete for females (Dawbin, 1966). Clapham (1996) describes the species mating behaviour as a flexible form of ‘Lek’. The main characteristic of this strategy is that males engage in competitive behaviours with the goal of being chosen by females. Males not only engage in agonistic displays towards competitors for mating, but also produce complex vocal calls that are believed to be part of courtship behaviour. These calls consist of a song structure with various conserved vocalisations that change across different populations, as these songs are culturally inherited, and evolve over the years (Dawbin, 1966; Garland et al., 2015; Garland et al., 2011). Courtship generally occurs in breeding grounds during winter, when females are in oestrus and sexually receptive (Clapham, Palsboll, Mattila, & Vasquez, 1992). Gestation lasts between 11 and 12 months, and pregnant mothers generally give birth once back in the wintering grounds (Chittleborough, 1958). After birth, mothers spend six months nursing the calf (i.e., lactating) and are often accompanied by one or more courting males, commonly referred to as ‘escorts’ (Tyack & Whitehead, 1982). Mothers invest a significant amount of energies and experience a linear decline in body size to lactate the calf and ready it for the migration back to the summer feeding grounds (Christiansen, Dujon, Sprogis, Arnould, & Bejder, 2016). That is, feeding opportunities are scarce for humpback whales in their winter breeding grounds and mothers spend the majority of their time resting and nursing their calf (Bejder et al., 2019; Videsen, Bejder, Johnson, Madsen, & Goldbogen, 2017). After one year, the calf becomes independent and at an average of five years, females will reach sexual maturity (Chittleborough, 1958; Clapham, 1996). The mean inter-birth interval for female humpback whales is about three years (Rankin, Maldini, & Kaufman, 2013), but annual calving has been documented on some occasions (Weinrich, 1991).

Within the species of humpback whales, several distinctive populations have been identified worldwide. The IWC has tentatively defined 12 major breeding stocks (BS) migrating to 12 different feeding areas (FA) (Figure 3, p. 14).

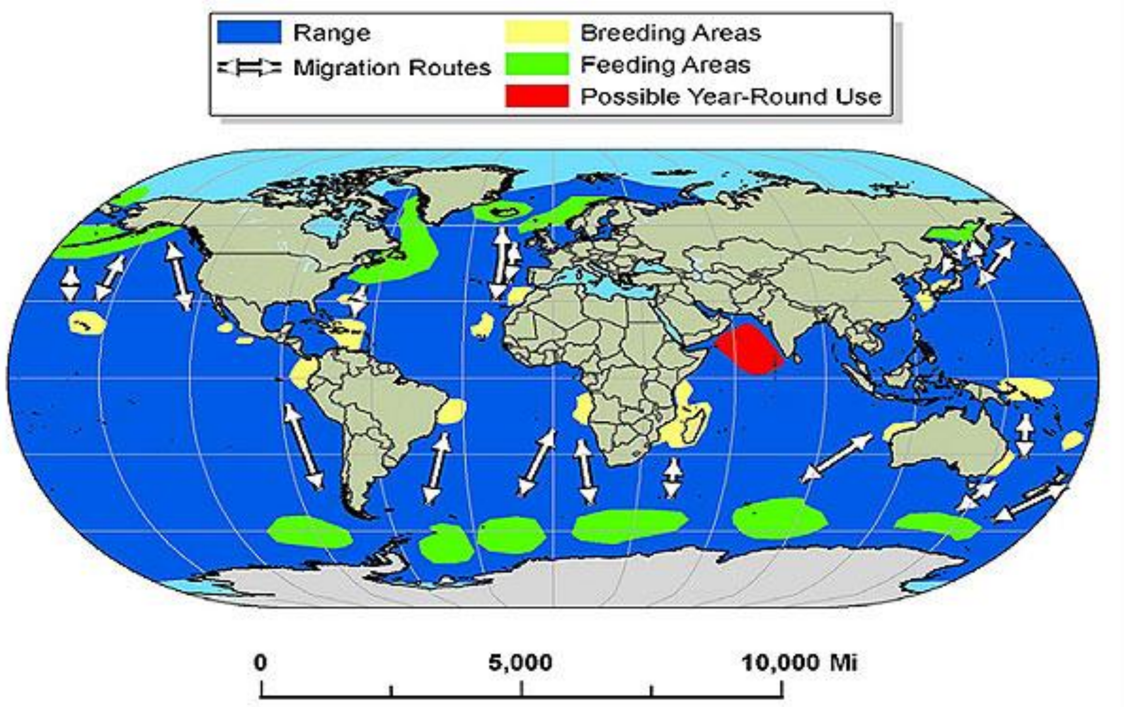


Figure 3. Humpback whale (*Megaptera novaeangliae*) IWC breeding stocks and feeding areas worldwide. Source: Schaumburg (2005).

Northern and Southern humpback whales are considered distinct as the two populations are unlikely to mingle due to their asynchronous migration to low latitude breeding grounds (Chittleborough, 1965). In addition, recent research on mitochondrial and nuclear DNA have demonstrated that some IWC breeding stocks are comprised of different identifiable sub-populations (e.g., Baker et al., 1998; Olavarria et al., 2007). In particular, the South Pacific humpback whales are divided into several distinct populations as the Eastern Australian and Oceania populations show an extremely low rate of interchange (Garrigue, Franklin, et al., 2011) and have a considerable difference in population size.

2.1.2 The Oceania humpback whale meta-population

Photo-identification (Garrigue et al., 2002) and mitochondrial DNA (Olavarria et al., 2007) studies have identified four Oceania breeding stocks with high regional fidelity and low rate of demographic interchange between adjacent regions. These four breeding stocks are as follows: New Caledonia (BSE2), Tonga (BSE3), Cook Islands (BSF1), and French Polynesia (BSF2) (Figure 4, p. 16). Research focused on male songs has also confirmed the existence of distinct populations and has described an East to West transmission patterns of new vocal themes (Garland et al., 2011; 2015). However, recent satellite tagging experiments have highlighted that the Cook Islands do not represent a breeding ground, but seem to be part of a migratory corridor towards Samoa (Hauser, Zerbini, Geyer, Heide-Jorgensen, & Clapham, 2010). The New Caledonian population seems to share the Antarctica Feeding Area V with the Eastern Australia breeding stock (BSE1), while the other Oceania sub-populations migrate to the Area VI (Anderson et al., 2010).

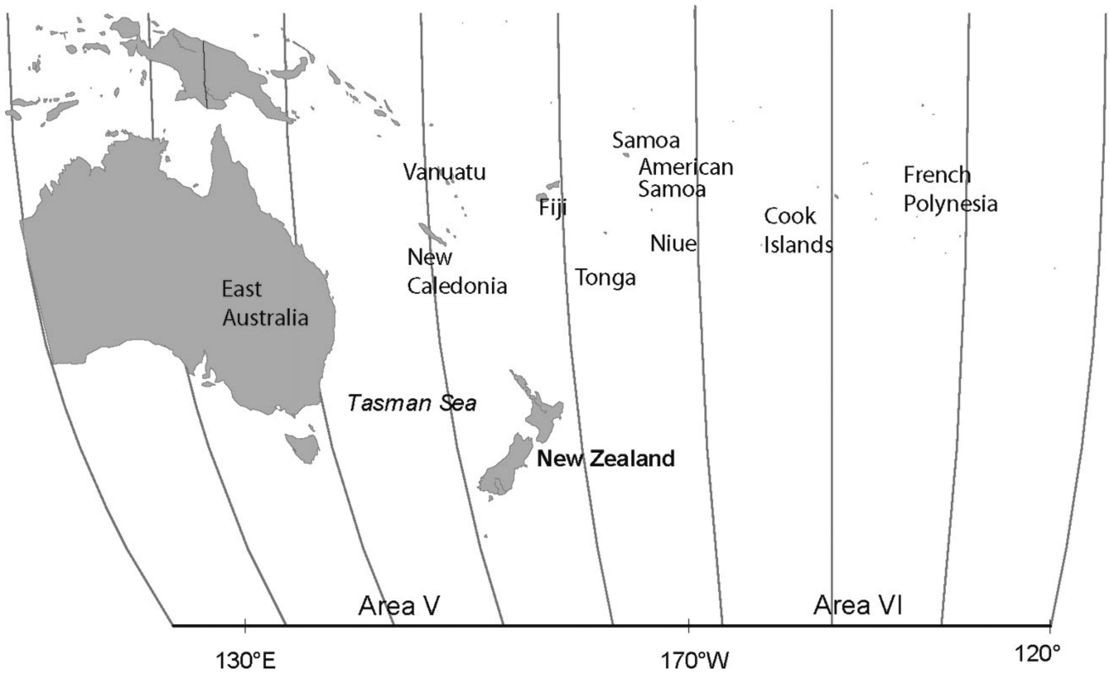


Figure 4. Sites surveyed (1999-2005) by the South Pacific Whale Research Consortium in the Oceania region (Constantine et al., 2012).

Robust estimates for the Eastern Australia population size are available and show an extremely high rate of growth (10.9% per year), close to the species' biological limit (Noad, Dunlop, Paton, & Kniest, 2011). In contrast to the availability of information regarding population estimates in other areas, the vastness of the Oceania region and the remoteness of the breeding grounds pose several challenges to the study of population dynamics and rate of recovery (Constantine et al., 2010). Moreover, the migration routes often follow sea mounts far from any inhabited coastlines (Garrigue, Clapham, Geyer, Kennedy, & Zerbini, 2015), which means that efficient, land-based surveys are not possible. To date, the best estimates for the whole Oceania meta-population is 4,329 whales (Constantine et al., 2012), well below the 14,522 individuals estimated for the adjacent Eastern Australia breeding stock (Noad et al., 2011). The cause of the relatively low rate of recovery of the Oceania humpback whales is still unclear (Constantine et al., 2012; Jackson et al., 2013).

Between 1947 and 1973, both Area V and VI have been heavily targeted by commercial whaling operations, and more than 25,000 humpback whales were killed in just two seasons during1959 and 1960 (Clapham et al., 2009). Interestingly, Garrigue, Albertson, and Jackson (2012) have reported an anomalous increase of the New Caledonia humpback whale numbers in 2010, and they suggest that it could represent the consequence of a spill-over event from the adjacent expanding Eastern Australia population. A previous eight-year study comparing the microsatellite genotype matches between Eastern Australia (n = 734), and Oceania (n = 1,086) detected a total of eleven individual exchange events with New Caledonia, while showing only two exchange events with Tonga (Anderson et al., 2010). Furthermore, photo-identification (n = 776) conducted between 1999 and 2004 found only eleven cases of individual resighting between the four Oceania breeding grounds, confirming their high degree of independence between these stocks/populations (Garrigue, Constantine, et al., 2011).

2.1.3 Humpback whales in Vava'u, Kingdom of Tonga

Almost half of the Oceania humpback whales are estimated to breed in Tongan waters (Figure 5a, p. 19), in particular around the Vava'u archipelago (Figure 5b, p. 19). Using photo-identification and DNA profiling studies conducted between 1999 and 2005, Constantine et al. (2010) have calculated that the Tongan sub-population could be between 1,168 and 1,840 and individuals. Moreover, the findings suggested that the Kingdom of Tonga acts as an important junction area for the Oceania humpback whales as 80% of the movements between the South Pacific breeding grounds involved whales sighted in Tongan waters (Garrigue, Constantine, et al., 2011).

Like other whale populations, the Tongan humpback whale breeding stock has been severely depleted by commercial whaling operations (Donoghue, 2000); between 1911 and 1963 an estimated 3,600 whales were killed during their migration along New Zealand’s coast (Donoghue, 2000). Intensive whaling operations were also expanded into the Antarctica feeding grounds by several national fisheries between 1947 and 1973, and a reported 38,146 and 7,195 whales were killed in Area V and Area VI, respectively (Clapham et al., 2009). Baker et al. (1998) analysed the mitochondrial DNA of Tongan humpback whales and found a reduced haplotype diversity, probably as consequence of a bottleneck effect (i.e., extremely low genetic variation amongst individuals of a population caused by the destruction of most of the population itself). Additionally, it was estimated by the same study that only 25 mature females were left at the end of the commercial whaling era (Baker et al., 1998). Even after the IWC ban in 1966, whaling in Tonga continued on a local basis until it was prohibited by Royal Decree in 1978 (Reeves, 2002). This ban probably saved the Tongan humpback whale population from complete eradication (Orams, 2002). As a result, of the estimated population of 10,000 whales at the beginning of commercial whaling, less than 250 animals were still migrating to Tongan islands to breed and give birth between July and October of 1978 (Donoghue, 2000).

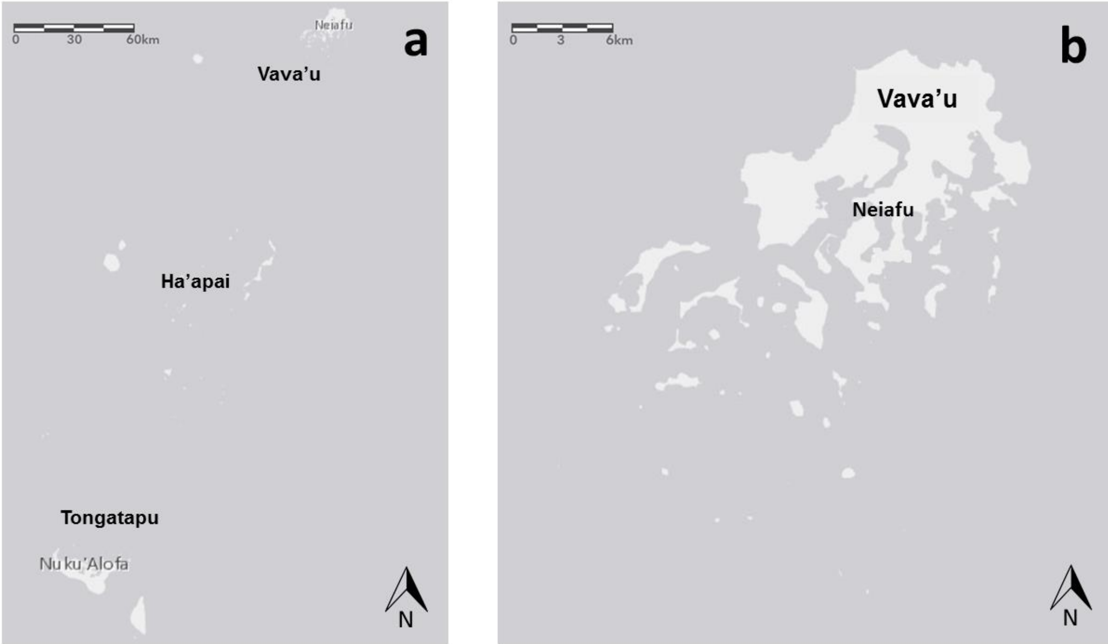


Figure 5. (**a**) The Kingdom of Tonga is constituted of three main island groups and the remote Niuatoputapu islands (not included in the map). Refer to Figure 4 (p. 16) for the location of Tonga in the South Pacific. (**b**) Vava'u Main Island (18°39'S, 173°59'W) and its archipelago.

The Tongan humpback whale population is slowly recovering but still faces threats. Diseases, ship strikes, entanglement in fishing gear, marine debris, acoustic pollution, and tourism are the key threats highlighted by the IWC (SPREP, 2014). Although the population is well below the pre-whaling size, there is ongoing pressure by some Tongan communities to resume whaling as a local food source (Orams, 2004). However, the proposal to return to a subsistence form of whaling appears controversial (Orams, 2002). In the past, the Tongan population only utilised stranded whales and did not actively hunt until North American and New Zealand fleets initiated commercial whaling operations in the area during the early 1800s (Reeves, 2002).

After the wide-scale whaling operations and the subsequent ban of whaling, the Kingdom of Tonga gained international fame as a whale-watching destination and a proposal to legalise whaling, to any extent, would likely face strong opposition from the tourism industry (Orams, 2002). In the past, hunting of humpback whales was only marginally important for the kingdom's economy (Reeves, 2002), while the Tongan whale-watching industry was estimated to have contributed 15% of the national total foreign income in 2008 (O'Connor et al., 2009). Following global trends, whale-watching industries that are focused on humpback whales have also flourished in other South Pacific countries (O'Connor et al., 2009). The Kingdom of Tonga, however, has drawn international attention for the promotion of swim-with-whales tourism activities – primarily targeting mothers and calves (Kessler & Harcourt, 2012). Tourism interactions with mothers and calves are considered to be potentially detrimental for baleen whale species (Orams et al., 2014), as they can disrupt vital activities like nursing (Kessler et al., 2013; Mangott et al., 2011) and resting (Lundquist et al., 2013). While little is known about the long-term effects of swim-with tourism activities involving humpback whales, several countries such as USA and UK have followed a precautionary approach and have prohibited in-water interaction with baleen whales in general (Hendrix & Rose, 2014). The number of licensed tour operators in the Kingdom of Tonga has, on the other hand, steadily increased (Hendrix & Rose, 2014). As a result, concern has been raised about the sustainability of the industry, especially in the light of the low rate of recovery of the Tongan humpback whale population (SPREP, 2014).

2.2 The whale-watching industry and the tourism interactions with cetaceans: behavioural responses of whales and dolphins

The whale-watching industry has been growing worldwide in the last four decades, generating an annual global revenue greater than US$ 2.1 billion from more than 13 million tourists in 2008 (O'Connor et al., 2009). Although the growth of the cetacean-human interactive tourism industry seems to have declined in some areas such as Hervey Bay, Australia (Peake, 2011), whale-watching tourism operations still have room to increase on a global scale (Cisneros-Montemayor, Sumaila, Kaschner, & Pauly, 2010). O’Connor et al. (2009) found that in 2008, 3,000 tour companies were operating in 119 countries, with the majority of them (65%) in developing countries (Mustika, Birtles, Welters, & Marsh, 2012). Commercial swim-with-cetaceans tourism activities has also dramatically increased during the past decade (Hendrix & Rose, 2014; Wiener, 2013). As documented by Wiener (2013), some countries have a long history of swim-with-dolphins tourism (e.g., USA, New Zealand, and Australia). However, only few countries permit swim-with-whales, including Australia, Canada, Dominican Republic, French Polynesia, Iceland, Kingdom of Tonga, and Sri Lanka (Hendrix & Rose, 2014). The authors also reported that as of 2014, 67 tour operators were offering in-water interactions with whales worldwide – an increase of 55% compared to 2005 – and humpback whales was the species that was most frequently targeted by this type of operation. In 2016, the Kingdom of Tonga was the country with the largest number (23) of licensed swim-with-whales tour operators (Tongan Ministry of Tourism, personal communication, October 10, 2015), followed by the Dominican Republic with 16 operators (Hendrix & Rose, 2014). In Australia, industry-led initiatives succeeded in legalising swim-with-humpback whales and in 2014, the Queensland government has issued the first permits to licensed whale-watching tour operators in Hervey Bay (Bochenski, 2014), aiming to stop the slight industry decline (Peake, 2011). Following the legalisation of whale-watching tour operations, Western Australian tour operators have claimed that the whale population is fully recovered and swim-with-humpback whales tourism trials have taken place in 2016 (*Humpback whale swimming tours set to begin off WA's Ningaloo coast*, 2015). The massive amount of media featuring wild cetaceans not only helped raise public awareness about their conservation, but also contributed to a growth in public demand for such intimate interactions (Hu, Boehle, Cox, & Pan, 2009; Wiener, 2013). In a survey of whale-watching tourists, Finkler and Higham (2004) discussed ‘the whale watcher’s paradox’, which is described as the desire to get as close as possible to the animals, even while recognising that the interaction may have detrimental consequences for the species.

Most of the literature (90%) that is concerned with interactions between tourists and cetaceans refers to commercial operations conducted by licensed tour operators in the form of whale-watching and swim-with activities (Senigaglia et al., 2016). Short-term behavioural responses in response to boats and swimmers have been widely documented for delphinids such as bottlenose dolphins (*Tursiops truncatus*) (e.g., Constantine, 2001; Lemon, Lynch, Cato, & Harcourt, 2006; Lusseau, 2003; S. Nowacek, Wells, & Solow, 2001; Pirotta et al., 2015; Samuels & Bejder, 2004), common dolphins (*Delphinus delphis*) (e.g., Meissner et al., 2015; Neumann & Orams, 2005; Stockin et al., 2008), burrunan dolphins (*Tursiops australis*) (e.g., Filby et al., 2014; Peters et al., 2012; Scarpaci et al., 2000), Hector’s dolphins (*Cephalorynchus hectori hectori*) (e.g., Bejder, Dawson, & Harraway, 1999; Martinez et al., 2010), Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) (Christiansen et al., 2010), dusky dolphins (*Lagenorynchus obscurus*) (Lundquist et al., 2012), spinner dolphins (*Stenella longirostris*) (Fumagalli et al., 2018), and killer whales (*Orcinus orca*) (e.g. Lusseau et al., 2009; Noren, Johnson, Rehder, & Larson, 2009; Williams et al., 2002). Sperm whales have also been recorded to be affected by vessel approaches ((Richter, Dawson, & Slooten, 2003, 2006). Turning to baleen whales, avoidance of vessels and changes in patterns of surface behaviours have been observed in humpback whales (eg., Avila et al., 2015; Baker & Herman, 1989; Corkeron, 1995; Schaffar et al., 2010; Scheidat et al., 2004; Stamation et al., 2010), southern right whales (*Eubalaena australis*) (Lundquist et al., 2013) and minke whales (*Balaenoptera acutorostrata*) (Christensen, Rasmussen, & Lusseau, 2014). Finally, some authors have demonstrated that short-term effects can lead to long-term consequences at the population level (Bejder et al., 2006; Lusseau, 2004, 2005), such as decrease of female reproductive success and avoidance of particular areas.

The next section is organised into two parts dedicated to cetacean behavioural responses to boats and swimmers, respectively. A third part summarises past research pertaining to the long-term effects of whale-watching and swim-with-cetaceans tourism activities.

2.2.1 Behavioural responses to whale-watching

Vessels are a source of visual and acoustic stimuli for cetaceans. Whale-watching tourism activities in particular constitute sustained vessel interaction as the operators deliberately approach the animals and manoeuvre the boat to remain close to them (Richardson & Würsig, 1997). Researchers have widely used the responses defined as avoidance or attraction to document the effects of vessel approaches (Arias et al., 2018; e.g., Bejder et al., 1999; Filby et al., 2014; Martinez et al., 2010; Neumann & Orams, 2005; Schaffar et al., 2010; Stamation et al., 2010; Steckenreuter, Möller, & Harcourt, 2012; Williams et al., 2002). However, avoidance and attraction of the cetaceans to the vessels may not be mutually exclusive during whale-watching interactions. For instance, small and medium-size delphinids (e.g., Hector’s, common, and bottlenose dolphins) often approach a vessel (e.g., bow riding) before losing interest and avoiding it (Bejder et al., 1999; Filby et al., 2014; Neumann & Orams, 2005). Sometimes, individuals within a group may approach the vessel while the rest of the group remains neutral or leaves the vicinity of the boat. Furthermore, the responses to specific boat proximity may not be clearly assessable by a researcher (Stamation et al., 2010), especially when on-board the whale-watching platform itself. This difficulty is due to the acoustic stimuli generated by the vessel engine/s, which can reach animals at great distances, often out of the visual range of the observer (Richardson & Würsig, 1997).

Respiration (e.g., frequencies of dives, and blows) and swim parametres (e.g., course directness, and speed) have been defined to quantify the responses of cetaceans to vessel approaches and compare the results with the data collected in the absence of vessels (control). Increases in the number of dives, also referred as vertical avoidance, have been reported for humpback whales (Au & Green, 2000; Baker & Herman, 1989; Corkeron, 1995; Schaffar et al., 2010; Stamation et al., 2010) and sperm whales (Richter et al., 2003, 2006) in proximity to vessels. Humpback whales (Avila et al., 2015; Schaffar et al., 2010; Scheidat et al., 2004; Sprogis, Bejder, Hanf, & Christiansen, 2020) and killer whales (Williams et al., 2002) also show a less direct swim path, a behaviour known as horizontal avoidance, when approached by whale-watching vessels.

Interestingly, a study conducted on sperm whales in Kaikoura, New Zealand, found that the responses to whale-watching operations varies depending on the targeted individual whale, with transient whales seeming to avoid vessels more frequently than resident ones (Richter et al., 2003). Research in other areas has further shown that whales can become habituated (Bejder, Samuels, Whitehead, Finn, & Allen, 2009) towards vessels that have been operating in close proximity for several years (e.g., Ellison, Southall, Clark, & Frankel, 2012; Lusseau & Bejder, 2007; Tougaard, Wright, & Madsen, 2015).

Another variant of vessel avoidance behaviour was described by Williams et al. (2002), who noted that male and female resident killer whales in Johnstone Strait, British Columbia, Canada, use different horizontal avoidance strategies to cope with the high level of boat traffic. Females tend to increase the swimming speed and angles between subsequent dives, while males adopt a less predictable path maintaining the same swimming speed. Lusseau (2003) also described how female and male bottlenose dolphin in Doubtful Sound, New Zealand, use different avoidance strategies in response to vessel approaches. Although both sexes were found to adopt vertical avoidance (i.e., increased mean diving interval), females reacted only after the interaction with vessels become more intrusive. The author suggests that different tolerance levels between sexes might reflect metabolic regime differences. In other words, the cetacean responses to boat approaches are influenced by factors independent of the stimulus itself, such as species, ecotype, and sex of the targeted animal. A similar pattern was observed by Corkeron (1995) and Stamation et al. (2010) who have highlighted the existence of correlation between the group composition and the response strength. The study focused on the Eastern Australia humpback whale population during the annual southward migration from the low latitude breeding grounds to the Antarctic feeding areas. The authors observed that mother and calf pairs increased their diving frequency more than adult and juvenile aggregations when exposed to whale-watching vessels. Furthermore, groups of whales without calves showed an increase of the frequency of aerial behaviours (e.g., breaching, fluke slapping, pectoral slapping, peduncle slaps) during boat approaches. Similar changes have also been reported by Noren et al. (2009) with regard to Southern resident killer whales off the coast of San Juan Island, Washington, USA. Both Corkeron (1995) and Noren et al. (2009) suggest that an increase of the frequency of behaviours such as fluke slaps, peduncle slaps might be agonistic responses towards vessels.

Other studies compare the behavioural state transition probabilities and the behavioural budgets (i.e., the proportion of time spent in each behavioural state) during vessel interactions and in the absence of tourism activity. This approach relies on the definition of mutually exclusive and cumulatively inclusive behavioural states (e.g., foraging, resting, travelling, milling, socialising) (Lusseau, 2003). A significant reduction in the time spent resting and foraging in response to the vessel has been observed in bottlenose dolphins (Lusseau, 2003; Pirotta et al., 2015), common dolphins (Cecchetti et al., 2017; Meissner et al., 2015; Stockin et al., 2008), Indo-Pacific bottlenose dolphins (F. Christiansen et al., 2010), burrunan dolphins (Steckenreuter et al., 2012), dusky dolphins (Lundquist et al., 2012), spinner dolphins, and killer whales (Lusseau et al., 2009). Studies conducted on common dolphins in the Hauraki Gulf and the Bay of Plenty, New Zealand, found that the time to resume foraging behaviour increased significantly in the presence of the whale-watching boat (Meissner et al., 2015; Stockin et al., 2008). Some authors have also reported that dolphin social behaviour decreased during the vessel interactions (Christiansen et al., 2010; Lusseau, 2003; Lusseau & Higham, 2004; Steckenreuter et al., 2012). Travelling behaviour, on the other hand, was found to increase when the vessels were present by the majority of studies (refer to Senigaglia et al. (2016) for a meta-analysis study). In the case of dusky dolphins off Kaikoura, New Zealand, the effects on behavioural budgets were influenced by factors such as the time of the day and the season (Lundquist et al., 2012). The authors found that resting behaviour was not affected during the autumn, and travelling behaviour only increased in the summer, when more whale-watching vessels were operating simultaneously. The authors proposed that these results might be related to the different intensity of whale-watching operations throughout the year.

In summary, cetaceans exhibit a wide range of behavioural responses to vessels, from horizontal and vertical avoidance to the disruption of vital behaviours. It is also worth noting that the effects of vessel approaches on their behaviour may vary depending on factors such as the season (e.g., Lundquist et al., 2012; Richter et al., 2003), pod composition (e.g., Corkeron, 1995; Stamation et al., 2010), ecotype (e.g., Richter et al., 2006), and sex (e.g., Lusseau, 2003; Williams et al., 2002) of the targeted cetaceans.

2.2.2 Behavioural responses to swim-with-whales tourism activities

Several authors agree that swim-with-cetaceans tourism activities are highly invasive for the targeted populations (e.g., Constantine, 2001; Curnock, Birtles, & Valentine, 2013; Sprogis et al., 2020). These interactions are highly invasive because an in-water interaction is considered successful when at least one dolphin or whale is within five metres of a swimmer for more than 10 seconds (Constantine, 2001; Constantine & Baker, 1997; Lundquist et al., 2013). The need to deploy the swimmers near the cetaceans means that the tour operators may attempt multiple approaches towards the same individuals, increasing the scale and the duration of the potential disturbance for the targeted cetaceans (Constantine, 2001; Martinez et al., 2010; Peters & Stockin, 2016). Moreover, approach speeds are generally higher on swim-with-cetaceans boats than on conventional whale-watching vessels (Lundquist et al., 2013) which increases the noise generated underwater by the engines and often triggers avoidance responses in cetaceans (Richardson et al., 1995).

Avoidance responses to swimmers have been observed in bottlenose dolphins (Constantine, 2001), common dolphins (Constantine & Baker, 1997; Neumann & Orams, 2005), Burrunan dolphin (Filby et al., 2014; Steckenreuter et al., 2012), and Hector's dolphins (Martinez et al., 2010). The boat approach and the swimmer placement have a great influence on the response strength of the cetaceans. Constantine (2001) and Martinez et al. (2010) observed that bottlenose dolphins and Hector's dolphins, respectively, were more likely to avoid swimmers placed in their path. Additionally, the use of avoidance strategies can be observed more frequently for small pods than for large affiliations (Filby et al., 2014; Martinez et al., 2010; Peters et al., 2012). With species such as the bottlenose dolphins, juveniles tend to interact more with swimmers than the adults (Constantine, 2001). In contrast, common dolphins were found to show little interest in swimmers, regardless of their age class (Constantine & Baker, 1997; Neumann & Orams, 2005). As a result, the average duration of in-water interactions with common dolphins is lower than the mean time for other dolphin species (Meissner et al., 2015).

Varying behavioural responses are documented for Burrunan dolphins, including the increase of whistling vocal behaviour (Scarpaci et al., 2000) and enhanced pod cohesion (Steckenreuter et al., 2012). Filby et al. (2014) suggest that dolphins, in particular small pods, might perceive vessels and swimmers as a threat and, as a result, adopt defensive strategies such as tightening the swimming formation and positioning the calves in the middle of the pod. In some cases, cetaceans may also exhibit aggressive behaviour towards swimmers and cause injuries ranging from small to life-threatening (e.g., Orams, 1997; Scheer, 2010; Shane, Tepley, & Costello, 1993).

Baleen whale behavioural responses to swim-with tourism activities are largely unknown. Mangott et al. (2011) and Curnock et al. (2013) reported that dwarf minke whales (*Balaenoptera acutorostrata*) voluntarily interact with vessels and swimmers in the Great Barrier Reef, Queensland, Australia. The whale-watching tour operators often wait for the whales along the Ribbons Reefs until the animals approach the vessel. These in-water interactions take place with the use of floating ropes – also called mermaid lines. Generally, the whales aggregate around swimmers (Mangott et al., 2011) with encounters that can last up to ten hours, with an average duration of two hours (Curnock et al., 2013).

Curnock et al. (2013) also found an increased level of effort among the licensed operators to document encounters with dwarf minke whales in the Great Barrier Reef. This resulted in a dramatic increase of the number of whale encounters that almost doubled over six seasons, raising concerns about the potential adverse effects on the whales if additional swim-with-whales permits would be granted to other tour operators. As the authors noted, the attraction response of dwarf minke whales to swimmers strongly differs from what has been documented for human interaction with other cetacean species (e.g., Lundquist et al., 2013).

To determine behaviours that concern humpback whales, Kessler et al. (2013) performed experimental swimming approaches in the Ha'apai island group, Kingdom of Tonga. An increased rate of surface-active behaviours was recorded during the trials. Furthermore, the in-water interactions lasted significantly less time when swimmers were approaching while splashing, but avoidance responses when swimmers approached quietly were not statistically significant. The vessel presence was identified as a confounding factor, as the control data were collected with the vessel in close proximity to the whales.

In what may be the most comprehensive study about the effect of in-water interaction on whale behaviour (Hendrix & Rose, 2014), Lundquist et al. (2013) used a theodolite land-based station to record the responses of southern right whales to a number of swim-with tourism simulations (N = 184) off the Península Valdés, Argentina. Seventeen percent (n = 31) of the whale pods avoided the vessel to such an extent that the in-water interaction could not be attempted. Mother and calf pairs showed the highest degree of avoidance amongst all the pod types (n = 26, 27% of mother and calf pairs). The authors also reported several cases of vertical avoidance by large, solitary adults which were presumably pregnant females. Moreover, the behavioural transition state probabilities and the behavioural budgets during successful swim attempts (n = 93) – defined as simulations lasting at least 10 minutes – were compared with those recorded before and after the trial. The probability that the cetacean would remain resting and socialising decreased by more than 10% between the control (before segment) and the simulation (during segment), while the transition to travelling behaviour also significantly increased. Whale pods also changed swim direction more frequently during the in-water activity than after the vessel had left the interaction area (after segment). When considering behavioural budgets, the whales spent significantly less time resting and socialising – 5% and 3% respectively – and travelled significantly more (6%) in the during segment compared to the before segment. The socialising activity significantly affected juveniles (-9%), and consequently lead to a greater proportion of time spent travelling (11%). Anecdotally, the authors have observed several episodes of disruption of male courtship behaviour during the swim attempts towards mating groups.

To summarise key findings, cetaceans often respond to swim-with tourism activities by adopting avoidance strategies and this disrupts vital behaviours. The response strength appears to be related to factors such as species (e.g., Mangott et al., 2011; Neumann & Orams, 2005), pod size (e.g., Filby et al., 2014; Martinez et al., 2010; Peters et al., 2012) and composition (e.g., Lundquist et al., 2013), age class (e.g., Constantine, 2001), animal's initial behaviour (e.g., Lundquist et al., 2012), and approach type (e.g., Constantine, 2001; Kessler et al., 2013; Martinez et al., 2010).

