


Spatial and temporal variation of marine megafauna off coastal beaches of south-eastern Queensland, Australia

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ABSTRACT

Context. Coastal beach environments provide habitats for marine megafauna, including turtles, rays, marine mammals and sharks. However, accessing these variable energy zones has been difficult for researchers by using traditional methods. **Aims.** This study used drone-based aerial surveys to assess spatio-temporal variation of marine megafauna across south-eastern Queensland, Australia. **Methods.** Drones were operated at five south-eastern Queensland beaches. Megafauna sightings and key variables including location, month and turbidity were analysed to assess variation across locations. **Key results.** Overall, 3815 individual megafauna were detected from 3273 flights. There were significant differences in the composition of megafauna assemblages throughout the year and among beaches, with megafaunal sightings in >80% of flights conducted off North Stradbroke Island. **Conclusions.** Strong temporal presence was found that is congruent with other studies examining seasonality. This supports the use of drones to provide ecological data for many hard-to-study megafauna species and help inform long-term sustainable management of coastal ecosystems. **Implications.** Results indicated that environmental conditions can influence the probability of sighting marine megafauna during aerial surveys.

Keywords: aerial survey, beaches, continental shelf, drones, ecological, RPA, temporal, UAV.

Introduction

Marine megafauna off coastal beaches

Marine megafauna are key components of marine ecosystems and include many charismatic species that are socially, economically and culturally valued by humans worldwide (Pimiento *et al.* 2020). Herein, we refer to 'megafauna' as groups of large animals, including mammals, rays, sharks, turtles, seabirds and large pelagic fishes (Fuentes *et al.* 2016). Coastal beaches worldwide provide important nesting and feeding grounds for the seven sea turtle species, including the green (*Chelonia mydas*) and loggerhead turtle (*Caretta caretta*) (Limpus and Coffee 2019; Schofield *et al.* 2019). These waters also support a diverse assemblage of elasmobranchs, which act as high-level trophic predators critical to maintain the balance in coastal food webs (Barreto *et al.* 2021). The shallow and productive waters of coastal beaches provide critical habitat for both resident and migratory shark and ray species that use these areas as nursery and foraging grounds (DiGiacomo *et al.* 2020), including tiger sharks (*Galeocerdo cuvier*), shovelnose rays (*Rhinopristiformes*) and green turtles (*Chelonia mydas*) (Holmes *et al.* 2014; Limpus and Coffee 2019; Colefax *et al.* 2020a). Nursery habitats provide an advantage to young because they reduce early mortality rate by decreasing the risk of predation and generally provide an abundance of prey sources (Yokota and Lessa 2006). According to the International Union for Conservation and Nature (IUCN), approximately one-third of marine megafauna species are at risk of extinction (see <https://www.iucnredlist.org>, accessed 17 September 2023). As shore-based activities and coastal developments increase, baseline knowledge of megafauna that inhabit these ecosystems and the processes that manage their populations is sorely needed.

Influence of environmental factors on marine megafauna

To understand the spatial dynamics of marine megafauna in coastal ecosystems, it must be recognised that shallow-water environments are exposed to highly variable oceanic conditions. The patchy distribution of megafaunal species is influenced by biotic and abiotic environmental cues occurring at various temporal and spatial scales (Haulsee *et al.* 2015). At the scale of hours, weeks or years, these coastal ecosystems can experience major changes in temperature, depth, turbidity and bathymetry. Fluctuations in rainfall, tidal changes and seasonal weather patterns also occur on varied temporal scales (DiGiacomo *et al.* 2020). Hays *et al.* (2016) stated that these factors can interact both directly (physiology of megafauna) and indirectly (physiology of megafauna prey) with marine megafauna across varied temporal scales. As the majority of large marine animals has been documented to migrate long-distances, it is often thought that their directed movements are influenced by spatial and temporal variations in essential prey resources (Couturier *et al.* 2011).

Rainfall events and warmer temperatures are linked to increases in phytoplankton, a vital biological component that establishes ocean food webs (Lee *et al.* 2018). Blooms in phytoplankton enhance productivity, providing megafauna with food sources and favourable foraging grounds (Meynecke *et al.* 2006). The variation in marine megafaunal assemblages can also change because of spatial factors, such as distance from other habitats (coral reefs, seagrass beds and estuaries), proximity to continental shelf and the presence of marine protected areas (Barnes 2017). Some coastal waters are also heavily influenced by estuarine plumes, which make substantial nutrient and energy contributions to nearby habitats (Connolly *et al.* 2009). These inputs, and the resulting enhanced biological activity, may play a role in the variation of megafauna presence across time and space (Loneragan 1999).

Studying marine megafauna in coastal waters

Faunal assemblages off coastal beaches have been primarily assessed using boat-based fishing surveys, or other passive methods such as baited remote underwater video systems (BRUVS) (Olds *et al.* 2018). However, these methods are not always suitable for large marine animals because of their wide range, protection status and spatial presence in coastal ecosystems (Kelaheer *et al.* 2020). Telemetry methods, such as satellite and acoustic tracking, offer efficient monitoring of species movement, location and aggregations (Dudgeon *et al.* 2008; Kock *et al.* 2013). However, both are costly and restricted by animal-capture considerations and tag-retention duration (Gredzens *et al.* 2014; Pereira *et al.* 2023). Effective sampling of air-breathing megafauna has traditionally been conducted by active surveillance (e.g. land- and vessel-based) (Hawkins and Gartside 2008). However, once underwater,

accurate observation of behaviours is challenging, with animals hard to track until they re-surface. Traditional aerial surveys have typically been conducted using manned aircrafts (e.g. helicopters and light planes), consisting of a pilot and an observer (Kelaheer *et al.* 2023). In recent times, remotely piloted aerial systems (RPAS), hereafter called drones, have become increasingly used as a tool for marine science research (Barreto *et al.* 2021; Kelaheer *et al.* 2023).

