Assessing variation in assemblages of large marine fauna off ocean beaches using drones

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Abstract. The turbulent waters off ocean beaches provide habitat for large marine fauna, including dolphins, sharks, rays, turtles and game fish. Although, historically, these assemblages have proven difficult to quantify, we used a new drone-based approach to assess spatial and temporal variation in assemblages of large marine fauna off four exposed beaches in New South Wales, Australia. In total, 4388 individual large marine animals were identified from 216 drone flights. The most common taxa, bottlenose dolphins (\textit{Tursiops} spp.) and Australian cow-nose rays (\textit{Rhinoptera neglecta}), occurred in 25.5 and 19.9\% of flights respectively. White (\textit{Carcharodon carcharias}), bull (\textit{Carcharhinus leucas}) and other whaler (\textit{Carcharhinus} spp.) sharks were observed in <1\% of flights. There was significant variation in the structure of assemblages of large fauna among beaches, with those adjacent to riverine estuaries having greater richness and abundance of wildlife. Overall, drone surveys were successful in documenting the spatio-temporal dynamics of an impressive suite of large marine fauna. We contend that emerging drone technology can make a valuable contribution to the ecological information required to ensure the long-term sustainability of sandy-beach ecosystems and associated marine wildlife.

Additional keywords: \textit{Carcharodon}, dolphin, RPAS, ray, sandy-beach, shark, \textit{Tursiops}, turtle, UAV, UAS.

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Introduction

Sandy beaches account for 31\% of ice-free shorelines globally (Luijendijk \textit{et al.} 2018) and provide important feeding, nursery, nesting and breeding sites for marine and terrestrial wildlife (Schlacher \textit{et al.} 2013; McLachlan and Defeo 2017; Baring \textit{et al.} 2018). These valuable ecosystems (Barbier \textit{et al.} 2011) also support a range of commercial, recreational and indigenous activities, including, but not limited to, fishing, education, off-road driving, sunbathing, swimming, boating and walking, as well as the extraction of sand and minerals (Schlacher \textit{et al.} 2007; Nel \textit{et al.} 2014; Jones \textit{et al.} 2017). Beach-based activities, in combination with global climate change and coastal development, make sandy beaches and their dependent ecosystems among the most threatened on the planet (Schlacher \textit{et al.} 2006; Jones \textit{et al.} 2007; Defeo \textit{et al.} 2009). Although most focus has been on individual or cumulative human impacts on fauna inhabiting the more accessible intertidal and supratidal beach areas (Nel \textit{et al.} 2014; McLachlan and Defeo 2017), impacts such as overfishing, shark nets and habitat degradation also contribute to population declines of the large marine fauna (e.g. sharks and dolphins) using the shallow waters off sandy beaches (Defeo \textit{et al.} 2009; Olds \textit{et al.} 2018).

As impacts to sandy-beach ecosystems intensify (e.g. coastal development, declining water quality or increased fishing pressure), baseline knowledge of the large marine fauna that exert top-down control on these systems and the processes that govern their populations is needed (Britten \textit{et al.} 2014; Olds \textit{et al.} 2018). The populations of many large marine fauna that inhabit the waters off ocean beaches are in decline, with an increasing number being listed as threatened (e.g. white sharks, \textit{Carcharodon carcharias}; green turtles, \textit{Chelonia mydas}; and Australian sea lions, \textit{Neophoca cinerea}). The need for greater knowledge about large marine fauna off ocean beaches has also been escalated because numerous authorities consider it necessary to mitigate the risk of shark attacks (Cardno 2015). Despite this, very limited data are presently available on the identity, distribution and abundance of assemblages of large marine fauna found off ocean beaches, in part because of the methodological difficulties in sampling highly mobile and wide-ranging animals in a wave-swept environment (Olds \textit{et al.} 2018).