2.2.3 Short term responses and long-term effects

The short-term behavioural responses of cetaceans to tourism activities often overshadow more complex detrimental consequences at the overall population level (Higham & Bejder, 2008). For instance, the use of avoidance strategies and the increase of travelling behaviour can represent a significant loss in energy for the animals (Bejder et al., 1999). Moreover, the disturbance of core biological activities (e.g., the reduced proportion of time spent in behavioural states such as foraging and resting) is detrimental for the population fitness (Bejder et al., 2006; Higham, Bejder, & Lusseau, 2009; Steckenreuter et al., 2012). This change in biological activities, such as decreased resting, can affect calf survival, as females often feed their young while resting (Stensland & Berggren, 2007). Furthermore, interruptions of socialising activities may also affect the behavioural development of juveniles (Lundquist et al., 2013) and reduce the chances to mate for adults (Lusseau, 2003).

Some long-term studies have highlighted changes over time, as opposed to short-term behavioural studies, in the dolphin behavioural response to vessels and swimmers. Increasing levels of avoidance have been documented for bottlenose dolphins in Bay of Islands, New Zealand (Constantine, 2001) and Burrunan dolphins in Port Philip Bay, Australia (Filby et al., 2014). Such changes may be due to sensitisation processes in response to the high levels of swim-with-dolphins tourism activities recorded in these locations. However, to confirm the observations, long-term studies focused on recognizable individuals would be necessary to demonstrate the development of sensitisation, habituation, or tolerance of cetacean species exposed to high levels of human interaction (Bejder et al., 2009).

Negative effects at dolphin population level as consequence of high levels of tourism activities focused on dolphins have been noted. For example, a significant decline (7.5% annual rate) of the bottlenose dolphin population has been observed in the Bay of Islands (Tezanos-Pinto et al., 2013), and a recent study suggested that changes in the habitat use and the high calf mortality (75% before the first year of life) may be the underlying cause of the local decline (Peters & Stockin, 2016). Moreover, whale-watching tourism interactions have also been proven to shift dolphins' home range (Lusseau, 2004) and to lower female reproductive success (Bejder et al., 2006). Unfortunately, inferring the biological implications of short-term responses is difficult when long-term baseline data about the cetacean populations are not available (Lusseau & Higham, 2004). Furthermore, some studies have failed to find any relation between the low rate of growth of a population and the level of exposure to a potential disturbing activity such as whale-watching. For instance, Weinrich and Corbelli (2009) investigated humpback whale calf production and survival in their first and second year of life in feeding grounds off the Gulf of Maine, New England, USA. The results indicated that there was no correlation between the fitness parametres and the level of exposure to whale-watching.

To date, only two studies have been able to demonstrate the link between whale-based tourism activities and long-term consequences for targeted animals. The first study, conducted by Lusseau (2005), focused on two isolated bottlenose dolphin populations in Fiordland, New Zealand. The dolphins lived in two similar fjords, Doubtful Sound and Milford Sound, but were exposed to different levels of whale-watching activities. Both populations exhibited avoidance responses towards the tour operator vessels, and as a result, their behavioural budgets were significantly affected, as described in paragraph 2.2.1 (p. 23). Despite these similar short-term responses, dolphins living in Milford Sounds adopted also long-term strategies during periods of high whale-watching activity and avoided particular areas of the fjord. One year later, Bejder et al. (2006) published the results of a 14 year investigation on the resident bottlenose population of Shark Bay, Western Australia. During the study period, tourism levels increased from nil to two dolphin-watching licensed operators. Dolphin abundance was also compared with adjacent control sites where no tourism activities were allowed. Decades of behavioural observations were available as reference. The authors found that the presence of two tour operators resulted in a significant average population decline of almost 15% dolphins per squared kilometre[2]. In contrast, there was a not significant average population growth of 8.5% per squared kilometre within the control site.

The results of these studies provided crucial information for the management of whale-watching industry. Several authors endorsed the findings of Bejder et al. (2006) as the proof that tourism activities should not take place until their sustainability is ascertained. Consequently, a precautionary approach should be recommended, especially in the light of the massive increase of commercial whale-watching operations worldwide (Constantine & Bejder, 2007; Higham & Bejder, 2008; Higham et al., 2009; Martinez & Orams, 2011).

2.2.4 Conclusions

Humpback whales are an extremely valuable resource for the tourism industry in the South Pacific, especially for developing countries (O'Connor et al., 2009). Moreover, commercial whale-watching activities have increased the public level of awareness regarding the need to protect the humpback whale populations and their home range. Unfortunately, while supporting tourism and raising awareness, such activities can also represent a threat for the targeted animals, especially in countries where regulations are not enforced, or governments do not implement effective plans to manage whale-based tourism. In-water tourism interactions with humpback whales have become increasingly popular, despite the lack of research on the effects of these activities on the animal behaviour and the potential long-term consequences.

2.3 The use of unmanned aerial systems (UAS) in marine mammal research

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In the last decade, several studies have highlighted the advantages and drawbacks of the use of lightweight UAS for spatial ecology and wildlife monitoring (see respectively Anderson and Gaston (2013) and Linchant, Lisein, Semeki, Lejeune, and Vermeulen (2015) for comprehensive reviews). In particular, UAS has been proposed as a tool for marine mammal surveys, as they allow researchers to reach remote areas and observe animals from an advantageous perspective, while being less invasive than standard aircraft (Christiansen, Dujon, et al., 2016; Christiansen, Rojano-Doñate, Madsen, & Bejder, 2016; Durban, Fearnbach, Barrett-Lennard, Perryman, & LeRoi, 2015; Goebel et al., 2015; Koski et al., 2015; Nowacek, Christiansen, Bejder, Goldbogen, & Friedlaender, 2016; Smith et al., 2016). Despite the challenges of operating at sea (Marine Mammal Commission, 2016), UAS has been used for a number of marine mammal research applications, from abundance surveys (Adame, Pardo, Salvadeo, Beier, & Elorriaga-Verplancken, 2017; Goebel et al., 2015; Hodgson, Kelly, & Peel, 2013; Hodgson, Peel, & Kelly, 2017; Jones, Pearlstine, & Percival, 2006; McIntosh, Holmberg, & Dann, 2018; Moreland, Cameron, Angliss, & Boveng, 2015; Pomeroy, O'Connor, & Davies, 2015; Seymour, Dale, Hammill, Halpin, & Johnston, 2017; Sweeney et al., 2015) to the measurement of the individuals through use of photogrammetry methods (Christiansen, Dujon, et al., 2016; Christiansen et al., 2018; Dawson, Bowman, Leunissen, & Sirguey, 2017; Durban et al., 2015; Durban et al., 2016; Goebel et al., 2015; Krause, Hinke, Perryman, Goebel, & LeRoi, 2017; Pomeroy et al., 2015). Standard abundance estimates of marine mammals such as cetaceans, polar bears (*Ursus maritimus*), and ice seals rely on data collected surveying vast areas with low individual density, generally onboard ships or aircrafts, with high associated costs and risk for operators (e.g., Buckland et al., 2001; Dawson, Wade, Slooten, & Barlow, 2008; Hiby & Lovell, 1998; Panigada, Lauriano, Burt, Pierantonio, & Donovan, 2011; Pollock, Marsh, Lawler, & Alldredge, 2006; Rekdal et al., 2015). Therefore, long-range fixed-wing UAS's have been tested as a potential replacement of the conventional manned aircraft (Marine Mammal Commission, 2016; Hodgson et al., 2013; Hodgson et al., 2017; Koski et al., 2009; Moreland et al., 2015). Aerial photogrammetry is a valuable method used to collect data, which indicate the health status of individuals by extracting measurements of animal bodies from high resolution pictures taken from above (e.g., Christiansen, Dujon, et al., 2016; Durban et al., 2015; Miller, Best, Perryman, Baumgartner, & Moore, 2012; Perryman, Goebel, Ash, LeRoi, & Gardner, 2014). Unfortunately, this method is costly and can disturb the targeted animals, as it requires standard aircraft to hover over them eliciting strong behavioural responses (Patenaüde et al., 2002; Richardson & Würsig, 1997; Smultea, Mobley, Fertl, & Fulling, 2008; Würsig, Lynn, Jefferson, & Mullin, 1998). In contrast, small vertical take-off and landing (VTOL) UAS has proven to be an affordable, effective, and less invasive alternative to manned helicopters (Christiansen, Dujon, et al., 2016; Christiansen et al., 2018; Goebel et al., 2015; Koski et al., 2015). Furthermore, UAS has been proposed as a novel tool for the study of cetacean behaviour (Hodgson et al., 2017; Nowacek et al., 2016; Torres, Nieukirk, Lemos, & Chandler, 2018). Although the testing phase has been considered successful for close-range surveys and operation is being standardised, long-range missions still faces several limitations.

For instance, government agencies in the United States, such as the National Oceanic and Atmospheric Administration (NOAA), have been systematically using VTOL UAS for marine mammal surveys since 2014 (Marine Mammal Commission, 2016). In contrast, the use of UAS for long-range surveys is under debate, as the advantages provided by long endurance aircraft are offset by high operating costs and difficulties to obtain beyond visual line of sight (BVLOS) permits from the relevant civil aviation authorities (Marine Mammal Commission, 2016; Hodgson et al., 2013; Koski et al., 2015). On this section, I present a general overview of the three UAS classes that have been used for marine mammal surveys and the relevant literature. Advantages and limitations are highlighted for each class and application. Finally, I discuss the use of VTOL UAS as a novel tool to study marine mammal behaviour.

2.3.1 Unmanned Aerial Systems

UAS consists of the UAV, also referred to as remotely piloted aircraft (RPA), the sensor, or payload carried, and the ground control station (GCS) (Watts et al., 2010). The GCS includes launching and retrieving platforms that can be mounted on vessels or land transported on trailers. UAS classification is derived exclusively from existing military descriptions (Watts et al., 2010). UAS classes valuable for marine mammal research and details relevant for survey design are reported in this note:

- Low Altitude Long Endurance (LALE) UAS. Fixed-wing aircraft capable of long endurance (>4 hours) at low altitude (< 3,000 metres above ground level, AGL). Small aircraft (< 4 metres wingspan; 2 kilograms payload capacity; < 20 kilograms take-off weight, Figure 6, p. 39);

- Low Altitude Short Endurance (LASE) UAS. Fixed-wing aircraft capable of short endurance (1–2 hours) at low altitude. These aircraft are generally smaller than LALE (<

2.5 metres wingspan; < 1 kilogram payload; < 5 kilograms take-off weight), electrically powered and — in some cases — can be hand-launched (Figure 7, p. 42);

- VTOL UAS. VTOL class ranges from nano-aircraft fitting into the breadth of a hand, to larger unmanned helicopters. Electric helicopters with multiple rotors are becoming increasingly popular and usually have from three to eight propellers (Figure 8, p. 47).

2.3.2 Low Altitude Long Endurance (LALE) UAS

LALE UAS is the best candidates for long-range aerial surveys of geographically dispersed marine mammal species. Small fixed-wing aircraft can be handled by two operators and do not necessarily require an airstrip to take off or land (launching and retrieving equipment can be also mounted on a vessel). Furthermore, fuel-powered engines ensure a flight duration, which can range from six to more than twenty hours, depending on the UAV and the payload weight.

Figure 6. ScanEagle® unmanned aerial vehicle (UAV) (Boeing Insitu, Bingen, WA, USA) lands on skyhook for recovery. The SuperWedge® pneumatic launching catapult (left) can be mounted on vessels. Source: United States Navy.

A case in point is the Insitu (Boeing) Insight A-20 (ScanEagle®, Figure 6, p. 39), which represents the greatest flight duration (28 hours) and range (150 kilometres) on the market. So far, it has been tested and utilised for dugong (*Dugong dugon*) (A. Hodgson et al., 2013) and humpback whale (Hodgson et al., 2017) aerial abundance surveys in Australia, and for seal counts in the Bering Sea pack ice (Moreland et al., 2015). Simulations have also been run with inflatable kayaks as whale-like targets (Koski et al., 2009). These studies highlight the great potential of the ScanEagle® and LALE UAS. For instance, the possibility of keeping a permanent record of the survey with high-quality images may reduce significantly the 'perception' bias (i.e., the number of missed sightings by the observer), the human error component resulting in the underestimation of the sample (Marsh & Sinclair, 1989). Furthermore, the dugong and humpback whale sighting rate with UAS appeared to be less affected by the Beaufort sea state (BSS), which normally happens in manned surveys (Marsh & Sinclair, 1989; Pollock et al., 2006), and every sighting was precisely GPS referenced. Nevertheless, the authors agree that the strip width is narrower than what is normally achieved during manned surveys. Consequently, UAS takes around three hours to cover the same area, which two observers on an aircraft would cover in one hour flying at the same altitude (Angliss, Ferguson, & Kennedy, 2016; Koski, Abgrall, & Yazvenko, 2010; Moreland et al., 2015). Hodgson et al. (2013) proposes, therefore, the use of higher resolution cameras or multiple cameras to address this problem. However, the latter solution would significantly increase the payload weight and reduce the flight duration. In addition, the large amount of imagery recorded can lead to high post-processing costs (Seymour et al., 2017) which represents a challenge in terms of time and efficiency of analysis (Angliss et al., 2016; Linchant et al., 2015). The studies presented in this section do not provide any exhaustive comparisons of UAS surveys with manned aerial surveys, apart from noting that fuel consumption is significantly less for a UAV (Hodgson et al., 2013; Moreland et al., 2015) and the costs for operating UAS operations are similar to manned aircraft surveys (Hodgson et al., 2017). Since hiring a UAS operator, they have not made the initial investment required to purchase a complete system and obtain the necessary certifications. Even choosing a cheaper UAS than the ScanEagle®, the price tag of any single aircraft is currently ranges from US$ 100,000 and up, and more than one backup aircraft is necessary to cover the risk of loss or damage (Koski et al., 2010). Moreover, Moreland et al. (2015) noted that long flights in arctic and sub-arctic regions are prone to icing risk (i.e., formation of ice on the wings and flight control surfaces) and precautions are necessary to prevent UAV failures. To our knowledge, no data has been published regarding the use of other LALE UAS in marine mammal surveys. However, further comparisons with manned aerial surveys are necessary to evaluate whether the choice of LALE UAS can be economically competitive to conventional aerial survey methods.

Preliminary results have shown that UAS transport to remote locations costs more than using a standard aircraft already in place, not to mention the time and personnel necessary to analyse several hours of recorded imagery (Angliss et al., 2016). Finally, the use of LALE UAS for long-range marine mammal surveys is currently limited by safety issues relating to activity taking place inside controlled airspace, as aviation authorities tend to refrain from issuing BVLOS permits as a way to prevent collisions with other airspace users (Hodgson et al., 2013; Koski et al., 2010; Moreland et al., 2015; Sweeney et al., 2015; Watts, Ambrosia, & Hinkley, 2012). These regulations not only limit the UAS operation range, but also limits their potential to reach remote areas (Hodgson et al., 2013).

2.3.3 Low Altitude Short Endurance (LASE) UAS

Several authors have proposed the use of short endurance fixed-wing UAV or LASE UAS (Figure 7, p. 42) as survey platforms in open areas for big land Mammals (e.g., Barasona et al., 2014; Mulero-Pazmany, Stolper, van Essen, Negro, & Sassen, 2014; Vermulen, Lejeune, Lisein, Sawadogo, & Bouche, 2013), reptiles (e.g., Jones et al., 2006), and birds (e.g., Chabot & Bird, 2012; Chabot, Craik, & Bird, 2015; Sarda-Palomera et al., 2012). In spite of their short endurance (generally 40–90 minutes), LASE UAS presents several advantages with respect to long endurance systems or LALE UAS. Their price is significantly lower, with the current average cost of a complete system, including the launching device and the GCS, at approximately US$ 20,000. Some UAVs can be hand-launched (e.g., Barasona et al., 2014; Bollard et al., 2014; Chabot, Carignan, & Bird, 2014; Mulero-Pazmany et al., 2014), as the airframe has a take-off weight lower than 5 kilograms. Most of these aircrafts land on their belly and thus require runaways. Web-retrieving systems have been developed as a solution for rear-propulsion aircraft, as bellylandings strongly reduce the airframe lifespan (Vermulen et al., 2013) and runaways can be dangerous for bystanders (Funaki & Hirasawa, 2008). Such retrieving webs can fit on vessels and, therefore, allow an extension of the UAS operating range (Koski et al., 2010). Another advantage, with respect to long endurance UAS, is the propulsion system. Electric brushless motors require less maintenance than fuel-powered engines (Funaki & Hirasawa, 2008), and are far quieter. The electric power, however, limits these aircraft. Advances in materials used for lithium batteries (e.g., Kucinskis, Bajars, & Kleperis, 2013; Wu, Liu, & Guo, 2014) may significantly improve the flight duration, although at the present, the gain of weight resulting from carrying high capacity batteries often offsets the gain in endurance.

Figure 7. PolarFox UAV (Skycam UAV Ltd., Dunedin, New Zealand) can be hand launched with a bungee cord. It is equipped with a parachute for landing (Bollard et al., 2014).

Koski et al. (2015) evaluated in a study the use of a LASE UAS, Brican Flight Systems' TD100E, as a tool for photo-identification of bowhead whales (*Balaena mysticetus*). Five tests were performed, flight ranging from 120 to 210 metres AGL, using a GoPro and

Nikon D800 (50 millimetre lens) as sensors. Interestingly, the effective picture resolution, or ground sampling distance (GSD) (3.25 and 4.14 centimetres/pixel at 120 and 210 metres altitude, respectively) was much higher than what was previously achievable with a manned aircraft, and clarity of picture resolution would allow the individual whale photo-identification. In addition, when flying at such altitudes above sea level during the survey the electric brushless motor was almost inaudible. As a result, no whale response to the aircraft could be detected during a survey. Koski et al. (2015) further reported a maximum flight duration of two hours. In contrast to the other short endurance UAV considered in this note, the TD100E is relatively large (4.9 metres wingspan; 9.1 kilograms payload; 22.7 kilograms max take-off weight). A catapult launcher is, therefore, required for take-off, and a runaway must be established for landing in a field nearby the operation area.

Other light fixed-wing designs, for example the eBee (SenseFly), have been used for a census of grey seals (*Halichoerus grypus*) in two breeding colonies of the Gulf of St. Lawrence, Nova Scotia, Canada (Seymour et al., 2017). The aircraft was equipped with a Canon S110 and thermal infrared camera (640 × 512-pixel resolution), obtaining a GSD of 3 centimetres/pixel and 7 centimetres/pixel, respectively. Pix4D software is then used to create tridimensional orthomosaics with the recorded imagery, and the counts conducted by human analysts were compared with the results obtained by an automated detection model. The two census methods gave similar results (within 95% and 98% in the two locations), with most of the discrepancies being associated with the detection and discrimination of seal pups from adult and juvenile seals. The model has proven to be an effective and less costly alternative to human census, provided that the targeted animals thermally contrast with the landscape and are not thermally similar to other species (Seymour et al., 2017).

Given the operational constraints highlighted so far, it is evident that LASE UAVs cannot provide a survey platform suitable for long-range marine mammal abundance estimations. Alternatively, LASE UAS could be used to survey narrower areas (Barasona et al., 2014), such as marine mammal aggregation sites (e.g., breeding or molting pinniped colonies, cetacean seasonal aggregations) (e.g., Perryman et al., 2014; Seymour et al., 2017). Without the need to rapidly cover extensive areas, the aircraft can be flown at lower altitude, and could potentially operate at a lower elevation than the controlled airspace (<400 feet, 121.92 metres AGL), thus obtaining the necessary flight authorisations would be easier. Finally, the image resolution power would significantly increase, allowing the collection of more information (e.g., age class, size, marks) from the sightings in a non-invasive way.

2.3.4 Vertical Take-Off and Landing (VTOL) UAS

Multirotor, electric-powered helicopters show a remarkable flight stability when compared to fixed-wing UAVs, which allows the aircraft to capture high-quality videos and pictures. The small size of the airframe and the propellers also make it easy to launch and retrieve the UAV in confined spaces without posing a threat to the operators. Furthermore, small multirotor VTOL UAS are easily transportable, with no need for additionally sophisticated equipment for take-off and landing, and the GCS normally being around the size of a laptop. Hovering flight, however, requires a large amount of power and the duration is often limited to less than one hour, even for the most sophisticated UAV. In this note we concentrate on small VTOL UAV (1–5 kilograms) equipped with electric brushless motors, normally four or more, as they have several important properties which may be relevant to marine mammal research.

Perryman et al. (2014) and Goebel et al. (2015) investigated the use of a small customised hexacopter (APH-22) in the abundance estimation of seals in Antarctica. High-resolution (<1 centimetres/pixel with 45 millimetres lens at 45 metres altitude) images of the shore were used to count individuals and discriminate pups from adults in fur seal (*Arctocephalus gazella*) and Weddell seal (*Leptonychotes weddellii*) colonies. In addition, it was possible to measure with a high level of precision the size of some leopard seals (*Hydrurga leptonyx*). With regards to the noise impact, no reaction of pinnipeds was observed while flying at 23 metres AGL. NOAA has similarly been using the APH-22 for land and boat-based surveys on gray whales (*Eschrictius robustus*), southern resident killer whales (Durban et al., 2015), and blue whales (*Balaenoptera musculus*) (Durban et al., 2016). The authors suggest that flying at 35–40 metres above sea level allows the gathering of important information about size, health, and behaviour, while reducing disturbance levels and increasing the measurement precision when compared with manned aircraft (Durban et al., 2015). Image resolution (<1.4 centimetres/pixel with 25 millimetres lens at 35 metres altitude) was slightly lower than what was achieved by Goebel et al. (2015), but still sufficient to discriminate individuals and detect changes of their body condition during subsequent encounters (Durban et al., 2015).

A more recent study tested three different VTOL UAS platforms for the photo-identification and the measurement of gray seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) in the UK (Pomeroy et al., 2015). The photo-identification of gray seals was proven to be feasible flying at 30 metres AGL. In contrast with the results of Goebel et al. (2015), aerial measures of total animal body length were, however, significantly imprecise, differing from the ground direct measures by more than the 2% even when seals were lying on boards. Pomeroy et al. (2015) also described different reactions of the seals to the UAV, even for groups of animals of the same species, approached by the same airframe. Age, sex, and, in the case of gray seals, breeding, or moulting, condition seem to affect the intensity of the behavioural responses. Interestingly, this study emphasised how the need for higher image resolution (< 0.2 centimetres/pixel) may lead to the choice of larger camera sensors. This could mean that more lift power and larger aircraft are required, thereby raising the noise levels and, consequently, increasing the risk of stress for the animals. Alternatively, the UAV can be flown at lower altitude, even though increased visual and acoustic stimuli might cause disturbance of the targeted specimens. In addition, Pomeroy et al. (2015) pointed out that in absence of wind the aircraft noise is not masked and is more obvious.

Christiansen, Dujon, et al. (2016) tested a small waterproof quadcopter (Splashdrone, SwellPro, Shenzhen, China, Figure 8, p. 47) in Western Australia to measure humpback whales. The authors demonstrated that high resolution aerial photographs of whales can be used to assess the body condition of whales and estimate the energetic cost of reproduction. Notably, animals were approached with a research vessel to use it as a scale reference for the photographs. Alternatively, the implementation of laser range finders attached to the aircraft has been proposed to measure accurately the distance between the UAV and the whale to be meaured (Dawson et al., 2017). Furthermore, Christiansen, Rojano-Doñate, et al. (2016) performed tests for the underwater and airborne noise levels generated by Splashdrone flying at different heights. This procedure is a recommended practice in the assessment of noise impacts on wildlife (Pater, Grubb, & Delaney, 2009; Southall et al., 2007) and should represent an essential first step in the design of marine mammal surveys involving the use of UAVs. The authors suggested that noise (95 dB re μPa rms) may be heard underwater by toothed and baleen whales when flying at 10 metres AGL or lower, but the effect of the noise is likely to be minimal even for animals close to the surface (Christiansen, Rojano-Doñate, et al., 2016).

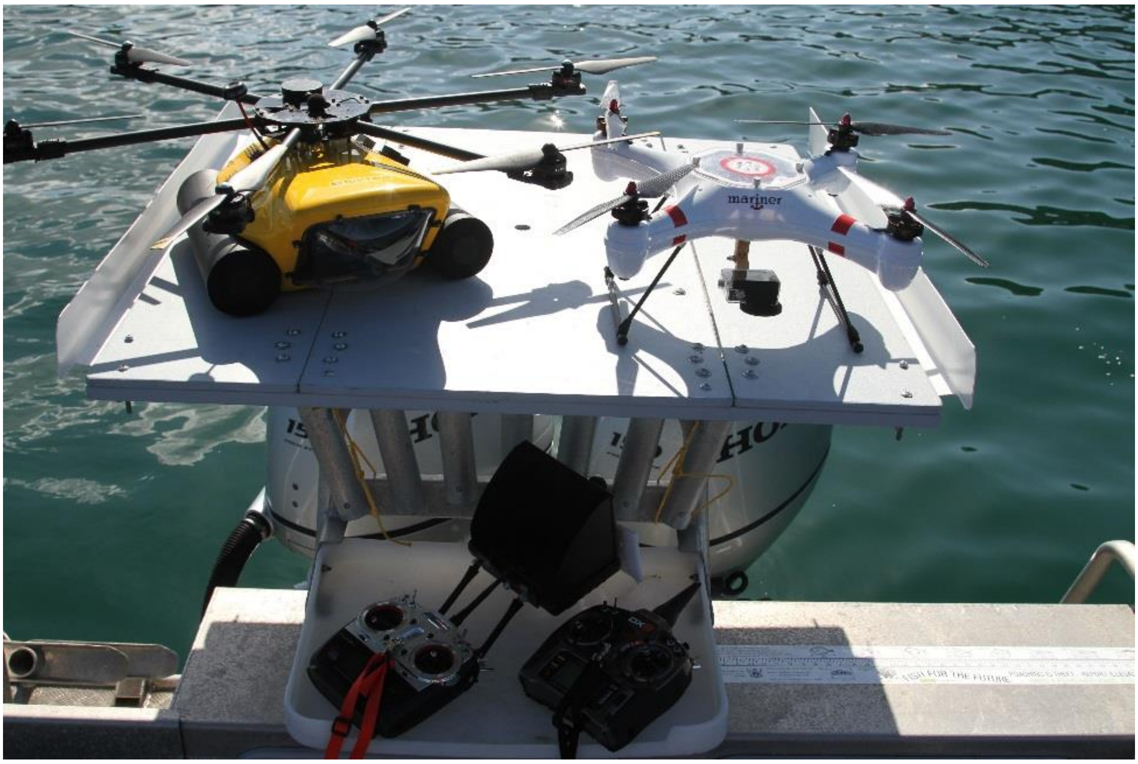

Figure 8. HexH2O™ (XtremeVision360, Worthing, UK) (left) and Splashdrone (SwellPro, Shenzhen, China) (right) on custom built foldable helipad. Photo credit: Ticiana Fettermann.

Whale plume sampling and behavioural studies

Acevedo-Whitehouse, Rocha-Gosselin, and Gendron (2010) propose the use of waterproof customised quadcopters to collect exhaled breath condensate from whales. The condensate can be an important source of information, as it contains dead cells (DNA) and hormones, which normally requires more invasive techniques, such as remote biopsy, in order to obtain such samples. However, the waterproof VTOL UAS market is still in its infancy and only a few similar models of UAV are available on the market, such as Splashdrone (SwellPro). While Splashdrone is available for less than US$ 2,000, its flight endurance is quite limited to approximately 12 minutes. In addition, the small size of the sealed unit allows minimal further implementation. To address this issue, Auckland University of Technology (AUT) is currently testing a waterproof hexacopter

(HexH2O™, Figure 9, p. 48) as a tool to investigate the behaviour of bottlenose dolphins (*Tursiops truncatus*) (Fettermann et al., 2019) and humpback whales (refer to Chapter 3, p. 58).

Figure 9. HexH2O™ has been used to observe the behaviour of humpback whales (*Megaptera novaeangliae*) in their Tongan breeding ground around the Vava'u archipelago (refer to Chapter 3, p. 58). Photo credit: Craig Koning.

For this purpose, the aircraft can be deployed from a foldable platform mounted on a small vessel. Another benefit of the aircraft is that the hexacopter is able to land and take off on the sea surface, keeping the engines well above the floating line and, therefore, reduces potential damage by minimizing its contact with saltwater. A large watertight compartment can also fit a couple of Li-Po batteries (6500–7000 milliamperes each), which ensure a flight time of approximately 25 minutes in good weather conditions.

Preliminary results have already highlighted how the aerial imagery allows the detection of the precise number of animals present in the pod and their age classes (Fettermann et al., 2019). In contrast, standard boat-based estimates are often biased, as the animals are not readily identifiable and they rarely breathe synchronously (Dawson et al., 2008). Additionally, important behaviours that normally take place underwater, and are therefore invisible from a boat-based platform, such as socialising, foraging, and nursing (Smultea et al., 2017; Torres et al., 2018), are more easily observable from an overhead angle (Figure 10, p. 50). Finally, tests are also being performed for flights at different heights to assess the potential behavioural responses of targeted animals to the aircraft presence (Fettermann et al., 2019). To date, the disturbance levels on the overflown animals have been poorly investigated and they should be assessed from other survey platforms, rather than being assessed from the source of potential disturbance itself (Patenaüde et al., 2002; Richardson & Würsig, 1997). This represents a common issue of detection of marine mammal behavioural responses to manned aircraft. That is, the noise of the aircarft can reach the animals, and eventually elicit a response, before that the observers onboard would be at eyesight distance to detect it. In particular, several factors that affect the responses have to be considered, such as the targeted species (Würsig et al., 1998), ecotypes and individuals (Richter et al., 2006), aircraft type (Patenaüde et al., 2002), and behavioural state at the time of the exposure (Würsig et al., 1998). Moreover, the acoustic stimuli can be modulated by characteristic of the surveyed area, such as sea state, wind speed, and geomorphology of the coastal environment (Smith et al., 2016).

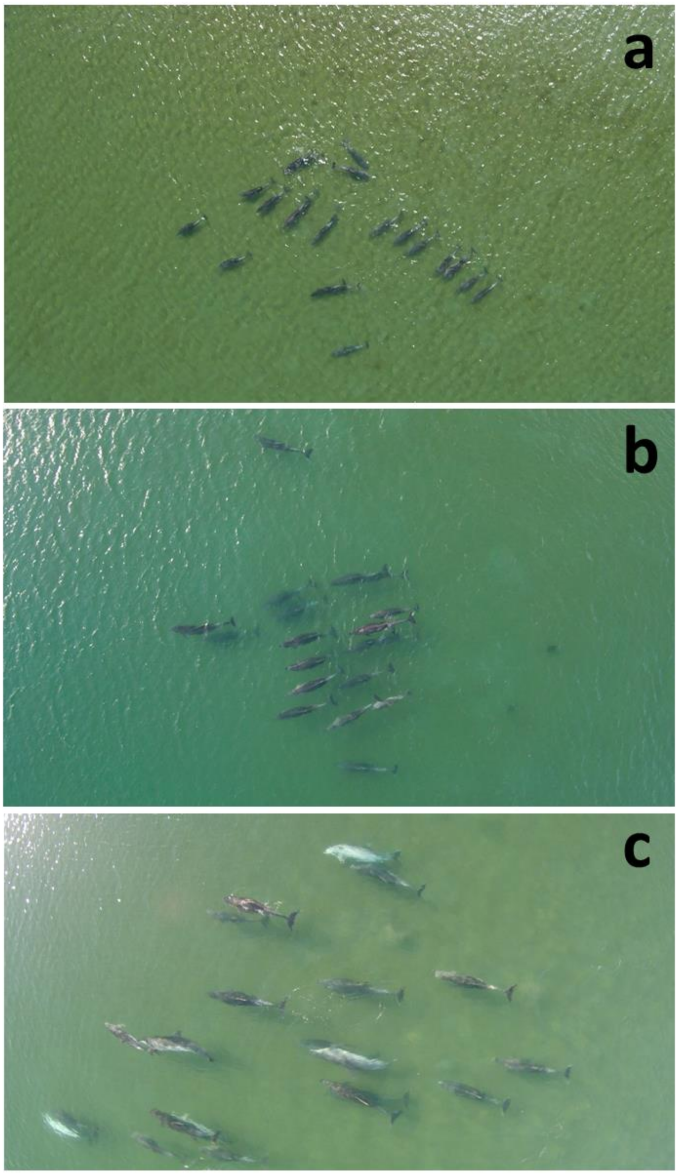

Figure 10. Bottlenose dolphins (*Tursiops truncatus*) photographed in Blind Bay, Great Barrier Island, New Zealand (36°15′ S, 175°26′ E), during UAV disturbance tests at (**a**) 40 metres; (**b**) 25 metres; and (**c**) 10 metres of altitude (Fettermann et al., 2019).

The idea of combining boat observation with aerial imagery for marine mammal behaviour surveys is not new. In the early 2000s, several studies on manatees (*Trichechus manatus latirostris*) and bottlenose dolphins were conducted using a video camera mounted on a tethered, helium-filled aerostat, also called a ‘blimp’ (Flamm, Owen, Owen, Wells, & Nowacek, 2000; Nowacek, 2002; Nowacek, Tyack, & Wells, 2001; Nowacek et al., 2004). This approach highlights the possibility of following animals during time spent underwater, although it depends on factors such as water depth and turbidity (Nowacek, 2002; Nowacek et al., 2001). The ‘blimp’ methodology, however, presents some disadvantages when compared with multirotor VTOL UAS. First of all, the shadow of the ‘blimp’ caused behaviour disruptions in dugongs (Hodgson, 2007), manatees, and bottlenose dolphins (Nowacek et al., 2001). While this may also represent an issue for multirotor aircraft, the aircraft is considerably smaller in size than the ‘blimp’ (Hodgson, 2007). Secondly, the aerial observation range is limited to a radius of approximately 200 metres around the vessel (Hodgson, 2007), while small multirotor aircrafts can be controlled at distances of about four kilometres. Therefore, it is possible to observe animals in a disturbance-free area and effectively eliminate the bias of the research boat presence (e.g., Guerra, Dawson, Brough, & Rayment, 2014).