Compared with traditional survey methods, drones are time-efficient, cost-effective and have shown significant value in detecting and observing fauna that may be dangerous or difficult to study (Butcher *et al.* 2021). Additionally, because many species of megafauna are threatened, drones provide a non-invasive approach to surveying these species with limited visual and auditory impact on the target individual (Bourke *et al.* 2023). Drones have been used in marine environments for quantifying fauna presence (Kelaheer *et al.* 2020; Ayres *et al.* 2021) and behaviour (Torres *et al.* 2018; Fettermann *et al.* 2019), as well as for detecting and monitoring sharks as a method of shark control for beach users (Colefax *et al.* 2020b; Butcher *et al.* 2021). A recent study conducted by the Queensland Government Department of Agriculture and Fisheries (DAF) and Surf Life Saving Queensland (SLSQ) demonstrated this, when comparing this non-lethal measure with traditional, lethal shark-bite mitigation measures such as nets and drumline shark-culling measures (SharkSmart drone trial, see Mitchell *et al.* 2022). Overall, drone detection of marine megafauna has the potential to play a significant role in the conservation of threatened species, calculate population estimates (Rees *et al.* 2018), guide management decisions (Monteforte *et al.* 2022), contribute to citizen science (Dudgeon *et al.* 2019) and assist in the designation of future Marine Protected Areas (MPAs) (Gredzens *et al.* 2014).

Given the paucity of our understanding of the spatial and temporal patterns of marine megafauna species off coastal beaches in south-eastern Queensland (SEQ), 12 months of drone surveys conducted as part of the SharkSmart drone trial were utilised to (1) determine temporal and spatial variations in marine megafauna assemblages (specifically species abundance and richness) across several SEQ beaches and (2) quantify the influence of environmental conditions on the sightability of marine megafauna.

Materials and methods

Drone-trial locations

Drones were operated at five SEQ beaches as part of the Queensland SharkSmart drone trial. A total of 3273 drone surveys occurred at two beaches on the Gold Coast (Southport Main Beach and Burleigh Beach), two beaches on the Sunshine Coast (Alexandra Headland and Coolum North) and one beach on North Stradbroke Island (Main Beach) (Fig. 1).

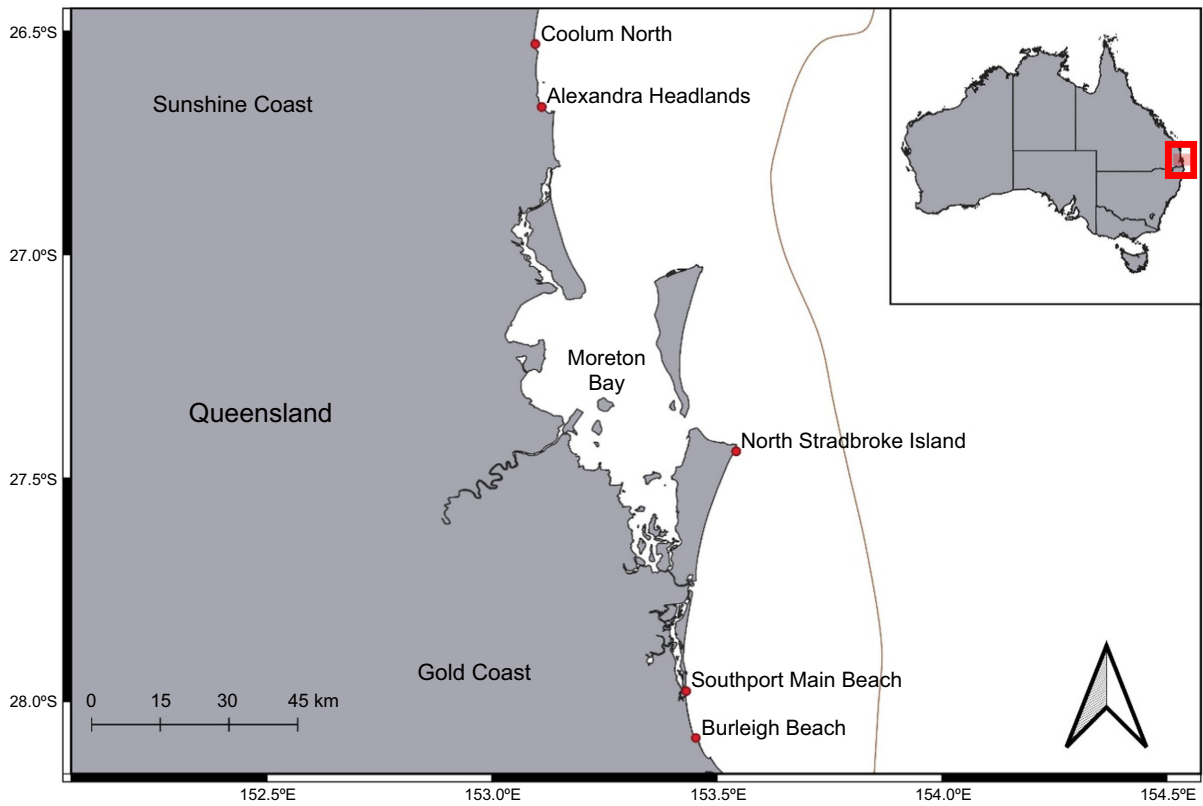


Fig. 1. Map of beach locations surveyed by the Queensland SharkSmart drone trial in south-eastern Queensland, Australia. The solid brown line indicates the edge of the continental shelf.