The quantification of spatio-temporal variation of assemblages of large marine fauna off ocean beaches has been restricted to targeted, scientific sampling techniques or incidental fishing practices that work well in swell-affected waters.
Commonly used methods for quantifying small and medium-sized fish off ocean beaches, such as seine nets and beam trawls (Olds et al. 2018), tend to be neither effective nor appropriate for quantifying large marine fauna, which are not common, range over large distances, and often have threatened or protected status. The recent use of baited remote underwater video systems (BRUVS) off ocean beaches has been a useful step forward (e.g. Vargas-Fonseca et al. 2016; Harasti et al. 2017), because BRUVS are a non-destructive method that effectively samples bony fish and ray species (e.g. Gladstone et al. 2012; Kelaher et al. 2014, 2015). However, the faunal assemblages sampled by BRUVS are generally too localised to capture variation in large predator abundances and are not designed to sample species that are less attracted to bait (e.g. sea turtles and manta rays). Shark nets and drumlines, installed off ocean beaches to decrease local shark populations (Dudley et al. 1998; Reid et al. 2011) or reduce the chances of a shark–human interaction (NSW Department of Primary Industries 2015), provide data on the relative abundance of some large marine fauna, primarily sharks and rays, but are likely to decrease in use over time because of increased community concerns over by-catch. Subtidal acoustic-telemetry stations (e.g. VR4G) allow for tracking of large marine fauna in real time (Bradford et al. 2011; Taylor et al. 2017), but the questions that can be answered using this technology relate to data collected from a small number of tagged individuals (i.e. movement, location and proximity to other tagged individuals, Bradford et al. 2011; Taylor et al. 2017).

Many of the above challenges for sampling large marine fauna off ocean beaches can be solved by land-, vessel-, or aerial-based surveillance (e.g. Hawkins and Gartside 2008; Robbins et al. 2014; Engelbrecht et al. 2017). Land- and vessel-based surveys can effectively sample the abundance, diving characteristics and surface behaviours of air-breathing marine animals, e.g. bottlenose dolphins (Hawkins and Gartside 2008). However, these methods are less useful for making accurate observations on large marine fauna below the water surface over large distances. These limitations are greatly reduced in aerial survey programs, although there are still methodological challenges (Colefax et al. 2018). For example, aerial surveys over coastal waters may be compromised by poor water clarity, breaking waves and sun glare (Colefax et al. 2018; Joyce et al. 2018), and are less effective for species residing deeper in the water column than for surface-dwelling species (Pollock et al. 2006; Fuentes et al. 2015). Many of these issues may be avoided by sampling on calm days and selecting viewing angles that reduce sun reflection (Alves et al. 2013; Westgate et al. 2014; Kiszka et al. 2016), particularly in clear, shallow waters (<5 m) off ocean beaches, where animals can generally be seen from the ocean surface to the seafloor.

Although historically undertaken by manned aircraft (e.g. Pollock et al. 2006; Rowat et al. 2009; Robbins et al. 2014; Fuentes et al. 2015), aerial surveys of marine habitats are increasingly undertaken by unmanned aerial systems (hearafter, drones, see Chapman 2014; Chabot 2018). The transition from manned aircraft to drones has been driven by significant cost-efficiencies associated with recent technological developments in commercially available drones, such as improved batteries, component miniaturisation and lighter cameras (Goebel et al. 2015; Kiszka et al. 2016; Fiori et al. 2017). Drones have been recently used to sample large marine wildlife, including whales (e.g. Hodgson et al. 2017; Pirotta et al. 2017), dolphins (e.g. Ramos et al. 2018), sharks and rays (e.g. Kiszka et al. 2016), sirensians (e.g. Hodgson et al. 2013; Ramos et al. 2018), birds (e.g. Ratcliffe et al. 2015; Hodgson et al. 2018), pinnipeds (e.g. Sweeney et al. 2016; McIntosh et al. 2018) and sea turtles (e.g. Rees et al. 2018). Compared with marine faunal surveys using manned planes and helicopters, surveys using drones improve workplace safety (e.g. reduced fatality risk, Jones et al. 2006; Watts et al. 2010) and reduce visual and auditory impact for both wildlife and people (Eirbe et al. 2017; McIntosh et al. 2018).

Here, we test the utility of aerial surveys using drones for documenting spatial and temporal variation in assemblages of large marine fauna off ocean beaches (e.g. dolphins, rays, sharks, sea turtles and game fish). Specifically, 216 aerial surveys using drones were undertaken to test whether the composition, richness and abundance of assemblages of large marine fauna varies (1) among ocean beaches, (2) among sampling periods and (3) with respect to sea-surface temperature, water clarity and ocean conditions.