2.3.5 Unmanned aerial systems regulations

The International Civil Aviation Organization (ICAO) established guidelines to standardise UAS regulation worldwide through standard and recommended practices (ICAO Cir 328, Unmanned Aircraft Systems (UAS), 2011). In many countries, aircrafts under 25 kilograms of weight at take-off are considered a small-UAV and have less strict regulations. Regardless of the weight, all operations have to obtain a certificate or waiver of authorisation (CoA) in order to take place and operators must be certified for flying UAV. These requirements also apply to operations outside controlled airspace, if they are not recreational flights.

In the United States, CoA and UAS controller certification exemptions are granted to recreational users complying with the guidelines summarised below:

- Outside controlled airspace: fly below 400 feet or 121.92 metres above ground level (AGL);
- Airport no fly zone (NFZ): do not fly closer than 5 nautical miles or 9.26 kilometres to airports;
- Fly in visual line of sight (VLOS): always maintain visual line of sight on the UAS;
- City NFZ: do not fly over densely populated areas;
- Building/vehicles NFZ: maintain safe distance from building and vehicles on the flight path.

Satisfying recreational use guidelines in commercial UAS operations, including scientific research, gives a remarkable boost to CoA assessment by a civil aviation authority. Nevertheless, those interested in using UAS for scientific research should contact the relevant regulatory bodies to clarify legal and safety issues in relation to the area and the methodology of the study. These factors are not negligible and have to be addressed in the early stages of the survey design conception.

2.3.6 Conclusions

Unmanned Aerial Systems, or UAS, represents a revolutionary tool for marine mammal research. Long endurance, fixed-wing UAVs can replace manned aircrafts for line transect aerial surveys, minimizing the human risk component and allowing researchers to access remote areas (Angliss et al., 2016; Hodgson et al., 2013; Hodgson et al., 2017; Moreland et al., 2015) (Table 1, p. 56). However, the issues highlighted in this section are not negligible. That is, regulations and costs still pose a serious limitation to the systematic use of LALE UAS. While it is reasonable to expect further lowering of LALE UAS costs, it is also necessary that the civil aviation authorities accommodate the regulations to the recent advances in UAV technology, which lead to an increase in their commercial use (Koski et al., 2010; Watts et al., 2012). A step in this direction has been taken by the US Federal Aviation Administration (FAA) with the amendment of UAS regulations in 2016 (*FAA Streamlines UAS COAs for Section 333*, 2015; Federal Aviation Administration - Operation and Certification of Small Unmanned Aircraft Systems, 2016). Waivers for commercial and, therefore research, UAS operations are now issued by the FAA for surveys taking place outside the controlled airspace. However, BVLOS permits are still extremely complicated to obtain and are limited to remote locations (Marine Mammal Commission, 2016).

Turning to smaller UAV, LASE UAS are a less expensive tool suitable for close-range abundance surveys of marine mammal aggregation sites (Seymour et al., 2017) (Table 1, p. 56). LASE UAS deployment in offshore waters is also feasible, provided that vessels can be equipped with adequate retrieving systems (Koski et al., 2010). Otherwise, VTOL UAS are more affordable (< US$ 15,000 GCS included) and manoeuvrable systems that can be operated safely even from small research vessels (< 6 metres). Lightweight VTOL

UAS has been successfully used for photo-identification, photogrammetry, and counts of marine mammals (Table 1, p. 56). GDS of less than one centimetre/pixel have been proven to be achievable flying at 45 metres AGL (Goebel et al., 2015), and even higher resolution can be obtained by lowering flight altitude or by increasing sensor size and focal length (Marine Mammal Commission, 2016; Pomeroy et al., 2015). Image resolution requirements should be assessed prior to choosing the surveying VTOL platform, and GDS calculators are available to assist this process (e.g., Pix4D). However, a conservative approach is recommended, as environmental factors, flight parametres, and aircraft specifications can lower the effective resolution of the images (Marine Mammal Commission, 2016). In addition to photogrammetry and censuses, they can provide high-quality video of marine mammal behaviour in a non-invasive way (Hodgson et al., 2017; Torres et al., 2018) and from a perspective that allows for the tracking of the position of the animals, even when they are submerged (Nowacek et al., 2016).

Nevertheless, VTOL UAS may allow researchers to eliminate the research boat bias and, therefore, can be an invaluable survey tool for shore-based observers, especially when a land vantage point is not available. Despite their value for research, concerns have been raised regarding the risk of disturbances of the targeted animals (e.g., Ditmer et al., 2015; Pomeroy et al., 2015; Smith et al., 2016). Consequently, scientific best practices for the use of UAS in wildlife surveys are being developed in order to minimise disturbance levels during surveys. That is, systematic assessment of the potential impacts on the targeted species is of paramount importance for the survey design (Christiansen, Rojano-Doñate, et al., 2016; Hodgson & Koh, 2016; Smith et al., 2016). Finally, the current low endurance of VTOL UAV still represents a limitation, which requires back-up options to be considered for long observations. When possible, traditional boat-based or land-based observation should be included in the survey design in order to collect data during the battery replacement time. Alternatively, the use of two aircrafts can be a more expensive, but highly effective, solution.

The variety of UAS and sensors on the market provides a wide choice of alternative survey platforms. UAS should not only be considered as a potential replacement of the human component for data collection in marine mammal research, but also as a valuable tool for novel research approaches.

Table 1. The use of UAS in marine mammal research.

Objective of the Study	**UAS Class/Model**	**Sensor**
Abundance surveys of manatees (*Trichechus manatus latirostris*) (Jones et al., 2006)	LASE [1]/FoldBat	Canon Elura 2
Collection of exhaled breath condensate of large whales (Acevedo-Whitehouse et al., 2010)	VTOL [2]/Aquacopter	N/A
Abundance surveys of dugongs (*Dugong dugon*) (Hodgson et al., 2013)	LALE [3]/ScanEagle	Nikon D90; 35 mm lens
Abundance surveys and photogrammetry of seals in Antarctica (Goebel et al., 2015; Perryman et al., 2014)	VTOL [2]/APH-22	Sony NEX-5, Canon EOS-M, Olympus E-P1; 22 mm or 45 mm lens
Photogrammetry and photo-identification of killer whales (*Orcinus orca*) (Durban et al., 2015)	VTOL [2]/APH-22	Olympus E-PM2 M.Zuiko 25 mm F1.8 lens
Photo-identification of bowhead whales (*Balaena mysticetus*) (Koski et al., 2015)	LASE [1]/TD100-E	Nikon D800; 35 mm lens
Abundance surveys of seals in the Bering Sea pack ice (Moreland et al., 2015)	LALE [3]/ScanEagle	Nikon D300; 35 mm lens
Abundance surveys, photogrammetry, and photo-identification of seals in UK (Pomeroy et al., 2015)	VTOL [2]/Cinestar 6 VTOL [2]/Skijib VTOL [2]/Vulcan 8	Sony HDR-CX760 and PJ650
Abundance surveys and photo-identification of Steller sea lions (*Eumetopias jubatus*) (Sweeney et al., 2015)	VTOL [2]/APH-22	Canon EOS M; EF-M f/2 STM 22 mm lens
Photogrammetry of humpback whales (Christiansen, Dujon, et al., 2016)	VTOL [2]/Splashdrone	Canon PowerShot D30
Photogrammetry of blue whales (*Balaenoptera musculus*) (Durban et al., 2016)	VTOL [2]/APH-22	Olympus E-PM2 M.Zuiko 25 mm F1.8 lens

Abundance surveys of California sea lions (*Zalophus californianus*) (Adame et al., 2017)	VTOL [2]/ DJI Phantom 3 Adv	DJI Phantom Vision FC200
Abundance surveys of humpback whales (Hodgson et al., 2017)	LALE [3]/ScanEagle	Nikon D90; 35 mm lens
Abundance surveys of grey seals (*Halichoerus grypus*) (Seymour et al., 2017)	LASE [1]/eBee	Canon S110; senseFly LCC Thermomapper
Photogrammetry of southern right whales (*Eubalaena australis*) (Christiansen et al., 2018)	VTOL [2]/Splashdrone	Canon PowerShot D30
Abundance surveys of Australian fur seals (*Arctocephalus pusillus doriferus*) (McIntosh et al., 2018)	VTOL [2]/Gryphon Dynamics X8-1400 VTOL [2]/ DJI Phantom 3 Pro VTOL[2]/ DJI Phantom 4 Pro	Canon EF 16-35 mm f2.8, Sony FE 16-35 mm f4; 16 and 28 mm lens Integrated 1/2.3″ CMOS 12.4 MP Integrated 1″ CMOS 20 MP
Behavioural survey of gray whales (*Eschrichtius robustus*) (Torres et al., 2018)	VTOL [2]/ DJI Phantom 3 Pro VTOL[2]/ DJI Phantom 4 Adv	Integrated 1/2.3″ CMOS Integrated 1″ CMOS
Behavioural survey of dusky dolphins (*Lagenorhynchus obscurus*) (Weir et al., 2018)	VTOL[2]/ DJI Phantom 4 Adv	Integrated 1″ CMOS
Behavioural survey of finless porpoises (Neophocaena phocaenoides) (Morimura & Mori, 2019)	VTOL[2]/ DJI Mavic Pro	Integrated 1/2.3″ CMOS

[1] Low Altitude Short Endurance, [2] Vertical Take-Off and Landing, [3] Low Altitude Long Endurance.

Chapter - 3 - Insights into the use of UAV to investigate the behaviour of humpback whales

Chapter 3 cover picture. A mother humpback whale (*Megaptera novaeangliae*) performs inverted fluke slaps off the South coast of Euakafa Island (18°75′ S, 174°03′ E), Vava'u, Kingdom of Tonga. Frame extracted from the aerial videos recorded by the UAV during this study.

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In this Chapter, the advantages of the use of a UAV platform when collecting humpback whale behavioural data are investigated (Thesis objective VI). Moreover, An assessment of the potential whale response to the UAV presence is presented (Thesis objective VII). This represents an essential first step in the setup of a behavioural survey using a UAV platform. That is, it is important to verify that the UAV presence does not elicit behavioural responses in the targeted whales and the data collected is not affected by the methodology used to gather them.

Thirty-three VTOL UAV surveys were conducted on humpback whales in Vava'u, Kingdom of Tonga. Interestingly, whale behaviours, such as socialising and nurturing, were not detected by trained observers on board the research vessel but were evident from the UAV. Nevertheless, no significant differences were detected in diving and swim parametres between absence and presence of UAV flying at 30 metres altitude. These results suggest that VTOL UAVs can be an important non-invasive tool to gather behavioural data on humpback whales.

3.1 Introduction

Recent advances in UAV technology are revolutionising marine mammal science. Several studies have been investigating the use of UAVs in marine mammal research and some applications seem promising (for example, refer to section 2.3, p. 35 for a review). In particular, VTOL UAVs (UAVs hereafter) are more manoeuvrable than fixed wing UAVs, and can be deployed from vessels under 10 metres in length (Marine Mammal Commission, 2016). Furthermore, UAVs have become more affordable and easier to operate in the past five years (Christiansen, Rojano-Doñate, et al., 2016). Consequently, multirotor, remotely piloted helicopters are increasingly being used to replace manned aircraft for marine mammal research. Examples of successful use include pinniped colony census research (e.g., Adame et al., 2017; Goebel et al., 2015; Sweeney et al., 2015) and measurement of cetaceans through photogrammetry (e.g., Christiansen, Dujon, et al., 2016; Dawson et al., 2017; Durban et al., 2015; Durban et al., 2016). In addition, their use as a research tool to study cetacean behaviour and ecology is proposed (Nowacek et al., 2016).

UAVs have the ability to provide an aerial view that facilitates counting individuals and estimating their age classes (refer to paragraph 2.3.4, p. 44). To date, studies of cetacean behaviour have largely relied on what an observer is able to see from aboard a vessel or from a distant shore-based observation point. Consequently, these observations are restricted to recording the cetaceans' surface, or near-surface, activity from an oblique angle and from a distance, which challenges the accuracy and consistency of the recorded behavioural data. As a result, important and often subtle behaviours such as socialising, nurturing and nursing, cooperative hunting, and avoidance are often difficult to identify (Smultea et al., 2017).

The majority of cetacean behavioural studies are conducted from a vessel and seek to maintain a distance that allows for observation and recording of behavioural, along with other data, but does not disturb the behaviour of the targeted animals. However, even with careful piloting, it is clear that the proximity of a manoeuvring research vessel can cause both avoidance and attraction responses in cetaceans (Dawson et al., 2008). In contrast, while researchers who have used UAV for cetacean studies report that they did not observe behavioural responses from the targeted animals during the flights (refer to Smith et al. (2016) for a review on the known effects on marine mammals), published, quantitative data that verify this information is only available for a few species and UAV platforms (e.g., Fettermann et al., 2019; Ramos, Maloney, Magnasco, & Reiss, 2018). A range of scientists and regulatory bodies have raised concerns regarding the lack of empirical data on the potential disturbance (Fettermann et al., 2019; Smith et al., 2016), in particular considering that some research applications require UAVs to fly at only a few metres from the targeted cetaceans (Acevedo-Whitehouse et al., 2010; Pirotta et al., 2017).

This study represents an evaluation of the potential effects of the use of UAV methods to investigate the behaviour of a whale species. Surveys on humpback whales were conducted during their breeding season (July to October) in Vava'u, Kingdom of Tonga. In addition, UAV surveys were compared with traditional vessel-based data collection methods for behavioural studies. Whale diving time, number of dives, respiration, and reorientation events were monitored in the presence and absence (control) of a 4.7 kilograms UAV flying at a 30 metres altitude. Finally, the time spent in specific behavioural states was collected from both platforms (vessel and UAV) and compared. The main hypotheses are that, firstly, the proportion of time spent in each behavioural state by whales would differ significantly between UAV-based and boat-based observations if the two methodology are not equally accurate. This hypothesis relies on the assumption that UAV-methodology can provide a more accurate description, because indications of certain behavioural states (for example, whales rubbing and touching each other) are more likely to occur underwater and are, therefore, more difficult to detect from a boat-based observation platform. Secondly, it was hypothesised that potential UAV-induced changes in whale behaviour can be detected through UAV absence and presence comparisons.

3.2 Methods

3.2.1 Study site and species

This study was conducted between July and October of 2016 in the Vava'u archipelago (18°39'S, 173°59'W), in the Kingdom of Tonga (Figure 11a, p. 63). Survey efforts were concentrated on the south side of the main island in inshore waters (Figure 11b, p. 63). The study area has been documented as an important breeding ground for the Oceania humpback whales (Constantine et al., 2012). From July to October, the sheltered waters between the islands represent the major calving site for the Tongan sub-population (Baker et al., 1998).

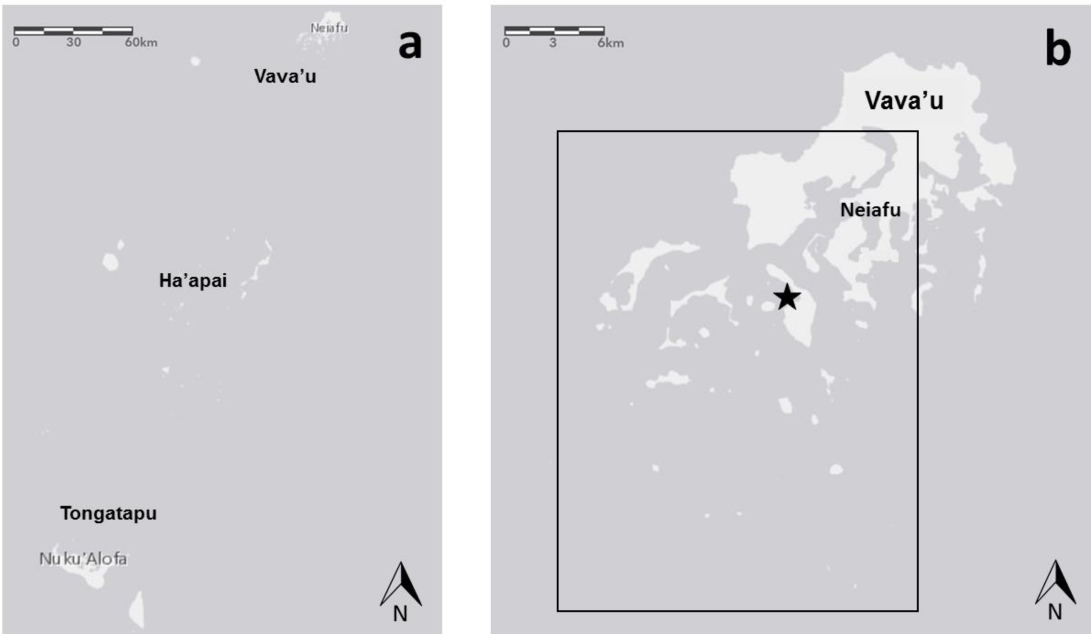

Figure 11. (**a**) The Kingdom of Tonga is constituted three main island groups and the remote Niuatoputapu islands. The study was conducted off of Vava'u Island (18°39'S, 173°59'W), (**b**) on the southern side (rectangle). Neiafu (18°39'S, 173°58'W) is the main township and the harbour from where tour vessels departed. Port Maurelle (18°42'S,

173°01’W), the anchorage from where most of the research dedicated surveys departed, is also indicated (star).

3.2.2 Survey design

Non-systematic surveys were conducted aboard a research dedicated 11-metre sailing trimaran and a 6-metre powerboat (powered by a 25 horsepower 2-stroke Mercury outboard motor), travelling at speeds less than 10 knots, depending on sea and wind conditions. The vessels were mainly operated from an anchorage in Port Maurelle (Figure 11b, p. 63). Surveys occurred only in good weather conditions (BSS < 4) and involved a skipper, the primary researcher (the UAV operator), and a trained observer. The observer’s eye height above the water surface was approximately two and a half metres on both vessels.

Once humpback whales were sighted, the vessel approached at idle speed (< 5 knots), following accepted protocols to minimise the potential effects on whale behaviour (Dawson et al., 2008; Stamation et al., 2010). A group was defined as one or more whales within 100 metres of each other, coordinating their behaviour, and moving in the same direction (Corkeron, 1995; Mobley & Herman, 1985; Whitehead, 1983). When within 300 metres from a focal group, the vessel was stopped, the engines were placed in neutral, and a survey was initiated (Figure 12a, p. 66), in accordance with Tongan regulations for non-whale watching vessels (*Tonga Whale Watching and Swimming Regulations 2013*, 2013). Distances were measured with a Rangemaster 1600-B laser rangefinder (Leica Camera, Wien, Austria). Date and time, location (GPS), environmental factors – such as sea state (Beaufort and Douglas scale), weather, wind speed (knots) and direction, and depth (metres) – were recorded at the beginning of each encounter, as well as the initial behavioural state and group composition of the focal group of whales. A calf was identified as a whale of less than 70% body length of an adult (full size) whale in close proximity which was defined as mother (i.e., lactating female) (Christiansen, et al., 2016; Sprogis, et al., 2020). Calves encountered during this study did not exceed 50% of their mother body length. (Corkeron, 1995). An individual adult whale consistently accompanying mother and calf pairs was defined as an escort (Tyack & Whitehead, 1982).

3.2.3 UAV operations

UAV operations were conducted under the research permit MOT-4/3, issued by the Tongan Ministry of Tourism. As Tonga lacked specific laws regarding the use of UAVs in its national airspace in 2016, operations complied with New Zealand Civil Aviation Authority (CAA) regulations. UAV surveys took place only in Visual Meteorological Conditions (VMC) (i.e., 10 kilometres skyline of sight, clear of clouds at the maximum legal flight altitude (122 metres), no rain) and 20 knots as the maximum wind speed. The primary researcher operating the UAV holds a Remote Pilot Certificate (license no. 839465) issued by the Australian Civil Aviation Safety Authority (CASA) in 2015. The UAV used was the HexH2O™ (ExtremeVision360, Worthing, UK), a six rotor waterproof helicopter (4.7 kilograms, diametre 110 centimetres propeller tip-to-tip, Figure 12b, p. 66) equipped with a gimballed GoPro Hero 4 Black camera (GoPro Inc, San Mateo, CA, USA). The camera has a 2.92 millimetres focal length and a mount with a polarised filter. The HexH2O™ is fitted with a Naza M-V2 flight controller, E600 tuned propulsion system, and carbon fibre propellers (DJI Innovation, Shenzhen, China). Two Turnigy Multistar Li-Po batteries (6 S, 6600 milliamperes, 10 C) allow a maximum flight time of 25 minutes. I chose the relatively large HexH2O™ for this study because it provid a more reliable, robust, and water-resistant aircraft with extended flight time (refer to paragraph 2.3.4, p. 44). This was particularly important in the remote study site of Vava'u, Tonga, where access to spare parts and repair expertise is virtually non-existent.

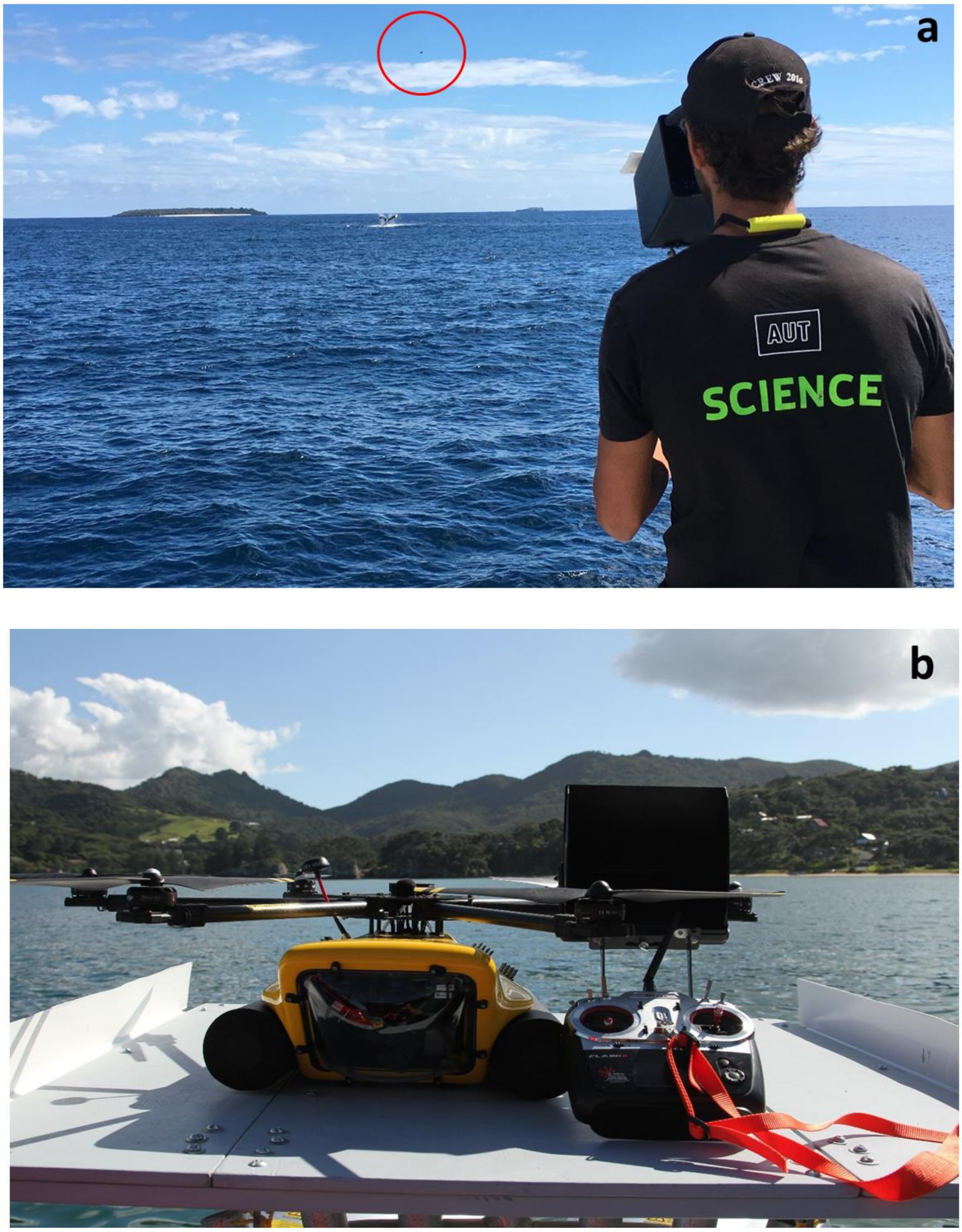

Figure 12. (**a**) The primary researcher conducting an aerial survey over humpback whales (*Megaptera novaeangliae*) in Vava'u, Kingdom of Tonga. The red circle indicates the UAV. Photo credit: Craig Koning. (**b**) HexH2O^{TM}, the UAV used in this study, during tests in New Zealand. Photo credit: Ticiana Fettermann.

The aircraft took off and landed from the vessel roof (powerboat platform) or the front webbing (sailing trimaran platform). The UAV was flown at 30 metres Above Sea Level

(ASL) from the moment it left the vessel until its return. The aerial videos recorded during the flights were analysed ashore after the vessel returned to dock so as not to influence the boat observer while collecting data.

3.2.4 Focal group follows

Vessel-based observational data on the focal group of whales were collected for a duration of 16 minutes prior to the UAV launch (absence or control), and during the 16 minutes exposure to aircraft (presence). Dive time (seconds), number of dives, respiration, and reorientation events (change in swim direction of 90° or more in respect to the original heading direction) were continuously recorded by an experienced observer on board the research vessel. The vessel observer was trained by the primary researcher in Vava'u to establish a consensus on humpback whale behaviour categorisation. Focal group size and behavioural state were recorded at approximately two minute scan sampling intervals (Altmann, 1974). That is, the intervals varied in time depending on the whale's presence at the surface and, therefore, the ability of the researcher to assess behavioural state and record data also varied. Behaviour was assumed to remain constant between observations (Lundquist et al., 2013). For example, any point sampling missed during a dive was allocated with the last behavioural state observed until the whales surfaced, and a new assessment can take place. During flights, the vessel observer collected data as soon as the UAV was above the focal group of whales. Exact time was recorded for comparison with the simultaneous aerial video recording.

Group behavioural state was defined as the behaviour in which more than 50% of the whales were involved, using focal group follow protocols developed by Mann (1999). Six mutually exclusive and cumulatively inclusive behavioural states (Lusseau, 2003) were defined to describe whale behaviour during the encounters: resting, travelling, surface-active, socialising (Sprogis, Bejder, & Christiansen, 2017; Stamation et al., 2010), feeding (Di Clemente et al., 2018), and nurturing (Table 2, p. 68). Feeding behaviour was included as a category but was unlikely to be observed due to the scarce distribution of humpback whale prey in tropical breeding grounds (Chittleborough, 1958; Matthews, 1937). A dive (i.e., whale arching the peduncle and/or fluking) was treated as a travelling behavioural state (Di Clemente et al., 2018), unless singing behaviour was detected. An H2A-XLR hydrophone (Aquarian Hydrophones, Anacortes, WA USA) was deployed in case of prolonged dives to detect singing behaviour. Singing whales were excluded from the behavioural categorisation, as this activity is not visually detectable. The vessel-based observer allocated the behavioural category in-situ during the observations and onto a data sheet.

Table 2. Definitions of behavioural states of individual humpback whales adapted from Sprogis et al. (2017), Stamation et al. (2010) and Di Clemente et al. (2018).

Resting (R)	Whale is motionless and horizontal at the water surface, may be also drifting or slightly below the water surfacing only to breathe.
Travelling (T)	Whale is travelling from location to location with persistent, directional movement making noticeable headway along a specific compass bearing at a constant speed, and may leave rows of “fluke-prints” at the surface.
Surface-Active (SA)	Whale is causing white water at the surface by rolling, breaching, spy hopping, caudal fin, pectoral flipper, or head slapping.
Socialising (S)	Whale is actively rubbing, touching, chasing, or circling around another whale (Figure 13, p. 70). Underwater bubble blows (Figure 13c, p. 70) can be observed (Supplementary material #1). Socialising category includes competitive groups of whales. These whale aggregations are composed by several whales involved in fast erratic movements and agonistic displays directed towards other whales (Tyack & Whitehead, 1982).
Feeding (F)	Whale is rapidly emerging with the ventral plates extended. The body at the act of surfacing can be lateral or vertical (Di Clemente et al., 2018).

Nurturing (N)	A whale mother and its calf are rubbing or touching (Figure 14, p. 71); this includes mother lifting the calf with its rostrum (Supplementary material #2). Possible suckling can be observed (Smultea et al., 2017; Zoidis & Lomac-MacNair, 2017).

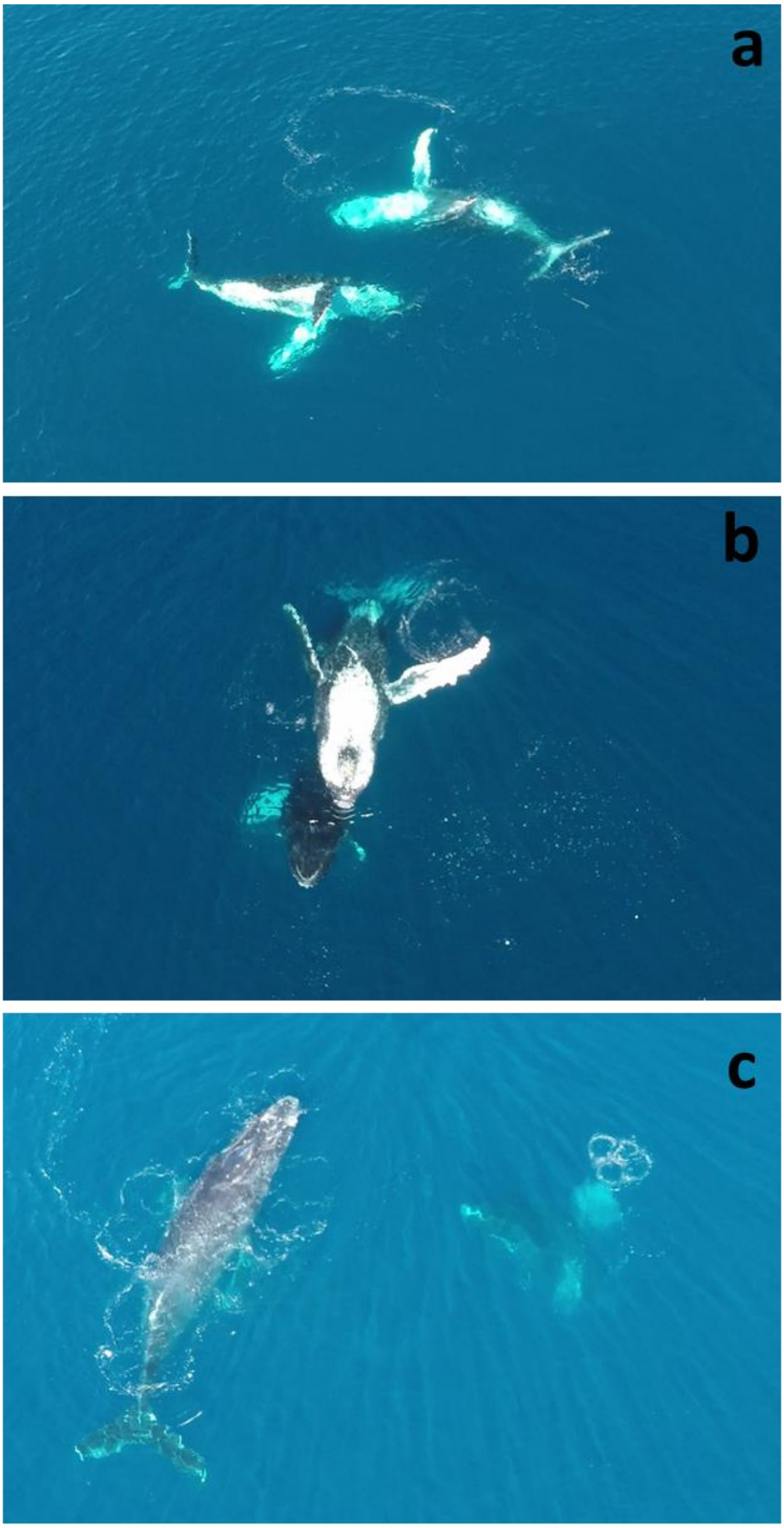

Figure 13. A couple of adult humpback whales (*Megaptera novaeangliae*) socialising along the shore of Taunga Island (18° 44'S, 174°01' W), Vava'u, Kingdom of Tonga. (**a**) Synchronized inverted swim; (**b**) rubbing on the other individual; (**c**) underwater blows. Frames extracted from the aerial videos recorded by the UAV during this study.