Trial sites were selected on the basis of the recommendations of the Cardno report of alternative approaches to shark control in Queensland (Cardno 2019), and Civil Aviation Safety Authority (CASA) regulations regarding restricted airspace and other no-fly areas, for example, within 5.5 km of an airport. Other key factors that determined the selection of these locations were the presence of Surf Life Saving Queensland (SLSQ) services, high year-round visitation of beach users, high water clarity, proximity to river mouths and historical catch of potentially dangerous sharks (Mitchell *et al.* 2022) (see Table 1 for location characteristics).

Experimental design

DJI Mavic 2 Enterprise Zoom drones were operated by certified SLSQ pilots from September 2020 to October 2021 on weekends, public holidays and school holidays to coincide with periods of highest public use of beaches. The lens of these drones had a field of view of ~77° and a sensor of 20 million effective pixels. No filters were added to the drones during the trial. Drones were deployed at 30-min intervals from when the beach opened (usually 07:00–08:00 hours) until 12:00 hours, because higher wind speeds typically occur in the afternoon in SEQ (>20 knots, ~37 km h⁻¹),

Table 1. Site characteristics of beach locations, including available habitats and proximity to river mouths, edge of the continental shelf and nearest town.

Location	Site characteristics			
	Proximity to river mouths (km)	Proximity to the edge of the continental shelf (km)	Proximity to nearest town (km)	Available habitats
Coolum North	1.12	58	0.64	Shallow rocky reefs, sandy beach
Alexandra Headland	2.11	53	0.32	Shallow rocky reefs, sandy beach
North Stradbroke Island	39	23	1.08	Rocky reefs, Point Lookout Headland, adjacent Moreton Bay, sandy beach
Southport Main Beach	9.8	42	0.51	Sandy beach
Burleigh Beach	1.48	39	0.47	Shallow rocky reefs, sandy beach

conditions in which these particular drones could not be operated. This resulted in six to eight flights per day. Flights conducted twice per hour allowed time in between for pilots to record environmental and flight log data and change drone batteries.

Flights lasted between 15 and 20 min, with flight paths being designed as 400-m transects behind the surf break (Fig. 2) (see Mitchell *et al.* 2022 for detailed drone transects). Flights were conducted with manual control as weather and tide variables significantly changed the position of the surf break. To stay within visual line of sight of the drone, flight paths covered a section of each beach close to the SLSQ swimming flags. Drones were flown at $\sim 10\text{--}20\text{ km h}^{-1}$ at a constant altitude of 60 m from where they were deployed, with the camera set at a 45° angle facing the direction of travel. These values provided a balanced height for identifying marine life, a field of view of $\sim 110\text{ m}$ and helped reduce glare. Drones were set to record continuously in 4K video to maximise the resolution for detecting megafauna and to allow identification to the species level.

Data collection

Videos were reviewed at double speed using VideoLan VLC media player (ver. 3.0.16, see <https://www.videolan.org/vlc/index.html>) until marine megafauna were sighted. Once

fauna were sighted, the footage was analysed, using frame by frame view if necessary to identify and count individual animals. During the review of video footage, all marine megafauna observed were recorded and identified to the lowest possible taxonomic resolution. In some cases, this was to a species level (e.g. Indo-Pacific leopard shark, *Stegostoma tigrinum*), whereas others were identified to genus level (e.g. whaler shark, *Carcharhinus* spp.). All marine megafauna were individually counted per flight conducted using MaxN statistic, where abundance is calculated as the maximum number of individuals of each taxa observed in a single frame of view (Shah Esmaili *et al.* 2021). Megafauna sightings (presence or absence) were recorded at the beach level to enable abundance and richness comparison among locations.

No animal ethics approval was required because the study was observational only.

Environmental data were recorded once per flight for each location. Specific environmental parameters included air temperature ($^\circ\text{C}$), sea state (Beaufort scale), wind speed (km h^{-1}), wind direction, turbidity (%), cloud cover (Oktas), barometric pressure (hPa), sea-surface temperature ($^\circ\text{C}$) and chlorophyll concentration (mg L^{-1}). Surface temperature and chlorophyll data were collected by satellite oceanography (Integrated Marine Observing System, Australian Ocean Data Network, see <https://portal.aodn.org.au/search>, accessed 20