Materials and methods

Beach locations and environmental conditions

To test hypotheses about the spatial and temporal variation of large marine fauna off exposed ocean beaches, four drones were used to simultaneously survey four beaches on a 55-km stretch of coastline in northern New South Wales, Australia (Fig. 1). Each of the four surveyed beaches, Byron Bay (28.642287°S, 153.620732°E), Lennox Head (28.784211°S, 153.593759°E), Ballina (28.868211°S, 153.592624°E) and Evans Head (29.11486°S, 153.434133°E), are places where people have been bitten by sharks in the past 5 years. Drone surveys were conducted in the following three distinct sampling periods: (1) 6 October–18 December 2016; (2) 30 June–17 July 2017; and (3) 23 September–8 October 2017. During the first sample period, drone surveys occurred every few days at Lennox Head, Ballina and Evans Head (94 surveys). During the second (68 surveys) and third (54 surveys) periods, surveys were undertaken on most days and at all beaches.

Drone surveys were undertaken in waters less than 6 m deep and across a range of wind speeds (0–37 km h⁻¹), wind directions (offshore, onshore and cross shore), cloud covers (ranging from 0 to 8 oktas) and air temperatures (ranging from 11°C to 39°C), which were measured at the start and end of each flight. During each drone survey, the sea state (ranging from 0 to 8 oktas) and air temperatures (ranging from 11°C to 39°C), were measured at the start and end of each flight. During each drone survey, the sea state (ranging from 0 to 5 on the Beaufort scale) and clarity of the water (scored from 1–5, where 1 was very poor and 5 was extremely clear) was estimated, with scores >2 indicating that animals could be observed from the seafloor to the surface. For each flight, the local daytime sea-surface temperature was determined using data sourced from Australia’s Integrated Marine Observing System (see https://portal.aodn.org.au/search, accessed 17 December 2018).

Marine wildlife-survey methods

On each day of sampling, a base station was established at each beach to ensure that its drone was within direct line-of-sight...
throughout the entire flight. All flights commenced at ~0900 hours in the morning. For each flight, a 2-km-long shore transect was flown at 60-m altitude and at a speed of 8 m s\(^{-1}\). The drone was flown manually to maintain the edge of the video footage on the back of the surf break. This meant that the location of each transect varied from day to day in response to tide and swell conditions. Given the drone’s fixed lens camera, the field of view of the video covered an area of ~110 m directly seaward of the surf break. The aerial surveys focused on this area, as it was not possible to reliably observe marine fauna under the white water of broken waves. To improve taxonomic identification of marine fauna, the drone was often lowered down to 15–20 m altitude for a short period when questionable fauna were observed by the pilot.

For each replicate flight, we used a Phantom 4 quadcopter (DJI, Shenzhen, Guangdong, PR China) equipped with a ND4 circular polarising filter (Polar Pro, Costa Mesa, CA, USA). Each drone was controlled by a multifunctional remote, utilising 2.4 GHz wireless communication, and drone pilots viewed a live video feed from the drone’s camera on an iPad (Apple Inc., Cupertino, CA, USA) that was shaded from sun glare. The camera of each drone was oriented straight down (i.e. nadir) and the entirety of each flight was video-recorded in 4K resolution (3840 × 2160 pixels) at 25 frames per second. The video files were later carefully reviewed in the laboratory on a 58.5-cm (diagonal), 1920 × 1080-pixel resolution LED display. Post hoc analysis of drone video footage provides more accurate estimates of marine wildlife abundances than do observations in real time. This method also has the added advantage of providing a permanent record of observations for verification purposes or for more in-depth analysis in the future (e.g. using flight and image-capture information to estimate the body size of wildlife, Krause et al. 2017).

During the review of video footage from each flight, observations were recorded for all large marine animals that were at or below the surface (Fig. 1). This included dolphins (e.g. bottlenose dolphins, *Tursiops* spp.), rays (e.g. spotted eagle rays, *Aetobatus narinari*; Australian cow nose rays, *Rhinoptera neglecta*), sharks (e.g. white sharks, *Carcharodon carcharias*; bull sharks, *Carcharhinus leucas*), sea turtles (e.g. green turtles, *Chelonia mydas*), game fish (e.g. yellowtail kingfish, *Seriola lalandi*; silver trevally, *Pseudocaranx georgianus*; tailor, *Pomatomus saltatrix*) and schools of bait fish (Table 1). Marine wildlife were identified to the lowest possible taxonomic resolution. In some cases, this was species (e.g. white sharks, *C. carcharias*), whereas, in others, it was genus (e.g. whaler sharks, *Carcharhinus* spp.). Sometimes it was possible to identify an animal only to a broad taxonomic group (e.g. shark), particularly when the
animals remained in deep water or the ocean was turbid. For bottlenose dolphins (*Tursiops* spp.), it was not possible to reliably distinguish the ‘inshore’ (*T. aduncus*) from the ‘off-shore’ species (*T. truncatus*) by using drone footage. All large marine fauna were individually counted. However, this was not possible for bait fish, which were counted per individual school.