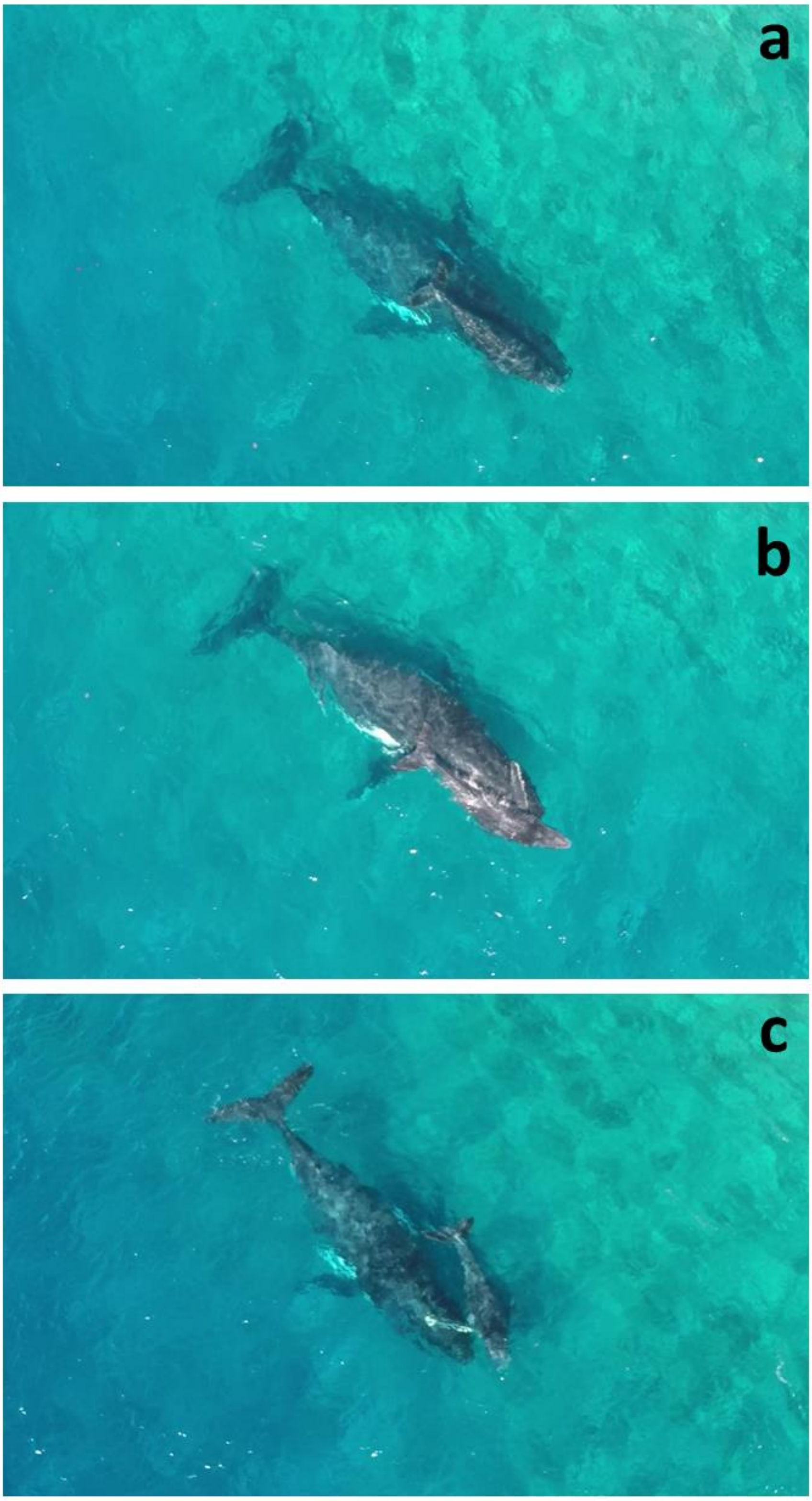

Figure 14. Humpback whales (*Megaptera novaeangliae*) mother and calf interacting close to the shore of Foelifuka Island (18°42'S, 173°01'W), Vava'u, Kingdom of Tonga. (**a**) Calf is above mother's rostrum; (**b**) mother lifts calf's left pectoral flipper with its rostrum; (**c**) calf rubs right pectoral flipper on mother's rostrum. Frames extracted from the aerial videos recorded by the UAV during this study.

3.2.5 Video analysis

UAV videos were recorded continuously at 60 frames per second (fps) during the flight. The GoPro camera was set in medium Field of View (FOV), which corresponds to a focal length equivalent of 21.9 millimetres and resolution was 2.7 K, 2704 × 1520 pixels. The imagery was analysed later on the same day, ashore, or on the live-aboard vessel, using an EliteBook 850 (Hawlett-Packard, Palo Alto, CA, USA) with a screen resolution of 1366 x 768 pixels and 125 pixels per inch (PPI). Behavioural categorisations were made using the same two-minute interval adopted by the vessel observer during focal group follows. Videos were analysed in presence of the vessel observer to verify consensus between the researchers.

3.2.6 Statistical approach

Platform assessment method

The hypothesis that UAV-based and vessel-based observations are equally accurate was tested comparing the proportion of time whales spent in each behavioural state. That is, two set of proportions were calculated: one using data collected from the vessel and one using the footage simultaneously recorded by the UAV. The proportion of time spent in each state was then compared with a binomial *z*-test for proportions and 95% confidence intervals were calculated.

Response to UAV method

Potential UAV-induced changes in whale behaviour could be detected through UAV absence/presence comparisons. The respiration rate (blows × whales in the group^{-1}), the number of diving and reorientation events, as well as the total diving time, were modelled as a function of the absence or presence of the UAV. Only data collected by the vessel observer were used to conduct UAV disturbance analysis. Graphical validation tools were used to assess the underlying assumptions of variance homogeneity (plot residuals vs. fitted values) and normality (quantile-quantile plot of the residuals) for dive time and respiration rate. Shapiro-Wilk and Levene's tests were also performed to test for normality and homoschedasticity, respectively. No violations of normality and homoscedasticity assumptions were detected. An ANOVA was run to compare UAV absence and presence data for whale dive time and respiration rate. Generalized Linear Models (GLM) with negative binomial distribution and log link function were used to compare the absence and presence data for counts of diving and reorientation events. Statistical analyses were conducted using SPSS Statistic 24 software (IBM, Armonk, NY, USA. 2016). For all analyses, statistical significance was assumed at $\alpha = 0.05$ level.

3.3 Results

Thirty-three focal group follows were conducted during 578.6 kilometres of survey effort across 19 days aboard research dedicated vessels in 2016. During the 27.8 hours spent with whales, thirty-three UAV operations were undertaken for a total flight time of 10.2 hours. In three instances, data were excluded from further analysis, as motorised whale-watching vessels approached the focal group during the aerial survey.

3.3.1 Platform assessment

High-resolution aerial imagery collected during UAV operations was analysed using the same method used during the surveys. Whale dive time and surfacing matched with what was recorded by the vessel observer in all the tests (n = 33). However, behavioural state assessment from the UAV perspective appeared significantly different (z-test, $P < 0.05$) from what was recorded by the vessel observer (Figure 15a and b, p. 75). Therefore, the proportions of time spent in each behavioural state were compared between the two methods, and were further divided into two groups; those without a calf, or calves, present (Table 3, p. 76) and those with a calf, or calves, present (Table 4, p. 76). Data were pooled in two subsets, as groups of whales without calves do not spend time in nurturing behavioural state and groups of whales with a calf were not observed in a socialising behavioural state. To illustrate, whale groups observed without calves spent 22.2% of their time socialising when observed from the aerial perspective, while this behavioural state was only detected for 1.1% of the time from the vessel-based observations (95% CI: 12.1 – 30.1%, $z = 4.41$, $P < 0.001$).

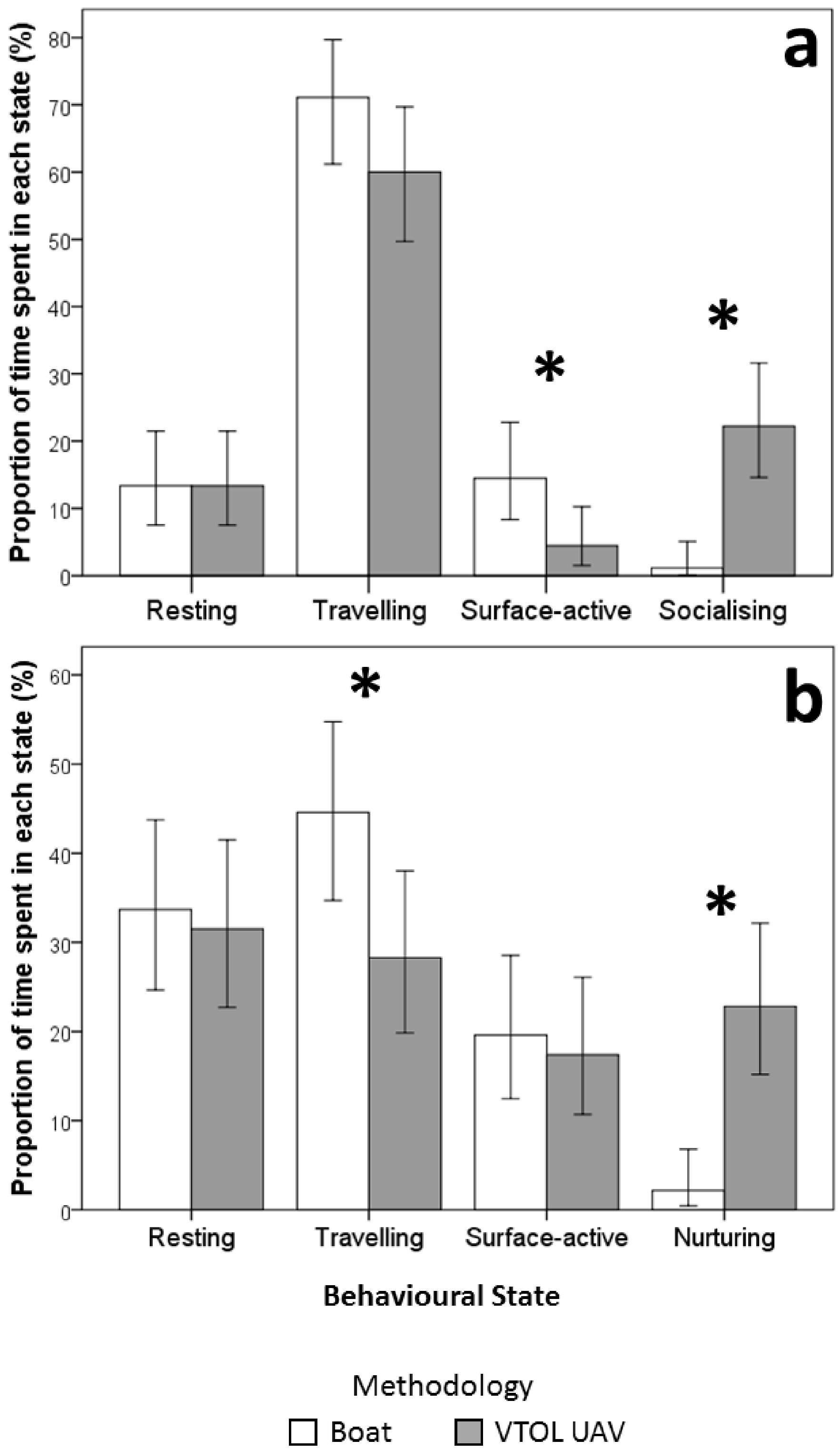

Figure 15. Proportion of time humpback whales (*Megaptera novaeangliae*) spent in each behavioural state by (**a**) non-calf groups, and (**b**) mother-calf groups recorded from a vessel and VTOL UAV platforms in Vava'u, Kingdom of Tonga. Error bars represent 95% confidence intervals. Significant differences ($P < 0.05$) between methodologies are denoted by an (*).

Table 3. Proportion of time spent by groups of humpback whales (*Megaptera novaeangliae*) without calves in each behavioural state recorded from a vessel and UAV platforms in Vava'u, Kingdom of Tonga. Significant differences ($P < 0.05$) between methodologies are denoted by an (*).

Behavioural state	**Boat-based data**	**UAV-based data**
Resting (R)	13.3%	13.3%
Travelling (T)	71.1%	60.0%
Surface-Active (SA)	14.4%*	4.4%*
Socialising (S)	1.1%*	22.2%*

Table 4. Proportion of time spent by groups of humpback whales (*Megaptera novaeangliae*) with a calf in each behavioural state recorded from a vessel and UAV platforms in Vava'u, Kingdom of Tonga. Significant differences ($P < 0.05$) between methodologies are denoted by an (*).

Behavioural state	**Boat-based data**	**UAV-based data**
Resting (R)	33.7%	31.5%
Travelling (T)	44.6%*	28.3%*
Surface-Active (SA)	19.6%	17.4%
Nurturing (N)	2.2%*	22.8%*

Socialising was mistakenly categorised as either travelling (52.6%) or surface-active (47.4%) from the vessel-based observations when review of the UAV data clearly indicated that socialising was the correct behavioural state. Moreover, the proportion of time spent in a surface-active state was assessed as being significantly lower (10.0% less) from the UAV aerial perspective (95% CI: 1.5 – 18.5%, $z = -2.29$, $P = 0.022$). Groups containing calves spent 22.8% of their time in a nurturing behavioural state when observed from the UAV, but this behavioural state accounted only for 2.2% of time when the data were collected by vessel-based observations (95% CI: 11.4 – 29.9%, $z = 4.23$, $P < 0.001$). Nurturing was most commonly recorded by the vessel-based observations as resting (68.4%), followed by travelling (21.1%), and surface-active (10.5%). The behavioural state categorised as travelling decreased significantly (by 16.3%) when the behaviour was assessed from the UAV (95% CI: 2.4 – 30.2%, z = - 2.29, P = 0.022). Finally, socialising and nursing behaviours were not observed in mother-calf groups from either the UAV or vessel-based platforms. Similarly, feeding behaviour was never observed during the entirety of the study.

3.3.2 Response to UAV presence

No significant difference ($F_{1,58}$ = 0.243, P = 0.624; $F_{1,58}$ = 0.358, P = 0.552) was detected for both respiration rate and mean dive time in the presence or absence of the UAV at 30 metres altitude (Figure 16a and b, p. 78). In addition, the number of dives and reorientation events were analysed using GLMs with binomial probability distribution. The comparison between the intercept only model and the model with UAV present indicated that the number of dives (Figure 16c, p. 78) was not significantly affected by the UAV at 30 metres altitude (Likelihood Ratio: χ^2_1 = 0.13, P = 0.910). A similar result was obtained for the number of reorientation events (Likelihood Ratio: χ^2_1 = 1.055, P = 0.304) (Figure 16d, p. 78v). No sudden changes in behaviour of the whales were noticed as the UAV first appeared above them.

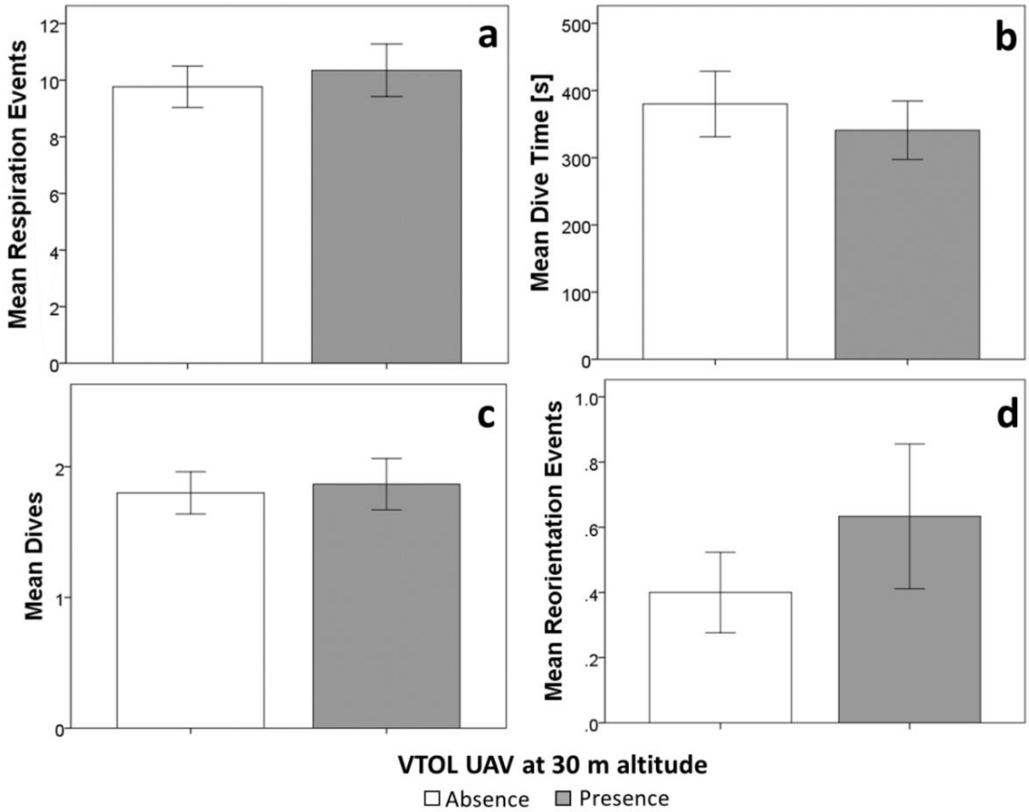

Figure 16. Representation of mean of (**a**) respiration events, (**b**) dive time, (**c**) number of dives, and (**d**) reorientation events in presence and absence of VTOL UAV flying at a 30-metre altitude above a group of humpback whales (*Megaptera novaeangliae*) in Vava'u, Kingdom of Tonga. Error bars represent the standard error of the mean.

3.4 Discussion

3.4.1 Platform assessment

While the vessel-based observations were efficient and timely in detecting surface behaviours such as dives, respiration, and reorientation events, the behavioural state assessment was significantly different from the UAV-based data. That is, socialising and nurturing categories were under-represented when data collected by the vessel-observer were considered.

Travelling, resting, and surface-active have been widely used as categories to describe humpback whale behaviour (e.g., Corkeron, 1995; Sprogis et al., 2020; Stamation et al., 2010). More recently, several authors have introduced the socialising behavioural state to describe whale intraspecific interactions such as courtship behaviour and mating competition between males (Sprogis et al., 2020). In addition, because of the importance of Vava'u as a breeding ground for humpback whales, nurturing is being used in this study to categorise and record mother-calf interactions. The results of the comparison between the vessel-based observations of behaviour with the UAV-based observations indicate that the behavioural states of socialising and nurturing were frequently recorded as other behavioural states in the vessel-based data set (Figure 15a and b, p. 75). The ability to examine and re-examine the UAV video recording of whale behaviour, post-flight, and off the water, is beneficial, and it facilitates a more accurate and trustworthy categorisation of whale behaviour states. In addition, the ability to review a video recording allows multiple researchers to assess the content and increase the accuracy and confidence of the behavioural state categorisation through consensus, or agreement, among colleagues. Finally, through the elevated and near vertical perspective above the whales they provided, UAVs allow for more continuous visibility, including for behaviour under and at the surface. This enhanced view allows researchers to investigate behavioural transitions in a much broader context and to gain insight into previously undetected effects on behaviour, such as additional whales approaching the focal group from depths.

Results suggest that some behavioural states (in this case, socialising and nurturing) are more difficult to observe and accurately record from a vessel-based observation platform than with a UAV. This is plausible because a vessel-based observer is unlikely to be able to view or accurately assess the behaviour of whales that are submerged, at a great distance, or are at an oblique angle in relation to the vessel. That is, the observer's height above the water's surface and the distance from the whales are considered as factors influencing behavioural assessment. For instance, in accordance to Tongan laws, research platforms did not actively approach the focal groups closer than 300 metres. Moreover, vessel observer eyes were at the approximate height of 2.5 metres above the water surface. Therefore, the differences between vessel-based and UAV-based data found by this study could have been reduced by approaching at closer distance from the whales and positioning the observer at a greater height.

In addition, this research found that the UAV permitted the observer to follow the whale movements, even during the time spent underwater, and to detect subtle physical contact between individual whales (depending on the depth of the whales below the surface and water clarity). However, while mother-calf interactions were clearly visible and quantifiable, it was not possible using the UAV (and certainly not from the vessel-based platform) to observe the calf in positions that may have indicated nursing behaviour. Only in one occasion white suspension patches were detected in proximity of a calf's mouth (Supplementary material #3). At the time of the observation, the mother was not visible from the aerial perspective, suggesting nursing was taking place at a depth. Humpback whale nursing behaviour has been observed in Hawai`i at depths between 10 and 15 metres (Zoidis & Lomac-MacNair, 2017). If this depth is typical for humpback whale nursing, the detection of this behaviour from an aerial platform, such as a UAV, will be difficult, especially when water visibility is low. During this study, underwater visibility was dependent on the location, sea-surface state, the angle of sunlight on the water surface (i.e., time of the day), and the weather. Interestingly, whales motionless at depth were observed on several occasions during this study, and this could also explain the significant over-representation of travelling behaviour detected for mother and calf pods by the vessel observer.

Finally, UAVs provide an enhanced perspective on the focal group, but they also tend to reduce the observer's field of view. That is, the presence of other individuals in proximity of the focal pod might not be detected. While this did not present an issue during this study, it might be a limitation for behavioural surveys on other cetacean species in different contexts (i.e., large and/or highly dispersed pods).

To summarise the findings of this study, the data suggest that the biases involved with vessel-based observations result in the assessment of certain whale behaviours that can significantly differ from when observations are conducted from a more advantageous, or overhead, perspective. Attempting to categorise and quantify the behaviour of an animal that spends the majority of its time beneath the surface by observing and recording only its surface behaviour is inherently flawed. With the exception of shore-based observation stations, which are always distant and at an oblique angle from the observed whales (or other cetaceans), the great majority of behavioural research on cetaceans to date has utilised a vessel-based platform (Guerra et al., 2014). The research comparing a vessel-based, traditional method with a UAV-assisted approach indicates that these new tools have the potential to make major advances in cetacean behavioural research and improve, or change significantly, our understanding of their behavioural ecology.

3.4.2 Response to UAV presence

Following concerns raised by several authors (Mulero-Pazmany et al., 2017; Smith et al., 2016), this study also investigated the potential effects of a UAV on the behaviour of the focal group of whales. The potential of both vertical and horizontal avoidance reactions was assessed by measuring and comparing whale dive time, diving and respiration rates, and the number of reorientation events in both the absence and presence of the UAV. No significant differences were detected for these parameters when flying the UAV at a 30-metre altitude over whales. As a result, it can be concluded that there was no evidence of avoidance responses from the whales due to the presence of the UAV. This finding is consistent with what has been anecdotally reported by other researchers who have flown lightweight UAV at 30- and 50-metre altitudes over humpback whales (Christiansen, Dujon, et al., 2016).

Despite the lack of statistical significance detected in the present study, the mean difference of number of reorientation events was slightly larger in the presence of UAV than in the absence of the UAV. This warranted further investigation. An analysis of the aerial video recorded from the UAV flights indicated that, on two occasions, groups of whales would change direction in the presence of the UAV, but these evasive manoeuvres observed proved to be a response to pursuing behaviour from an individual adult? whale. Future research on the effects of UAVs on cetacean behaviour, however, should consider other variable responses (e.g., swimming speed, frequency of aerial behaviours such as fluke slaps, breaches, peduncle slaps and side rolls).

The findings of this study support the hypothesis that UAVs, operating at a safe distance, can be used to assess humpback whale behaviour remotely and non-invasively, potentially eliminating the need for close approach by research vessels to collect behavioural data. It is important, however, to recognise that factors such as flight altitude, aircraft type, environmental conditions, species identity, location, and life-stage may all affect marine mammal behaviour and their reaction to UAVs approaching them (Pomeroy et al., 2015). In addition, while cetaceans might respond physiologically to the UAV presence, they do not display any detectable behavioural change, as documented in black bears (*Ursus americanus*) by Ditmer et al. (2015). That is, bears reacted to a UAV flying at 20 metres above them increasing three times their heart rates but no behavioural response was detected in most of the tests. The choice of 30 metres ASL for humpback whale surveys was made due to the need to capture, in the same video camera frame (mounted on the UAV), all the individuals of the focal group and provide clear visual recordings of behaviour. Furthermore, a conservative approach was chosen by flying at 30 metres altitude, because behavioural responses have been documented in bottlenose dolphins exposed to a Splashdrone, a UAV, flying at 10 metres altitude (Fettermann et al., 2019). Also, the UAV used in this study, the HexH2O™, is considerably larger than the Splashdrone. While this does not necessarily imply a higher noise level (Perryman et al., 2014), disturbance of cetaceans from aerial sources could originate from both visual and acoustic stimuli (Richardson & Würsig, 1997; Southall et al., 2007). Finally, another consideration in the choice of flying 30 metres ASL was that bottlenose dolphins have been documented to also respond to the Splashdrone's shadow by turning onto their sides in what seemed an attempt to visualise the UAV flying overhead (Fettermann et al., 2019). Interestingly, in one occasion, the HexH2O™ shadow was over a humpback whale mother's rostrum, but no behavioural response was detected (Supplementary material #4).

3.5 Conclusions

The use of UAVs has further extended the opportunities for marine mammal aerial observational research that was developed during the late 20th century with ‘blimp’-based research platforms (Flamm et al., 2000; Hodgson, 2007; Nowacek et al., 2001). UAVs have the additional advantages of greater manoeuvrability and the possibility to track marine mammals over greater distances (refer to paragraph 2.3.4, p. 44). The findings presented in this study provide empirical evidence that UAVs represent an innovative, non-invasive, and effective tool to investigate cetacean behaviour, as proposed also by other researchers (e.g., Hodgson et al., 2017; Nowacek et al., 2016). Although the post-flight data processing efforts can be time-consuming and cost-intensive (Marine Mammal Commission, 2016; Linchant et al., 2015), the opportunity to use close aerial video recordings of behaviour significantly improves the quality and accuracy of data for cetacean behavioural studies. Furthermore, the ‘birds-eye’ point of view provided by UAVs more readily allows the observation and recording of subtle and cryptic behaviours, such as socialising and nurturing. Finally, the results of the assessment of the potential disturbance, with the flight of a UAV at a 30 metres altitude overhead are most compatible with no important effect on humpback whale behaviour. These encouraging findings highlight the tremendous potential of this new research tool in improving data accuracy and gaining new insights into cetacean behaviour. However, the highly diverse cetacean morphology, and behavioural ecology, together with their wide distribution, require careful tailoring and evaluation of the UAV setup, including operating altitude on a case-by-case basis. Further investigations on the use UAVs at lower altitudes, over different species, and in other locations will be important to extend our confidence in the application of these tools for cetacean research.

Chapter - 4 - Effects of whale-based tourism in Vava’u: Behavioural responses of humpback whales to vessel and swimming tourism activities

Chapter 4 cover picture. A group of swimmers observes a mother humpback whale (*Megaptera novaeangliae*) lifting her calf with her rostrum close to the South side of Mu’omu’a Island (18°45′ S, 174°08′ E), Vava’u, Kingdom of Tonga. Photo credit: Barbara Lësser.

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In this Chapter, the main research question of this thesis is addressed: the interaction levels between whales and swim-with-whales vessels (Thesis objectives I) and the short-term behavioural responses of humpback whales to swim-with-whales vessels and swimmer approaches (Thesis objectives II) are quantified using a traditional boat-based observational methodology. That is, the data presented in this Chapter were collected by a vessel observer during fifty-six surveys taking place in Vava'u, Kingdom of Tonga, in the 2016 and 2017 whale breeding seasons aboard dedicated research and opportunistic platforms (swim-with-whales vessels). Although a UAV platform was used to collect whale behavioural data in this study (refer to Chapter 5, p. **Error! Bookmark not defined.**), the presence of a vessel observer to document the encounters with whales was still necessary. As described in the literature review section of this thesis, the use of UAVs for cetacean behavioural surveys faces some limitations. In particular, the flight time of 25 minutes does not permit following the focal group of whales throughout the total time of the encounters, especially during swim-with-whales tourism activities. Therefore, a back-up option is necessary to collect data during the UAV launch, retrieval, and replacement of batteries. In addition, it was not always possible to recharge batteries onboard the vessels, limiting the maximum number of UAV operations per survey. Additionally, the levels of industry compliance with whale-watching regulations and guidelines are quantified in this Chapter to determine the effectiveness of the current management regime in Vava'u (Thesis objectives IV).

In this study whale diving time, number of reorientation events, and respiration rates (blows × minute^{-1}) were documented in both the absence (control) and presence of vessels and swimmers. Vessel approach type, swimmer placement, and whale avoidance responses were also recorded. Results indicate that the average diving time and the proportion of time spent diving in the presence of in-water tourism activities increased significantly for mother-calf pairs. Moreover, avoidance responses of whales towards swim-with-whales vessels were observed for one third of vessel approaches, and the avoidance rate of the whales was significantly affected by the vessel approach type. Finally, low levels of compliance to the existing Tongan swim-with-whales regulations were documented, in particular, the stipulated whale resting time between interactions with tour operator vessels and swimmers was often not respected (38.4%).

4.1 Introduction

The whale-watching tourism industry’s focus on humpback whales has escalated worldwide in the last three decades according to O'Connor et al. (2009). This global trend has been supported by the recovery of some whale populations (Magera et al., 2013) and the increasing public demand for tours offering close interactions with whales (Higham & Bejder, 2008; Orams et al., 2014). Consequently, tourism activities focusing on humpback whales have increased, both in regions representing important breeding grounds for this species and on migration routes (Hendrix & Rose, 2014).

The Kingdom of Tonga promotes swimming activities with humpback whales during their breeding season, with mothers and calves being the primary focus (Kessler & Harcourt, 2012). The growth of whale-based tourism in Tonga from the 1990s to now represents a major source of foreign income for the nation (Kessler & Harcourt, 2012; Orams, 2002). Vava’u, a northern archipelago of the Kingdom, is where the first swim-with-whales commercial activity started in 1993 (Kessler et al., 2013). By 2017, the island group had 20 commercial tour operators offering in-water encounters with humpback whales (Tongan Ministry of Tourism, personal communication, October 8, 2017), more than any other whale-watching destinations worldwide (Hendrix & Rose, 2014). Each operator can obtain up to two licences for swimming activities and is permitted to have two tour vessels operating at the same time. In addition, a low level of compliance with the existing Tongan regulations has been reported in the past (Walker & Moscardo, 2011).

Swimming activities with whales are still prohibited in most countries where whale-watching occurs (Hendrix & Rose, 2014) and the scientific community has expressed the need for a more precautious approach for the management of commercial tourism operations (Constantine & Bejder, 2007; Higham et al., 2009; Martinez & Orams, 2011). There is widespread concern amongst the scientific community (e.g., Constantine, 2001; Fumagalli et al., 2018; Lundquist et al., 2013; Martinez et al., 2010; Meissner et al., 2015; Peters et al., 2012; Sprogis et al., 2020) that swim-with-cetaceans tourism can disrupt vital behaviour and cause avoidance responses in targeted cetaceans. For example, increases in the number of dives (also referred as vertical avoidance) have been reported for humpback whales (Au & Green, 2000; Baker & Herman, 1989; Corkeron, 1995; Schaffar et al., 2010; Stamation et al., 2010) and sperm whales (Richter et al., 2006) exposed to approaches from tourism vessels. Humpback whales (Avila et al., 2015; Schaffar et al., 2010; Scheidat et al., 2004) also show a less direct swim path (a behaviour known as horizontal avoidance) when approached by whale-watching boats. Similar responses have been observed during swim-with trials conducted with humpback whales in Western Australia (Sprogis et al., 2020). Moreover, the need to place swimmers in close proximity to the whales can encourage vessel approaches that are less tolerated by the whales and are considered highly invasive (Curnock et al., 2013; Richardson, Greene, Malme, & Thomson, 1995; Sprogis et al., 2020). For instance, tour operators may increase their approach speed to overtake the whales and position the boat in the whale’s path of travel in attempt to increase the success of the swim-with activity for the tourists (Lundquist et al., 2013). This behaviour has been defined as a “J approach” by Scarpaci, Nugegoda, & Corkeron (2003) and it is strongly discouraged by whale-watching regulations worldwide (Carlson, 2013).

Some studies have also demonstrated that short-term responses to vessel approaches can lead to long-term effects for dolphins at both the individual and population levels (Bejder et al., 2006; Filby et al., 2014; Lusseau, 2004; Tyne, Johnston, Christiansen, & Bejder, 2017). However, only a few studies have focused on the behavioural responses of baleen whales to swim-with tourism activities (Kessler et al., 2013; Lundquist et al., 2013;

Mangott et al., 2011). Responses to swimmer approaches appear to depend on the targeted species. For example, when comparing two different species' response to swimmer approach, significant changes in the behavioural budget have been observed in southern right whales in Península Valdés, Argentina (Lundquist et al., 2013), upon approach, while dwarf minke whales appear to deliberately approach vessels and swimmers in the Great Barrier Reef, Australia (Mangott et al., 2011). This research is significant because there are a growing number of locations which are opening up swim-with-humpback whales tourism (e.g., Queensland, Western Australia, Nuie, French Polynesia, the Dominican Republic) (Bochenski, 2014; Hendrix & Rose, 2014). Vava'u, Tonga is an appropriate location to conduct this research because it has a long-established and intensive swim-with-humpback whales tourism sector (Kessler & Harcourt, 2012; Orams, 2002; Walker & Moscardo, 2011). More importantly, these commercial swim-with-whales operations take place in a humpback whale breeding and calving ground (Baker et al., 1998), and what makes the Tongan sub-population especially critical to protect is that it still shows little signs of recovery after the cessation of whaling (Clapham et al., 2009; Constantine et al., 2012; Jackson et al., 2013).

This study represents an assessment of the behavioural responses of humpback whales to vessel and swimmer approaches in Vava'u, Kingdom of Tonga. First, the effects of vessel and swimmer approach type chosen by tour operators on whales' reaction were investigated. The hypothesis was that if the approach type would not influence the whale response to the approach, the avoidance rate would not differ significantly between different type of approaches. Secondly, whales' diving, respiration, and reorientation parameters were quantified, and the effects of swimming tourism activities on these response variables were assessed. The hypothesis was that, if vessel or swimmer presence (experimental situations) do not affect whales' behaviour, then no significant differences for dive time, diving frequency, proportion of time spent diving, respiration rate, or reorientation rate would be detected in comparison with the absence of tourism activities (control situations). Finally, the level of compliance with Tongan regulations was evaluated.

4.2 Methods

4.2.1 Study site and species

The study was conducted during humpback whale breeding seasons (between July and October) in 2016 and 2017 on the South side of Vava'u (18°39'S, 173°59'W), Kingdom of Tonga (Figure 5, p. 19). The study was undertaken under the permit MOT 4/3 issued by the Tongan Ministry of Tourism.

4.2.2 Survey design

Control data (samples in the absence of vessels and swimmers) were collected in the absence of commercial tour vessels or private vessels within a 1,000 meters radius of the focal group of whales. Data were gathered aboard a dedicated research vessel, which was an 11-metre sailing trimaran and a six- metre powerboat (powered by a 2-stroke Mercury 25 horsepower). Surveys were conducted as described in paragraph 3.2.2 (p. 64). Control observations lasted 30 minutes, then the research vessel left the area to search for other whale groups. This protocol was based on other studies on the behavioural responses of humpback whales (Sprogis et al., 2017) and southern right whales (Lundquist et al., 2013) to swimming tourism activities. A 30 minutes observation was deemed appropriate to gather sufficient data about whale behaviour at the surface and surface respiration patterns, while also considering the maximum observed dive time of humpback whales in Vava'u during this study. Moreover, this protocol aimed to minimise potential disturbance to the whales, especially mother-calf pairs.