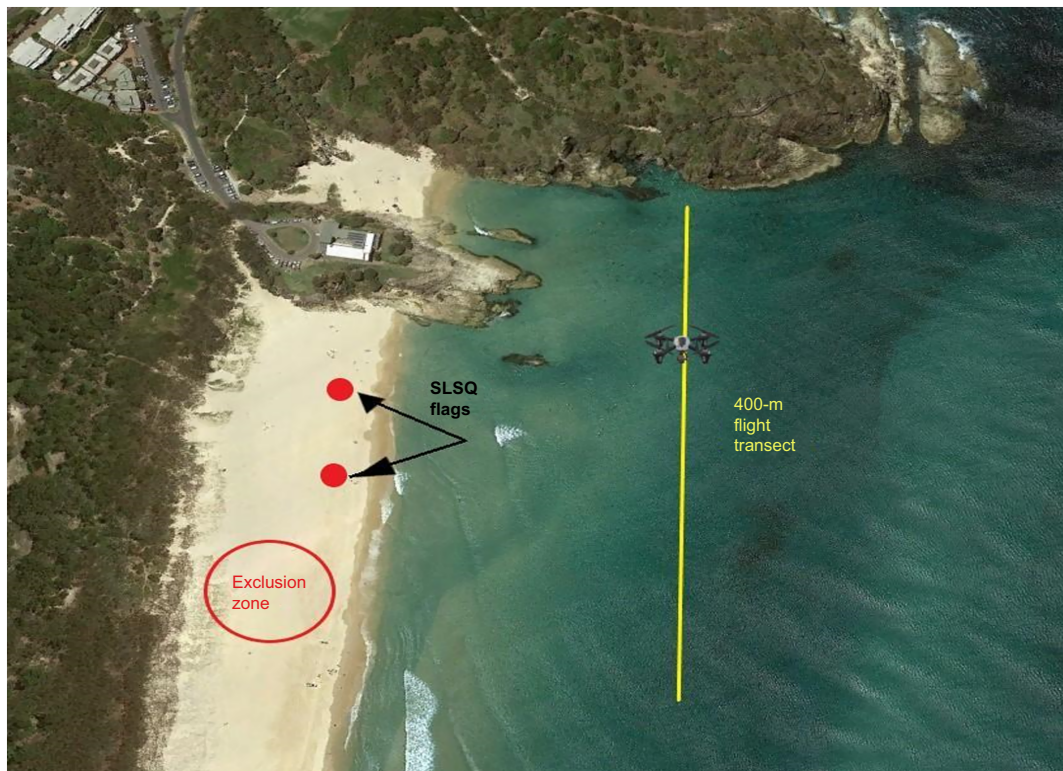


Fig. 2. Schematic diagram showing the path of the drone transect behind the surf break at Main Beach, North Stradbroke Island, Queensland. Red circle indicates the 30-m public exclusion zone from where the drones were launched and retrieved.

December 2022), but high cloud cover and subsequent light reflectance resulted in data being unavailable for many days of this study. Rainfall data for the preceding 7 days for each beach location was downloaded from The Bureau of Meteorology (BOM) website (see <http://www.bom.gov.au/climate/data/index.shtml>, accessed 19 September 2022). This enabled an assessment of the influence of turbidity on sightability of megafauna at time periods >1 day because there can be a time lag between rain falling over land and the subsequent increase in turbidity from river outflows.

Statistical analysis

Generalised linear models (GLMs) were applied to determine which key environmental variables influenced the probability of sighting marine megafauna (Table 2). Response variables for analysis included megafauna species sightability (separated into air breathing v. non-air-breathing fauna), calculated as the presence or absence of individuals, and megafauna species abundance (specifically for leopard sharks, *S. tigrinum*, and turtles, Cheloniidae). These two groups were selected for abundance because a large number of them were sighted.

Species richness, calculated as the number of different species found in a location, was also used to examine the variation in species composition across each location.

Response variables in the GLMs were modelled using a Poisson distribution. The distributions of predictor variables were checked, and a log + 1 transformation was applied to rainfall to account for overdispersion. The correlation of predictor variables were also checked using the `cor()` function to ensure all variable combinations had a Pearson correlation coefficient of <0.4. A series of models were run following a backwards stepwise model selection to drop predictor variables. The model of best fit was indicated by having the lowest Akaike information criterion (AIC, Akaike 1974). All statistical analyses were performed in *RStudio* (ver. 1.4.1711, Posit Software, PBC, Boston, MA, USA, see <https://posit.co/products/open-source/rstudio/>) in *R* (ver. 4.0.5, R Foundation for Statistical Computing, Vienna, Austria, see <https://www.r-project.org/>). GLMs were implemented with the R package *lme4* (ver. 1.1-30, see <https://CRAN.R-project.org/package=lme4>; Bates *et al.* 2015). The *tidyverse* package (ver. 1.3.2, see <https://cran.r-project.org/package=tidyverse>; Wickham *et al.* 2019) was also used in analysis for organising and plotting data.

Table 2. List of environmental variables influencing the sightability and variation of marine megafauna, including the metric used, hypothesised importance to the study and the data source.

Variable or predictor	Unit of measurement	Rationale	Data source
Location	Beach	The five locations have differences in depth, habitat type, level of exposure and continental shelf distance, which can influence the behaviour and movement of megafauna	Recorded by pilot
Time of day	Flight number (1–8)	The behaviour and movement of megafauna vary with the time of day. Time of day also affects the angle of sun, which can influence the intensity of glare thus limit visibility into the water column.	Recorded by pilot
Month	January–December	In south-eastern Queensland, there are seasonal changes in weather patterns, for example, high pressure systems occur in winter and bring low winds, dry weather and still sea states.	Recorded by pilot
Air temperature	°C	Rising temperatures are associated with some weather patterns and can lead to heavy rainfall, higher winds and affect the amount of dissolved oxygen in the water column (Garcia-Soto <i>et al.</i> 2021).	Bureau of Meteorology
Rainfall	Cumulative rainfall of previous week (mm)	Cumulative rainfall over the previous week can influence turbidity levels, for example, high rainfall can lead to large plumes of organic materials from rivers, therefore influencing the probability of sighting megafauna.	Bureau of Meteorology
Turbidity	0–100%	Visibility into the water column from a drone is affected by turbidity.	Estimated by pilot
Wind speed	km h ⁻¹	Wind speed is associated with most waves, for example, higher winds can lead to increased surface disturbance and therefore inhibit the likelihood of sighting megafauna. Drones could operate safely with winds up to 20 km h ⁻¹ .	Bureau of Meteorology
Sea state	Beaufort scale (low = 1, high = 12)	Surface disturbance and turbidity of the water column is affected by sea state.	Bureau of Meteorology
Cloud cover	Oktas	Cloud cover affects the amount of sunlight that penetrates the water column, thus influencing megafauna sightability.	Estimated by pilot
Glare	1 (low)–5 (high) scale	Visibility into the water column from drones can be affected by the amount of sun glare on the water surface.	Estimated by pilot
Atmospheric pressure	hPa	Weather patterns are affected by atmospheric pressure, for example, low pressure systems can cause high winds, rough sea states and heavy rain. Barometric pressure can also influence the movement and behaviour of megafauna (Heupel <i>et al.</i> 2003).	Bureau of Meteorology