**Analysis of data**

Permutational multivariate analysis of variance (PERMANOVA, Anderson et al. 2008) was used to test hypotheses about spatial and temporal variations in the composition of faunal assemblages off ocean beaches. The analysis included the following three factors: beach, sampling period and day nested within period. Because the same beach was sampled on multiple days within a sampling period, analyses were conservatively treated as a repeated-measure design, following the procedures of Anderson et al. (2008). There was no evidence that flights on consecutive days were more similar to those flown on days further apart, which would be expected for highly mobile, large marine fauna that could move in and out of the transects within minutes. Multivariate analysis was run on a dataset of distinct taxa (Table 1) that excluded unusual observations that occurred only once in the monitoring program (e.g. a single pod of humpback whales, a free-swimming moray eel and a large jellyfish). Prior to analysis, data were transformed with a presence or absence function, which (1) reduced the over-dispersion associated with species in large schools (e.g. schools of Australian cow nose rays could exceed 300 individuals), (2) allowed schools of bait fish to be included in analyses without bias and (3) down-weighted the contribution of the most abundant taxa in multivariate analyses to provide a more balanced view of taxonomic composition (Clarke 1993). Nonmetric multidimensional scaling (nMDS; Field et al. 1982) was used to generate two-dimensional ordination plots. The SIMPER routine (Clarke and Gorley 2006) determined the relative contribution of individual taxa to overall dissimilarity in faunal assemblages among beaches and periods. All PERMANOVA, nMDS and SIMPER analyses were based on the Bray–Curtis similarity coefficient (Bray and Curtis 1957). These analyses were conducted using PRIMER (ver. 6.0, K. R. Clarke and R. N. Gorley, PRIMER-E, Plymouth, UK) and PERMANOVA (M. J. Anderson, R. N. Gorley, and K. R. Clarke, PRIMER-E) software.

Generalised linear models (GLM) were used to determine the relationships between univariate response variables (faunal richness (taxa per transect), faunal abundance (individuals per transect), dolphins, rays, sharks and turtles) and key predictor variables (beach, sampling period, water clarity, water temperature and sea state). It was decided *a priori* that these predictor variables represented the most relevant factors for (1) explaining variability in marine faunal abundance and (2) accounting for sampling artefacts associated with ocean clarity and condition (wind and swell), while keeping the model relatively simple to account for limited observations, given the many flights where no marine fauna were observed. GLMs were run using the lme4 and MASS packages in R (ver. 3.5.1, R Foundation for Statistical Computing, Vienna, Austria). For these analyses, predictor variables were not co-linear (Pearson *r*’s all between –0.3 and 0.2). As the data were count-based, models were initially run using a Poisson distribution, but these GLMs were consistently over-dispersed. To address this, the GLMs were then run using a negative binomial distribution (Zuur and Ieno 2016), which satisfied assumptions, appropriately converged and validated. The one exception was the GLM for the abundance of rays, where the model needed to be further simplified to converge by dropping the water temperature and sea-state terms. These two terms were dropped because they were not significant in any other model (Table 2).

**Results**

In total, 216 individual drone flights were completed with a mean (±s.e.) flight time of 14.4 ± 1.7 min. During these flights, 4388 individual large marine animals and 16 schools of bait fish were observed. Animals were observed only in 62.0% of flights,
with no marine fauna detected in 82 flights. Bottlenose dolphins (Tursiops spp.) were the most frequently observed marine animal, occurring in 25.5% of flights (Table 1), followed by Australian cow nose rays (R. neglecta), which occurred in 19.9% of the flights and represented 3643 of the 4388 large individual animals observed. Australian cow nose rays were mostly observed in fercas of over 100 individuals. Spotted (A. narinari) and southern (Myliobatis spp.) eagle rays were the next most common rays and occurred either as solitary individuals or in small groups of less than five rays (Table 1, Fig. 1). Green turtles (C. mydas), schools of bait fish and game fish were observed in 7.4, 6.9 and 4.2% of the 216 flights respectively. The schools of bait fish ranged from a few square metres to hundreds of square metres in size and were often associated with predatory species (e.g. bottlenose dolphins, Fig. 1). Sharks were rare off ocean beaches, with white (C. carcharias), bull (C. leucas) and whaler (Carcharhinus spp.) sharks each occurring in <1% of flights (Table 1). These sharks were almost always observed as solitary individuals.