Experimental data (samples in the presence of tour vessels and swimmers) were collected by the primary researcher and the observer from two swim-with-humpback whales tour operator vessels, hereafter referred to as vessel A and vessel B. As for the research vessels, the observer's eyes were at a height of two and a half metres above the surface of the water. The two tour boats share similar sizes (10 metres in length), but they differ substantially in terms of engines and hydrodynamics. Vessel A is a catamaran design and it is gasoline-powered by two 4-stroke Yamaha 250 horsepower outboard engines. Vessel B is a single hulled boat and is powered by two inboard diesel engines (Cummins 350 horsepower). The boats were voluntarily offered by tour operators to be utilised as platform of opportunity for this research. Therefore, researchers had no control over the type of vessel, speed of approach, minimum distance to the whales, or placement of swimmers into the water. As per control observations, a 30-minute protocol was followed to collect data during swim tourism activities.

4.2.3 Focal group follows and data collection

The beginning of an encounter between a tour vessel and whales is the point at which a vessel was approximately 1,000 metres from the focal group of whales. A focal group was represented by one or more whales within 100 metres from each other, coordinating their behaviour and moving in the same direction (Corkeron, 1995; Mobley & Herman, 1985; Whitehead, 1983). Date, time, location (latitude and longitude using GPS), sea-state (Beaufort and Douglas scales), weather, wind speed, wind direction, and depth were recorded and assessed at the beginning of each encounter, as well as the composition of the whale group. A calf was identified as a whale of less than 70% body length of an adult (full size) whale aside, which was defined as mother (i.e., lactating female) (Christiansen, et al., 2016; Sprogis, et al., 2020). Calves encountered during this study did not exceed 50% of their mother body length. An adult whale consistently accompanying a mother and calf pair was defined as an escort (Tyack & Whitehead, 1982).

The initial behavioural state of the focal group of whales was assessed as described in paragraph 3.2.4 (p. 67). Behavioural categories (resting, travelling, surface-active, socialising, feeding, and nurturing) were allocated following definitions presented in Table 2 (p. 68). An H2A-XLR hydrophone (Aquarian Hydrophones, Anacortes, WA USA) was deployed in case of prolonged dives to detect singing behaviour.

Whale responses to vessel and swimmer approaches were categorised as either ‘avoidance’ or ‘no avoidance’. An ‘avoidance’ response was defined as a movement away from the approaching vessel or swimmers (Stamation et al., 2010). A ‘no avoidance’ response included any other potential category (i.e., attraction and neutral). The boat approach type was recorded as direct, parallel or J (Table 5, p. 93) (Scarpaci et al., 2003). The distance between vessel and the closest whale was measured by the primary researcher using the laser rangefinder every time whales were present and visible at the surface. Similarly, whales joining or leaving the focal group, as well as the quantity and names of tour boats arriving or departing in the area (1,000 metres around the focal group), were recorded through the encounters.

Table 5. Definitions of vessel approach type (Scarpaci et al., 2003).

Parallel	The tour vessel is positioned to the side of the focal whale group, parallel to the whales’ direction of travel.
Direct	The tour vessel is maneuvered directly in the middle of the focal whale group. This may happen from any direction with respect to the heading of the whale group.
J	The tour vessel travels parallel to the focal whale group direction of travel, overtakes the whales and is then turned in front of the group.

Swimmer placement (Table 6, p. 94) was generally associated with the tour vessel approach type: ‘in path’ (during vessel J approaches), ‘line abreast’ (during vessel parallel approaches), and ‘around boat’ (during vessel direct approaches) (Constantine, 2001).

Table 6. Definitions of swimmer placement type adapted from Constantine (2001).

Line abreast	On the side, parallel to the direction of travel of the focal whale group, slightly ahead of the whales.
In path	In the path of travel of the focal whale group.
Around boat	The tour boat is stationary with the focal whale group circling around it.

Dive time (seconds), number of dives, respirations (number of “blow” exhalations during a surfacing period), and group reorientation events (change in swim direction of 90° or more in respect to the original heading direction) were recorded continuously (Altmann, 1974). Average dive time (total dive time × number of dives^{-1}), diving frequency (dives × hour^{-1}), and respiration rate (blows × individuals^{-1} × minute^{-1}) were calculated. As asynchronous diving behaviour was observed for mothers and calves, a focal individual (i.e., the mother) was selected to record the dive time. The decision to focus on one individual in a pair was made, as it was problematic for the observer to record the dive time of two or more whales while collecting other data, simultaneously. Therefore, in the case of groups containing a calf, the mother was chosen as the focal individual; the calf and the escort were always observed, if present, following the mother, and she was readily recognisable by the observer. Multiple mother-calf pairs were never observed in the same group of whales, neither they were accompanied by more than one other individual (i.e., escort).

4.2.4 Statistical approach

Avoidance responses to vessel and swimmer approaches

Generalized Linear Models (GLM) were used to test the hypothesis that the vessel approach type had no effect on whales' response. That is, the presence or absence of an avoidance response was modelled as a function of approach type (AT), vessel A or B (V), distance between vessels and the closest whale (DI) and water depth (DP), using a binomial distribution with logit link function. Two two-way interactions were also tested (AT × V and V × D). Due to the low sample size of direct approaches, only parallel and J approaches were considered for analysis. GLMs were compared using Akaike's Information Criterion (AIC). The best fitting model had the lowest AIC and models falling within two units were considered to have substantial support (Burnham & Anderson, 1998). That is, AIC assist in the identification of the model that provides more information using less parameters. Models falling within the two-unit range were considered to provide an equal amount of information and parameters were further evaluated to choose the most parsimonious model. Any significant effect of a parameter on the avoidance response occurrence was further investigated by comparing the avoidance rate with a *z*-test for proportions. Confidence intervals (95%) were also calculated.

Similarly, GLMs with binomial distribution and logit link function were used to test the dependence of whales' response to swimmer approaches. The presence or absence of avoidance response was modelled as a function of swimmer placement (SP), vessel (V), distance of the boat from the whales at swimmer drop (DD), and water depth (DP). Two two-way interactions were also considered – swimmer placement × vessel and vessel × distance of the boat from the whales at swimmer drop (SP × V and V × DD). Due to the low number of swims “around the boat”, only “line abreast” and “in path” placements were analysed. In addition, “line abreast” approaches were modelled to test the whale’s response as a function of vessel (V), vessel distance at swimmer drop (DD), depth (DP), presence of calf (C), and whale’s behaviour at the time of the approach (B). Another two-way interaction was also tested: vessel × distance of the boat from the whales at swimmer drop (V × DD). Repeated approaches targeting the same whale pods were excluded from the analysis to ensure that the samples were not dependent on the repetitive approach of the vessel. Therefore, only the first approaches by vessel, or swimmers, to whales were included in the analysis.

Diving, respiration and reorientation rates

Average diving time (seconds), diving frequency (dives × hour^{-1}), respiration rates (blows × individuals^{-1} × minute^{-1}), and number of group reorientation events were compared with control and experimental (vessel and swimmers) samples. In addition, the proportion of time spent diving by the focal group was calculated (total dive time/encounter time) and compared between the three situations (control, vessel, swimmers). Data gathered from the research vessel in the absence of tourism activity (1,000 metres radius from the focal group) were considered as the control data set. Experimental data collected from the swim-with-whales vessel were divided in two groups; those where swimming with whales occurred (swimmers) and those where swimming with the whales did not occur (vessel), which was regarded as the control data set. The analysis focuses on whale groups containing a calf that were approached in parallel by the primary swim-with-whales vessel (A), which was necessary due to the high number of potentially influential variables and the non-homogeneous sample. That is, whale mother-calf pairs were the preferred focus by tour operators for swim-with activities (68.8% of time spent with whales and 79.3% of swim time), and most of the encounters occurred when aboard swim-with-whales vessel (A). Focal group follows were also filtered to include those with a minimum of 30 minutes of data, as per the control protocols. As a consequence, vessel and swimmer data for groups without a calf present were limited in numbers and time of observation, and the sample size of the data was deemed too small to conduct valid analyses with enough statistical power (Zar, 2010). The effect of water depth on response variables was also tested as it might influence the possibility to dive for the whales.

The proportion of time spent diving was log-transformed, as the models used for the analysis require a continuous dependent variable. Graphical validation tools were used to assess the underlying assumptions of variance homogeneity (plot residuals versus fitted values) and normality (quantile-quantile plot of the residuals) for average dive time, log-transformed proportion of time spent diving, diving, and respiration rates. Shapiro-Wilk and Levene's tests were also performed to test for normality and homoscedasticity. No violations of normality were detected for control, vessel, or swimmer data sets. Deviations from homoscedasticity were found for diving frequency, average diving time, and log-transformed proportion of time spent diving. Therefore, Weighted Least Squares (WLSQ) models were used to test if these response variables differed significantly between control, vessel, and swimmers' samples. ANOVAs and post-hoc Tukey's tests were then conducted. A Linear Model (LM) was also used to investigate the hypothesis that respiration rate would not change between the three samples. Finally, the number of group reorientation events during the first 30 minutes of the encounter was modelled as a function of sample type using GLMs with negative binomial distribution and log link function. Statistical analyses were conducted using SPSS Statistic 24 software (IBM, Armonk, NY, US. 2016). For all analyses, statistical significance was assumed at $\alpha = 0.05$ level.

4.3 Results

Between July and October of 2016 and 2017, 44 encounters with whales (28.3 hours) were recorded during 641 kilometres of survey effort across 20 days aboard research vessels. Nine encounters were excluded from the control data set, as tour vessels interacted with the whales during those observations. Control observations, overall, lasted a total time of 19.1 hours (mean = 0.5, SD = 0.1 hours). During the 36 days aboard swim-with-whales vessels (i.e., Vessel A and Vessel B) 2,516 kilometres were travelled and 146 separate encounters with whales (95.4 hours) were documented. During the two seasons of the study a total of 62 groups containing a calf were encountered (mother-calf pairs n = 46; mother-calf and escort = 16), versus 128 groups encountered without a calf (single n = 62; duos n = 43; trios n = 11; four to nine individuals n = 12).

Vessel A and B spent an average of 2.6 hours per day in encounters with whales (4 encounters per day lasting 0.6 hours on average). Swimming activities were attempted 162 times, with a total cumulative swim time of 24.8 hours. Vessel A conducted most of the swimming activities with whales (17.3 hours) over the two seasons. This tour operator focused particularly on mother-calf pairs (34.9 hours; 68.8% of the total encounter time), and most of the swim activities took place with whale groups containing a calf (13.8 hours; 79.3% of total swim time).

4.3.1 Avoidance responses to vessel and swimmer approaches

Vessels A and B approached a focal group of whales a total of 206 times over the two seasons of data collection. The majority of approach types were parallel (70.9%, n = 146) and the J approach was also used in 18.0% of the cases (n = 37), while direct approaches accounted for the remaining 11.1% (n = 23). Whales were recorded as actively avoiding vessel approaches for 33.5% of all approaches, and the whales avoided the boat more frequently when the skipper used a J approach (67.6% of the J approaches elicited avoidance) in comparison to parallel (26.0% of the parallel approaches elicited avoidance) and direct approaches (26.1% of the direct approaches elicited avoidance). The choice of vessel's approach was influenced by the initial behavioural state and group composition of the whales (Figure 18a and b, p. 102) targeted. For example, resting and travelling whales were approached by a vessel most frequently with parallel placement (98.6% and 68.5% of the resting and travelling whales, respectively), J approach types were more frequently used when whales were socialising (89.5%) or travelling (20.7%) (Figure 17a, p. 100), and direct approaches mainly used with singing whales (75.0% of the singing whales). However, singing individual whales were encountered on a few occasions (n = 6) and, therefore, were excluded from further statistical analysis due to the low sample size. Nurturing behaviour was never observed at the beginning of an encounter with the tour vessel and feeding behaviour was never observed in the entirety of the study.

Vessels A and B approached whale groups containing a calf primarily with the parallel technique (83.0%; Figure 17b, p. 100). Interestingly, in every instance recorded (n = 16) the mother-calf pairs always responded by avoiding the vessel when direct and J approaches were used. The proportion of direct and J approaches used by the vessels increased significantly (Pearson's χ^2: χ^2_2=12.638, P = 0.002) for groups without a calf (Figure 17b, p. 100).

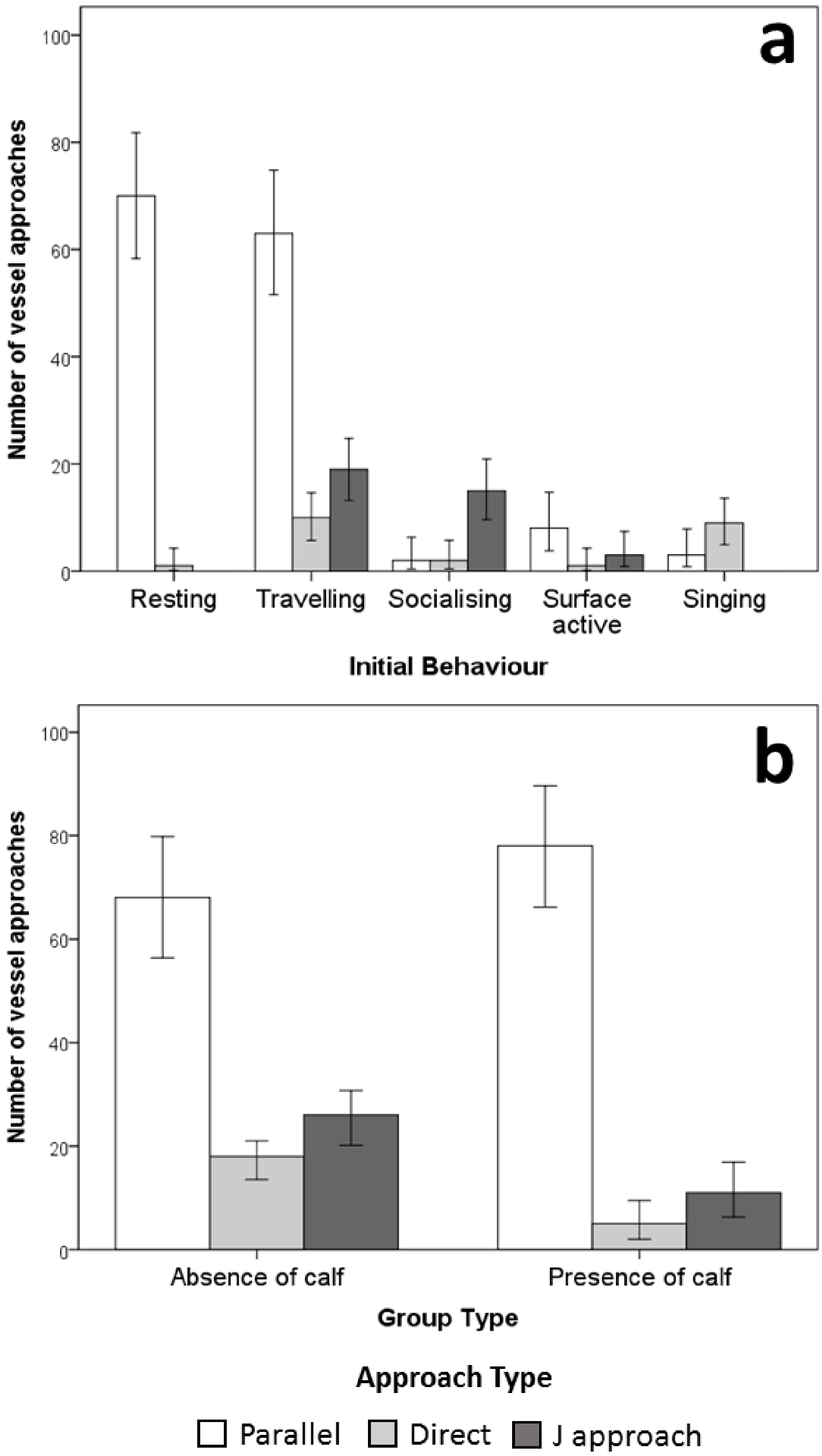

Figure 17. Number of documented swim-with-whales vessel approaches towards humpback whales (*Megaptera novaeangliae*) in Vava'u, Kingdom of Tonga. Shades

indicate the approach type (parallel, direct, J). (**a**) The horizontal axis is represented the initial behaviour of the targeted whales. Resting whales (n = 71) were approached almost exclusively in parallel (98.6%). Travelling whales (n = 92) were approached more frequently in parallel (68.5%) and with J approaches (20.7%). Socialising whales (n = 19) were approached more frequently with J approaches (89.5%). Direct approaches were used mainly with singing and travelling whales. (**b**) Horizontal axis indicates absence (n = 112) or presence of whale calves (n = 94) in the group targeted by the tour operators. Groups containing a calf were mainly approached in parallel (83.0%). J and direct approaches were used more frequently with groups without calves (39.3%). Error bars represent 95% confidence intervals.

The GLM that best fitted the data concerning the first approach on each group (n = 124) included the main effect approach type (AT) and the interaction vessel (V) × approach type (AT) (Table 7, p. 101). The second model provided an equal amount of information but included also the main effect vessel (V) as predictor variable. As a result, the model was less parsimonious and was discarded.

Table 7. Akaike's Information Criterion (AIC) values and Variation AIC for best fitting models in comparison to full model.

Model	**AIC**	**ΔAIC**
AT + (V × AT)	132.919	0
AT + V + (V × AT)	132.919	0
AT + V	133.912	1.070
AT + V + DI + DP + (V × AT) + (V × DI)	137.494	4.575

In particular, J approaches corresponded to an avoidance rate (76.5%) significantly higher (95% CI: 20.7 – 69.2%, $z = 3.50$, $P < 0.001$) than for parallel approaches (31.4%; Figure 18a, p. 102). Moreover, vessel B was avoided by whales more frequently than vessel A (95% CI: 7.8 – 45.6%, $z = 2.75$, $P = 0.006$) when using parallel approaches (Figure 18b, p. 102).

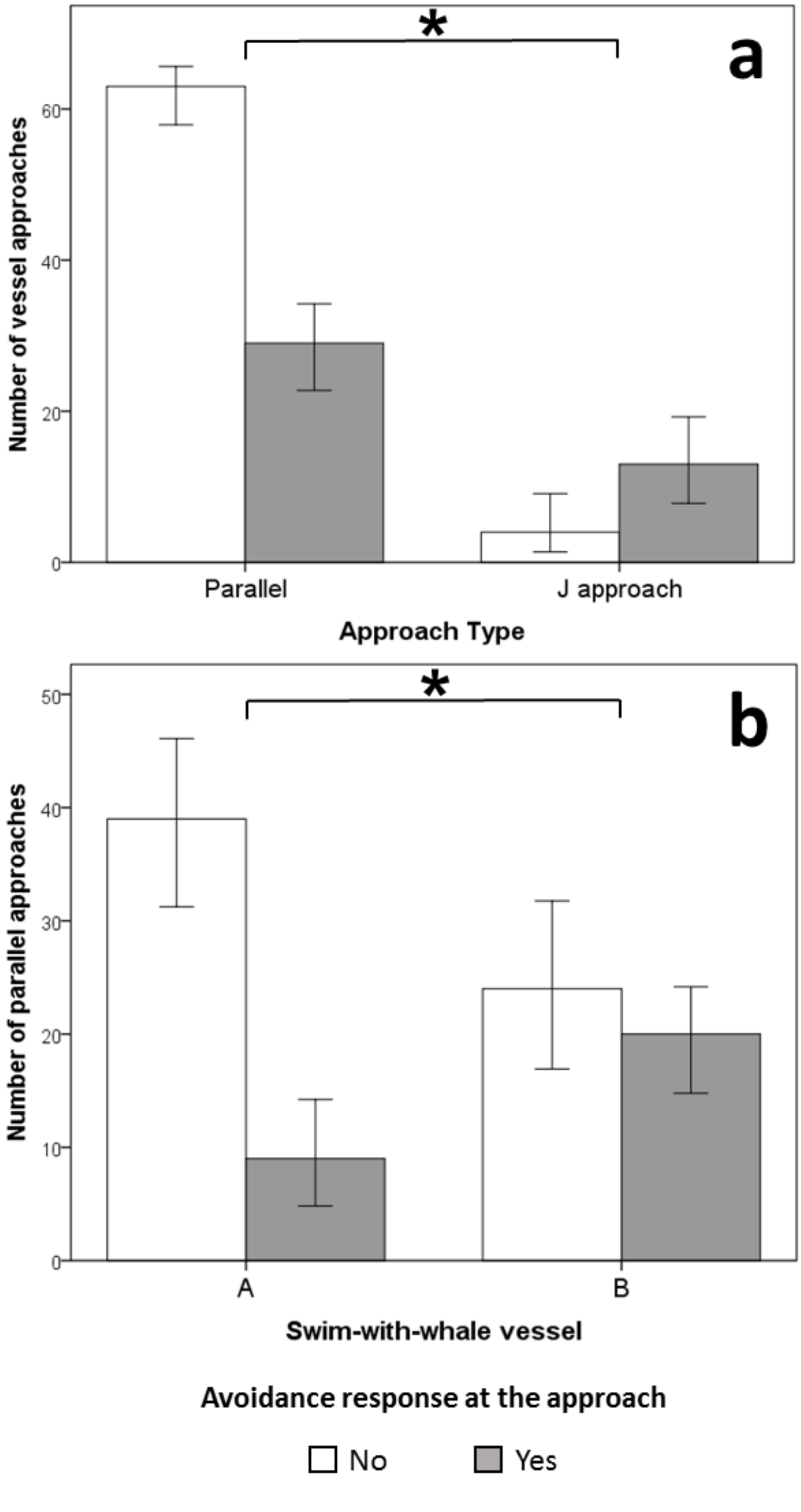

Figure 18. Number of documented swim-with-whales vessel first approaches towards groups of humpback whales (*Megaptera novaeangliae*) in Vava'u, Kingdom of Tonga. Shades represent the whale's response ("avoidance", "no avoidance"). (**a**) Comparison between whale responses to parallel (n = 92) and J (n = 17) approaches. 76.5% of J approaches elicited an avoidance response, while parallel approaches were significantly less avoided by whales (31.4%). (**b**) Whale responses to parallel approach by tour operator boat A (n = 48) and B (n = 44) are compared. Whale avoidance rate to vessel B parallel approach (45.4%) was significantly higher than the rate observed for vessel A

(18.7%). Error bars represent 95% confidence intervals. Significant differences ($P < 0.05$) between avoidance rates detected by *z*-test for proportions are denoted by an (*).

The minimum boat distance (DI) reached during an approach (mean = 91.6 ± SE 7.9, SD = 82.1 metres) and depth (mean = 84.3 ± SE 10.5, SD = 109.6 metres) had no significant effect on vessel avoidance rates.

Regarding whale avoidance responses towards swimmers, a total of 162 swim approaches were observed. Whales showed avoidance behaviour to swimmers 35.5% of the time. GLM selection procedures did not highlight any significant effect of swimmer placement, vessel, vessel distance from the whales at swimmer drop, water depth, presence of calves, or initial group behavioural state at the time of the first approach on the occurrence of whale avoidance response to swimmers. That is, both models fitting data relative to 'line abreast' and 'in path' swimmer placement and data relative to "line abreast" alone were not significantly different from intercept only models (Likelihood Ratio for full models: $\chi^2_6 = 6.338$, $P = 0.386$ and $\chi^2_6 = 3.371$, $P = 0.761$, respectively).

4.3.2 Diving, respiration and reorientation rates

The presence of vessel A and swimmers had a significant effect ($F_{2,36} = 18.183$, $P < 0.001$) on the dive time of a whale mother (i.e., A female adult whale with her calf present) (Figure 19a, p. 105). Average dive time increased almost two-fold upon tour vessel approach (parallel approach type) (351 ± SE = 26 seconds) and three-fold during swimming activities (line abreast placement type) (561 ± SE = 73 seconds) when compared to control data sets (189 ± SE = 24 seconds). WLSQ model explained 52.4% of the variance observed for the dive time in the three situations. Although the diving frequency decreased in the presence of a tour vessel (4.75 ± SE = 0.53 dives × hour^{-1}) and in the presence of swimmers (3.77 ± SE = 0.28 dives × hour^{-1}) with respect to controls (6.03 ± SE = 1.42 dives × hour^{-1}), this change was not statistically significant ($F_{2,36}$ = 2.219, P = 0.125) (Figure 19b, p. 105). However, whale mothers spent significantly more time diving ($F_{2,36}$ = 5.462, P = 0.009) in the presence of both tour vessels and swimmers (vessel: 50.4 ± SE 6.7%; swimmers: 58.6 ± SE 6.0%) when compared to their time spent at the surface in control observations (27.9 ± SE 5.2%) (Figure 19c, p. 105). The model explained 24.9% of the variance in the data for the proportion of time spent diving in the three situations. Whale's respiration rate (blows × individuals^{-1} × minute^{-1}) decreased when whales were in the presence of a vessel (0.51 ± SE = 0.07) and swimmers (0.49 ± SE = 0.04) compared to the control situation (0.67 ± SE = 0.07) (Figure 19d, p. 105). However, this difference was not significant ($F_{2,36}$ = 0.208, P = 0.140).

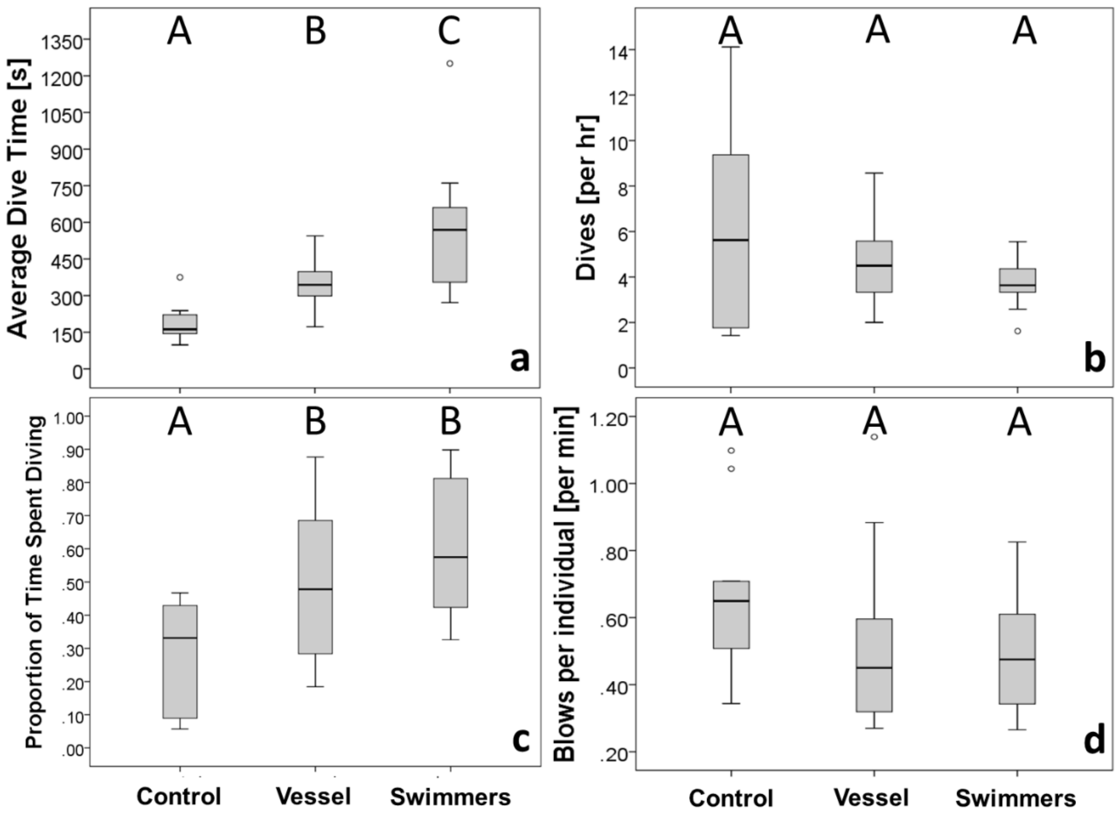

Figure 19. Box plots representation of (**a**) dive time, (**b**) diving frequency, (**c**) proportion of time spent diving, and (**d**) respiration rate in absence of tourism activity (control), in presence of swim-with-whales vessel A and during swimming activities (swimmers) for humpback whales (*Megaptera novaeangliae*) mother-calf pairs in Vava'u, Kingdom of Tonga. Capital letters indicate the results of Tukey's post-hoc analysis. Different letters are associated with significant differences ($P < 0.05$).

Finally, the mean number of re-orientation events was higher when whale groups were approached by the tour vessel (1.77 ± SE 0.26) and swimmers (2.15 ± SE 0.35) than in their absence (1.0 ± SE 0.42; Figure 20, p. 106). However, a GLM analysis did not detect any significant effect of vessel or swimmer presence (Likelihood Ratio: $\chi^2_2 = 1.915$, $P = 0.384$). Finally, no significant effect of water depth (mean = 66.4 ± SE 4.4, SD = 26.7 metres) was found on all the response variables investigated.

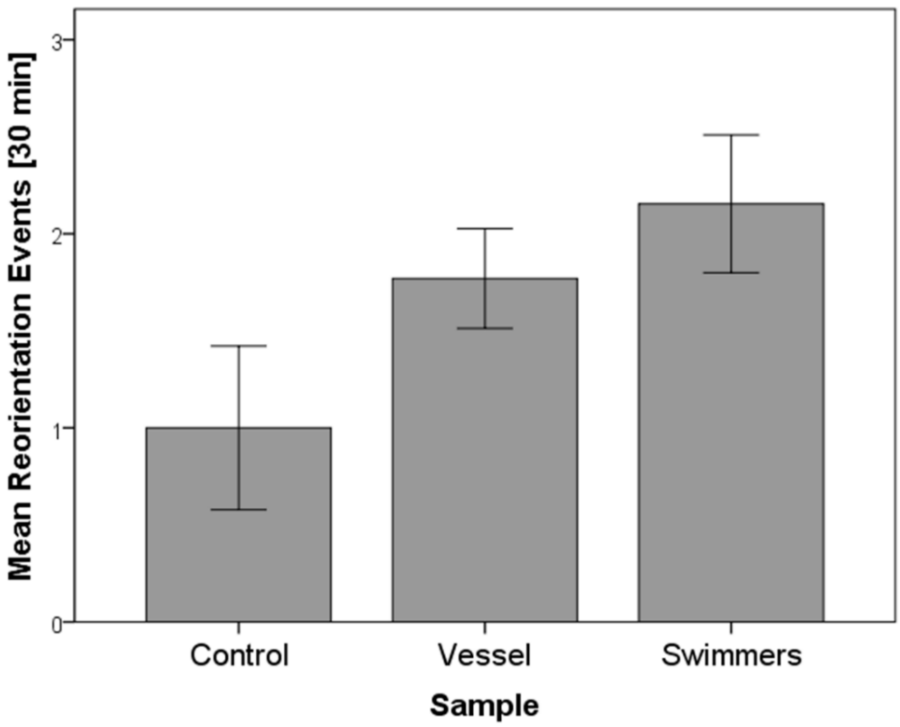

Figure 20. Mean values for re-orientation events observed in 30 minutes for mother-calf pairs in absence of tourism activity (control), in presence of a swim-with-whales vessel (experimental), and swimmers (experimental) for humpback whales (*Megaptera novaeangliae*) mother-calf pairs in Vava'u, Kingdom of Tonga. Error bars represent the standard error of the mean.

4.3.3 Compliance with regulations

Data collected from aboard tour vessels A and B indicated that 10.4% of encounters with whales (n = 146) lasted longer than an hour and a half, the maximum interaction time permitted under the Tongan swim-with-whales regulations (*Tonga Whale Watching and Swimming Regulations 2013*, 2013). Furthermore, during 38.4% of the encounters recorded (n = 56), additional tour vessels (up to six) queued within 300 metres of the whale group waiting to drop swimmers into the water with the same whales (Figure 21, p. 107). This contravenes the Tongan swim-with-whales regulations, which requires a minimum whale resting time (no swimmers or vessels within 300 metres of the whales) of an hour and a half between each interaction with tour vessels.

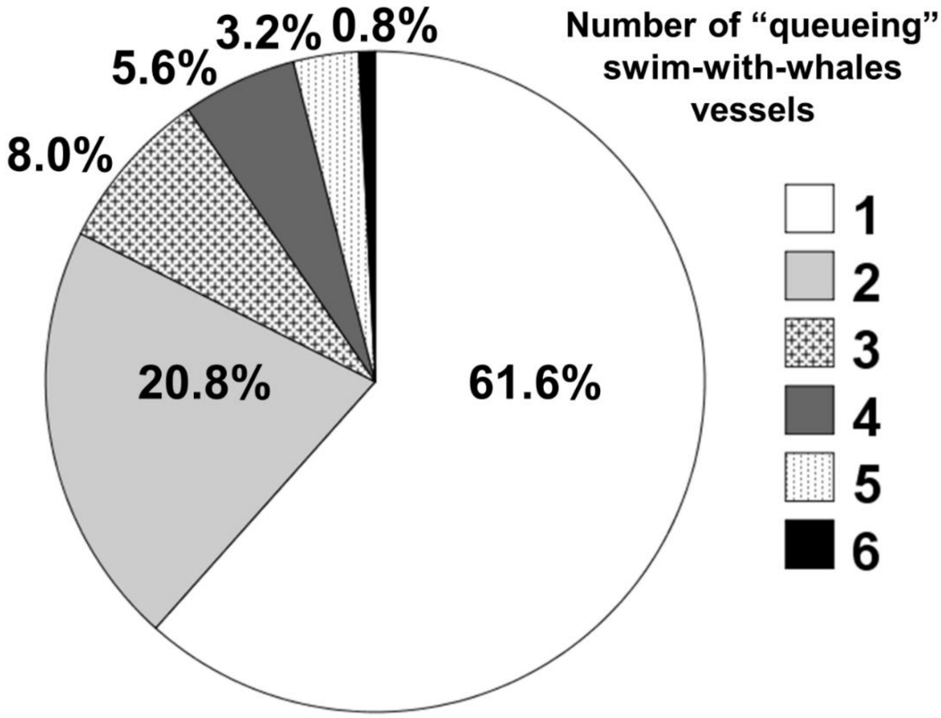

Figure 21. Percentage of encounters with humpback whales (*Megaptera novaeangliae*) in Vava'u, Kingdom of Tonga, during 2016 and 2017 seasons with number of tour vessels present in the area waiting to interact. The number includes the tour operator boat boarded by the researcher (vessel A or B).