Results

Marine megafauna sightings

In total, 3815 megafauna were observed across the five locations (Table 3). The number of sightings varied substantially across beaches, ranging from 227 megafauna sightings at Alexandra Headland, to 2273 sightings at North Stradbroke Island. Maximum megafaunal richness was eight across all locations, varying from three at both Alexandra Headland and Southport Main Beach, to eight at North Stradbroke Island. In total, megafauna were sighted on 23.3% of all flights. Megafauna sighting rates were highly variable across locations, ranging from 11.3% at Alexandra Headland and Southport Main Beach, to 84% at North Stradbroke Island (Table 3).

Overall, megafauna sightings and the abundance of rays, sharks, turtles, cetacean and fish varied substantially across locations (Table 4). The most abundant and diverse marine megafauna assemblages were observed at North Stradbroke Island, followed by Burleigh Beach, whereas Alexandra

Headland and Southport Main Beach had the least abundant and rich assemblages. Turtles (Cheloniidae) were the most commonly sighted megafauna, occurring in 49.5% of flights at North Stradbroke Island, 9.4% at Coolum North and 7.9% at Alexandra Headland. This was followed by stingrays (Dasyatidae), which occurred in 40.9% of flights at North Stradbroke Island, 14.6% at Burleigh Beach and 4.8% at Coolum North. North Stradbroke Island had significantly higher sightings of the majority of megafauna taxa despite having the fewest number of flights (Table 3).

Leopard sharks were the most frequently sighted shark species at North Stradbroke Island, being sighted in 22.5% of flights. Whaler sharks (*Carcharhinus* spp.) were the second-most frequently sighted sharks at North Stradbroke Island, occurring in 19.1% of flights, followed by 6% of flights at Burleigh Beach. Marine mammals were predominantly sighted at North Stradbroke Island, with dolphins (Delphinidae), dugongs (*D. dugong*) and humpback whales (*M. novaeangliae*) occurring in 19.1, 0.6 and 1.2% of flights respectively (Table 4).

Table 3. Total megafauna abundance, richness, percentage of flights with megafauna sighted and number of flights for each location.

Location	Total megafauna abundance	Maximum megafaunal richness	Percentage of flights with megafauna sighted (%)	Total number of flights conducted at each location
Coolum North	358	4	18.3	727
Alexandra Headland	227	3	11.3	825
North Stradbroke Island	2273	8	84	325
Southport Main Beach	327	3	11.3	698
Burleigh Beach	630	4	26.2	698
All SEQ locations combined	3815	8	23.3	3273

Table 4. Percentage of flights (%) in which marine megafauna were sighted at each location.

Taxon	Location				
	Coolum North	Alexandra Headland	North Stradbroke Island	Southport Main Beach	Burleigh Beach
Stingray (Dasyatidae)	4.8	1	40.9	4.4	14.6
Manta and devil ray (Mobulidae)	1.4	0.1	14.8	0	0.3
Eagle ray (Myliobatidae)	3.3	1.6	32.6	2	5.2
Shovelnose ray and wedgefish (<i>Rhinopristiformes</i>)	0	0	17.5	0	0.7
Cownose ray (<i>Rhinoptera neglecta</i>)	0.1	0.1	2.2	1.3	5.2
Leopard shark (<i>Stegostoma tigrinum</i>)	0	0	22.5	0.4	0.3
Hammerhead shark (<i>Sphyrna</i> spp.)	0	0.1	0.3	0	0
White shark (<i>Carcharodon carcharias</i>)	0	0	0	0.1	0
Whaler shark (<i>Carcharhinus</i> spp.)	0	0.4	19.1	0	6
Turtle (Cheloniidae)	9.4	7.9	49.5	1.3	0.7
Dolphin (Delphinidae)	0.6	0.1	19.1	0.6	0.1
Dugong (<i>Dugong dugong</i>)	0	0	0.6	0	0
Humpback whale (<i>Megaptera novaeangliae</i>)	0	0	1.2	0	0
Large fish (e.g. tuna and cobia)	5.4	3	22.8	3.2	4.7

Temporal variation of marine megafauna

The majority of megafauna groups exhibited temporal variation. Stingrays were sighted at most locations throughout the year. However, July had the highest number of sightings at North Stradbroke Island, whereas more were sighted at Burleigh in the January (Fig. 3). The highest sighting rates of cownose (*R. neglecta*) and devil rays (*Mobula* spp.) occurred at Burleigh during December and January respectively. Reef manta rays (*M. alfredi*) were most sighted at North Stradbroke Island during September and decreased notably in number as the year passed. This species also had more sightings at Coolum in June. Eagle (Myliobatidae) and shovelnose ray (*Rhinopristiformes*) sightings were highest at North Stradbroke Island during summer (January and December respectively), whereas at Burleigh sightings were highest in April (Fig. 3).

The sighting rate of dolphins was highest at North Stradbroke Island during January (Fig. 4). Dolphins were sighted at Coolum and Alexandra Headland only in winter (June–August). Dugongs were sighted only in August and June at North Stradbroke Island, along with the highest sightings of humpback whales, although a small number of whales were sighted in September. Sightings of large fish were similar year-round for all locations; however, North Stradbroke Island had the highest sighting rate during September. Higher sightings of fish were observed at the other four locations during autumn and winter (Fig. 4).

