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Drone Surveys Are More Accurate Than Boat-Based Surveys of Bottlenose Dolphins (*Tursiops truncatus*)

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Abstract: Generating accurate estimates of group sizes or behaviours of cetaceans from boat-based surveys can be challenging because much of their activity occurs below the water surface and observations are distorted by horizontal perspectives. Automated observation using drones is an emerging research tool for animal behavioural investigations. However, drone-based and boat-based survey methods have not been quantitatively compared for small, highly mobile cetaceans, such as Delphinidae. Here, we conduct paired concurrent boat-based and drone-based surveys, measuring the number of individuals in 21 groups and the behaviour within 13 groups of bottlenose dolphin (*Tursiops truncatus*). We additionally assessed the ability to detect behaviour events by the drone that would not be detectable from the boat. Drone-derived abundance counts detected 26.4% more individuals per group on average than boat-based counts ($p = 0.003$). Drone-based behaviour observations detected travelling 55.2% more frequently and association in subgroups 80.4% more frequently than boat-based observations ($p < 0.001$ for both comparisons). Whereas foraging was recorded 58.3% and resting 15.1% less frequently by the drone than by boat-based surveys, respectively ($p = 0.014$ and 0.024). A considerable number of underwater behaviours ranging from individual play activities to intra- and inter-species interactions (including those with humans) were observed from the drone that could not be detected from the boat. Our findings demonstrate that drone surveys can improve the accuracy of population counts and behavioural data for small cetaceans and the magnitude of the discrepancies between the two methods highlights the need for cautious interpretation of studies that have relied on boat-derived data.

Keywords: *Tursiops truncatus*; unmanned aerial systems; drone; behavioural ecology; marine mammals

1. Introduction

Because most cetacean activity occurs underwater, on-board vessel observations may not produce accurate or consistent recording of behavioural data [1], group behavioural state categorization may be biased towards an overestimation of the number of animals involved in a particular activity [2], and important, often subtle, behaviours may be missed [3,4]. Dolphin daily behaviour patterns are complex, as they live in a highly dynamic fission-fusion society, where individuals move in small groups that continually change in composition and behaviour [5].

The presence of a research vessel may elicit a behavioural response in the animals that influences the results [6,7]. Surveys are commonly conducted by human spotters from vessels and follow strict protocols, such as maintaining a sufficient distance from the animals so as not to disturb the animals or to elicit a behaviour response from them [7]. However, vessel presence and associated noise are known to impact on cetacean behaviour patterns, behavioural budgets, group size, composition, habitat loss, and range shifts [8–13].

Drones can improve data collection in field studies by facilitating the rapid survey of areas, adding aerial perspectives, detecting cryptic animals, and allowing access to sites previously considered inaccessible (for example, remote islands, marine protected areas, and rocky shallow waters). Drones provide a safe method for scientists to acquire high-resolution data at a lower cost with greater operational flexibility [14]. Drone data, therefore, have the potential to improve population and behavioural studies and enhance ongoing conservation programs [15,16]. For cetacean surveys, drones are particularly advantageous as they allow researchers to provide localised, detailed biological information at finer spatial scales than observations made from aircraft or satellites at higher altitudes [17,18].

Vertical take-off and landing drones are of particular interest as research tools for studying marine animals because they can be deployed from small vessels and fly over target species groups while maintaining high levels of stability [19–21]. To date, vertical take-off and landing drones have been used to identify individuals [22,23]; assess live entanglement events [24] quantify entanglement rates [25]; collect blow samples from whales [26,27] and dolphins [28,29]; assess whale health using thermal imagery [30], create three-dimensional images using photogrammetry [31–33]; study dolphin populations [34–36]; and record behaviour [1,37–39].

In New Zealand, bottlenose dolphins (*Tursiops truncatus*, Montagu, 1821) are nationally endangered [40], and are distributed in three genetically distinct populations [41]. The largest population inhabits the northern North Island [41]; a semi-resident population of 317 dolphins [41] that travel and change habitat during the seasons within a home range of 500 km. However, concerns over this population have been reported due to a decline in the resight rate of some individuals and the increase in tourism pressure [41–43]. Great Barrier Island has been described as a hotspot for the bottlenose dolphin's northern North Island population, acting as social hub where small groups fuse for socializing. In this region there are year-round sightings, high levels of site fidelity for individuals (possibly related to food availability), large average group sizes and high use by groups containing neonates and calves [44]. The island has a low human population density and remains relatively undisturbed from human activities and whale watching tour operators. Because populations are declining, it is important that there is long-term research undertaken on population sizes of groups occupying the waters near Great Barrier Island. In addition, the region offers a unique opportunity to study population size changes relative to other regions where dolphins are heavily exposed to tourism [44] and other anthropogenic impacts and/or natural disturbances.

From a management perspective, knowledge about population dynamics and behavioural patterns is crucial for identifying the conservation status of a given population [45,46] and for improving the management of adverse human activities [47,48]. With such information, researchers can define residency patterns as well as home ranges and core areas [49], establish baseline knowledge, and inform effective species-specific conservation management plans.

The recent advances of drone technology are revolutionizing marine mammal science [50], and over the last five years drones have become common tools for both marine mammal research and whale-watching. Despite the rapid uptake of drone technology by researchers, there remains a lack of studies directly comparing drone derived group size estimates or behavioural observations to paired boat-based surveys, especially for small, agile, and often widely disperse odontocetes, such as Delphinidae. Direct comparisons between drone-derived data and boat-based observations are important to identify discrepancies between the results derived from the two methods.

Here, we compare the performance of a drone survey approach to the boat-based method of collecting small cetacean population and behavioural data. Our target species is the bottlenose dolphin, and the study site is offshore of Great Barrier Island, Aotearoa New Zealand. We tested three hypotheses: (1) that drone-derived observations will produce greater group-size estimates; (2) frequency counts of behaviour states and of group dispersion/aggregation states will differ between boat-based and drone-based surveys;

and (3) underwater behavioural events will be detected from drones that cannot be seen from boats.