Vessels A and B were recorded approaching the focal group of whales closer than the minimum distance specified under the Tongan swim-with-whales regulations (ten metres for whale groups without a calf, 50 metres for whale groups containing a calf) in 13.1% of the cases documented (n = 206). In addition, during 19 of 162 swims observed (11.7%) swimmer regulations were violated, and more than five swimmers at the same time were dropped in the water (Tongan swim-with-whales regulations specify a maximum of four swimmers and one guide at one time). On one occasion, ten swimmers were recorded in the water, concurrently. Finally, on no occasions during this study were any official monitoring or enforcement vessels seen observing whale tourism activities in Vava'u.

4.4 Discussion

4.4.1 Avoidance responses to vessel and swimmer approaches

The hypothesis that the tour vessel approach type does not affect humpback whale behaviour (specifically avoidance rates) was rejected by the data presented in this study. The J approaches caused an avoidance response most frequently (+ 35.1%), while parallel approaches resulted in the least number of avoidance responses (Figure 18a, p. 102). Cetaceans are known to respond to erratic and fast movements of boats manoeuvring closely around them with avoidance behaviour, especially when vessel manoeuvring happens in the middle of a group or directly in the path of their direction of travel. Not surprisingly, most whale-watching regulations and codes of conduct worldwide recommend the use of parallel approaches when interacting with whales and dolphins (Carlson, 2013). However, the Tongan regulations for commercial swimming activities do not explicitly provide indications on how to approach whales when dropping swimmers (*Tonga Whale Watching and Swimming Regulations 2013*, 2013). Despite the lack of regulation, the recommended parallel approach type was the most frequently used by Vava'u tour operators (70.9%).

The frequency of use of the parallel approach by Vava'u tour operators differs from reports by Sprogis et al. (2020) during the first trials of swim-with-humpback whales tourism activities in Ningaloo Marine Park, Western Australia. The study reports that at Ningaloo Marine Park, tour operators interacted with humpback whales using mainly a J approach (89.8%), positioning swimmers in the path of travel of the whales. Several factors may explain the difference in approaches between the Tongan and Ningaloo whale swim operations. One factor is that Western Australian swim-with-whales regulations did not permit swimming with groups containing calves (*In-water humpback whale interaction. Ningaloo Marine Park trial 2016*, 2016). In contrast, tour operators in Vava'u interact primarily with mother-calf pairs (79.3% of total swim time). The predominant activity of a mother-calf pair in Vava'u is resting, and this situation facilitates the use of a parallel approach by swim-with-whales tour operators. In addition, mother-calf pairs seem to be particularly sensitive to direct and J approaches, exhibiting avoidance responses in all the cases (n = 16) observed in Vava'u. This suggests that tour operators use a parallel approach because it results in a higher probability of success for their swim-with customers' interaction with the mother-calf pairs. Similarly to the frequently used approaches in Ningaloo (Sprogis et al., 2020), Vava'u swim-with-whales operators use a J approach more frequently when targeting whale groups without a calf (Figure 17b, p. 100). This is likely to be related to the more common socialising and travelling behavioural states of whale groups without calves in Vava'u, and, potentially, also in Western Australia.

A further factor that may explain the difference between Vava'u and Ningaloo is the significance of their respective location in the whale's annual migratory cycle. Ningaloo represents a resting and nursing area for Western Australian humpback whales along their southward migration, especially for mother-calf pairs (Christiansen, Dujon, et al., 2016). In contrast, the Vava'u archipelago is a breeding and calving ground for the Tongan humpback whale sub-population (Baker et al., 1998; Constantine et al., 2012). Consequently, Western Australian whales exhibit a different behavioural scenario with respect to their Tongan conspecifics, most probably because they are at a different stage of their annual migration.

In Vava'u, vessel approach type was not the only factor affecting whale avoidance rates. Whale focal groups displayed more frequent avoidance responses towards tour vessel B (+27.5%), than vessel A, when it approached using the parallel technique (Figure 18b, p.

102), while J approaches caused a similar avoidance rate for both tour vessels. This finding may reflect differences between the design (vessel A = catamaran; vessel B = monohull) or propulsion type for each vessel (vessel A = gasoline fuelled outboard motors; vessel B = diesel fuelled inboard engines) or potentially the different hydrodynamic characteristics related to the hull shapes. Differences in engine type and hull design affect the intensity and the frequency of the noise generated in the water (Wladichuck, Hannay, MacGillivray, Li, & Thornton, 2019), which is known to elicit behavioural responses in humpback whales (Sousa-Lima et al., 2002). An additional potentially influential variable may have been the longevity of vessel in the area as a swim-with-whales platform. Vessel A had been conducting swim activities in Vava'u for over a decade, while vessel B was only in the second year of operations. Research in other areas has shown that whales can become habituated (Bejder et al., 2009) towards vessels that have been operating in close proximity for several years (e.g., Ellison et al., 2012; Lusseau & Bejder, 2007; Tougaard et al., 2015).

Factors such as the tour vessel type, swimmer placement, and vessel distance at swimmer drop had no significant effect on the avoidance rate. These findings contrast with research conducted by Constantine (2001) on bottlenose dolphins in the Bay of Islands, New Zealand, who found higher levels of avoidance towards 'in path' swimmer placements when compared with 'line abreast' and 'around the boat' placements. Any assessment of swimmer placement technique is further complicated by the presence and manoeuvring of the vessel that is being used to place swimmers in the water (Kessler et al., 2013). While the findings of the present study did not detect any significant relationship between swimmer placement technique and whale avoidance behaviour, other variables, which may be influential, were not tested. For example, the behaviour of the swimmers in the water and their distance to the whales might influence whale responses. Unfortunately, such variable could not be assessed accurately from the tour vessel as an observation platform. Interestingly, a study into the effects of swimmer behaviour on humpback whales in the Ha'apai island group, Kingdom of Tonga, indicated that whales moved away from swimmers significantly earlier when swimmers were splashing instead of being calm during their in-water encounters with the whales (Kessler et al., 2013).

4.4.2 Diving, respiration and reorientation rates

The hypotheses that swim-with-whales tourism activities had no effect on humpback whale dive time or on the proportion of time spent diving was rejected because of observed behavioural changes in mother-calf pairs. The results indicate that whale mothers increase their average dive duration two-fold when in the presence of tour vessel and three-fold when in the presence of swimmers in comparison to control observations (Figure 19a, p. 105). In addition, the proportion of total time spent diving during tourism encounters doubled in the presence of swimmers and tour vessel (Figure 19c, p. 105). As a result of the observed behavioural changes, the present study provided evidence that whale mothers in Vava'u adopt a vertical avoidance strategy in response to swim-with-whales vessel approaches and, most frequently, to swimmer approaches. Similar findings have been reported for humpback whales exposed to whale-watching vessels in other breeding grounds (Au & Green, 2000; Schaffar et al., 2010) and also in humpback whale migratory corridors (Stamation et al., 2010). Although the biological consequences of such avoidance behaviour is not clear, such strategies may increase energy expenditure for the lactating mother and for her dependent offspring (Cartwright & Sullivan, 2009; Noren, Biedenbach, Redfern, & Edwards, 2008). Evidence from other parts of the world suggests it is likely such energy-expending behaviour is detrimental for the affected whales. For instance, Braithwaite, Meeuwig, and Hipsey (2015) estimate that the increase of swimming speed and the reduction in the time spent resting for mother-calf pairs can result in a significant decrease in the calf's growth rate.

Humpback whales in Western Australia, on the other hand, reacted to swimming activities by decreasing their average dive duration and increasing the deviation index (the mean of turning angles between consecutive positions during the follow) with respect to the approaching vessel (Sprogis et al., 2020). Although the present study documented an increase of reorientation events in presence of a tour vessel and swimmers (Figure 20, p. 106), this finding was not statistically significant. However, reorientation may not be the only observable behavioural change that may indicate a reaction to the presence of vessels or swimmers. Whale swim speed, for instance, could also be investigated as potential indicator of horizontal avoidance. Scheidat et al. (2004), for example, documents that humpback whales almost double their swim speed in the presence of whale-watching boats during observations, while the number of reorientation events did not significantly increase. An additional study on humpback whales in their breeding grounds off Bahía Málaga, Colombia found an increase in both swim speed and reorientation rates, and a decrease of whale respiration rates in response to the presence of vessels (Avila et al., 2015). During the research in Vava'u, a slight decrease in whale respiration rates in the presence of tour vessels and swimmers was recorded, but this was not statistically significant (Figure 19d, p. 105). It is important to note that the absence of a statistically significant change in whale respiration rates at the group level may not be synonymous with the lack of changes at the individual level, especially if different age classes are considered (Lundquist et al., 2013). In the present study, the group respiration rate was calculated by dividing the total number of respiration events by the total number of whales in the group. Consequently, while this may be representative for whales' synchronised breathing, changes in respiration rates for individuals, which have different respiration patterns throughout the wider group which includes calves, can be underestimated.

Unfortunately, it was not possible to investigate the effects of swimming on focal groups of whales not containing calves because it occurred so rarely and briefly that the sample size was too small for any valid statistical analysis. This low sample size was also a consequence of swim-with-whales tour operators' opportunistic preference for targeting mother-calf pairs in Vava'u.

4.4.3 Compliance with regulations

Low levels of compliance with Tongan key swim-with-whales regulations in Vava'u ("Tonga Whale Watching and Swimming Regulations 2013," 2013) were documented supporting the findings reported by Walker and Moscardo (2011). In particular, during 38.4% of the encounters tour operators did not comply with the minimum rest time between interactions with tour vessels, which is stipulated as an hour and a half under the regulations implemented in 2013. Up to six vessels were observed waiting ("queueing") to interact with a focal whale group, which already had a tour vessel interacting with it. These queueing vessels would then move in immediately after the original vessel departed the area, or, in some cases, they would alternate with the original vessel by placing swimmers in the water as soon as the initial vessel swimmers exited the water. In addition, on a number of occasions (38.4% of the encounters) tour vessels were queued up within 300 metres from the whales waiting to commence in-water interactions with whales after the tour vessel boarded by the researchers departed the area. Up to 28 commercial swim-with-whales vessels were counted on the water simultaneously during the peak of the 2017 season. That is, the level of exposure of humpback whales to swim-with tourism activities in Vava'u is extremely high during daylight hours, both in terms of the number of tour boats and the time spent with the whales (mean = 2.6 hours per day per vessel).

While compliance with minimum rest-time was poor, adherence with other regulations was higher. For example, the maximum number of five swimmers (including the guide) in the water at a single time was respected by tour operator vessels A and B in 88.3% of the interactions. Notably, breaches to this regulation of maximum number of swimmers generally occurred when five swimmers were on board the tour boat. Tour operators A and B opted to let all the swimmers enter the water with the guide (thereby exceeding the five-person maximum) instead of dividing them in two groups and reducing the interaction time for each group. On one occasion, two groups of five swimmers were in the water at the same time because of a second tour operator, who was initiating the swimming activity before the first operator could retrieve its participants. Despite this, the four-to-one swimmers-to-guide ratio seemed to be adhered to most of the time by tour operators. Therefore, compliance with this regulation was generally high, as documented also by Sprogis et al. (2017) in Western Australia.

The regulated minimum distance between a vessel and whales (ten metres for whale groups without a calf, 50 metres for whale groups containing a calf in Tonga) was adhered to by vessels A and B in 86.9% of their approaches. This level of compliance in Vava'u was higher than that reported for Ningaloo, Western Australia (68.5%) (Sprogis et al., 2017). However, Western Australia regulations (*In-water humpback whale interaction. Ningaloo Marine Park trial 2016*, 2016) are more restrictive than in Tongan waters (i.e., 50 metres for parallel approach, 150 metres for J approach). It is possible that adhering to closer distances, as in the Tongan regulations, might be easier for operators (Scarpaci, Nugegoda, & Corkeron, 2004), especially considering that boat crews rarely use laser rangefinders to assess the distance from the whales during their approaches (Sprogis et al., 2017). Finally, it is important to note that the influence of researchers on board the tour vessels cannot be excluded, which may have resulted in operators being more likely to comply with license conditions. Moreover, data were collected only for two operators in Vava'u that accepted to host researchers onboard. Therefore, no information is available to document how the other 18 operators behaved during the encounters with whales in terms of approach, distance, duration of the encounters, and number of swimmers simultaneously in water.

4.5 Conclusions

This study highlights that both observational and interactive activities cause avoidance responses from humpback whales in Vava'u, Kingdom of Tonga. In particular, mother-calf pairs showed significant vertical avoidance responses, with humpback whale mothers diving for significantly longer periods of time in the presence of vessels and swimmers. Whether the short-term behavioural responses observed in Vava'u humpback whales could cause a long-term detrimental effect at the population level is unknown and needs further investigation. Again, evidence from other studies on the negative effects of cetacean based tourism suggests that the findings from the present study in Vava'u should be cause for concern, also documenting low levels of compliance to Tongan regulations regarding minimum resting time for whales between interactions with commercial vessels.

The Tongan sub-population of humpback whales still shows little evidence of recovery after the cessation of whaling, in contrast to other regions such as the East and West coasts of Australia (Clapham et al., 2009; Constantine et al., 2012; Jackson et al., 2013). Moreover, the Vava'u island group represents one of the most important breeding and calving grounds for this population, as the sheltered waters of the archipelago are favoured for birth and rearing of calves while readying them for the long southward migration to Antarctica (Baker et al., 1998). The behavioural responses documented in this study show an underlying risk of detrimental effects on whale populations targeted by swim-with-whales tourism. The rapid growth of swim-with-whales industry experienced by Vava'u over a short period of time (Hendrix & Rose, 2014) and the tour operator focus on mother-calf pairs is concerning, especially in the light of the poor compliance with regulations and the lack of enforcement of formal regulations documented by this study (Tongan Ministry of Tourism, personal communication, October 8, 2017). Some management actions have been recommended by the primary researcher and co-authors, and are currently under consideration by the Tongan Ministry of Tourism:

a) Focus on increasing compliance with the existing whale-watching regulations;
b) Reduce the number of swim-with-whales licensed vessels;
c) Introduce a break time in the middle of the day (e.g., from12 to 2 pm) when swim-with-whales operations are not allowed.

Overall, the findings of this study reinforce the urge for a more cautious and effective approach to the management of swimming activities with humpback whales, both for Tongan authorities and other governments willing to permit these activities.

Chapter - 5 - Using UAVs to assess humpback whale behavioural responses to swim-with interactions in Vava'u, Kingdom of Tonga

Chapter 5 cover picture. A group of swimmers approaches two humpback whales (*Megaptera novaeangliae*) resting in Vaitukakau Bay (18°60′ S, 174°01′ E), Vava'u, Kingdom of Tonga. Frame extracted from the aerial videos recorded by the UAV during this study.

A version of this Chapter is published as:

Fiori, L., Martinez, E., Orams, M. B., Bollard, B. (2020). Using Unmanned Aerial Vehicles (UAVs) to assess humpback whale behavioural responses to swim-with interactions in Vava'u, Kingdom of Tonga. Journal of Sustainable Tourism. DOI:10.1080/09669582.2020.1758706

In this Chapter, the main research question (Thesis objectives II and III) of this thesis is addressed using a lightweight UAV. Data were collected during eighty-two aerial surveys taking place in Vava'u, Kingdom of Tonga, in the 2016 and 2017 whale breeding seasons. The UAV was launched from aboard dedicated research and opportunistic platforms (swim-with-whales vessels). Whales' behavioural state were assessed from aerial videos, and the proportions of time spent in each behavioural state in the presence and absence (control) of swim-with-whales tourism activities were compared.

Results indicate that in-water tourism activities significantly alter the proportion of time spent in each behavioural state by humpback whales in Vava'u. In particular, mother-calf pairs significantly decreased ($P < 0.001$) the proportion of time spent nurturing, while the time spent travelling increased two-fold when approached by swimmers. Agonistic behaviours of whales directed towards swimmers and the injury of a swimmer were also documented.

5.1 Introduction

Whale-watching (considered to include all forms of tourism activity focused on non-lethal interaction with wild-free ranging cetaceans) has grown rapidly since the latter part of the 20th century (see section 2.2, p. 21, for a more detailed description). It is now estimated to generate billions of dollars of annual revenue for a significant global whale-watching industry (O'Connor, et al., 2009). As the growth of whale-based tourism progressed, a wide range of research studies investigated how these interactions with humans might affect the behaviour of the tourism-focused cetaceans. In particular, research has assessed the effects of vessel approaches on whale and dolphin behaviour (refer to Senigaglia et al. (2016) for a meta-analysis study). As a sub-set of the overall growth of whale-watching, interest in swim-with-whales opportunities has increased during the last two decades. While the great majority of countries where whale-watching occurs do not permit commercial swim-with-whales, the demand for such opportunities, fuelled also by media releases on social media networks and television channels (Wiener, 2013), has seen an expansion of such tourism. Consequently, a growing number of tour operators worldwide are now offering the opportunity to swim with whales (Hendrix and Rose, 2014). However, the scientific literature pertaining the effects of such interactions on whale behaviour is scarce. To date, only a few studies have been published and their findings suggest that whale responses to swimmers vary depending on the species of interest, location, and seasonal behaviour. For instance, Mangott, et al. (2011) and Curnock, et al. (2013) reported that dwarf minke whales voluntarily interact with vessels and swimmers in the Great Barrier Reef, Queensland, Australia. In contrast, southern right whales showed significant changes in their behavioural budget in response to swim-with-whales trials in Península Valdés, Argentina (Lundquist et al., 2013). In particular, whales spent less time resting and socialising, and increased their time spent travelling in the presence of swimmers. Furthermore, horizontal avoidance strategies were observed and quantified during the trials. Mother-calf pairs exhibited stronger responses towards swimmers and higher avoidance rates (27%) to the approaching vessel than adult-only groups (Lundquist, et al., 2013). More recently, Sprogis, et al. (2020) have documented the behavioural responses of humpback whales to the first swim-with-whales trials in Ningaloo, Western Australia. Similar to what was reported for southern right whales, humpback whales responded to in-water interactions by adopting vertical and horizontal avoidance strategies. The authors found that whales decreased significantly the duration of their dives and the predictability of their paths, while they increased both their swim speed and turning angles away from approaching vessels. To date, only one published study has investigated the effects of in-water tourism interactions on the behaviour of humpback whales in Vava'u, Kingdom of Tonga (refer to Chapter - 4 - In the study, high levels of avoidance (i.e. whale/s move away from approaching swimmers and/or vessels) towards swimmers (35.5%) and vessels (33.5%) were found. In contrast with the findings of Sprogis, et al. (2020), whale mothers responded by increasing their dive time when approached by boats and/or swimmers in Vava'u. That is, mother dive time and the proportion of time they spent diving increased significantly in presence of vessels and swimmers (Figure 19, p. 105).

This study extends the research presented in Chapter 4 and represents an application of UAV data collection to investigate cetacean behavioural responses to whale-watching tourism activities. That is, while the original assessment of the effects of swim-with-whales tourism on humpback whale behaviour was achieved using standard boat-based observational data, in this study, we analysed data collected using UAVs flying over the whales, both in absence and presence of in-water interactions. The advantages provided by this relatively new technology have been already illustrated in paragraph 2.3.4 (p. 44) and Chapter 3 (p. 58). In particular, the aerial perspective provided by UAVs and the high-resolution video recordings and still images they capture allow for better detection of the often cryptic humpback whale behaviours such as socialising and nurturing, in a non-invasive way. In addition, individuals of interest (i.e., calves) can be easily tracked during encounters. These capabilities represent an advantage during both data collection and post-processing. That is, the imagery collected by the UAV helps researchers to review and retrieve data that could have been missed or not sampled in the field (Hodgson, 2007).

The original research presented in Chapter 4 (p. 85) aimed to quantify the short-term behavioural responses of humpback whale mother-calf pairs to swimmer and vessel approaches, as the local swim-with-whales industry focuses especially on this group type (Kessler et al., 2013). While the study found that whale mothers respond using a vertical avoidance strategy in response to swim-with-whales tourism activities, the calf behavioural responses were not investigated. Vava'u represents one of the most important calving grounds for Oceania humpback whales (Constantine et al., 2012) and whale mothers have the crucial task to ready their calves for the southward summer migration towards Antarctica. Therefore, research on the whale calves' behavioural responses to swimmer approaches is fundamental to understand whether swim-with-whales tourism activities might affect humpback whales in this important stage of their life. Moreover, the potential changes in the proportion of time that whales spend in different behavioural states (resting, travelling, surface-active, socialising, nurturing) during in-water tourism interactions have, to date, not been assessed in Vava'u.

This study aimed to quantify the proportion of time spent in each behavioural state by humpback whales in Vava'u and compare it in absence (control) and presence of swimmers. In addition, calf respiration and dive patterns during swim-with-whales activities and in control situations were also monitored and compared. A three-fold increase of mother's dive time in presence of swimmers was documented in the previous chapter (paragraph 4.3.2, p. 103). As calves were expected to have a limited diving capability when compared to adult whales, it was predicted that this might have resulted in a spatial separation between mothers and their calves. Therefore, the proportion of time spent by the calf at the surface without the mother aside in absence and presence of swimmers was also calculated and compared. Finally, whale agonistic behaviours (e.g., fluke swishes, fluke slaps, peduncle slaps) directed towards swimmers were documented as they might underlie that whales perceive humans as a potential threat. Moreover, such behaviours can pose risk of injury or death to tourists participating to in-water interactions.

5.2 Methods

5.2.1 Study site and species

The study was conducted during humpback whale breeding seasons in 2016 and 2017 (between July and October) in the Vava'u island group (18°39'S, 173°59'W), Kingdom of Tonga (Figure 11a, p. 63). Surveys took place on the South side of the main island (Figure 11b, p. 63) where most of the swim-with-whales vessels operate.

5.2.2 UAV operations

UAV operations were conducted under the research permit MOT-4/3 issued by the Tongan Ministry of Tourism. All operations complied with CAA regulations and took place in maximum wind speed of 20 knots, as described in paragraph 3.2.3 (p. 65). The UAV was flown at 30 metres ASL from the moment it left the vessel until its return. The operator of the UAV is the primary researcher and holds a Remote Pilot Certificate (license no. 839465) issued by CASA in 2015.

5.2.3 Survey design

Control data were collected with a UAV operating from onboard a 11-metre sailing trimaran and a six-metre powerboat(powered by a 2-stroke Mercury 25 horse power), both dedicated for research, as described in paragraph 3.2.2 of this thesis (p. 64). The UAV used for control observations (in absence of tourism activities) was the HexH2O™ (ExtremeVision360, Worthing, UK) (Figure 22, p. 126), and its specifications are presented in paragraph 3.2.3 (p. 65). The aircraft took off from and landed on the vessel roof (powerboat platform) or the front webbing (sailing trimaran platform). The research vessels both travelled at speeds of less than 10 knots, depending on sea and wind conditions, and were operated from an anchorage in Port Maurelle (Figure 11b, p. 63). Surveys were conducted only in suitable sea conditions (Beaufort Sea State, BSS, < 4) and involved a skipper, the primary researcher (the UAV operator), and a trained assistant to the UAV operator. When a group of whales was sighted, the vessel approached at idle speed until at 300 metres distance from the whales. The vessel was stopped at 300 metres from the whales, in accordance with Tongan regulations for non-whale watching vessels. After 16 minutes of observation, the UAV was launched and aerial observations also lasted 16 min. This timing allowed the UAV to cover the distance between the whale focal group and the research vessel at a maximum cruise speed of ten metres per second, with sufficient battery charge to land safely. After the flight, the research vessel exited the area searching for other whale groups and only a single flight was conducted on a particular group of whales, as described in paragraph 3.2.2 (p. 64). The aerial footage collected in absence of tourism activities constituted whale behaviour control data.

Figure 22. The VTOL UAVs used during the study: (right) the waterproof HexH2O™ (ExtremeVision360, Worthing, UK); (left) Phantom4™ (DJI Innovations, Shenzhen, China). Photo credit: Ashray Doshi.

Data collected in presence of swimmers were gathered via a UAV, which was operated from a tour operator vessel or vessel A (refer to paragraph 4.2.2 of this thesis, p. 91). The UAV used to document swimming activities was the Phantom4™ (DJI Innovations, Shenzhen, China), which is a quadcopter (1.4 kilograms, diameter 35 centimetres engine-to-engine), equipped with a polarised filter mounted on the built-in camera (Figure 22, p. 126) and Li-Po batteries (4 S, 5870 milliamperes, 10 C). The Phantom4™ had a maximum flight time of 25 minutes. The choice of Phantom 4™ over the HexH2O™, was dictated by the need for a smaller aircraft, which could be hand-launched and retrieved from the tour vessel. The aircraft was launched and retrieved by the UAV operator assistant as soon as the first swimmer, a licensed swim-with-whales guide, entered the water. The UAV operator assistant took position with the aircraft ready to launch behind the swimmer preparing to enter the water, and facing the whales with the UAV camera. Video recording was initiated before take-off to avoid the loss of data regarding whale's initial response to swimmers entering the water. As for control observations, the aerial survey also lasted 16 minutes, with the exception of shorter interactions interrupted by the tour operator as consequence of the whales leaving the area, and the impossibility to place swimmers in their proximity.

UAV videos were recorded continuously at 60 fps (HexH2O^{TM}) and 30 fps (Phantom4^{TM}) during the flight, with a video resolution of 2.7 K, 2704 × 1520 pixels and 4 K, 4096 × 2304 pixels for the HexH2O^{TM} and Phantom4^{TM}, respectively.

5.2.4 Video analysis

The imagery was analysed with an iMac desktop (Apple Computer Inc, Cupertino, CA, US) 21.5-inch (diagonal) with Retina screen at 4 K resolution. Date, time, location (GPS), and environmental factors – such as sea state (BSS and Douglas scale), overall weather conditions, wind speed and direction, and depth – were recorded by the UAV operator assistant at the beginning of each encounter. Group composition and number of whales were determined post-flight from the aerial imagery by the primary researcher. Based on the criteria used, a calf was defined as a whale of less than 70% body length of accompanying adult (full size), which was categorised as the mother (i.e. lactating female) (Christiansen et al., 2016; Sprogis et al., 2020). Calves encountered during this study did not exceed 50% of their mother body length.

Group behavioural state was defined as the behaviour which more than 50% of the whales in the focal group were participating in (Mann, 1999). Six mutually exclusive and cumulatively inclusive behavioural states (D. Lusseau, 2003) were defined to describe whale behaviour during the encounters (refer to Table 2, p. 68): resting, travelling, surface-active, socialising (Figure 23, p. 129), feeding, and nurturing (Figure 24, p. 130).

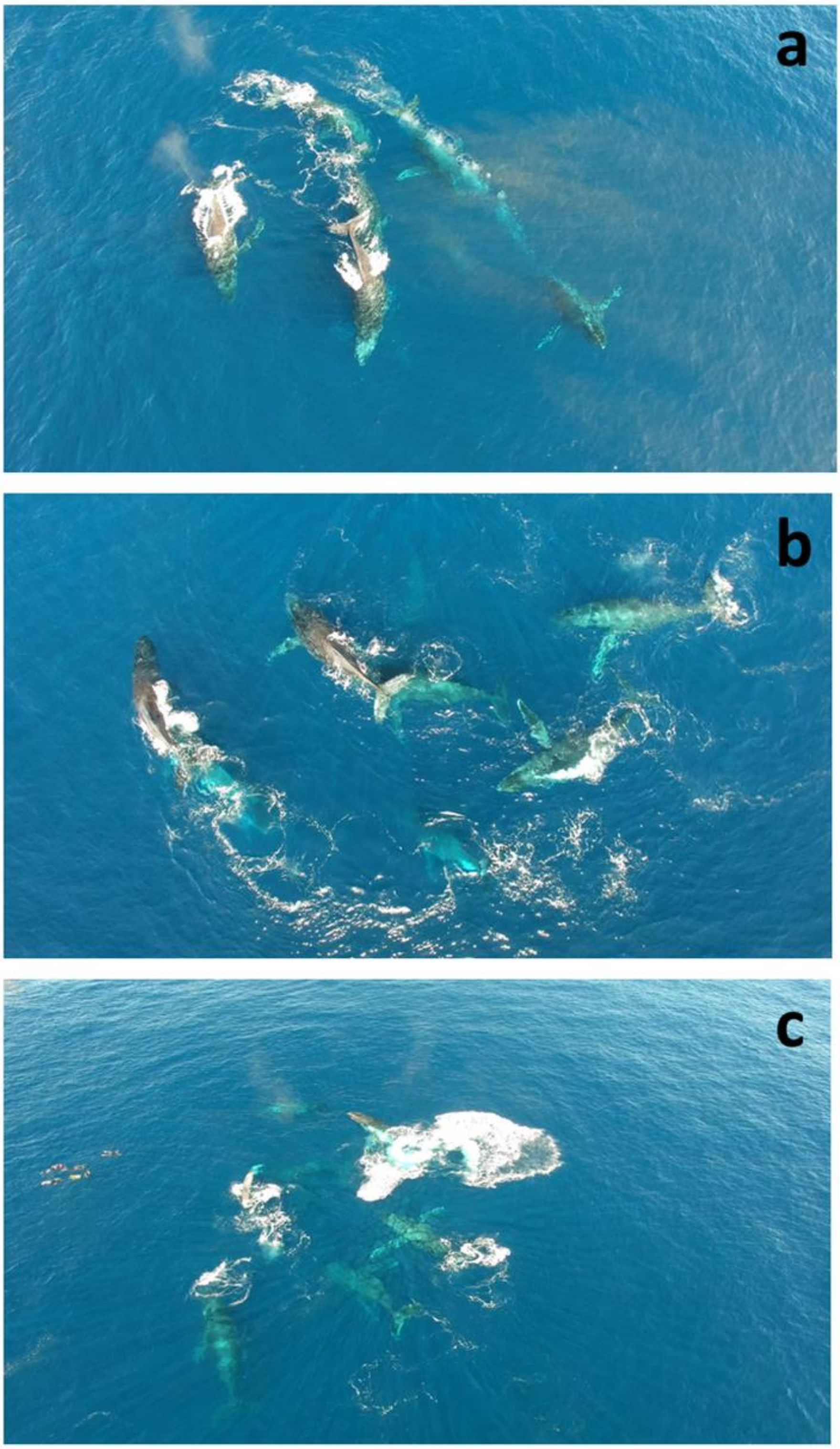

Figure 23. A competitive group of humpback whales (*Megaptera novaeangliae*) socialising along the south side of Euaeiki Island (18° 46'S, 174°01' W), Vava'u, Kingdom of Tonga. (**a**) A row of underwater blows is produced by one individual; (**b**) individuals are fast chasing and changing direction abruptly; (**c**) two individuals perform

peduncle slaps in proximity of swimmers (left). Frames extracted from the aerial videos recorded by the UAV during this study.

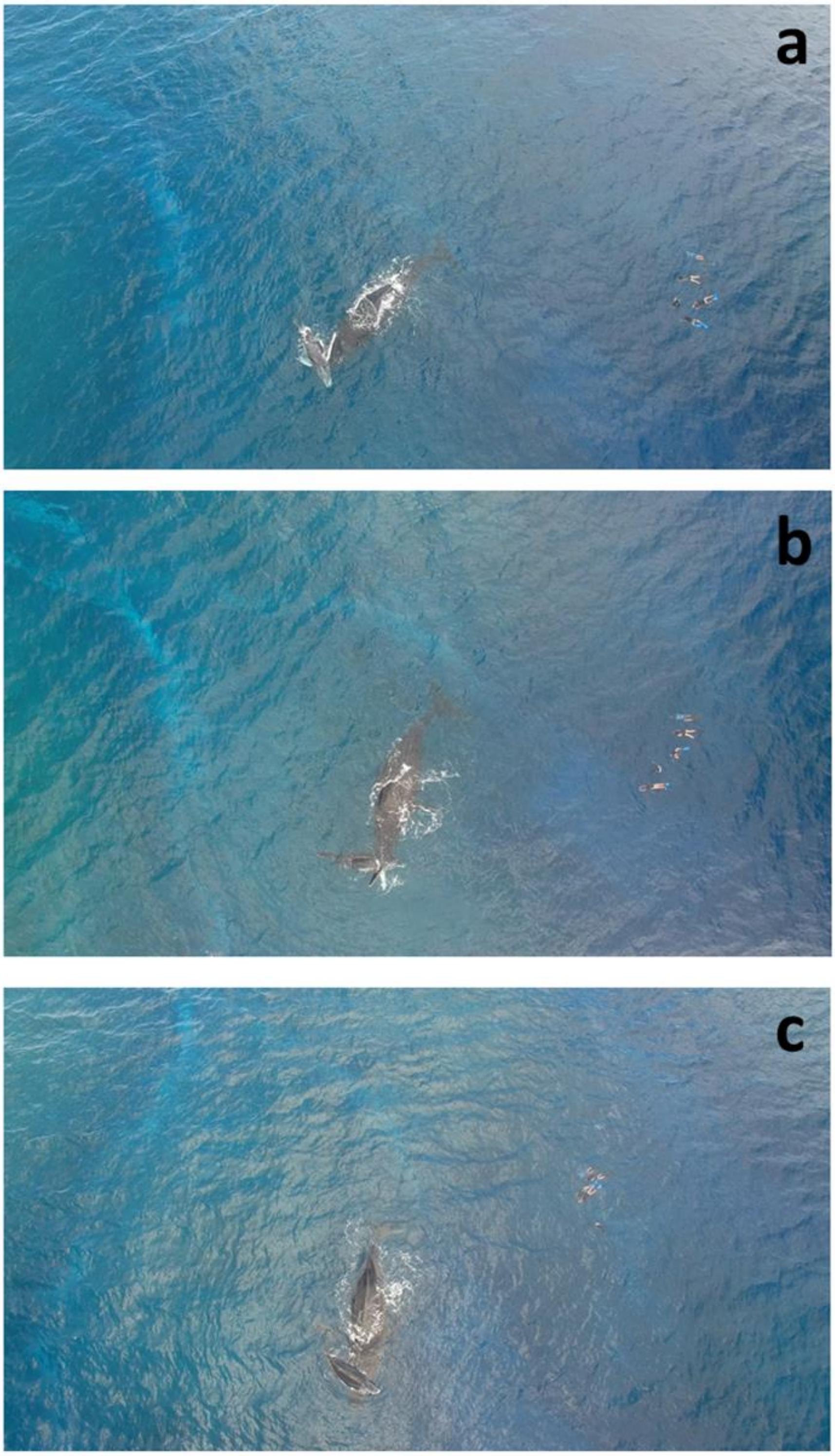

Figure 24. Mother and calf humpback whales (*Megaptera novaeangliae*) nurturing close to the south side of Foelifuka Island (18°42'S, 173°01'W), Vava'u, Kingdom of Tonga,

in presence of swimmers (right). (**a**) Calf rolls upside down above mother's rostrum; (**b**) calf lays sideway on top of its mother's rostrum; (**c**) mother lifts calf above the surface with her rostrum. Frames extracted from the aerial videos recorded by the UAV during this study.