The most important factor influencing sightability of leopard sharks (*S. tigrinum*) and turtles (Cheloniidae) was month, explaining 58 and 22% of the deviance in the response variable respectively (Fig. 5, see Supplementary Tables S3 and

S4 for further model outputs). Models including this variable had the lowest AIC. The probability of sighting leopard sharks was highest in December (0.1 ± 0.04) and lowest in August ($<0.001 \pm <0.001$). The probability of sighting turtles was highest in November (0.95 ± 0.15) and lowest in March (0.07 ± 0.04).

Environmental factors influencing the sightability of marine megafauna

Generalised linear model outputs indicated that turbidity, month and location were the most important factors influencing the sightability of air-breathing marine megafauna (mammals and turtles), explaining 42% of the deviance in the response variable (see Table S1 for further model outputs). The model including these variables had the lowest AIC. Turbidity had a negative linear effect on the probability of sighting air-breathing megafauna, decreasing from 0.86 (± 0.15 s.e.) when turbidity was 0%, to 0.39 (± 0.11) when turbidity was highest (Fig. 6a). The likelihood of sighting air-breathing fauna was highest during October (0.91 ± 0.16) and lowest during May (0.35 ± 0.13) (Fig. 6b). The probability of sighting megafauna was highest at North Stradbroke Island (0.69 ± 0.11), followed by Coolum North and Alexandra Headland. The lowest probability of sighting megafauna was at Burleigh Beach (0.01 ± 0.004), followed by Southport Main Beach (Fig. 6c).

Model selection based on AIC for sightability of non-air-breathing megafauna (elasmobranchs and fish) included rainfall, turbidity, location and month, which collectively accounted for 44% of the deviance in the response variable

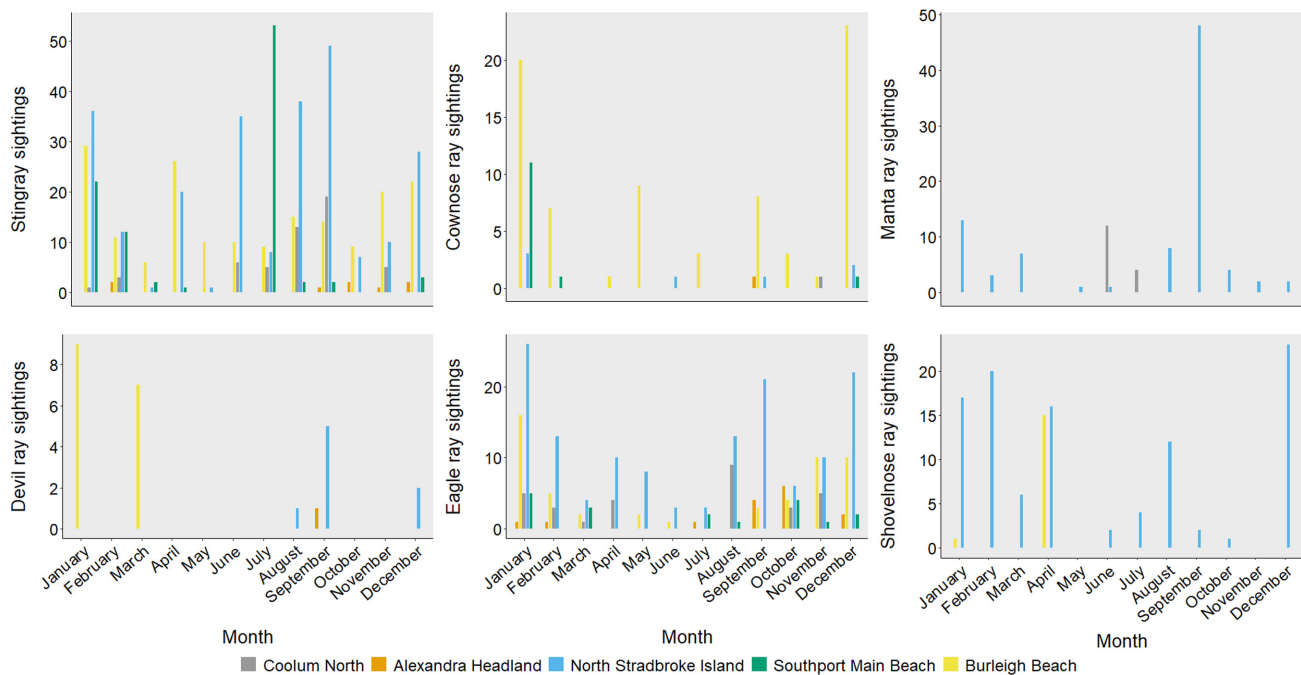


Fig. 3. Temporal variation of ray groups across all locations.