2. Materials and Methods

Data were collected between July 2015 and March 2017 in the inshore waters of the western side of Great Barrier Island, North Island, Aotearoa New Zealand (36°10′ S, 174°23′ E; Figure 1). Great Barrier Island is located approximately 90 km northeast of Auckland City (36°85′ S, 174°76′ E) within the outer Hauraki Gulf. This region is considered a potential hotspot for nationally endangered bottlenose dolphins [44].
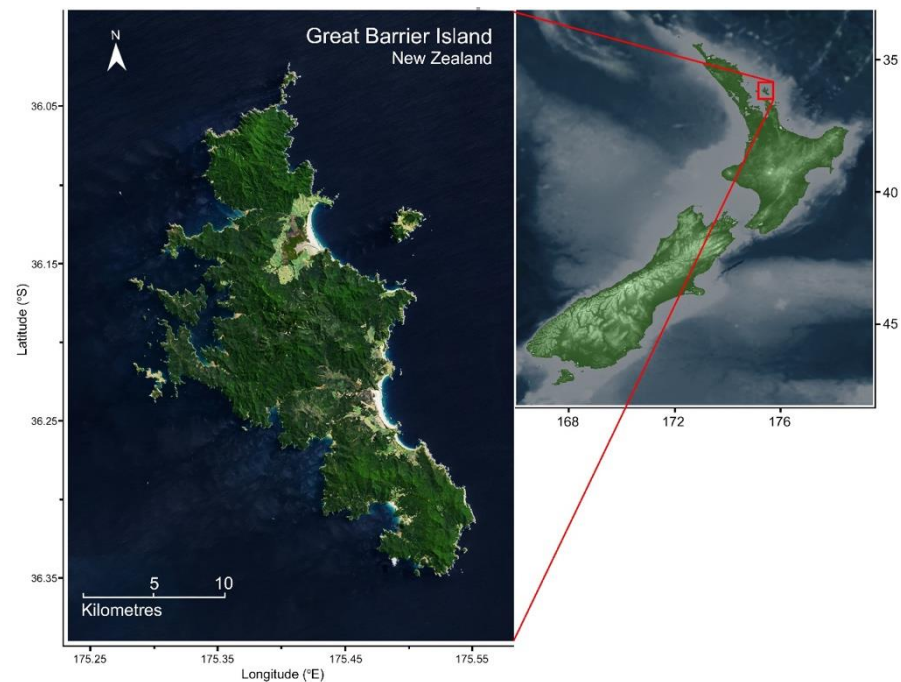

Figure 1. Map of the Great Barrier Island, Aotearoa New Zealand.

For a total of 16 days, boat- and drone-based surveys were conducted, resulting in a total of 21 independent group encounters. Non-systematic surveys for bottlenose dolphins were conducted on board a research vessel (Osprey 8.5 m) in conditions of Beaufort Sea State 3 or less. Once a dolphin group was sighted, the vessel approached in accordance with the New Zealand Marine Mammal Protection Regulations (1992), moving at idle speed to minimise behavioural impact [2,6]. At 100 m from the target group, an 'encounter' was commenced, and the time and GPS position were recorded. Initial behavioural data and group size were recorded, with group defined as any number of dolphins observed in association, moving in the same direction and engaged in similar behaviour [51]. Independent groups were determined when groups were temporally and spatially separated (>20 km). Out of the 21 groups surveyed, only 2 were surveyed on the same day.

The boat remained at a minimum of 100 m from the group at all times, unless the animals approached the boat, in which case the engines were either placed in neutral or switched off. Encounters lasted until weather conditions deteriorated and/or crew were unable to maintain visual contact with the dolphins without approaching closer than 100 m. The decision to terminate an encounter also included a significant change in dolphin behaviour (for example, a change in the direction of travel, an increase in speed, or avoidance of the boat).

Drone flights were conducted only in fine conditions with no precipitation and light to moderate wind (<15 knots). One of two drones were used: (1) HexH$_2$O TM (XtremeVision360, Worthing, UK), with six rotor waterproof drone (4.7 kg, diameter 110 cm propeller

tip-to-tip) equipped with a gimballed GoPro Hero 4 Black camera (GoPro Inc., San Mateo, CA, USA) and a polarised filter, and (2) Phantom 4 (DJI, Shenzhen, China), with four-rotor drone (1.38 kg; diameter: 35 cm engine-to-engine) equipped with a polarised filter mounted on the built-in camera. The drone was launched and retrieved from a custom-built platform on the research vessel. All flights were conducted between 25 and 40 m above sea level to minimise potential disturbance [52] and lasted approximately 10 min.

2.1. Group Counts

Dolphin group sizes were estimated from the boat based on a minimum and maximum number of individuals observed and categorised to the nearest five animals (1–5, 6–10, 11–15, etc.), unless all individuals in the group were readily identifiable and the observers agreed on an exact number. For each encounter, 1–2 drone flights were conducted to record and count the number of individuals in the group. Drone-derived group size counts were extracted from video playback at normal speed. Where necessary, footage was stopped for enlarging and enhancing, and then examined frame by frame to maximise detection of animals. At least two observers independently verified the counts (i.e., blind counts) using the same methodology and using high resolution monitors.

2.2. Behavioural Surveys

Synchronous paired observations of behavioural state and group dispersion were made by the boat observer and post hoc examination of aerial video recording by the drone. Behavioural states were recorded using a one-minute interval instantaneous scan of the whole group [2,53]. Aerial imagery was analysed only after the vessel returned from the field to ensure the boat observer counts and behaviour observations were not influenced via drone collected data. Behavioural state was determined by what more than 50% of the individual animals within the group were engaged in at the instantaneous sampling [2]. Five mutually exclusive categories of behavioural state were defined: socializing, milling, foraging, resting, and travelling (Table 1, Figure 2) [43,54,55]. Group dispersion was recorded as tight, moderate, loose, or sub-group (Table 2) [51].

Table 1. Definitions of behavioural states recorded for bottlenose dolphins (*Tursiops truncatus*) in the Great Barrier Island, New Zealand.

| Behavioural State	Definition
Socialising	Dolphins observed chasing, copulating, and/or engaged in any other physical contact with another dolphin, such as rubbing and touching (excluding mother-calf pairs). Aerial behavioural events, such as horizontal and vertical jumps, may occur.
Milling	Dolphins exhibited non-directional movements, with frequent changes in bearing that prevented dolphins from making headway in any specific direction. Most of the time appears to be 'transition' behaviour between behavioural states.
Foraging	Dolphins involved in any effort to pursue, capture, and/or consume prey. Diving for long periods of time, showing repeated unsynchronised dives in different directions in a determined location, exhibiting behaviour such as fluke out dives.
Resting	Dolphins observed in a tight group, engaged moving slowly and in a constant direction. Surfacing is generally more predictable, often more synchronous than observed in other behavioural states.
Travelling	Dolphins engaged in persistent, directional movement, making noticeable headway along a specific compass bearing. Group space varies and individuals swim with short and relatively constant dive intervals.
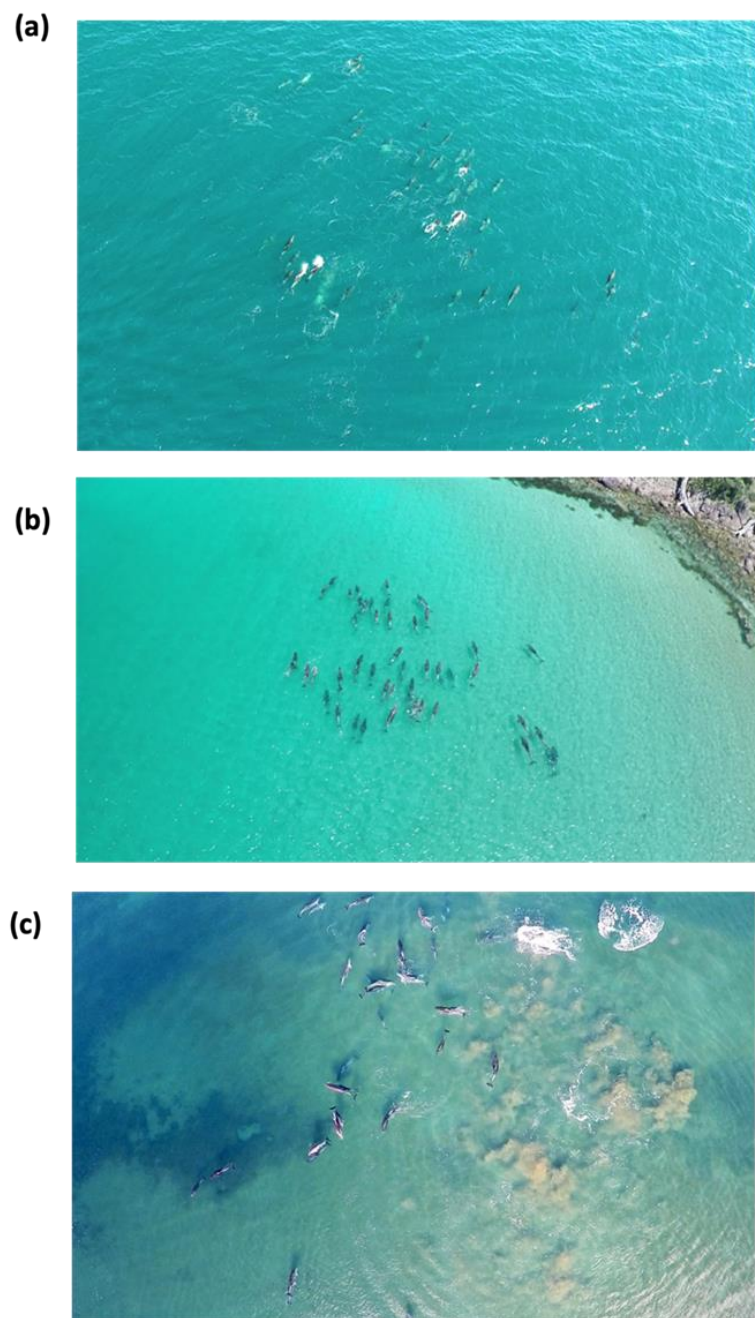
Figure 2. Bottlenose dolphins (*Tursiops truncatus*) photographed at Great Barrier Island (GBI), New Zealand during this study at 40 m of altitude and illustrating (**a**) travelling, (**b**) resting, and (**c**) socialising behavioural state.