The assemblage composition of large marine wildlife varied significantly among beaches (PERMANOVA, $P < 0.001$, Fig. 2), but did not interact significantly between beaches and sample periods (PERMANOVA, $P = 0.12$). The marine wildlife composition did not differ significantly between Byron Bay and Lennox Head (PERMANOVA, $P = 0.53$, Fig. 2), but the beaches at Ballina and Evans Head had their own unique assemblages ($P < 0.05$ for all PERMANOVA pairwise tests, Fig. 2). When averaged over all six pairwise comparisons among beaches, the occurrence of bottlenose dolphins and Australian cow nose rays contributed 32.5 and 21.4% of the dissimilarity respectively. Green turtles, bait fish, spotted eagle rays and game fish all had contributions that exceeded 5% of the overall dissimilarity among beaches (Table 1). Sharks contributed <1.5% of the average dissimilarity among beaches (Table 1).

Despite Periods 1 and 3 being in the austral spring and Period 2 being in the austral winter, the composition of marine faunal assemblages did not vary significantly among sampling periods (PERMANOVA, $P = 0.23$, Fig. 2). Notably, mean ocean temperature and water clarity also did not vary much among sampling periods, although seas were rougher in

### Table 2. Results of generalised linear modelling for the faunal richness and abundance per transect of key groups of marine wildlife and categorical (beach and sampling period) and continuous (water clarity, sea surface temperature and Beaufort sea state) predictor variables. $–$ indicates that less important terms were dropped from the model to facilitate convergence. Significant effects are in bold.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Beach</th>
<th>Period</th>
<th>Clarity</th>
<th>Temperature</th>
<th>Sea-state</th>
</tr>
</thead>
<tbody>
<tr>
<td>Faunal richness</td>
<td>$&lt;0.001$</td>
<td>0.07</td>
<td>$&lt;0.001$</td>
<td>0.21</td>
<td>0.74</td>
</tr>
<tr>
<td>Faunal abundance</td>
<td>$&lt;0.001$</td>
<td>$&lt;0.001$</td>
<td>$&lt;0.001$</td>
<td>0.89</td>
<td>0.30</td>
</tr>
<tr>
<td>Dolphins</td>
<td>$&lt;0.001$</td>
<td>0.66</td>
<td>$&lt;0.001$</td>
<td>0.52</td>
<td>0.74</td>
</tr>
<tr>
<td>Rays</td>
<td>$&lt;0.001$</td>
<td>$&lt;0.001$</td>
<td>$&lt;0.001$</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Sharks</td>
<td>$&lt;0.05$</td>
<td>0.15</td>
<td>$&lt;0.05$</td>
<td>0.55</td>
<td>0.26</td>
</tr>
<tr>
<td>Turtles</td>
<td>$&lt;0.01$</td>
<td>0.95</td>
<td>0.37</td>
<td>0.62</td>
<td>0.98</td>
</tr>
</tbody>
</table>

Sampling period 3 (Table S1, available as Supplementary material to this paper). Similar to the average dissimilarity of marine faunal composition among beaches, the occurrence of bottlenose dolphins (24.6%) and Australian cow nose rays (22.9%) had the largest contributions to dissimilarity among sampling periods. Green turtles, bait fish, spotted eagle rays and game fish all had contributions that exceeded 5% of the overall dissimilarity among periods (Table 1). The contribution of sharks to the overall assemblage dissimilarity among periods was <2%.

Taxonomic richness, overall faunal abundance and the abundances of bottlenose dolphins, rays, sharks and turtles all varied significantly among beaches (Table 2, Fig. 2). The most rich and abundant marine faunal assemblages were at Evans Head, which also had the largest numbers of rays, sharks and turtles (Fig. 3). Although taxonomic richness did not vary among the other three beaches, Ballina had the next most abundant fauna, the highest number of dolphins and the second-highest number of rays of any sites, with Byron Bay and Lennox Head having the lowest total fauna and numbers of rays (Fig. 3). The lowest mean numbers of dolphins were observed at Evans Head (Fig. 3). Relative to the beach location, the influence of sampling period was small, with only rays and overall faunal abundance showing significant variation among periods (Fig. 3). For overall faunal abundance (FA) and rays (R), the highest mean ($±$s.e.) abundances were in the third period ($FA = 34.8 ± 12.8$, $R = 36.2 ± 12.8$), followed by the second ($FA = 17.5 ± 10.4$, $R = 15.2 ± 10.3$) and then the first ($FA = 11.7 ± 2.3$, $R = 7.7 ± 2.0$) periods.