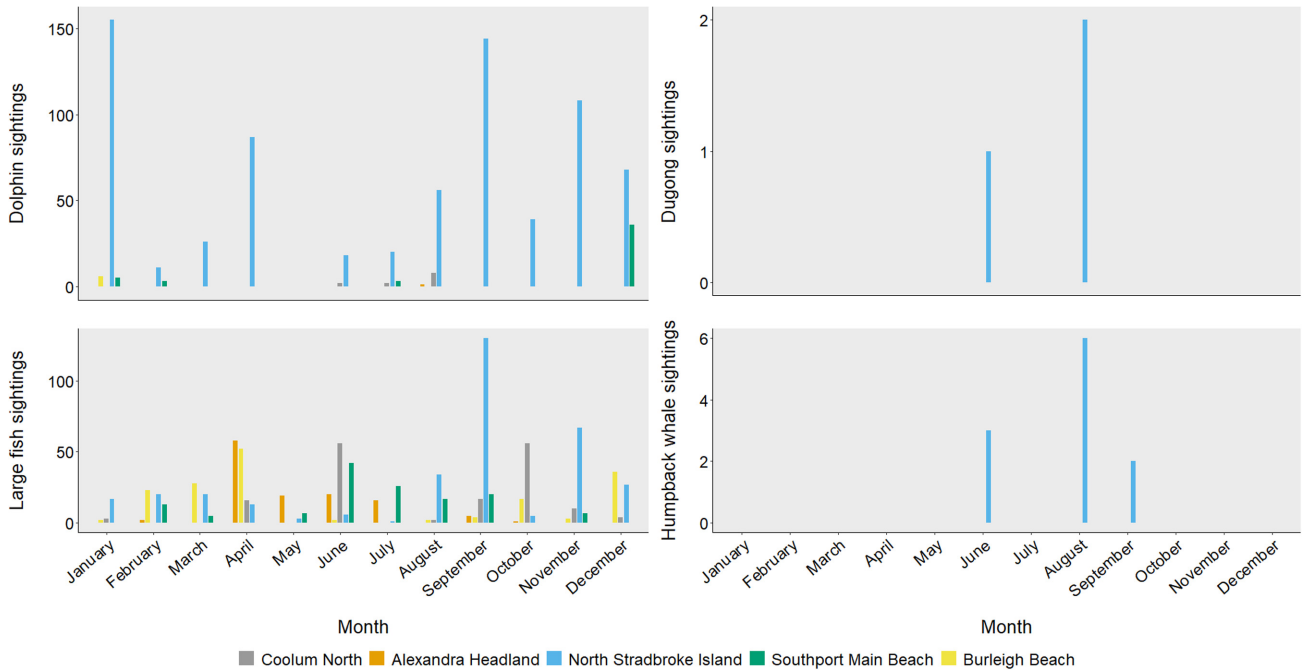


Fig. 4. Temporal variation of marine mammals and bony fish across all locations.

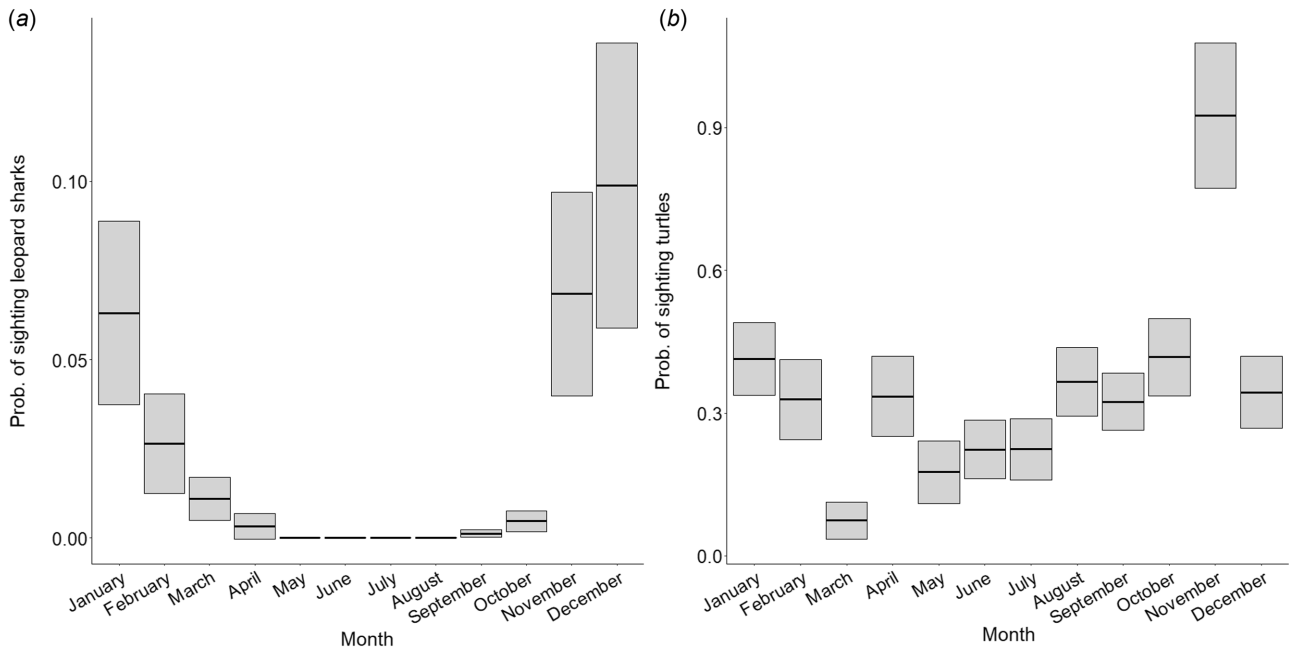


Fig. 5. Influence of month on the sightability of (a) leopard sharks (*S. tigrinum*) and (b) turtles (Cheloniidae). Solid black lines indicate model-fitted values. Grey shaded areas indicate 95% confidence intervals.