Table 2. Group dispersion categories recorded for bottlenose dolphins (*Tursiops truncatus*) in the Great Barrier Island, New Zealand.

Group Dispersion	Definition
Tight	Less than one body length between individuals.
Moderate	One to five body lengths between individuals.
Loose	More than five body lengths between individuals.
Sub-group	Dolphins are divided in two or more groups but act as part of a single pod.

Out of the 21 independent groups encountered and filmed, 8 were discarded from the comparative behavioural study due to the proximity of other boats or recreational

users (for example, swimmers, stand up paddleboards and kayaks) to the dolphins, or due to the short duration of the flight (<5 min) enforced by bad weather or loss of daylight. All 21 encounters with dolphin groups were used to assess the detection of behaviour events from the drone that were not detectable from the boat. A total of 5.9 h (354 min) of synchronous boat-based and drone-derived behaviour sampling were collected during 30 flights over 13 independent encounters. Flights ranged in duration from 7 to 16 min (mean = 12, SD = 2.2). The time spent following and sampling groups ranged from 10 to 67 min (mean = 27, SD = 20), and involved 1 to 6 flights (mean = 2, SD = 1.6).

2.3. Data Analysis

All data were tested for normality and equality of variances using the Shapiro–Wilk test and Levene's test, respectively. Statistical analyses were carried out using IBM SPSS Statistics 23 software. Boat-based group size estimations and drone-derived counts were considered linked to each encounter because flights were performed immediately following boat derived group estimates. The two samples being compared were not random samples from two distributions, but different detection results from the same group conducted simultaneously. A parametric paired *t*-test was used to compare group size. To assess if behavioural states occurred more, or less often than expected for the sampling method, Pearson chi-square tests were performed.

3. Results

3.1. Group Counts

Drone counts produced on average 26.4% more individuals (7.8 dolphins) per group (M = 37.4, SD = 19.16) than boat-based counts (M = 29.6, SD = 14.74) (n = 21 groups, p = 0.003). Drone-based counts were higher than their associated boat-based counts in 71.4% of cases, with only two cases, when the group size was small (six individuals), resulting in congruent estimates between the two methods (Figure 3).
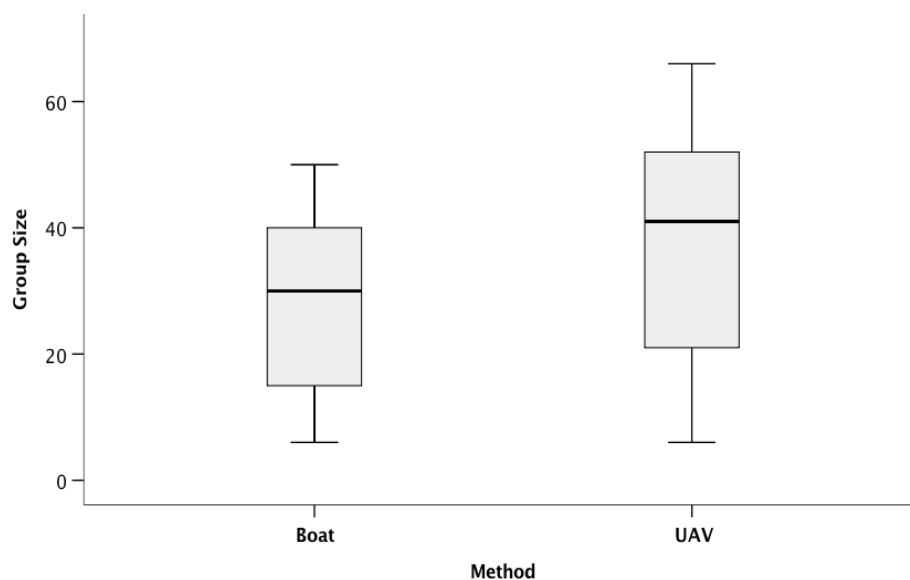
Figure 3. Median group size recorded from boat-based and drone-based (UAV) surveys from 21 independent bottlenose dolphin (*Tursiops truncatus*) group encounters between July 2015 and March 2017 at Great Barrier Island, Aotearoa New Zealand. Maximum and minimum bars and 75% quartile boxes are shown.

3.2. Behavioural Surveys

The proportion of time spent in each behavioural state differed between methods in 26.3% of samples (Pearson's χ^2_4 24 = 21.97, p < 0.001). Drone-derived behaviour observa-

tions detected travelling 55.2% more frequently than boat-based observations (Pearson's $\chi^2_1 = 15.11$, $p < 0.001$), whereas foraging and resting were recorded 58.3% and 15.1% less often by drone than by boat-based surveys, respectively (Pearson's $\chi^2_1 = 6.05$, $p = 0.014$ and $\chi^2_1 = 5.09$, $p = 0.024$, respectively) (Figures 3 and 4, Table A1 Appendix A). Differences in socialising and milling were not statistically significant.