There was a significant effect of water clarity on the taxonomic richness, overall abundance and the number of dolphins, rays and sharks detected (Table 2). The effect was positive, such that the number of sighted animals increased as the water clarity improved. Marine fauna could typically be observed from the seafloor to the surface, except when the water
clarity was very poor. Neither ocean temperature nor sea state were significantly related to any of the univariate response variables.

Discussion

Drone surveys were effective in quantifying assemblages of large marine fauna off ocean beaches, which included green turtles (*C. mydas*) and white sharks (*C. carcharias*), both being listed as vulnerable species in Australia. The assemblages of large fauna were numerically dominated by bottlenose dolphins (*Tursiops* spp.) and Australian cownose rays (*R. neglecta*). In particular, Australian cownose rays were usually seen in large schools that often exceeded 100 individuals. In contrast, sharks were rarely observed and usually solitary. Far from consistent, the assemblages of large fauna off ocean beaches varied substantially from day to day. Of the 4388 large marine animals observed on flights, 694 were from a single flight, and 38% of the 216 drone flights yielded no animals at all. Given this substantial variation among replicate flights, the clear significant differences in faunal-assemblage structure among beaches is a notable result.

The assemblages of large marine fauna off Evans Head differed from those at Ballina, as well as from those at Lennox Head and Byron Bay. This assemblage-level pattern was also apparent for the richness and abundance of marine fauna, which was highest at Evans Head. There could be numerous explanations for differences in marine faunal assemblages among these ocean beaches, such as physical characteristics or the degree of adjacent urbanisation, each of which are known to influence other aspects of beach ecology (McLachlan et al. 1993; Huijbers et al. 2013). Nonetheless, the proximity to river estuaries with substantial nutrient loading was a likely contributor because the ocean beaches at Evans Head and Ballina were directly adjacent to the entrances of the Evans and Richmond Rivers respectively.
whereas this was not the case for Lennox Head or Byron Bay. The nutrients and organic material provided by rivers stimulates primary and secondary production in near-shore areas, including sandy beaches (Connolly et al. 2009; Schlacher and Connolly 2009), which may increase the prey availability for large marine predators. Developing a larger monitoring program of marine fauna and environmental parameters off ocean beaches in close proximity and distant from riverine estuaries could provide valuable insight into factors influencing the richness and abundance of large marine predators in near-shore areas.

Bottlenose dolphins (Tursiops spp.) were observed in more drone flights (24.6% of the 216 flights) than any other taxa, and represented the most prominent marine predator off the surveyed ocean beaches. Given their abundance, metabolic requirements and generalist diet (e.g. many species of bony fish and cephalopods; Amir et al. 2005), bottlenose dolphins may have an important role in shaping fish assemblages in surf zones off ocean beaches. Bottlenose dolphins were most abundant at Ballina and least abundant off Evans Head. Previous research has identified groups of bottlenose dolphins that associate with Ballina and the Richmond River (home range of >177 km²) and those that associate with Byron Bay (home range of >320 km²), with mixing occurring around Lennox Head (Hawkins and Gartside 2008). The abundance, composition and size of bottlenose dolphin groups can change routinely, depending on prey availability, foraging techniques, habitat type, behaviour, reproductive state and time of day (Connor et al. 1992; Möller et al. 2002; Bearzi et al. 2005; Hawkins and Gartside 2008). Although bottlenose dolphin abundance displays seasonal variation in sheltered waters (e.g. Möller et al. 2002; Lodi et al. 2014; Vermeulen 2018), our study did not find this to be the case for the exposed sandy beaches sampled.