As explained in paragraphs 3.3.1 and 4.3.1 (p. 74 and p. 99, respectively), feeding behaviour was never observed during the study and, consequently, was excluded from the whale ethogram. A dive (i.e., whale arching the peduncle and/or fluking can be seen gaining depth while propelling forward and increasing its swim speed) was treated as a travelling behavioural state (Di Clemente et al., 2018), unless singing behaviour was detected. An H2A-XLR hydrophone (Aquarian Hydrophones, Anacortes, WA, USA) was deployed in case of prolonged dives to detect singing behaviour. Similarly to the discussion provided in paragraphs 3.3.1 and 4.3.1 (p. 74 and p. 99, respectively), singing whales were excluded from the behavioural categorisation as this activity is not visually detectable. Singing whales (n = 4) were, therefore, excluded from the data set.

Behavioural state was assessed, allocated, and recorded at approximately two-minute sampling intervals (Altmann, 1974). Sampling intervals could vary in time depending on the whale's visibility and, therefore, the ability of the analyst to assess behavioural state. Behaviour was assumed to remain constant between observations (Lundquist et al., 2013), and any point that sampling was missed during a dive was allocated to the last behavioural state observed (until whales became visible again and a new assessment could take place). For example, if whales were last observed diving, travelling was the behavioural state allocated (Di Clemente et al., 2018) during the interval until the whales became visible again.

In addition to the behavioural state data, individual focal follows (as described in paragraph 3.2.4, p. 67) were conducted on calves in which dive time (seconds), diving frequency (dives × hour^{-1}), and respiration rate (blows × minute^{-1}) were monitored. The proportions of time spent diving for both mothers and calves were also calculated. This allowed to quantify the time spent by the calf at the surface without the mother at its side. Change of whale heading direction was not investigated as the analysis presented in Chapter 4 (paragraph 4.3.2 abovep. 103) did not found significant differences when comparing control and swimmer situations. Furthermore, whale swim speed could not be included in the analysis as it was not possible to calculate distances from the aerial footage. That is, the UAVs were not flown perpendicularly above the whales at all time to avoid glare and allow for the best possible underwater visibility. Finally, during the reviews and analysis conducted on the UAV video records, whale agonistic behaviours (Table 8, p. 132) targeting swimmers were noted.

Table 8. Definitions of agonistic behaviours of humpback whales (*Megaptera novaeangliae*) adapted from Corkeron (1995) and Pitman et al. (2015).

Fluke slap	Whale strikes the surface of the water with the ventral side of its flukes.
Fluke swish	Whale moves the fluke rapidly through the water in a sideways movement.
Peduncle slap	Whale strikes the surface of the water with the lateral side of its tail stock.

5.2.5 Statistical approach

Proportion of time in each behavioural state

The hypothesis that swimming tourism interactions alter the time spent in each behavioural state by humpback whales was tested comparing the proportion of time spent in each behavioural state between control and swim-with-whales samples. That is, two sets of proportions were calculated in the absence (control) and presence of swimmers. The proportion of time spent in each state was then compared with a binomial *z*-test for proportions and 95% confidence intervals were calculated. Both the control and experimental data were pooled in two groups (and analysed separately) depending on the presence or absence of a calf, because this has been found to affect the proportion of time spent in each behavioural state by whales in Vava'u (Figure 15, p. 75).

Calf dive time, diving frequency and respiration rates

It was further hypothesised that calf mean dive time, diving frequency and respiration rate would be affected by the presence of swimmers if swim-with-whales activities do elicit a behavioural responses in humpback whale calves. In addition, a difference in the time spent by the calf at surface without the mother in presence and absence of swimmers was expected, as a consequence of the three-fold increase of whale mother dive time documented in section 4.3.2 (p. 103). That is, it was hypothesised that whale calves have a limited diving capability in comparison with adult whales and cannot follow their mothers during prolonged dives. To test these hypotheses, calf mean dive time (seconds), diving frequency (dives × hour^{-1}), and respiration rates (blows × minute^{-1}) were compared between control and presence of swimmer data sets. The proportion of time spent by the calf at the surface without the mother at its side was calculated and log transformed. This transformation was necessary to analyse the data with statistical models that required a continuous dependent variable. Graphical validation tools were used to assess the underlying assumptions of variance homogeneity (plot residuals versus fitted values) and normality (quantile-quantile plot of the residuals) for all the dependent variables. Shapiro-Wilk and Levene's tests were also performed to test for normality and homoscedasticity, respectively. No violation of normality and homoscedasticity were detected. Linear models (LM) and one-way ANOVAs were then performed to determine whether the hypotheses were to be accepted or rejected. Statistical analyses were conducted using SPSS Statistic 24 software (IBM, Armonk, NY, US. 2016). For all analyses, statistical significance was assumed at $\alpha = 0.05$ level.

5.3 Results

Thirty-four UAV flights (10.5 hours) were conducted during 19 surveys aboard research-dedicated vessels. Four flights in absence of tourism activity had to be discarded from further analysis due to the arrival of other vessels in proximity of the whales (< 1000 meters from the focal group). Furthermore, three different whales were detected singing during prolonged deep dives and were not included in the behavioural state analysis. An additional 21 surveys aboard the tour-operator vessel, resulting in 30 UAV flights over different whales groups, were conducted to document swim-with-whales activities (7.9 hours). In four instances, swim-with-whales activity was aborted as the whales left the area and it was not possible to position the swimmers in their proximity. Therefore, the aerial footage was excluded from the analysis. After filtering the data, 27 UAV flights were pooled as control samples and 26 were pooled as swimmer samples. Whale groups size ranged from one (n = 10) to nine (n = 1) averaging at 2.3 whales per group. Pairs were the most frequently sampled (n = 28), followed by trios (n = 12). Larger groups of five and nine whales only occurred in three occasions.

5.3.1 Proportion of time spent in each behavioural state

The proportion of time spent in each behavioural state by whales differed significantly in the absence and presence of swimmers (Figure 25, p. 137). Results were influenced by the presence of a calf in the focal group of whales (Pearson's χ^2: χ^2_3= 41.959, P < 0.001 for whale groups containing a calf; Pearson's χ^2: χ^2_3= 14.625, P = 0.002 for groups without calves). In particular, the proportion of time spent travelling by groups containing a calf (Figure 25a, p. 137) increased from 28.3%, in the control scenario, to 50.0% in the presence of swimmers (95% CI: 9.0 – 34.4%, z = 3.30, P = 0.001). In addition, nurturing behavioural state accounted for 21.9% of the time in absence of tourism activity, but whales spent significantly less time nurturing (17.2% less) when being the focus of in-water interactions (95% CI: 8.9 – 25.6%, z = - 3.94, $P < 0.001$). Furthermore, the proportion of time spent in a surface-active behavioural state for the same group type decreased from 16.3% in the absence of swimmers to 0.7% with swimmers present (95% CI: 9.3 – 21.9%, z = - 4.65, $P < 0.001$). Socialising behaviour was not observed in groups of whales containing a calf. In contrast, whale groups without calves (Figure 25b, p. 137) spent significantly more time (14.3% more) in a surface-active behavioural state in presence of swimmers (95% CI: 6.2 – 22.3%, z = 3.42, $P = 0.001$) than in their absence, which accounted for 3.9% of the total time of observation in the control scenario. No further significant differences were detected.

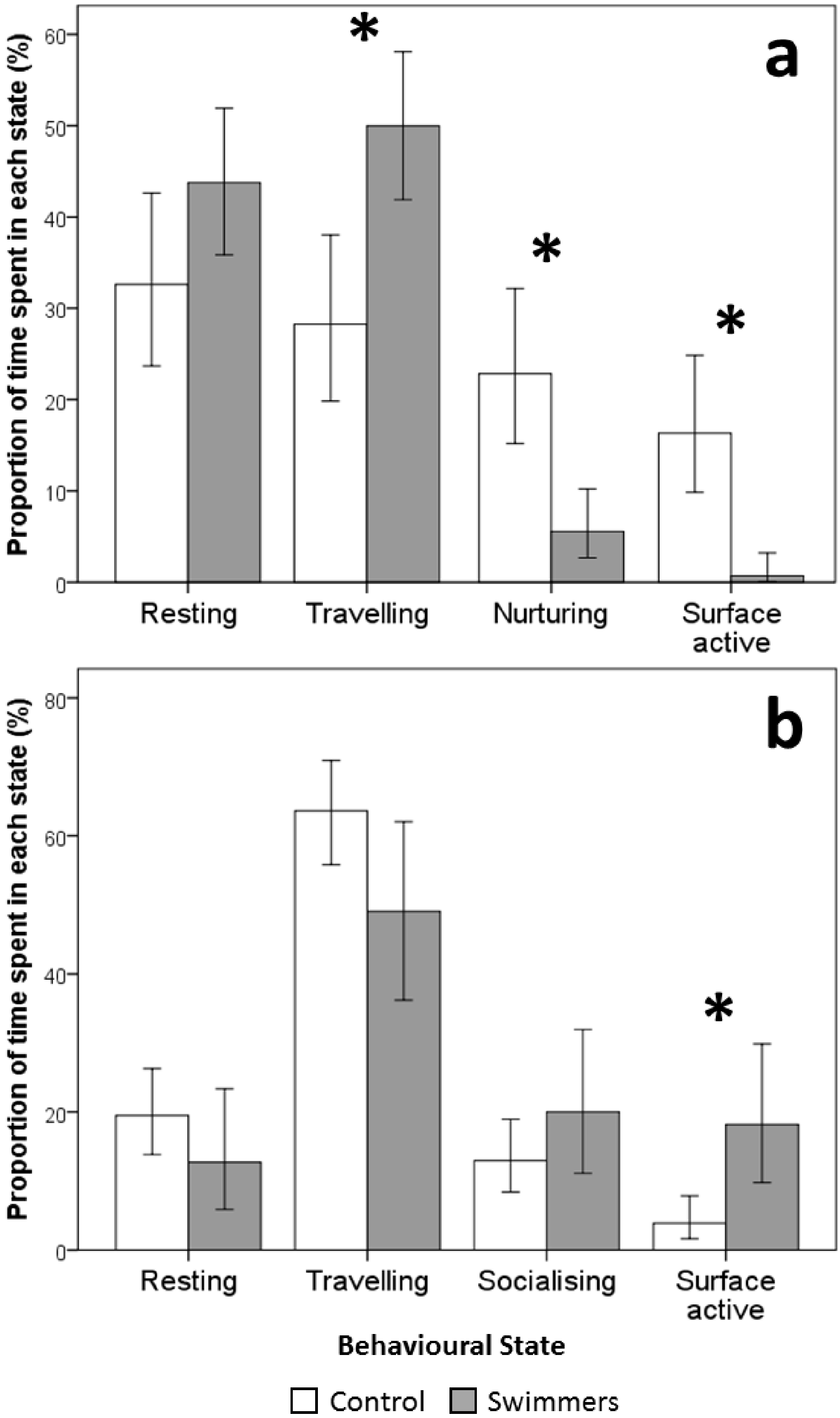

Figure 25. Proportion of time humpback whales (*Megaptera novaeangliae*) spent in each behavioural state by (**a**) groups containing calves; and (**b**) groups without calves recorded from a VTOL UAV platform in Vava'u, Kingdom of Tonga, in presence and absence (control) of swim-with-whales tourism activities. Error bars represent 95% confidence

intervals. Significant differences ($P < 0.05$) between presence and absence of swimmers are denoted by an (*).

5.3.2 Calf dive time, diving frequency and respiration rate

The presence of swimmers had no significant effect ($F_{1,20} = 0.213$, $P = 0.649$) on calf mean dive time (Figure 26a, p. 139). Similarly, while the mean diving frequency for calves (Figure 26b, p. 139) increased during swim-with tourism activities (9.07 ± SE = 1.26 dives × hour^{-1}) compared to control situations (5.87 ± SE = 1.20 dives × hour^{-1}), this difference was not statistically significant ($F_{1,22} = 3.124$, $P = 0.091$, $R^2 = 0.124$). However, calf respiration rate (Figure 26c, p. 139) decreased significantly ($F_{1,22} = 17.081$, $P < 0.001$) from 1.83 ± SE = 0.15 blows × minute^{-1} (control) to 1.18 ± SE = 0.08 blow × minute^{-1} (swimmers). The linear model explained 43.7% of the variance in the data. Furthermore, the calves' time spent at the surface without their mother at its side (Figure 26d, p. 139) was also significantly affected by swimmer presence ($F_{1,22} = 14.493$, $P = 0.001$), increasing more than four times during in-water interactions (28.3 ± SE = 5.8% versus 6.0 ± SE = 1.8%, control). The LM explained 39.7% of the variance. No effect of water depth (mean = 66.7 metres ± SE = 5.8, SD = 28.4 metres) on all response variables investigated was detected.

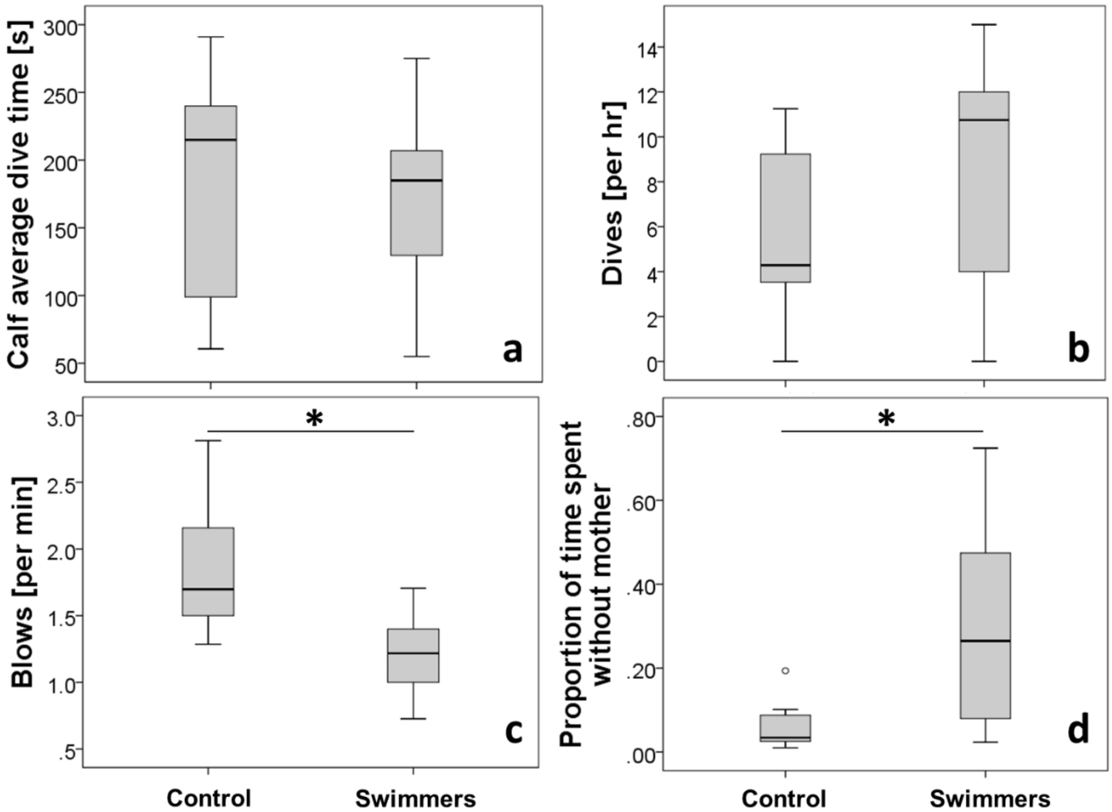

Figure 26. Box plots representation of calf (**a**) dive time; (**b**) diving frequency; (**c**) respiration rate; and (**d**) proportion of time spent at surface without the mother in absence of tourism activity (control) and during the swimming interactions (swimmers) for humpback whales (*Megaptera novaeangliae*) in Vava'u, Kingdom of Tonga. Significant differences ($P < 0.05$) between presence and absence of swimmers are denoted by an (*).

5.3.3 Whale agonistic behaviour towards swimmers

Thirty-two agonistic behavioural events were observed over 1.6 hours of aerial video recordings in six different encounters. The most dramatic of these was a particular occasion on the 31st of July 2017, when a single female adult whale was recorded directing fluke slaps and peduncle slaps in the direction of swimmers 19 times over a 16 min-aerial observation (Supplementary material #6). This behaviour culminated in the whale fluke hitting a swimmer with force (Figure 27, p. 140). The video record showed that the swimmer lost both fins due to the impact and needed to be assisted by the tour operator to leave the water and board the tour vessel. The swimmer appeared to have suffered an injury, which meant he was unable to swim with his legs. In addition to this incident, on five separate occasions, calves were recorded exhibiting similar agonistic behaviours directed at swimmers (Supplementary material # 8, 9, and 10). Finally, in one occasion, on the 25th July 2017, it was documented a swimming interaction with a competitive group of nine whales involved in agonistic behaviours such as peduncle slaps directed towards other individual whales (Figure 23c, p. 129).

Figure 27. A female humpback whale (*Megaptera novaeangliae*) hits with her flukes a participant to swim-with-whales tourism activity in proximity of the South-western tip of Nuapapu island (18°42'S, 174°06'W), Vava'u, Kingdom of Tonga (31st July 2017). (**a**) The whale approaches the swimmer sideways, opening wide the left pectoral fin; (**b**) the swimmer attempts to touch the whale's left pectoral fin with his left hand; (**c**) the whale keeps its momentum and passes by, the peduncle is flexed to the right; (**d**) the swimmer tries to move backward but the whale intercepts him with a fluke swish. Frames extracted from the aerial videos recorded by the UAV during this study.

5.4 Discussion

5.4.1 Proportion of time spent in each behavioural state

The findings highlighted that swim-with-whales tourism activities in Vava'u significantly alter the proportion of time spent in each behavioural state by humpback whales (Figure 25, p. 137). These findings are consistent with results documented by several other studies conducted on cetacean species targeted by whale-watching vessels (Di Clemente et al., 2018; Senigaglia et al., 2016) and in-water tourism interactions (Lundquist et al., 2013; Meissner et al., 2015). However, research on the effect of tourism on the activity budget of humpback whales is scarce. Only recently has this survey approach been applied to this species in the Juneau feeding ground, Alaska, USA (Di Clemente et al., 2018). The authors did not report any decrease in the proportion of time spent feeding by the whales, but they did find a significant increase of surface-active behaviour in response to the presence of vessels. A similar pattern was noted for in killer whales (*Orcinus orca*) in British Columbia, Canada (Noren et al., 2009). The results of the present study provide additional evidence of this effect and indicate that humpback whale groups without calves in Vava'u spent significantly more time (from 3.9% to 18.2%) in a surface-active behavioural state during in-water tourism interactions (Figure 25b, p. 137). This increase might be the result of the aerial agonistic displays such as peduncle slaps, fluke slaps, and fluke swishes that whales exhibit towards potential threats (Pitman, et al., 2015). While such an alteration of the proportion of time spent in each behavioural state by whales can lead to an increase of whale energetic expenditure (Di Clemente et al., 2018), it also poses a potential danger for participants in swim-with-whales activities. That is, humpback whale surface-active behaviours such as breaches, peduncle slaps, fluke swishes, fluke slaps, and pectoral fin slaps can put swimmers at risk of injury (as documented and discussed further by this study) or death, if direct contact is made with a swimmer.

In contrast to the above results, the proportion of time spent in a surface-active behavioural state for humpback whale groups containing a calf decreased significantly (from 16.3% to 0.7%) in the presence of swimmers (Figure 25a, p. 137). Mothers likely perform aerial displays to teach their calves social communication skills. Swimmer approaches might interfere with such behaviour and elicit an avoidance response. Notably, in Hervey Bay, Australia, it has been documented that humpback whale groups with calves decrease the frequency of their surface-active behaviours when approached by whale-watching vessels (Corkeron, 1995). Furthermore, the results of this study indicate that the proportion of time spent in each behavioural state by humpback whale groups containing a calf is the most affected by swim-with-whales tourism activity in Vava'u in comparison to groups without calves (Figure 25, p. 137). That is, the proportion of time spent travelling by these whale groups almost doubled from 28.3% in the control situation to 50.0% when in the presence of swimmers (Figure 25a, p. 137). This finding is consistent with several studies on other cetacean species that reported an increase of travelling behaviour in response to swimmers' presence (Lundquist et al., 2013; Meissner et al., 2015) and whale-watching vessel approaches (Christiansen et al., 2010; Lusseau, 2003). It has also been observed that the proportion of time cetaceans spent resting (Lundquist et al., 2013; Lusseau, 2003; Meissner et al., 2015) and socialising (Christiansen et al., 2010; Lundquist et al., 2013; Lusseau, 2003) decreased in the presence of swimmers and whale-watching vessels. In this study, the proportion of time spent resting by humpback whale mother-calf pairs was not significantly affected by swimmer presence, but nurturing behaviour did decrease significantly from 21.9% in control situations to 4.7% during swim-with-whales activities (Figure 25a, p. 137). These findings need to be considered in the context of the nuances of different cetacean species

– e.g., southern right whales (Lundquist et al., 2013) and delphinids (Christiansen et al., 2010; Lusseau, 2003; Meissner et al., 2015) – and different locations that might influence the behavioural responses to swimmers. However, the different findings between the present study and others might be related also to data collection methods. More specifically, the studies, which found changes to resting behaviour, were boat- and land-based observational studies and they did not include nurturing as a behavioural state in their ethograms. Nurturing is a subtle behavioural state and could be easily interpreted as resting, surface-active, or even travelling by a boat or land observer, especially if the whales are slightly under the surface and/or difficult to observe clearly (refer to Chapter 3, p. 58). During this study, the use of UAVs allowed us to gain more accurate observations on whale behaviour and to detect the subtle differences between resting and nurturing. In addition, because Vava'u is a breeding and nursing ground for humpback whales, the use of a nurturing category is appropriate, whereas for other cetacean species, and in other locations, such activities might be less frequently observed.

The almost five-fold decrease of the time spent in a nurturing behavioural state in comparison to control conditions could have negative consequences for calf development. Nurturing is a critical behavioural state for humpback whale calves, not only because of the nutritional requirements for growth and development, but also because of the important bonding such behaviour engenders between a mother and her calf (Cartwright & Sullivan, 2009). Examples of important bonding behaviours commonly observed during nurturing bouts in Vava'u included the calf being lifted on the mother's rostrum. Resting on mother's back or head in what seems to be an aid to flotation provided by the mother while slowly travelling have also been documented for baleen whale species (Smultea et al., 2017). Moreover, other researchers have placed multisensory DTAGs on humpback whale calves in the Exmouth Gulf, Western Australia, and have found that calves spend around 20% of the total tagging time seeking milk from their mothers when they are stationary, either at the surface or at depth (Videsen et al., 2017). While in Vava'u it was not possible to ascertain suckling behaviour from the UAV perspective, the disruption of nurturing behaviour that has been observed could reduce the time available to the calf to be fed by its mother. Therefore, the significant reduction in the time spent nurturing recorded in this study may have implications not only for the bonding process between the calf and its mother, but also for the physical development of the calf and its swimming energy expenditure (Noren et al., 2008) and, consequently, for its growth rate (Braithwaite et al., 2015).

Groups of whales containing a calf in Vava'u likely experience an increase in energy expenditure as consequence of the increased time spent travelling when in the presence of swim-with-whales tourism activities and the high level of exposure to such interactions. Twenty-eight swim-with-whales boats were operating in Vava'u in 2017 and the number of licensed vessels has increased to 37 in 2019 (Tongan Ministry of Tourism, personal communication, 24th July, 2019). In section 4.3.3 (p. 106) queues of up to six vessels waiting to interact or simultaneously interacting with the same group of whales were documented in almost 40% of the encounters. This is of concern during this phase of the calf's growth and development, when energy conservation is important so the calf can put on as much weight as possible in preparation for its first migration to Antarctic waters (Braithwaite et al., 2015; Christiansen, Dujon, et al., 2016; Videsen et al., 2017). An aerial photogrammetry study conducted in the breeding/resting ground of the Exmouth Gulf, Western Australia, documented a linear decrease of body condition for lactating humpback whales (Christiansen, Dujon, et al., 2016). In the same region, Bejder et al. (2019) used DTAGs to assess the proportion of time spent in each behavioural state by humpback whales and found that whale mothers spend most of their time in a resting behavioural state (mean = 35%). Interestingly, a similar proportion of time spent resting (mean = 31%) has been observed via UAVs for humpback whale groups containing a calf in Vava'u (refer to Table 4, p. 76). Bejder et al. (2019) suggested that whales adopt a hypo-metabolic behaviour to reduce their energy expenditures while they simultaneously provide milk to the calf and sustain their own life functions. Therefore, the two-fold increase of the time spent travelling detected in presence of swimmers during this study might be detrimental not only for the calf growth rate, but also for the mother's fitness level.

5.4.2 Calf dive time, diving frequency and respiration rate

Calf respiration rate changed significantly in the presence of swimmers, decreasing an average of 35.3% in comparison to control observations. Similar changes in respiration patterns have been widely documented for humpback whales (Avila, et al., 2015) and other cetacean species exposed to tourism activities (Nowacek et al., 2001; Richter et al., 2003). However, the biological implications of these behavioural responses for calves remains unclear. Nevertheless, the findings of this study should be considered in the light of the research conducted on the same groups of whales using data collected by a boat-based observer. The results presented in section 4.3.2 (p. 103) highlighted that the group respiration rate (blows × individuals^{-1} × minute^{-1}) did not change significantly between control and swimmer samples. However, the mean dive time of humpback whale mothers was found to have increased three-fold in presence of swimmers, from 189 (± SE = 24 seconds) to 561 (± SE = 73 seconds). Furthermore, the proportion of time humpback whale mothers spent diving when in the presence of swimmers doubled, indicating the use of a vertical avoidance strategy in response to swimmer approaches. In contrast, the present study did not find a significant increase in calf dive time. These might be a result of the limited breath-holding and diving capacity that calves have (the longest recorded calf dive was 291 seconds) and, as a consequence, they are physically unable to follow their mothers for longer dives. Calves may be responding to the vertical avoidance strategy adopted by their mother by increasing the frequency of their dives and reducing the respiration rate as they spend more time diving than the time they spend at the surface.

During some swim-with tourism activities (n = 9) humpback whale mothers were detected via the UAV in a stationary position at depth. Such behaviour was never observed for calves, neither was recorded in control situations. Whale mothers observed in a resting behavioural state at depth during swimming activities could be more tolerant to the presence of swimmers than those actively avoiding the approaches (Bejder et al., 2009). It is plausible that, after several years of commercial swim-with-whales tourism conducted in Vava'u, some humpback whale mothers have developed a certain degree of habituation (e.g., Ellison et al., 2012; Higham et al., 2009; Tougaardet al., 2015). Moreover, some whales could have learned to rest at depth to avoid potential disturbance at the surface, as documented for southern right whale mothers in response to kelp gull (*Larus dominicanus*) attacks in Peninsula Valdez, Patagonia (Marón et al., 2015). However, this aspect needs further investigation and would require whales' photo-identification to asses if different individuals would show different behavioural responses to swimmer approaches. Moreover, the use of DTAGs could complement the information provided by our study with valuable insights on whale mothers' diving profile, swim speed and underwater behaviour. Future studies should also take in consideration swimmers' distance from the whales and swimmers' behaviour during the approaches.

Calves are most likely unable to remain at depth for prolonged time, which is consistent with the difference in the proportion of time spent diving observed for mother and calves. A 371.7% increase in the time calves spent at surface without their mothers when exposed to swim-with-whales activities is important to note (Figure 6d). This finding might be a result of mother's vertical avoidance towards swimmer approaches, which their calves are unable to engage in yet. Similarly, when whale mothers rest at depth, their calves are generally unable to remain at their side. As a consequence, calves are left unaccompanied by their mothers at the surface in a situation where the presence of swimmers is a potential disturbance. In contrast, whale mothers were mostly observed resting at the surface next to their calf in control situations.

5.4.3 Whale agonistic behaviour towards swimmers

Behaviours such as fluke swishes and slaps directed towards swimmers were recorded during one in-water interaction with a single female whale (refer to Supplementary material #6). As highlighted in the previous section, calves spent significantly more time without their mothers at the surface in presence of swimmers. Interestingly, similar agonistic displays were observed from five calves during swim-with-whales activities and always in absence of the mother at the surface. Peduncle slaps, fluke slaps, and fluke swishes have been interpreted by researchers as defensive behaviours used by humpback whales to intimidate predators, such as killer whales (Pitman et al., 2015). Whether humpback whales recognise swimmers as potential threats is unclear. However, aggressive behaviours directed towards humans have been already documented in delphinids (Orams, 1997; Scheer, 2010), especially as consequence of pursuit and physical contact from swimmers (Parker, 1994; Shane, Tepley, & Costello, 1993). Furthermore, surface behaviours from whales that put swimmers at risk of injury or even death were observed in southern right whales after they were touched by swimmers (Lundquist et al., 2013). There is, therefore, evidence that any pursuit of and attempted physical contact from swimmers with humpback whales can be extremely dangerous for the swimmers, as documented in this study and reported by Sprogis at al., (2017) for humpback whales in Western Australia. During this study, we also documented a swim-with activity conducted with a competitive whale group (Figure 23c, p. 129). These whale aggregations are composed by several males (nine individuals at a single time were observed) involved in fast erratic movements and highly aggressive displays (Figure 23c, p. 129) directed towards other individuals (Tyack & Whitehead, 1982). Accordingly, Sprogis et al. (2017) defined whale high-risk behaviours and documented their occurrence during the first swim-with-humpback whales trials in Ningaloo, Western Australia. The report highlighted that such high-risk behaviours were initiated by whales after the swimmers entered the water in 20.7% of the in-water interactions. Moreover, the rate of occurrence of potentially dangerous surface behaviours tripled when the whale-watching vessel was at a distance of less than 100 m from the whales. An increase of whale breaching behaviour in response to whale-watching boat approaches was also observed by Avila et al. (2015) in the humpback whale breeding ground of Bahía Málaga ,Colombia. While we did not observe whales breaching at less than 100 meters of swimmers and tour operator vessels during this study, there have been several reports of such events happening (e.g., CBSNews, 2010), even in Vava’u (Pilgrim, 2016). It is evident that if a whale landed accidentally on a swimmer or a group of swimmers, there would be a high potential risk of fatalities and near certain injuries to the people involved.

5.5 Conclusions

The findings from this study provide an empirical assessment of the effects of swim-with-whales tourism activities on the proportion of time spent in each behavioural state by humpback whales in Vava'u. The growth of these activities over the past two decades has raised concerns amongst marine mammal scientists. The results reported here confirm some of these concerns and need to be considered carefully because the waters of Vava'u archipelago represent an important calving ground for the Tongan sub-population of humpback whales that still shows little sign of recovery from whaling (Baker et al., 1998; Constantine et al., 2012; Jackson et al., 2013). Management actions such as a) the reduction of the number of swim-with-whales licensed vessels operating simultaneously (37 at the moment) and b) the decrease of the maximum interaction time per vessel (currently set at 1.5 hours by 2013 Tongan regulations) could prevent that the short term effects documented in this study will lead to long term consequences, in particular for whale mothers and their calves. In addition to the evidence of negative effects on the whales, the injury to a swimmer caused by a whale and recorded during this study highlights how further research on humpback whale agonistic behaviours would be valuable to reduce the potential negative consequences of whale-based tourism in Vava'u and other locations, both for the whales and the tourists who wish to interact with them.

Chapter - 6 - Discussion and conclusions

Chapter 6 cover picture. Myself, Lisa – one of the employees of Vava'u Environmental Protection Agency (VEPA) – and the Phantom 4™ in Neiafu (18°64′ S, 173°98′ E), Vava'u, Kingdom of Tonga. Photo credit: Karen Stone.

The last chapter of this thesis is a general discussion of the results presented in the previous chapters (Chapters 3, 4 and 5) and is divided in two sections. The first section examines the findings presented in Chapter 3 and focuses on the use of UAVs for humpback whale behavioural surveys. The second section discusses the results from Chapters 4 and 5, and the implications of this research for whale-based tourism in Vava'u, Kingdom of Tonga. Finally, the last sections evaluate the efficiency of the existing swim-with-whales regulations and provide recommendations for the management of in-water tourism activities in the Kingdom of Tonga and other countries where swim-with-whales is permitted.

6.1 The use of UAVs for humpback whale behavioural studies

6.1.1 UAV Platform assessment

The comparison of behavioural data collected using the UAV methodology and the boat-based methodology supports the assumption that the use of multi-rotor UAVs improves the accuracy of humpback whale behaviour assessment. The behavioural state assessment conducted by the boat-based observer was significantly different to the data collected by the UAV. In particular, socialising and nurturing categories were under-represented with boat-based observations as socialising and nurturing were frequently recorded as other behavioural states (Figure 15, p. 75).

The difficulty of detecting and recording some behavioural states from a viewing platform based on a boat is most likely due to the position of the observer, who is unable to see whales that are submerged and at an oblique angle. In contrast, the use of an UAV allows for improved visibility of the whales and permits the observer to follow their movements, even when they swim underwater. Although this advantage can be limited by factors such as the depth of the whales below the surface and water clarity, the elevated perspective offered by the UAV enhances the ability of the observer to detect subtle physical contacts and behaviours between whales. Such subtle interactions are indicative of socialising and nurturing behavioural states (Table 2, p. 68), and as such are relevant for a through and accurate behavioural assessment. The ability to analyse and review UAV video-recordings of whale behaviour after data collection further facilitates the categorisation of behavioural states. Finally, video-recordings of whale behaviour taken by the UAVs can be assessed by different researchers, increasing the accuracy of the categorisation.