(a)

(b)
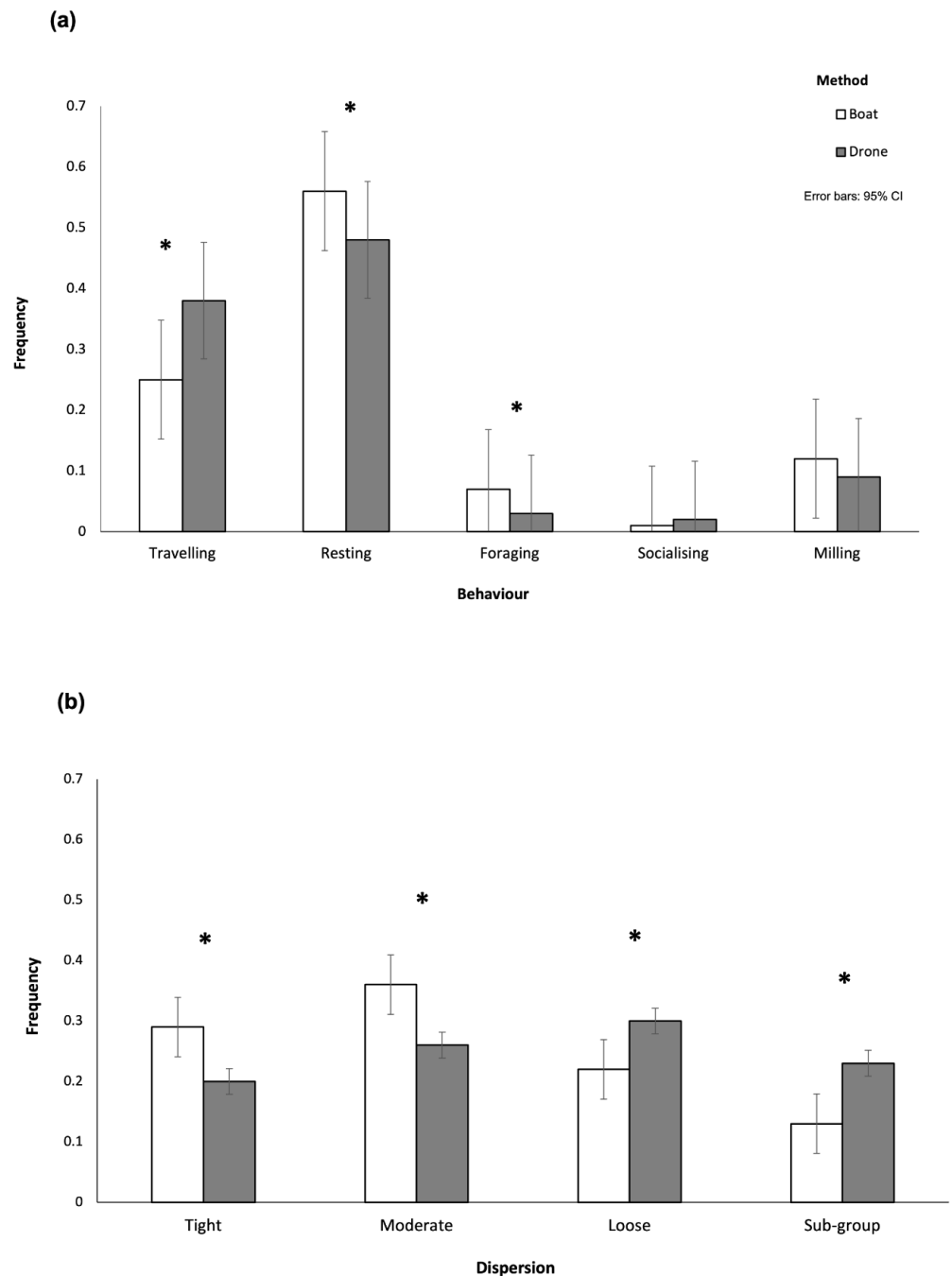
Figure 4. Bottlenose dolphins (*Tursiops truncatus*) behavioural state frequency (**a**) and dispersion state frequency (**b**) recorded from the boat- and drone-based surveys near Great Barrier Island, NZ. Error bars represent 95% confidence intervals. Significant differences (*p* < 0.05) between methods are denoted by an (*).

Frequencies for dispersion/association behavioural states differed between the boat-based and drone-based methods by 46.3% (Pearson's $\chi^2_3 = 25.62$, $p < 0.001$). Aggregation into sub-groups was recorded 80.4% more frequently using drone-derived samples than

from boat-based observations (Pearson's χ^2_1 = 12.97, p < 0.001) and dolphins swimming in a loose formation were recorded 35.4% more often by drone surveys (Pearson's χ^2_1 = 5.71, p = 0.017). Tight and moderate associations also differed significantly between methods (Figure 4, Table A2 Appendix A).

3.3. Additional Behavioural Events Recorded by the Drone

Several subsurface behaviours were observed using the drone imagery that were not detected from the boat. These included: social rubbing, underwater chases, interactions between calves and juveniles, exhaling air underwater, playing with seaweed, nursing, and copulation attempts. Underwater interactions with and/or responses to other species such as fish, sharks and birds were additionally observed with the drone. For example, dolphins were recorded swimming past a school of fish while travelling around the coast, sharing the same area for resting with juvenile hammerhead sharks (*Sphyrna zygaena*) and chasing stingrays (*Myliobatis tenuicaudatus*). These activities could not be observed from a boat unless the dolphins were directly below it. Many interactions and responses to human activity were also recorded by drone imagery that were not evident by observation from the boat.

4. Discussion

4.1. Group Counts

We found that the counts from drone-derived surveys of bottlenose dolphins were significantly different to the boat-derived counts. The results support our hypothesis that drone-based surveys of small cetaceans identify more individuals than boat-based counts. This is consistent with prior observations, where a post hoc analysis of drone imagery demonstrated improved accuracy of counts of dolphins in groups relative to counts performed from helicopters [56] and improved precision and accuracy for monitoring seabirds and pinnipeds relative to land-based observations [57,58].

The perspective of drone imagery can reduce the likelihood of missing animals present in the study area [56] or missing counts due to topography and/or other individuals obscuring the observer's line of sight [58]. Differentiating between animals can also be difficult from a boat when multiple individuals are surfacing within a group simultaneously. Dolphins move quickly, often changing direction and/or speed, and surface asynchronously [59]. When using boat-based estimates, group sizes are usually estimated and later confirmed or amended by photo-identification. However, not all species are equally suited to photo-identification [60] and all individuals in a group are often not captured. Conversely, drone-based counts of small cetaceans enable all the individuals to be accurately counted and are, therefore, especially useful when studying large animal groups.

Group organization and size can provide insight into habitat use and the role a species plays within an ecosystem [61]. Group size is usually related to food availability, social interactions, and/or based on predator defence [62]. It can vary both temporally and spatially and a significant change over time in a home range can indicate a shift in dolphin ecology related to environmental or biological conditions. For example, the mean group size in the Bay of Islands was reported to be 14.8 individuals between 2012 and 2015 [63], which was smaller than reported from previous studies [32,41], indicating a shift in the fine scale habitat use. Accurate counts of group sizes are important because they are used to assess the adequacy of current protected areas in the region for protecting dolphin populations [64].

4.2. Behavioural Observations

In our study, behavioural state data collected from the drone disagreed with boat-based observations in 26.3% of our one-minute scans. Specifically, the drone methodology recorded substantially more travelling and less resting and foraging than the boat-based method.