Although there was substantial variation in marine faunal assemblages among flights, there was no significant variation in assemblages among sampling periods, other than for rays (which had the largest contribution to overall abundance). The lack of temporal variation was despite one period being in the austral winter (late June to early July) and the others in the austral spring–summer (late September to early December). At more temperate latitudes, where water temperature varies substantially throughout the year, there would be an expectation of a clearer seasonal variation in the structure of faunal assemblages (e.g. Magill and Sayer 2002). At the subtropical latitudes of the present study, the temperature differential between winter and spring is not large, which is likely to explain why water temperature was not a significant predictor. In general, there is a fairly limited seasonal influence on elasmobranch and fish assemblages off the coast of New South Wales, Australia (Gray and Otway 1994; Kelaher et al. 2015). Nonetheless, there are exceptions, such as sea mullet (Mugil cephalus) runs that occur on ocean beaches in late summer to early winter (Stewart et al. 2018) and are likely to have fallen between our sampling periods.

Environmental variables, such as water clarity, sun glare and sea state, can influence the detectability of large marine fauna during aerial surveys (Hodgson et al. 2013; Kiszka et al. 2016; Lubow and Ransom 2016). Only on 2 days did the sea state reach 5 on the Beaufort scale (wind = 29–38 km h⁻¹, wave height = 2–3 m), with most survey efforts being conducted during mild morning conditions with light winds. Given this, it is not surprising that sea state did not account for significant variation in the richness and abundance of large marine fauna. This result is consistent with previous drone-based marine surveys that have also found no difference in faunal sighting rates among sea states (Hodgson et al. 2013; Fiori et al. 2017; Hodgson et al. 2017). In contrast, water clarity significantly influenced both detectability and ability to identify marine fauna from drone footage. This parameter is particularly important for aerial surveys of deep waters, because animals can dive below the sightability threshold, which becomes increasingly shallower as visibility declines (Pollock et al. 2006; Rowat et al. 2009). Water clarity is generally considered less of an issue in clear, shallow waters off ocean beaches, where animals can often be seen from the seafloor to the surface by using drones. However, there were days when the water quality was so poor that it hindered the detection of fauna. For some species (e.g. Dugong dugon), it is possible to empirically develop correction factors to reduce observation errors associated with increased water turbidity (e.g. Pollock et al. 2006). It is possible that drone-based sensors that can sample specific spectral frequencies using hyperspectral imagery may effectively increase image contrasting, and thereby improve the detection of large marine fauna as water clarity declines (Schoonmaker et al. 2011; Chabot and Francis 2016; Colefax et al. 2018). However, this technology is unlikely to help the visual detection of marine fauna over turbid water, which could be an important consideration for drone sampling off tropical beaches, where rainfall and turbidity plumes are highly seasonal (e.g. Lane et al. 2002).

As water clarity declined, it not only influenced the detectability of marine fauna, but also the capacity to make accurate taxonomic identifications. On the clearest days, species situated throughout the water column could be distinctly identified (e.g. spotted eagle rays, A. marina, distinguished from southern eagle rays, Myliobatis spp.). However, on days when the ocean was more turbid, it was possible to assign animals deep in the water column only into broad categories (e.g. shark, ray, or turtle). Because there is no immediate solution to this issue, before commencing a drone monitoring program of large marine fauna, it would be prudent to carefully consider whether the taxonomic resolution that can be reliably obtained is adequate to achieve the goals of the study. Furthermore, it is also worth considering limiting drone surveys to days when the water clarity is reasonable, so as to reduce sampling biases associated with faunal detectability and species identification.

Our drone surveys successfully documented patterns of spatial and temporal variation of large marine fauna off ocean beaches. These faunal assemblages included protected species (e.g. bottlenose dolphins) and threatened species (e.g. green turtles and white sharks), highlighting the value of ocean beach ecosystems. In our study, bottlenose dolphins were the most common large predator off ocean beaches, whereas sharks were rare. Additionally, patterns of variation among beaches suggested that proximity to riverine estuaries could influence the diversity and abundance of large marine wildlife. Given that ocean-beach environments are being increasingly threatened by human activities (Schlacher et al. 2007; Defeo et al. 2009; Schoeman et al. 2014), it is becoming necessary to implement evidence-based management strategies to ensure the
sustainability of these ecosystems and conservation of associated wildlife (Peterson and Bishop 2005; Jones et al. 2017). Obtaining robust ecological information to support such management from the wave-affected waters off exposed ocean beaches has always been challenging (McLachlan and Defeo 2017; Olds et al. 2018). We contend that emerging drone technology provides a useful new tool to help understand the ecology of sandy-beach ecosystems.

Conflicts of interest
The authors declare that they have no conflicts of interest.

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