6.1.2 Response to UAV presence

The study investigated the potential of both vertical and horizontal avoidance reactions from the whales with a UAV overhead. This aspect was explored by measuring and comparing whale diving frequencies, respiration rates, dive time, and the number of reorientation events in both the absence and presence of the UAV situations. No significant differences were detected for these parameters when flying the UAV at 30 metres altitude over whales (Figure 16, p. 78). In other words, there was no evidence of avoidance responses from the whales due to the presence of the UAV.

6.1.3 Contributions to knowledge of the study

UAV platform assessment for humpback whale behavioural studies

Travelling, resting, surface-active (e.g., Corkeron, 1995; Sprogis et al., 2017; Stamation et al., 2010) and, more recently, socialising (Sprogis et al., 2017) behaviours have been used by several authors to categorise humpback whale behaviour. Considering that Vava'u represents an important breeding ground for humpback whales (Baker et al., 2006; Constantine et al., 2012; Olavarria et al., 2007), it seemed important to include the category nurturing to describe and record mother-calf interactions. The introduction of the nurturing behavioural state categorisation represents a significant refinement of humpback whale traditional ethograms, especially for studies taking place in their breeding grounds. However, the results of this study demonstrated that boat-based observations fail to detect interactions between whales that are indicative of nurturing and socialising, whereas UAV-based observations are able to detect these behavioural states during the same encounters, which means that the use of UAVs improve the accuracy of observations.

The idea of using a remotely controlled aerial platform to observe marine mammal behaviour is not necessarily new as previous studies have utilised helium-filled aerostatic balloons (Flamm et al., 2000; Hodgson, 2007; Nowacek et al., 2001). However, UAVs have the additional advantages of greater manoeuvrability and the possibility to track marine mammals for greater distances (refer to paragraph 2.3.4, p. 44). Therefore, the findings support the idea that UAVs represent an innovative and effective tool to refine conventional investigative methods of cetacean behaviour (Hodgson et al., 2017; Nowacek et al., 2016; Torres et al., 2018).

Humpback whale behavioural responses to UAV presence

Several authors raised concerns on the potential effect of UAVs on marine mammal behaviour (Mulero-Pazmany et al., 2017; Pomeroy et al., 2015; Smith et al., 2016) and highlighted the lack of systematic assessments focusing on the potential disturbance caused by the UAV on the targeted cetaceans. The present research study addressed this concern by including a systematic comparison of aerial vs boat-based data. Results show no evidence of vertical or horizontal avoidance behaviours when flying the UAV at 30 metres altitude over the whales. Thus, the findings suggest that VTOL UAVs can be utilised as a non-invasive tool to investigate humpback whale behaviour. Moreover, these findings are consistent with what has been reported by other researchers who have flown lightweight VTOL UAV at 30 and 50 metres altitudes over humpback whales (Christiansen, Dujon, et al., 2016). VTOL UAVs can eliminate the need to approach whales with a research boat, which have been shown to potentially alter their behaviour (Dawson et al., 2008; Guerra et al., 2014).

6.1.4 Study limitations and future studies

The “birds-eye” point of view provided by the UAV allowed the analyst to clearly detect and quantify humpback whale mother-calf interactions. However, calves were not observed in positions that may have indicated nursing behaviour. Recent studies conducted at a Hawaiian breeding ground documented that humpback whales nurse calves at depths between 10 and 15 metres (Zoidis & Lomac-MacNair, 2017). If this depth is typical for humpback whale nursing, the detection of this behaviour from an aerial platform, such as a UAV, would be difficult and strictly dependent on water visibility and light attenuation through the water column. For instance, underwater visibility was estimated to range from 2 to 30 metres in Vava’u, depending on the location, sea-surface state, the angle of sunlight on the surface, and the weather. Moreover, subtle details of interactions between whales could be better observed flying at altitudes lower than 30 meters ASL, and this consideration is particularly relevant when the behaviour of smaller cetacean species is investigated using a UAV platform. The choice of 30 metres ASL for humpback whale surveys was dictated by the need to capture all the individuals of the whale group in the same video camera frame. Additionally, behavioural reactions have been documented in bottlenose dolphins exposed to a Splashdrone, a VTOL UAV, flying at a 10 metre altitude (Fettermann et al., 2019), and the UAV used in the present study, HexH2O^{TM}, is considerably larger than the Splashdrone. Therefore, a conservative approach was followed in this study and 30 metre altitude ASL was set as the minimum altitude over whales to reduce the risk of altering their behaviour.

When the first surveys took place in Vava’u (July 2016), HexH2O^{TM} was the best VTOL UAV platform available on the market for the study because it provided a more reliable, robust, and water-resistant design with extended flight time (refer to paragraph 2.3.4, p.

44). This was particularly important for a remote study site, such as Vava'u, where access to spare parts and major repair expertise would be unavailable. However, smaller VTOL UAVs, such as the DJI Innovations Phantom4™ (Figure 22, p. 126), now have a comparable flight endurance and reliability, representing a cheap, and easier to handle, alternative to the HexH2O™. While the aircraft size does not necessarily imply different noise levels (Perryman et al., 2014), the use of a smaller UAV may allow scientists to fly closer to cetaceans without eliciting behavioural responses. Nevertheless, disturbance of cetaceans from aerial sources could originate from both visual and acoustic stimuli (Richardson & Würsig, 1997; Southall et al., 2007).

In summary, further research should carefully consider factors such as flight altitude, aircraft type, environmental conditions, species identity, location, and life-stage, as each factor may all affect marine mammal behaviour differently in regard to their reaction to UAVs in close proximity (Pomeroy et al., 2015). In particular, the highly diverse cetacean morphology and behavioural ecology requires a case-by-case evaluation of the UAV setup. Further investigations on the use of VTOL UAVs at lower altitudes, with different species and in other locations, is crucial to extend our confidence in the application of these tools for cetacean research.

6.2 The effects of humpback whale-based tourism in Vava'u

6.2.1 Behavioural responses to vessel approaches

The hypothesis that the tour vessel approach type does not affect humpback whale behavioural response to swim-with-whales tourism activities was rejected as shown by the results presented in Chapter 4. J approaches caused an avoidance response most frequently (67.6%), while parallel approaches resulted in the least number (26.0%) of avoidance responses (Figure 18, p. 102). Nevertheless, humpback whale mother-calf pairs seemed to be particularly sensitive to direct and J approaches, avoiding the tour vessels in all cases (n = 16) observed during the study. In addition, whales in Vava'u exhibited avoidance responses towards swim-with-whales vessel B more frequently (+27.5%) than towards swim-with-whales vessel A when they approached using the parallel technique (Figure 18, p. 102). In contrast, J approaches elicited similar avoidance rates for both vessel A and B. Whether this finding reflects differences between the vessel hull shape (vessel A = catamaran; vessel B = monohull), propulsion type (vessel A = gasoline fuelled outboard motors; vessel B = diesel fuelled inboard engines), or even the different hydrodynamic characteristics related to the hull shapes, remains unclear.

Furthermore, the hypothesis that swim-with-whales tourism activities do not elicit changes in the diving behaviour of humpback whale can be rejected for mother-calf pairs. Data presented in Chapter 4 shows that whale mothers increased their average dive time two-fold in the presence of tour vessels, in comparison to control observations (Figure 19, p. 105). The proportion of total time spent diving also doubled in presence of whale-watching vessels (Figure 19, p. 105). The study provided evidence that humpback whale mothers in Vava'u adopt a vertical avoidance strategy in response to tour boats.

6.2.2 Behavioural responses to swimmers

Data presented in Chapter 4 highlights how factors such as vessel, swimmer placement, and vessel distance at swimmer drop had no significant effect on whale avoidance rate of swimmers. However, the presence of swimmers resulted in an increase of humpback whale mother dive time and doubled the proportion of time spent diving for mother-calf pairs. Results show that whale mothers increased their average dive duration three-fold with swimmers in the water in comparison to control observations (Figure 19, p. 105), changing from 189 ± SE = 24 seconds to 561 ± SE = 73 seconds. Moreover, the proportion of total time spent diving during encounters doubled in the presence of swimmers, from 27.9 ± SE 5.2% (controls) to 58.6 ± SE 6.0% (swimmers) (Figure 19, p. 105).

While these findings indicate that whale mothers in Vava'u adopt a vertical avoidance strategy in response to swimmer approaches, it was not possible to investigate calf responses to in-water interactions from boat-based observations. Therefore, aerial video recordings, collected via UAV, have been used to conduct individual calf follows in the presence and absence of swimmers, as presented in Chapter 5. The hypothesis that calf respiration rate would not change significantly in the presence of swimmers was also rejected. Calf average respiration rate was found to have decreased (35.3% less), going from 1.83 ± SE = 0.15 in control situations to 1.18 ± SE = 0.08 blows × minute during in-water interactions (Figure 26, p. 139). In contrast with previous documentation of whale mothers, no significant increase of calf dive time was found (mean 171 ± SE = 16 seconds) (Figure 19, p. 105) or calf diving frequency during in-water interactions (Figure 26, p. 139). Finally, calves spent 28.3% of the time at the surface without their mothers when exposed to swim-with-whales activities, but only 6.0% of the time under control conditions (Figure 26, p. 139).

In Chapter 5, the overall proportions of time spent in each behavioural state by humpback whales in the presence and absence of swimmers were compared assessing whale behaviour from the aerial video recordings collected via UAV. The advantages of this methodology for humpback whale behavioural studies are highlighted in Chapter 3. The hypothesis that swim-with-whales tourism activities in Vava'u did alter significantly the proportion of time spent in each behavioural state by humpback whales was supported by the data presented in Chapter 5 (Figure 25, p. 137). Results indicate that the proportion of time spent in each behavioural state by whale groups containing a calf was the most affected by swim-with-whales tourism activity in Vava'u. That is, the proportion of time spent travelling by the whales almost doubled, going from 28.3% in control situations to 50.0% in presence of swimmers (Figure 26, p. 139). While the humpback whale mother-calf pair proportion of time spent resting was not significantly affected by swimmer presence, nurturing behaviour decreased from 21.9% in control situations to 4.7% during swim-with-whales activities (Figure 25, p. 137). Finally, the proportion of time spent in a surface-active behavioural state also decreased significantly (from 16.3% to 0.7%) in the presence of swimmers when compared to control observations (Figure 25, p. 137). In contrast, whale groups without calves spent significantly more time (from 3.9 to 18.2%) in a surface-active behavioural state during in-water tourism interactions (Figure 25, p. 137).

Humpback whales in a surface-active behavioural state typically exhibit displays such peduncle slaps, fluke swishes, and slaps. Such behaviours can pose risk of injuries or death for participants to swim-with-whales tourism activities, and it is important to note that during one 16-minute aerial survey a female whale was observed and filmed directing 19 fluke swishes and slaps towards swimmers (Supplementary material #6). The encounter culminated with the injury of one swimmer, who was hit by the fluke of the whale (Figure 27, p. 140, Supplementary material #7). Similar agonistic displays were detected in calves during swim-with-whales activities, always in the absence of the mother at the surface (Supplementary material #8, 9 and 10). This situation was significantly more frequent in the presence of swimmers (28.3%) compared to control observations (6.0%), as shown in Chapter 5 (Figure 26, p. 139).

6.2.3 Contributions to knowledge of the study

Level of exposure of humpback whales to in-water tourism interactions in Vava'u, Kingdom of Tonga

During the two years of data collection for the study, the level of exposure of humpback whales to swim-with-whales tourism activities in the Vava'u, Kingdom of Tonga, was quantified. Swim-with-whales vessels A and B spent an average of 2.6 hours per day with whales. If the time spent with whales by vessel A and B is similar to the time spent by other tour operators, there is evidence that humpback whales in Vava'u are exposed to an extremely high level of commercial in-water interactions. This can be exemplified by the sighting of up to 28 swim-with-whales vessels, simultaneously, on the water during a single day at the peak of the season (August-September).

Humpback whale avoidance rates towards vessel and swimmer approaches

The rates of avoidance towards swim-with-whales vessels A and B (33.5%), as well as swimmers (35.5%) were quantified. Both vessels A and B most frequently caused an avoidance response when approaching with the J technique (+35.1%), while parallel approaches resulted in the least number of avoidance responses (Figure 18, p. 102). This finding provides supporting evidence to what is documented in the literature, which noted that whales and dolphins respond with avoidance behaviour to the erratic, fast movements of boats manoeuvring closely around them, in particular when vessels are placed directly in the path of their direction of travel (Richardson et al., 1995). Nevertheless, most of whale-watching regulations and guidelines worldwide recommend the use of parallel technique when approaching cetaceans by boat (Carlson, 2013). However, the parallel approach type was the most frequently used by Vava'u swim-with-whales tour operators A and B (70.9%). This differs with Sprogis et al.'s (2020) observations during the first commercial swim-with-humpback whales trials in Ningaloo, Western Australia. Swim-with tour operators in Ningaloo interacted with humpback whales using mainly a J approach (89.8%) and positioned swimmers in the path of travel of the whales (Sprogis et al., 2020). In Chapter 4, some factors that might explain this difference between Tongan and Australian swim-with-humpback whales operations have been highlighted. One of the main differences noted was that Western Australian swim-with-whales regulations did not permit in-water interactions with groups of whales containing calves (*In-water humpback whale interaction. Ningaloo Marine Park trial 2016*, 2016). In contrast, tour operators A and B in Vava'u, where swim-with-whales activities with mother-calf pairs are legal, interacted most frequently with groups containing a calf (79.3% of total swim time). As shown in Chapter 3, mother-calf pairs in Vava'u spend most of their time in resting and nurturing behavioural states (Table 4, p. 76). While this situation facilitates the use of a parallel approach by swim-with-whales tour operators, mother-calf pairs exhibited avoidance responses in 100% of the cases (n = 16) when approached by boats using the J technique in Vava'u. Therefore, Tongan tour operators A and B used a parallel approach because it guarantees a higher probability of success for their clients. Similarly to what was documented by Sprogis et al. (2020) in Ningaloo, Vava'u tour operators use a J approach more frequently when focusing on whale groups without a calf (Figure 17, p. 100). This is likely to be related to the more common socialising and travelling behavioural states observed for whale groups without calves in Vava'u, as shown in Chapter 3 (Table 3, p. 76).

Humpback whale behavioural responses to vessel and swimmer approaches: mother-calf pair diving and respiration patterns

Chapter 4 provides quantitative data indicating that humpback whale mothers in Vava'u adopt a vertical avoidance strategy in response to vessel and swimmer approaches. That is, swim-with-whales tourism activities resulted in a significant increase of whale dive time and the proportion of time spent by whales diving. Results showed that whale mothers increased their average dive duration two-fold when in the presence of tour vessels and three-fold when in the presence of swimmers in comparison to control observations (Figure 19, p. 105). The proportion of time spent diving during tourism encounters doubled in the presence of swimmers and swim-with-whales vessels (Figure 19, p. 105). Notably, humpback whales exposed to whale-watching vessels in other breeding grounds (Au & Green, 2000; Schaffar et al., 2010) and also in their migratory corridors (Stamation et al., 2010) showed similar behavioural responses.

In-water interactions with humpback whales in Western Australia, however, elicited horizontal avoidance responses in the targeted whales. Sprogis et al. (2020) documented a significant increase of the whale deviation index (the mean of turning angles between consecutive positions during the follow) with respect to the approaching vessel. Although an increase of reorientation events in the presence of vessel and swimmers was observed (Figure 20, p. 106), this finding was not statistically significant. Similarly, no significant differences in the group respiration rates between control and experimental (vessel and swimmers) situations were found (Figure 19, p. 105). However, the analysis of the UAV aerial footage highlighted significant differences in whale calf respiration rates, as presented in Chapter 5. Calf average respiration rate decreased 35.3% during in-water interactions in comparison to control observations (Figure 26, p. 139). Similar changes in respiration patterns have been reported for humpback whales (Avila et al., 2015; Sprogis et al., 2020) and other cetacean species exposed to whale-watching tourism activities (Nowacek et al., 2001; Richter et al., 2003). While the average dive time for humpback whale mothers in Vava'u was three-times longer in the presence of swimmers (Figure 19, p. 105), No significant increase of calf dive time (mean 171 ± SE = 16 seconds) was found during in-water interactions (Figure 26, p. 139). This finding likely shows that calves have an inferior diving capability in comparison to their mothers (the longest calf dive that recorded in this study was 291 seconds). While humpback whale mothers can dive longer and adopt a vertical avoidance strategy in response to swimmer approaches, calves are forced to surface earlier. A calf may cope with its mother's vertical avoidance response, reducing the respiration rate and potentially increasing the diving frequency. Although the difference was not significant ($F_{1,22}$ = 3.124, P = 0.091, R^2 = 0.124), an increase of average calf diving frequency (Figure 26, p. 139) was documented during swim-with tourism activities (9.07 ± SE = 1.26 dives × $hour^{-1}$), with respect to control situations (5.87 ± SE = 1.20 dives × $hour^{-1}$). Moreover, adult humpback whales seem to be able to rest at depth, as observed via UAV during this study in Vava'u, a behaviour which was never documented for humpback whale calves. Finally, in comparison to control situations (6.0%), calves spent a significant larger proportion of time (28.3%) at the surface without their mothers when exposed to swim-with-whales activities (Figure 26, p. 139).

Humpback whale behavioural responses to swimmer approaches: proportion of time spent in each behavioural state

Chapter 5 documents how swim-with-whales tourism activities in Vava'u significantly altered the proportion of time spent in each behavioural state by humpback whales (Figure

25, p. 137). Similar findings have been reported for several cetacean species exposed to whale-watching vessels (Di Clemente et al., 2018; Senigaglia et al., 2016) and in-water tourism interactions (Lundquist et al., 2013; Meissner et al., 2015). However, research about the effects of whale-watching on the activity budget of humpback whales is limited. Recently, Di Clemente et al. (2018) compared the behavioural budgets of humpback whales in their Juneau feeding ground in Alaska, USA, in presence and absence of whale-watching activities. The study did not highlight any decrease in the proportion of time spent feeding by the whales when in the presence of whale-watching vessels, but a significant increase in the proportion of time spent in a surface-active behavioural state was documented. Surface activity is elicited in killer whales by approaching boats (Noren et al., 2009). Similarly, a significant increase in the proportion of time spent in a surface-active behavioural state (from 3.9 to 18.2%) was observed in groups of whales without calves during in-water tourism interactions in Vava'u (Figure 25, p. 137). An increase of breaching behaviour in response to whale-watching boat approaches was also observed by Avila et al. (2015) in the humpback whale breeding ground of Bahía Málaga, Colombia.

In contrast, the proportion of time spent in a surface-active behavioural state with groups containing a calf decreased significantly (from 16.3% to 0.7%) during swim-with-whales tourism activities in Vava'u (Figure 25, p. 137). Notably, in Hervey Bay, Australia humpback whale groups with calves decreased the frequency of surface-active behaviours when approached by whale-watching vessels (Corkeron, 1995). The proportion of time spent in each behavioural state by whale groups containing a calf emerged as the most affected by the presence of swimmers in Vava'u. Humpback whales almost doubled the proportion of time spent travelling when in the presence of the swimmers, from 28.3% in control situation to 50.0% during in-water interactions (Figure

25, p. 137). This finding supports what others have documented when other cetacean species are approached by swimmers (Lundquist et al., 2013; Meissner et al., 2015) or whale-watching vessels (Christiansen et al., 2010; Lusseau, 2003). Nurturing behaviour also decreased, from 21.9% in control situations to 4.7% in the presence of swimmers (Figure 25, p. 137).

Humpback whale behavioural responses to swimmer approaches: agonistic displays

Agonistic behaviours directed towards swimmers, such as peduncle slaps, fluke swishes, and slaps, were observed during one in-water interaction with an adult female whale. Peduncle slaps, fluke slaps, and swishes have been interpreted by researchers as defensive behaviours used by humpback whales to intimidate predators, such as killer whales (Pitman et al., 2015). Moreover, similar displays were documented in calves (n = 5) during swim-with-whales activities, always in the absence of the mother at the surface (See Supplementary material #8, 9 and 10). Aggressive behaviours directed towards humans have been reported for Delphinids (Orams, 1997; Scheer, 2010), in particular in response to swimmers seeking physical contact with the dolphins (Shane et al., 1993). In addition, surface behaviours that could harm participants of in-water swim-with-whales activities were observed in southern right whales after being touched by swimmers (Lundquist et al., 2013).

6.2.4 Study limitations and future studies

During this study, It was demonstrated that the vessel approach was the main factor affecting whale avoidance rates. However, humpback whales in Vava'u showed more frequent avoidance responses towards vessel B (+27.5%) when it approached using the parallel technique (Figure 18, p. 102). In contrast, J approaches caused similar avoidance rates for both vessels. Unfortunately, it was not possible to investigate if this finding reflected differences between the design (vessel A = catamaran; vessel B = monohull) or propulsion type for each vessel (vessel A = gasoline fuelled outboard motors; vessel B = diesel fuelled inboard engines). Vessel type should be considered for future research and for the development of guidelines for swim-with-humpback whales tourism activities, with the purpose of mitigating potential disturbances for the targeted whales.

In addition, swim-with-cetaceans activities require vessels to deploy swimmers near the animals, which may require several close approaches for the success of the interaction (Constantine, 2001; Martinez et al., 2010). The approach speeds are generally higher for swim-with-whales boats when compared with whale-watching vessels (Lundquist et al., 2013) and this can elicit avoidance responses in the approached whales (Richardson et al., 1995). Therefore, further research should compare the behaviour of whales in response to the approach of different types of swim-with-whales platforms.

The vessel manoeuvring closely to the whales to place swimmers in the water represents a confounding factor when assessing the responses of humpback whales to swimmer approaches (Kessler et al., 2013). To mitigate this effect, the analysis of several response variables (i.e., dive time, diving frequency, respiration rate, number of reorientation events) was restricted to vessel parallel approaches to the focal group of whales. As expected, this resulted also in a sample size reduction and it was thus possible to investigate the effects of swim-with-whales activities only on groups of whales containing a calf. This was a consequence both of tour operators' preference for focusing on mother-calf pairs and the frequent use of J approach technique with groups of whales without calves. It is suggested that other response variables might indicate a reaction to the presence of vessels or swimmers and should be measured in future investigations.

Whale swim speed, for example, could also be assessed as potential indicator of horizontal avoidance.

Although no significant relationship between swimmer placement and whale avoidance behaviour was established, other variables which may be influential were not investigated. For instance, swimmer behaviour in the water and their distance to the whales could have affected whale responses. Notably, Kessler et al. (2013) found that humpback whales moved away from swimmers significantly earlier when swimmers were splashing, instead of being calm, during in-water interactions in Ha'apai, Kingdom of Tonga. Thus, future investigations should focus also on how the swimmers approach the whales once in the water. This was not possible during the study, as any research on the behaviour of participants during in-water tourism interactions would have needed to be approved by a human ethic commission and authorised by the participants themselves. Moreover, measurements of distance between whales and swimmers could not be collected from the vessel as an observation platform, or from the aerial perspective of the UAV. The UAV could be flown perpendicularly above the animals only on a few occasions to avoid the glare over the water surface. This impeded to calculate the distance between swimmers and whales with similar precision to what is currently achieved with perpendicular photogrammetry (refer to paragraph 2.3.4, p. 44).

Finally, a low level of compliance with the Tongan swim-with-whales regulations pertaining the minimum whale resting time between interactions (1.5 hours) was documented. However, data were not collected for an entire day with a specific group of whales, and the findings may represent an underestimation or overestimation of the scale of tour operators' queueing behaviour in Vava'u. Moreover, it cannot be excluded that the presence of researchers aboard the swim-with-whales vessels may have influenced the tour operators and made them more likely to comply with license conditions.

6.2.5 Effectiveness of regulations and recommendations for the management of swim-with-humpback whales tourism

In Chapter 4, the levels of compliance with Tongan key swim-with-whales regulations in Vava'u were assessed. The findings highlight relatively high rates of transgression of some of the regulations and support those reported by Walker and Moscardo (2011). Thus, during 38.4% of the encounters, tour operators did not comply with the minimum rest time between interactions with tour vessels, which is stipulated as an hour and a half (*Tonga Whale Watching and Swimming Regulations 2013*, 2013). Up to five vessels were observed at a time waiting to interact with a whale group which already had a tour vessel interacting with it (Figure 21, p. 107). These queueing vessels would then move in immediately after the original vessel departed the area or, in some cases, they would alternate with the original vessel by placing swimmers in the water as soon as the initial vessel swimmers exited the water. It is plausible that tour operators disregarded this regulation, as there are too many commercial swim-with-whales vessels on the water simultaneously and the number of whales tolerating vessel approaches and in-water interactions is low in comparison to the number of boats seeking to place swimmers in their proximity. Up to 28 tour operator boats were counted on the water each day during the peak of the 2017 season, during which whale avoidance rates towards vessels and swimmers were fairly high (33.5% and 35.5%, respectively). Therefore, increasing the level of compliance with the existing regulations might not be feasible without reducing the number of licensed vessels operating at a single time.

However, compliance with other key regulations was high. For example, the maximum number of five swimmers (including the guide) in the water at a single time was adhered to by tour operator vessels A and B in 88.3% of the interactions. Interestingly, tour operators A and B disregarded this regulation to reduce the number of in-water approaches when five or six participants were on board. This choice may minimise the number of vessel and swimmer approaches necessary for a successful in-water interaction, and, consequently, reduce the whale exposure to swim-with-whales activities. In addition, swimmers should be briefed comprehensively about how to act once in the proximity of whales. The four-to-one swimmers-to-guide ratio is considered to be a safety measure to avoid swimmer misconduct during the interactions with whales, and it could be difficult for a guide to maintain control of more than four participants once in the water.

The maximum interaction time (an hour and a half) was adhered to by tour operators A and B during 89.6% of the encounters. However, an interaction time of an hour and a half could be excessive, especially in Vava'u where there are 28 swim-with-whales vessels on the water simultaneously during the peak of the season. For instance, in Ningaloo Reef, Western Australia, 11 companies conduct swim-with-humpback whales tourism activities and the maximum interaction time for a vessel with each group of whales is 60 minutes ("In-water humpback whale interaction. Ningaloo Marine Park trial 2016," 2016).

The stipulated minimum distance a vessel can approach whales (ten metres for whale groups without a calf, 50 metres for whale groups containing a calf) was respected in most of the cases. Tour operators A and B complied with this regulation in 86.9% of the approaches. Notably, both tour operators, A and B, did not utilise a laser rangefinder to assess distances from the whales. Therefore, the level of compliance to distance regulations appears to be reasonable. Nevertheless, the minimum distance of ten metres between vessels and groups of whales without calves seems inappropriate, especially as the J approach was frequently used in absence of calves (Figure 17, p. 100). The tour operator choice of J approach is likely to be related to the more common socialising and travelling behavioural states of whale groups without calves in Vava'u (Table 3, p. 76). However, J approaches elicited an avoidance response towards vessels in 67.6% of the cases in Vava'u and are known to cause avoidance behaviour in cetaceans (Richardson et al., 1995). While most whale-watching regulations and codes of conduct worldwide recommend the use of parallel approaches when interacting with whales and dolphins (Carlson, 2013), Tongan regulations do not explicitly discourage or forbid the use of the J approach (*Tonga Whale Watching and Swimming Regulations 2013*, 2013). Similarly, Ningaloo swim-with-humpback whales guidelines allow tour operators to use the J approach but set the minimum distance between the vessel and the whales to 150 metres (*In-water humpback whale interaction. Ningaloo Marine Park trial 2016*, 2016). Setting a minimum distance greater than 10 metres for J approaches to whale groups without calves could mitigate the incidence of whale avoidance behaviour towards vessel approaches and still permit tour operators to conduct successful in-water interactions with travelling and socialising whales. Nevertheless, results show that humpback whale mother-calf pairs avoided direct and J approaches in the 100% of the cases (n = 16) in Vava'u. Therefore, these approach techniques for whale groups containing a calf should be discouraged.

Furthermore, it is recommended that whale agonistic behaviours directed towards swimmers should cause the immediate termination of the in-water interaction by the tour operator. This was not the case during the incident that was documented during the study (Figure 27, p. 140, Supplementary material #7). Moreover, even after the incident, one swimmer was allowed by the tour operator to remain in the water while the whale continued its agonistic behaviour. Tongan regulations state that the in-water interaction should be terminated at any sign of distress of the whales but this decision is left to the tour operator's discretion. However, whale behaviours can still be misinterpreted and/or considered not posing risk to swimmers' safety. For instance, several tour operators were observed conducting in-water interactions with competitive whale groups (Figure 23, p. 129, Supplementary material #5). Whales in competitive groups are engaged in fast chasing movements (Tyack & Whitehead, 1982) and high-risk aerial behaviours such as peduncle slaps and fluke slaps (Sprogis et al., 2017). Even if these behaviours are generally directed towards other whales, they can accidentally involve swimmers who find themselves in the path of the whales. In conclusion, it is recommended that regulations explicitly state which whale behaviours (e.g., fluke and peduncle slaps, fluke swishes) should be considered aggressive and potentially harmful for participants involved in-water interactions. Moreover, aerial video recordings collected during this study could be used as explanatory material for skippers and guides conducting swim-with-humpback whales tourism activities (see Supplementary material).

Finally, on no occasion during this two-year study were any enforcement activities observed, which was also documented by the Tongan Ministry of Tourism (Tongan Ministry of Tourism, personal communication, October 8, 2017). That is, in the primary researcher experience, compliance with regulations in Vava'u was totally at the discretion of the tour operators. While patrolling the waters on a regular basis may not be feasible for the local authorities, both for logistic and economic reasons, alternative solutions should be explored in Vava'u. For example, some land lookouts offer excellent fields of vision over the waters where most of the swim-with-whales activities take place. Transgressions such as "queueing" would be easily detectable with no need to deploy a vessel and sustain the associated costs.

6.3 Conclusions

This work highlighted that both whale-watching vessels and swim-with-whales activities caused avoidance responses from humpback whales in Vava'u, Kingdom of Tonga. In particular, whale mothers showed significant vertical avoidance responses and increased their average dive time significantly in presence of swim-with-whales vessels and swimmers. Nevertheless, a significant reduction of calf respiration rate during in-water interactions was observed. While the biological consequences of these behavioural responses are not clear, such avoidance strategies may increase the energy expenditure for the lactating mother and her dependent offspring (Cartwright & Sullivan, 2009; Noren et al., 2008). The potential danger of this behavioural patter was highlighted by Braithwaite et al. (2015), who estimated that the increase of swimming speed and the reduction in the time spent resting for mother-calf pairs can result in a significant decrease in the calf's growth rate.

In addition, swim-with-whales tourism activities were found to significantly alter the proportion of time spent in each behavioural state by humpback whales in Vava'u. Groups of whales containing a calf seem to be more sensitive to disturbance. This observation supports the findings documented by other researchers for humpback whales (Stamation et al., 2010) and southern right whales (Lundquist et al., 2013) exposed to vessel and in-water tourism interactions. Groups of whales containing a calf in Vava'u even doubled the proportion of time spent travelling in presence of swim-with-whales tourism activities. Also, the time spent in a nurturing behavioural state by mother-calf pairs decreased almost five-times during in-water interactions with respect to control conditions. Nurturing state included behaviours such as the mother lifting the calf on her rostrum and/or the calf resting above its mother's back or head in what seems a flotation aid provided by the mother (Smultea et al., 2017). Therefore, the reduction of the time spent nurturing may have implications for the energy expenditure of the calf (Noren et al., 2008).

Finally, a significant increase of the proportion of time spent by calves at the surface without their mother during in-water interactions was documented. This physical separation in the presence of swimmers can represent a stress factor for the calf. The calf agonistic behaviours directed towards swimmers that were observed during the study seems to corroborate this hypothesis. The injury of a participant involved in a swim-with-whales activity was witnessed, as a consequence of an adult whale targeting swimmers with fluke swishes and peduncle slaps. Such agonistic displays were clearly directed towards humans and may indicate that sensitisation processes (Bejder et al., 2009) are occurring in some humpback whales in Vava’u. However, future long-term studies are needed to test this hypothesis. Moreover, it is recommended that Vava’u tour operators gain a better understanding of humpback whale behaviour to help them recognise signs of aggression and take appropriate measures to minimise the risk of lethal consequences for their clients.

To sum up, the behavioural responses shown by humpback whales towards swim-with-whales tourism activities in Vava’u may indicate that this kind of interactions have the risk of detrimental effects on the whales involved. High levels of exposure to commercial in-water interactions were documented, both in terms of the number of tour boats (28 licensed vessels in 2017) and the average time spent with the whales per day (mean = 2.6 hours per day). Thus, a reduction of a) the number of licensed tour operators and b) the maximum interaction time with a specific whale/group of whales is warranted. Furthermore, the Tongan subpopulation of humpback whales is still experiencing a slow recovery after being severely depleted by industrial whaling (Clapham et al., 2009; Constantine et al., 2012; Jackson et al., 2013) and the Vava’u island group represents one of the most important breeding and calving grounds for this population. That is, whales give birth and raise calves in the sheltered waters of the archipelago, readying them for the southward migration back to the Antarctica feeding grounds (Baker et al., 1998). Therefore, the rapid growth of swim-with-whales industry experienced by Vava'u over a short period of time (Hendrix & Rose, 2014) and the tour operator focus on mother-calf pairs are alarming, especially in the light of the poor compliance with regulations and lack of enforcement documented in this study. Whether the short-term behavioural responses observed in Vava'u humpback whales could cause a long-term detrimental effect at the population level needs to be investigated further. Additionally, research conducted on terrestrial mammals indicates that physiological changes do not necessarily correspond to detectable behavioural changes (MacArthur et al., 1982; Ditmer et al., 2015) and future studies should also attempt to assess whale physiological responses to swimming tourism activities. It cannot be excluded that whales showing tolerance to boat and swimmer approaches might have been alert as if in presence of a potential threat. Nevertheless, the whale agonistic displays directed towards swimmers documented in this study are consistent with responses to predators previously observed in humpback whales (Pitman et al., 2015). Evidence from other studies on the long-term effects of cetacean-based tourism (Bejder et al., 2006; Filby et al., 2014; Lusseau, 2004) suggests that the findings from the present study in Vava'u should be cause for concern for the scientific community, Tongan stakeholders and the government of those countries wishing to legalise swim-with-humpback whales tourism activities.

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