Behavioural studies of cetaceans have been challenging because these animals are only partially visible from boats for short periods of time [65], with some species spending up to 95% of their time below the surface [66]. Some behaviours are difficult to identify and easy to confuse, for example, milling and resting [62,67]. Additionally, the oblique perspective afforded from a boat can make it difficult to accurately characterise behaviours because it is only possible to record the behaviour of dolphins that are close to the surface and this may not represent the majority of the group [2]. Characterising group activity may be less problematic if all members of the group are doing the same thing, but more difficult when behaviour differs among individuals [62]. As a result, behavioural observations from boats are influenced by both observer bias and availability bias [2,62]. Bias in boat-based observations can usually be reduced using an individual focal-animal follow protocol [53]. However, this method provides information about far fewer animals in a given sampling period.

In our study, the aerial perspective of the drone-based survey and clear visibility of all dolphins in the water column from the drone, allowed observers to ensure the entire group was surveyed and the ability to retrospectively investigate drone imagery of dolphins postflight enabled accurate categorization of cetacean behaviour states without real-time observational biases. Consistent with our study, Hodgson et al. [68] argued that aerial drone observations of behaviour provide a more accurate assessment of availability than either land- or boat-based follows because they provide a direct measure of availability, minimizing assumptions about what occurs during the portions of the dive cycle when animals are out of sight under water.

Bottlenose dolphins in the North Island of Aotearoa New Zealand are heavily exposed to the tourism industry and vessel traffic, and show sensitisation and increased avoidance levels with prolonged exposure to swimmers [69] and dolphin watching tour boats [6,9,12]. The presence and noise of a research vessel may also affect dolphin behaviour and bias observations [7,70]. The prolonged exposure of these activities can have a significant impact on the population whereby it can interrupt biologically significant behaviours, such as resting, which may carry energetic costs and affect individual fitness. Short term-effects can have potentially long-term population consequences [11,41]. Our results show that our understanding of dolphin behaviour responses to those human activities has been underestimated by boat-based studies, and in many cases the boat observers are likely to have influenced the nature of the observations due to the proximity of the boat either attracting or deterring the target animals. By contrast, it has been demonstrated that drone-derived observations do not affect cetacean behaviour if flown above 25 m altitude. Drones can be deployed at a greater distance from target animals than required for direct boat-based observations, thereby causing less disturbance to the animals, and less bias in the data collected [34,52,71]. Finally, drone-base surveys can provide a better perspective on interactions and can refine the measurement of the anthropogenic impacts on target populations, thereby better informing appropriate management measures.

Assessment of dolphin dispersion differed between the drone and boat-based observations in 46% of the scans. Using the drone, we recorded more widely separated dolphins (loose) and smaller sub-groups than from the boat-based observations. We were able to record those differences due to the water clarity giving us continuous observation of the animals underwater, and throughout the water column. Recent studies have used drone observations to study the sociality of Risso's dolphins (*Grampus griseus*) by recording the relative positions of individuals, synchrony, and alignment in swimming patterns within a group of males [72]. Furthermore, drones have been successfully used to measure the proximity of mother and calf pairs of Southern right whales (*Eubalaena australis*) in order to better understand the level of calf dependency on its mother [73].

4.3. Additional Behavioural Events Detected from Drones

Because the use of a drone made it possible for dolphins to be followed and for continuous observations to be recorded, even when the animals were submerged, behavioural

events not seen from the boat were captured. These additional behaviours included: social rubbing, underwater chases, interactions between calves and juveniles, underwater exhalation, playing with seaweed, nursing; and copulation attempts. This finding is consistent with Fiori et al. [1], who reported underrepresentation of socializing by humpback whales (*Megaptera novaeangliae*) using boat-based studies. Even if behaviour is not the focus of a study, the permanent imagery provides the potential for it to be subsequently used for a variety of other behavioural objectives. Furthermore, although not reported here, the drone imagery can be used for diverse post-processing data mining, such as identifying the precise number of neonates, calves, and juveniles, and for identifying sexual maturity, mother/calf pairs, body shape, and nutritive condition of all dolphins in a group [21–23].

Conservation management seeks to regulate human activities to minimise direct and indirect negative impacts on threatened or vulnerable species. Assessing the non-lethal effects of disturbance and their population-level consequences is a significant ecological and conservation challenge which requires extensive baseline knowledge including but not limited to that of population dynamics and behaviour [74]. Several studies have explored how changes in behaviour (in response to disturbance) could affect energy reserves and the implications of this for fertility and survival (see [74]). Group size dynamics and behaviour have been applied as two critical markers upon which to assess disturbance in marine mammal populations [75,76]. For this reason, clarity on how methodologies to collect such data can produce varying results are critical for conservation management. Drone-based surveys can provide improved datasets and, thereby, advance our knowledge of marine mammals and improve the efforts made to minimize the impacts of human activities on them. Drone-based surveys have the additional advantage of being less intrusive [45]. Drones will therefore likely replace the need for boat-based surveys and will provide more robust data for conservation management.

5. Conclusions

In order for conservation management to regulate human activities and minimise direct and indirect negative impacts on threatened or vulnerable species, best practice methodologies are needed to collect critical data, such as group size and behaviour. Boat-based surveys can only record dolphin activity when the animals are near or above the surface of the water and rely on assumptions about contiguous activity by individuals while out of sight. By contrast, all dolphins regardless of where they are in the water column can be differentiated when drone-based video observations are recorded, and all activities of individuals can be extracted in a post hoc review of the video. Drone-based surveys therefore provide more accurate behaviour and abundance data than observations from boats.

Using paired drone and boat-based observations of dolphin groups, we have demonstrated that drone- and boat-based survey methods for Delphinids produce significantly different results; substantial differences were found in group size, time spent involved in different behavioural states, such as resting, and spatial aggregation patterns. These differences have important implications for understanding dolphin ecology and, therefore, their conservation. They suggest that some previous conclusions derived from boat-based surveys relating to dolphin ecology and behavioural responses to humans may require re-examination.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Behavioural state frequencies for boat-based and drone-based samples (n = 354 one-minute instantaneous whole group scans).

Behavioural State	Boat-Based Frequency	Drone-Based Frequency	Difference (%)	p-Value
Resting	0.56	0.48	−15.1	0.024
Travelling	0.25	0.38	55.2	<0.001
Foraging	0.07	0.03	−58.3	0.014
Socialising	0.01	0.02	166.7	0.129
Milling	0.12	0.09	−22.0	0.266

Table A2. Dispersion/association behavioural state frequencies for boat-based and drone-based samples (n = 354 one-minute instantaneous whole group scans).

Dispersion	Boat-Based Frequency	Drone-Based Frequency	Difference (%)	p-Value
Tight	0.29	0.20	−30.1	0.007
Moderate	0.36	0.26	−27.0	0.006
Loose	0.22	0.30	35.4	0.017
Sub-group	0.13	0.23	80.4	<0.001

References

1. Fiori, L.; Martinez, E.; Bader, M.; Orams, M.B.; Bollard, B. Insights into the use of an unmanned aerial vehicle (UAV) to investigate the behavior of humpback whales (*Megaptera novaeangliae*) in Vava'u, Kingdom of Tonga. *Mar. Mammal Sci.* **2019**, *36*, 209–223. [CrossRef]
2. Mann, J. Behavioral sampling methods for cetaceans: A review and critique. *Mar. Mammal Sci.* **1999**, *15*, 102–122. [CrossRef]
3. Smultea, M.A.; Fertl, D.; Bacon, C.E.; Moore, M.R.; James, V.R.; Wursig, B. Cetacean Mother-Calf Behavior Observed from a Small Aircraft off Southern California. *Anim. Behav. Cogn.* **2017**, *4*, 1–23. [CrossRef]
4. Weir, J.S.; Fiori, L.; Orbach, D.N.; Piwetz, S.; Protheroe, C.; Würsig, B. Dusky Dolphin (*Lagenorhynchus obscurus*) Mother–Calf Pairs: An Aerial Perspective. *Aquat. Mamm.* **2018**, *44*, 603–607. [CrossRef]
5. Wells, R.S.; Scott, M.D.; Irvine, A.B. The social structure of free-ranging bottlenose dolphins. In *Current Mammalogy*; Genoways, H.H., Ed.; Springer: Boston, MA, USA, 1987; pp. 247–305.
6. Guerra, M.; Dawson, S.M.; Brough, T.E.; Rayment, W.J. Effects of boats on the surface and acoustic behaviour of an endangered population of bottlenose dolphins. *Endanger. Species Res.* **2014**, *24*, 221–236. [CrossRef]
7. Dawson, S.; Wade, P.; Slooten, E.; Barlow, J. Design and field methods for sighting surveys of cetaceans in coastal and riverine habitats. *Mamm. Rev.* **2008**, *38*, 19–49. [CrossRef]
8. May-Collado, L.J.; Quinones-Lebron, S.G. Dolphin changes in whistle structure with watercraft activity depends on their behavioral state. *J. Acoust. Soc. Am.* **2014**, *135*, 193–198. [CrossRef]
9. Lusseau, D. The short-term behavioral reactions of Bottlenose dolphins to interactions with boats in Doubtful Sound, New Zealand. *Mar. Mammal Sci.* **2006**, *22*, 802–818. [CrossRef]
10. Guerra, M.; Dawson, S.M. Boat-based tourism and bottlenose dolphins in Doubtful Sound, New Zealand: The role of management in decreasing dolphin-boat interactions. *Tour. Manag.* **2016**, *57*, 3–9. [CrossRef]
11. Filby, N.E.; Stockin, K.A.; Scarpaci, C. Long-term responses of Burrunan dolphins (*Tursiops australis*) to swim-with dolphin tourism in Port Phillip Bay, Victoria, Australia: A population at risk. *Glob. Ecol. Conserv.* **2014**, *2*, 62–71. [CrossRef]

12. Constantine, R.; Brunton, D.H.; Dennis, T. Dolphin-watching tour boats change bottlenose dolphin (*Tursiops truncatus*) behaviour. *Biol. Conserv.* **2004**, *117*, 299–307. [CrossRef]

13. Dwyer, S.; Kozmian-Ledward, L.; Stockin, K. Short-term survival of severe propeller strike injuries and observations on wound progression in a bottlenose dolphin. *N. Z. J. Mar. Freshw. Res.* **2014**, *48*, 294–302. [CrossRef]

14. Klemas, V.V. Coastal and Environmental Remote Sensing from Unmanned Aerial Vehicles: An Overview. *J. Coast. Res.* **2015**, *31*, 1260–1267. [CrossRef]

15. Wich, S.; Dellatore, D.; Houghton, M.; Ardi, R.; Koh, L.P. A preliminary assessment of using conservation drones for Sumatran orang-utan (*Pongo abelii*) distribution and density. *J. Unmanned Veh. Syst.* **2016**, *4*, 45–52. [CrossRef]

16. Sweeney, K.L.; Helker, V.T.; Perryman, W.L.; LeRoi, D.J.; Fritz, L.W.; Gelatt, T.S.; Angliss, R.P. Flying beneath the clouds at the edge of the world: Using a hexacopter to supplement abundance surveys of Steller sea lions (*Eumetopias jubatus*) in Alaska. *J. Unmanned Veh. Syst.* **2015**, *4*, 1–12. [CrossRef]

17. Jones, G.P.; Pearlstine, L.G.; Percival, H.F. An Assessment of Small Unmanned Aerial Vehicles for Wildlife Research. *Wildl. Soc. Bull.* **2006**, *34*, 750–758. [CrossRef]

18. Clarke, P.J.; Cubaynes, H.C.; Stockin, K.A.; Olavarria, C.; de Vos, A.; Fretwell, P.T.; Jackson, J.A. Cetacean strandings from space: Challenges and opportunities of very high resolution satellites for the remote monitoring of cetacean mass strandings. *Front. Mar. Sci.* **2021**, *8*, 650735. [CrossRef]

19. Goebel, M.E.; Perryman, W.L.; Hinke, J.T.; Krause, D.J.; Hann, N.A.; Gardner, S.; LeRoi, D.J. A small unmanned aerial system for estimating abundance and size of Antarctic predators. *Polar Biol.* **2015**, *38*, 619–630. [CrossRef]

20. Koski, W.R.; Gamage, G.; Davis, A.R.; Mathews, T.; LeBlanc, B.; Ferguson, S.H. Evaluation of UAS for photographic re-identification of bowhead whales, *Balaena mysticetus*. *J. Unmanned Veh. Syst.* **2015**, *3*, 22–29. [CrossRef]

21. Watts, A.C.; Ambrosia, V.G.; Hinkley, E.A. Unmanned Aircraft Systems in Remote Sensing and Scientific Research: Classification and Considerations of Use. *Remote Sens.* **2012**, *4*, 1671–1692. [CrossRef]

22. Landeo-Yauri, S.S.; Ramos, E.A.; Castelblanco-Martínez, D.N.; Niño-Torres, C.A.; Searle, L. Using small drones to photo-identify Antillean manatees: A novel method for monitoring an endangered marine mammal in the Caribbean Sea. *Endanger. Species Res.* **2020**, *41*, 79–90. [CrossRef]

23. Durban, J.W.; Fearnbach, H.; Barrett-Lennard, L.G.; Perryman, W.L.; LeRoi, D.J. Photogrammetry of killer whales using a small hexacopter launched at sea. *J. Unmanned Veh. Syst.* **2015**, *3*, 131–135. [CrossRef]

24. Martins, M.C.I.; Sette, L.; Josephson, E.; Bogomolni, A.; Rose, K.; Sharp, S.M.; Niemeyer, M.; Moore, M. Unoccupied aerial system assessment of entanglement in Northwest Atlantic gray seals (*Halichoerus grypus*). *Mar. Mammal Sci.* **2019**, *35*, 1613–1624. [CrossRef]

25. Ramp, C.; Gaspard, D.; Gavrilchuk, K.; Unger, M.; Schleimer, A.; Delarue, J.; Landry, S.; Sears, R. Up in the air: Drone images reveal underestimation of entanglement rates in large rorqual whales. *Endanger. Species Res.* **2021**, *44*, 33–44. [CrossRef]

26. Acevedo-Whitehouse, K.; Rocha-Gosselin, A.; Gendron, D. A novel non-invasive tool for disease surveillance of free-ranging whales and its relevance to conservation programs. *Anim. Conserv.* **2010**, *13*, 217–225. [CrossRef]

27. Domínguez-Sánchez, C.A.; Acevedo-Whitehouse, K.A.; Gendron, D. Effect of drone-based blow sampling on blue whale (*Balaenoptera musculus*) behavior. *Mar. Mammal Sci.* **2018**, *34*, 841–850. [CrossRef]

28. Centelleghe, C.; Carraro, L.; Gonzalvo, J.; Rosso, M.; Esposti, E.; Gili, C.; Bonato, M.; Pedrotti, D.; Cardazzo, B.; Povinelli, M.; et al. The use of Unmanned Aerial Vehicles (UAVs) to sample the blow microbiome of small cetaceans. *PLoS ONE* **2020**, *15*, e0235537. [CrossRef]

29. Raudino, H.C.; Tyne, J.A.; Smith, A.; Ottewell, K.; McArthur, S.; Kopps, A.M.; Chabanne, D.; Harcourt, R.G.; Pirotta, V.; Waples, K. Challenges of collecting blow from small cetaceans. *Ecosphere* **2019**, *10*, e02901. [CrossRef]

30. Horton, T.W.; Hauser, N.; Cassel, S.; Klaus, K.F.; Fettermann, T.; Key, N. Doctor Drone: Non-Invasive Measurement of Humpback Whale Vital Signs Using Unoccupied Aerial System Infrared Thermography. *Front. Mar. Sci.* **2019**, *6*, 466. [CrossRef]

31. Dawson, S.M.; Bowman, M.H.; Leunissen, E.; Sirguey, P. Inexpensive Aerial Photogrammetry for Studies of Whales and Large Marine Animals. *Front. Mar. Sci.* **2017**, *4*, 366. [CrossRef]

32. Christiansen, F.; Dawson, S.M.; Durban, J.W.; Fearnbach, H.; Miller, C.A.; Bejder, L.; Uhart, M.; Sironi, M.; Corkeron, P.; Rayment, W.; et al. Population comparison of right whale body condition reveals poor state of the North Atlantic right whale. *Mar. Ecol. Prog. Ser.* **2020**, *640*, 1–16. [CrossRef]

33. Durban, J.W.; Moore, M.J.; Chiang, G.; Hickmott, L.S.; Bocconcelli, A.; Howes, G.; Bahamonde, P.A.; Perryman, W.L.; LeRoi, D.J. Photogrammetry of blue whales with an unmanned hexacopter. *Mar. Mammal Sci.* **2016**, *32*, 1510–1515. [CrossRef]

34. Ramos, E.A.; Maloney, B.; Magnasco, M.O.; Reiss, D. Bottlenose Dolphins and Antillean Manatees Respond to Small Multi-Rotor Unmanned Aerial Systems. *Front. Mar. Sci.* **2018**, *5*, 316. [CrossRef]

35. Oliveira-Da-Costa, M.; Marmontel, M.; Da-Rosa, D.S.X.; Coelho, A.; Wich, S.; Mosquera-Guerra, F.; Trujillo, F. Effectiveness of unmanned aerial vehicles to detect Amazon dolphins. *Oryx* **2019**, *54*, 696–698. [CrossRef]

36. Orbach, D.N.; Eaton, J.; Fiori, L.; Piwetz, S.; Weir, J.S.; Würsig, M.; Würsig, B. Mating patterns of dusky dolphins (*Lagenorhynchus obscurus*) explored using an unmanned aerial vehicle. *Mar. Mammal Sci.* **2020**, *36*, 1097–1110. [CrossRef]

37. Torres, L.G.; Nieukirk, S.L.; Lemos, L.; Chandler, T.E. Drone Up! Quantifying Whale Behavior from a New Perspective Improves Observational Capacity. *Front. Mar. Sci.* **2018**, *5*, 319. [CrossRef]

38. Frouin-Mouy, H.; Tenorio-Hallé, L.; Thode, A.; Swartz, S.; Urbán, J. Using two drones to simultaneously monitor visual and acoustic behaviour of gray whales (*Eschrichtius robustus*) in Baja California, Mexico. *J. Exp. Mar. Biol. Ecol.* **2020**, *525*, 151321. [CrossRef]

39. Torres, L.G.; Barlow, D.R.; Chandler, T.E.; Burnett, J.D. Insight into the kinematics of blue whale surface foraging through drone observations and prey data. *PeerJ* **2020**, *8*, e8906. [CrossRef]

40. Baker, C.S.; Bore, L.; Childerhouse, S.; Constantine, R.; van Helden, A.; Lundquist, D.; Rayment, W.; Rolfe, J.R. Conservation status of New Zealand marine invertebrates, 2019. *N. Z. J. Mar. Freshw. Res.* **2010**, *44*, 129–148. [CrossRef]

41. Tezanos-Pinto, G.; Constantine, R.; Brooks, L.; Jackson, J.; Mourão, F.; Wells, S.; Scott Baker, C. Decline in local abundance of bottlenose dolphins (*Tursiops truncatus*) in the Bay of Islands, New Zealand. *Mar. Mammal Sci.* **2013**, *29*, 390–410. [CrossRef]

42. Tezanos-Pinto, G.; Baker, C.S.; Russell, K.; Martien, K.; Baird, R.W.; Hutt, A.; Stone, G.; Mignucci-Giannoni, A.A.; Caballero, S.; Endo, T.; et al. A Worldwide Perspective on the Population Structure and Genetic Diversity of Bottlenose Dolphins (*Tursiops truncatus*) in New Zealand. *J. Hered.* **2009**, *100*, 11–24. [CrossRef]

43. Constantine, R. *The Behavioural Ecology of the Bottlenose Dolphins (Tursiops truncatus) of Northeastern New Zealand: A Population Exposed to Tourism*; The University of Auckland: Auckland, New Zealand, 2002.

44. Dwyer, S.L.; Tezanos-Pinto, G.; Visser, I.N.; Pawley, M.D.M.; Meissner, A.M.; Berghan, J.; Stockin, K.A. Overlooking a potential hotspot at Great Barrier Island for the nationally endangered bottlenose dolphin of New Zealand. *Endanger. Species Res.* **2014**, *25*, 97–114. [CrossRef]

45. Whitehead, H.; Reeves, R.R.; Tyack, P.L. Science and the Conservation, Protection, and Management of Wild Cetaceans. In *Cetacean Societies: Field Studies of Dolphins and Whales*; Mann, J., Connor, R.C., Tyack, P.L., Whitehead, H., Eds.; The University of Chicago Press: Chicago, IL, USA, 2000; pp. 308–332.

46. Berger-Tal, O.; Polak, T.; Oron, A.; Lubin, Y.; Kotler, B.P.; Saltz, D. Integrating animal behavior and conservation biology: A conceptual framework. *Behav. Ecol.* **2011**, *22*, 236–239. [CrossRef]

47. Barros, N.B.; Wells, R.S. Prey and feeding patterns of resident Bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *J. Mammal.* **1998**, *79*, 1045–1059. [CrossRef]

48. Rogan, E.; Ingram, S.; Holmes, B.; O'Flanagan, C.; Institute, M. *A Survey of Bottlenose Dolphins (Tursiops truncatus) in the Shannon Estuary*; National University of Ireland: Cork, Ireland, 2000.

49. Whitehead, H. Analysis of animal movement using opportunistic individual identification: Application to sperm whales. *Ecology* **2001**, *82*, 1417–1732. [CrossRef]

50. Fiori, L.; Doshi, A.; Martinez, E.; Orams, M.B.; Bollard-Breen, B. The Use of Unmanned Aerial Systems in Marine Mammal Research. *Remote Sens.* **2017**, *9*, 543. [CrossRef]

51. Shane, S.H. Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida. In *The Bottlenose Dolphin*; Leatherwood, S., Reeves, R.R., Eds.; Academic Press, Inc.: New York, NY, USA, 1990; pp. 245–265.

52. Fettermann, T.; Fiori, L.; Bader, M.; Doshi, A.; Breen, D.; Stockin, K.A.; Bollard, B. Behaviour reactions of bottlenose dolphins (*Tursiops truncatus*) to multirotor Unmanned Aerial Vehicles (UAVs). *Sci. Rep.* **2019**, *9*, 8558. [CrossRef]

53. Altmann, J. Observational study of behavior: Sampling methods. *Behaviour* **1974**, *49*, 227–267. [CrossRef]

54. Lusseau, D. Why do dolphins jump? Interpreting the behavioural repertoire of bottlenose dolphins (*Tursiops* sp.) in Doubtful Sound, New Zealand. *Behav. Process.* **2006**, *73*, 257–265. [CrossRef]

55. Shane, S.H.; Wells, R.S.; Wursig, B. Ecology, behavior and social organization of the bottlenose dolphin: A review. *Mar. Mammal Sci.* **1986**, *2*, 34–63. [CrossRef]

56. Kelaher, B.P.; Peddemors, V.M.; Hoade, B.; Colefax, A.P.; Butcher, P.A. Comparison of sampling precision for nearshore marine wildlife using unmanned and manned aerial surveys. *J. Unmanned Veh. Syst.* **2019**, *8*, 30–43. [CrossRef]

57. Sorrell, K.; Clarke, R.H.; Holmberg, R.; McIntosh, R.R. Remotely piloted aircraft improve precision of capture–mark–resight population estimates of Australian fur seals. *Ecosphere* **2019**, *10*, e02812. [CrossRef]

58. Hodgson, J.C.; Baylis, S.M.; Mott, R.; Herrod, A.; Clarke, R.H. Precision wildlife monitoring using unmanned aerial vehicles. *Sci. Rep.* **2016**, *6*, 22574. [CrossRef]

59. Wilson, B.; Hammond, P.S.; Thompson, P.M. Estimating size and assessing trends in a coastal bottlenose dolphin population (*Tursiops truncatus*). *Ecol. Appl.* **1999**, *9*, 288–300. [CrossRef]

60. Hupman, K.; Stockin, K.A.; Pollock, K.; Pawley, M.D.M.; Dwyer, S.L.; Lea, C.; Tezanos-Pinto, G. Challenges of implementing Mark-recapture studies on poorly marked gregarious delphinids. *PLoS ONE* **2018**, *13*, e0198167, Correction in *PLoS ONE* **2018**, *13*, e0203356. [CrossRef]

61. Hooker, S.K.; Gerber, L.R. Marine Reserves as a Tool for Ecosystem-Based Management: The Potential Importance of Megafauna. *Bioscience* **2004**, *54*, 27–39. [CrossRef]

62. Mann, J.; Connor, R.C.; Tyack, P.; Whitehead, H. Field studies of dolphins and whales. In *Cetacean Societies*; The University of Chicago Press: Chicago, IL, USA, 2000; p. 433.

63. Peters, C.H.; Stockin, K.A. *Response of Bottlenose Dolphin (Tursiops truncatus) to Vessel Activity in Northland, New Zealand*; Massey University: Auckland, New Zealand, 2016.

64. Hartel, E.F.; Constantine, R.; Torres, L.G. Changes in habitat use patterns by bottlenose dolphins over a 10-year period render static management boundaries ineffective. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **2014**, *25*, 701–711. [CrossRef]

65. Tayler, C.K.; Saayman, G.S. The social organisation and behaviour of dolphins (*Tursiops aduncus*) and baboons (*Papio ursinus*): Some comparisons and assessments. *Ann. Cape Prov. Museums* **1972**, *9*, 11–49.

66. Leatherwood, S.; Evans, W.E. Some recent uses and potentials of radiotelemetry in field studies of cetaceans. In *Behaviour of Marine Mammals: Current Perspectives in Research*; Olla, H.E.W., Olla, B.L., Eds.; Plenum Press: New York, NY, USA, 1979; Volume 3.

67. Bearzi, G.; Politi, E. Diurnal behavior of free-ranging bottlenose dolphins in the Kvarneric (Northern Adriatic Sea). *Mar. Mammal Sci.* **1999**, *15*, 1065–1097. [CrossRef]

68. Hodgson, A.; Peel, D.; Kelly, N. Unmanned aerial vehicles for surveying marine fauna: Assessing detection probability. *Ecol. Appl.* **2017**, *27*, 1253–1267. [CrossRef]

69. Constantine, R. Increased avoidance of swimmers by wild Bottlenose dolphins (*Tursiops truncatus*) due to long-term exposure to swim-with-dolphin tourism. *Mar. Mammal Sci.* **2001**, *17*, 689–702. [CrossRef]

70. Nowacek, D.P.; Christiansen, F.; Bejder, L.; Goldbogen, J.A.; Friedlaender, A.S. Studying cetacean behaviour: New technological approaches and conservation applications. *Anim. Behav.* **2016**, *120*, 235–244. [CrossRef]

71. Giles, A.B.; Butcher, P.A.; Colefax, A.P.; Pagendam, D.E.; Mayjor, M.; Kelaher, B.P. Responses of bottlenose dolphins (*Tursiops* spp.) to small drones. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **2020**, *31*, 677–684. [CrossRef]

72. Hartman, K.; van der Harst, P.; Vilela, R. Continuous Focal Group Follows Operated by a Drone Enable Analysis of the Relation Between Sociality and Position in a Group of Male Risso's Dolphins (*Grampus griseus*). *Front. Mar. Sci.* **2020**, *7*, 283. [CrossRef]

73. Nielsen, M.L.K.; Sprogis, K.R.; Bejder, L.; Madsen, P.T.; Christiansen, F. Behavioural development in southern right whale calves. *Mar. Ecol. Prog. Ser.* **2019**, *629*, 219–234. [CrossRef]

74. Booth, C.G.; Sinclair, R.R.; Harwood, J. Methods for Monitoring for the Population Consequences of Disturbance in Marine Mammals: A Review. *Front. Mar. Sci.* **2020**, *7*, 115. [CrossRef]

75. Erbe, C. Effects of underwater noise on marine mammals. *Adv. Exp. Med. Biol.* **2012**, *730*, 17–22. [CrossRef]

76. Pirotta, E.; Merchant, N.D.; Thompson, P.M.; Barton, T.R.; Lusseau, D. Quantifying the effect of boat disturbance on bottlenose dolphin foraging activity. *Biol. Conserv.* **2015**, *181*, 82–89. [CrossRef]