(see Table S2 for further model outputs). Rainfall had a negative linear effect on the relative probability of sighting non-air-breathing megafauna, decreasing from 3.78 (± 0.46 s.e.) when rainfall was lowest, to 1.49 (± 0.17) when rainfall was 6 mm (Fig. 7a). A similar trend was seen with turbidity, ranging from 3.4 (± 0.32) when there was no turbidity, to 1.46

(± 0.25) when turbidity was at 100% (Fig. 7b). The relative probability of sighting megafauna was highest at North Stradbroke Island (2.67 ± 0.25), followed by Burleigh Beach and Coolum North. Alexandra Headland (0.11 ± 0.02) had the lowest likelihood of sighting megafauna, followed by Southport Main Beach (Fig. 7c). The relative likelihood of

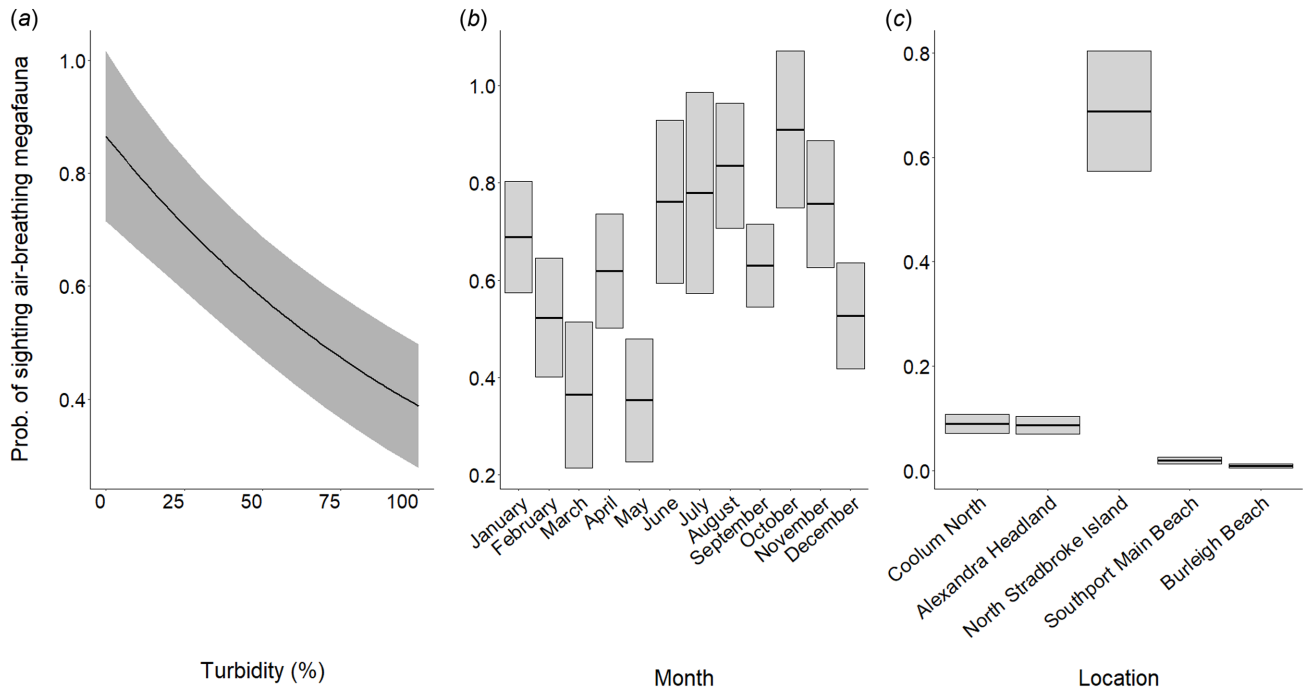


Fig. 6. Influence of predictor variables on the sightability of air-breathing marine megafauna: (a) turbidity, (b) month and (c) location. Solid black lines indicate model-fitted values. Grey shaded areas indicate 95% confidence intervals.

sighting non-air-breathing fauna was highest during March (2.78 ± 0.46) and lowest during September (0.8 ± 0.08) (Fig. 7d).

Discussion

Drone surveys found that assemblages of marine megafauna varied substantially among the sandy beaches surveyed and also by month. Spatiotemporal variation was identified in commonly sighted species including leopard sharks and reef manta rays, with some information being provided for rare faunal groups including dugongs.

Spatial variation of megafauna

North Stradbroke Island was found to have the highest detection of megafauna, as well as the greatest species richness and abundance of species compared with the other locations. There could be several explanations for the differences in megafaunal assemblages across these coastal beaches, such as the exposure to adjacent urbanisation or physical characteristics (e.g. wave climate), both of which are known to influence key aspects of beach ecology (Schlacher *et al.* 2007; Olds *et al.* 2018). Nevertheless, the availability of other habitats and the proximity to the edge of the continental shelf (23 v. >39 km) are plausible contributors to the high detection of all fauna species and groups at North Stradbroke Island (refer to Table 1 for site characteristics).

The presence of shallow rocky reefs and the Point Lookout headland on North Stradbroke Island create one of the most prominent and complex habitats for the region. This habitat is likely to be abundant with potential prey items (Chilvers *et al.* 2005), possibly explaining the high detection of marine megafauna (Amir *et al.* 2005; Kelaher *et al.* 2020). This availability of complex habitats may additionally provide megafauna with zones used as cleaning stations (Couturier *et al.* 2011; Couturier *et al.* 2014), refuges from predators (DiGiacomo *et al.* 2020), breeding and nursery grounds (Shah Esmaeili *et al.* 2021). Turtles and dugongs are resident inside adjacent Moreton Bay, which has extensive seagrass meadows (Lanyon 2003; Limpus and Coffee 2019). The variable detection of these species on the ocean side of North Stradbroke Island is likely to be due to the absence of seagrass beds in these high-energy environments (Barnes 2017). Instead, these zones are likely to be selected for reproduction purposes for turtles, and thermoregulation may partially explain the occurrence of dugongs off this sandy beach. Although few dugongs were recorded here, they have been documented previously to temporarily leave the protected bay to adjacent oceanic waters that are significantly warmer, so as to minimise heat loss to the environment (Zeh *et al.* 2018).

Proximity to continental shelves is known to attract animals closer to beaches, because it serves as a navigational aid during their migrations (e.g. sharks (Holmes *et al.* 2014) and humpback whales (Noad *et al.* 2006)). The shelf also facilitates the convergence of the warm East Australian

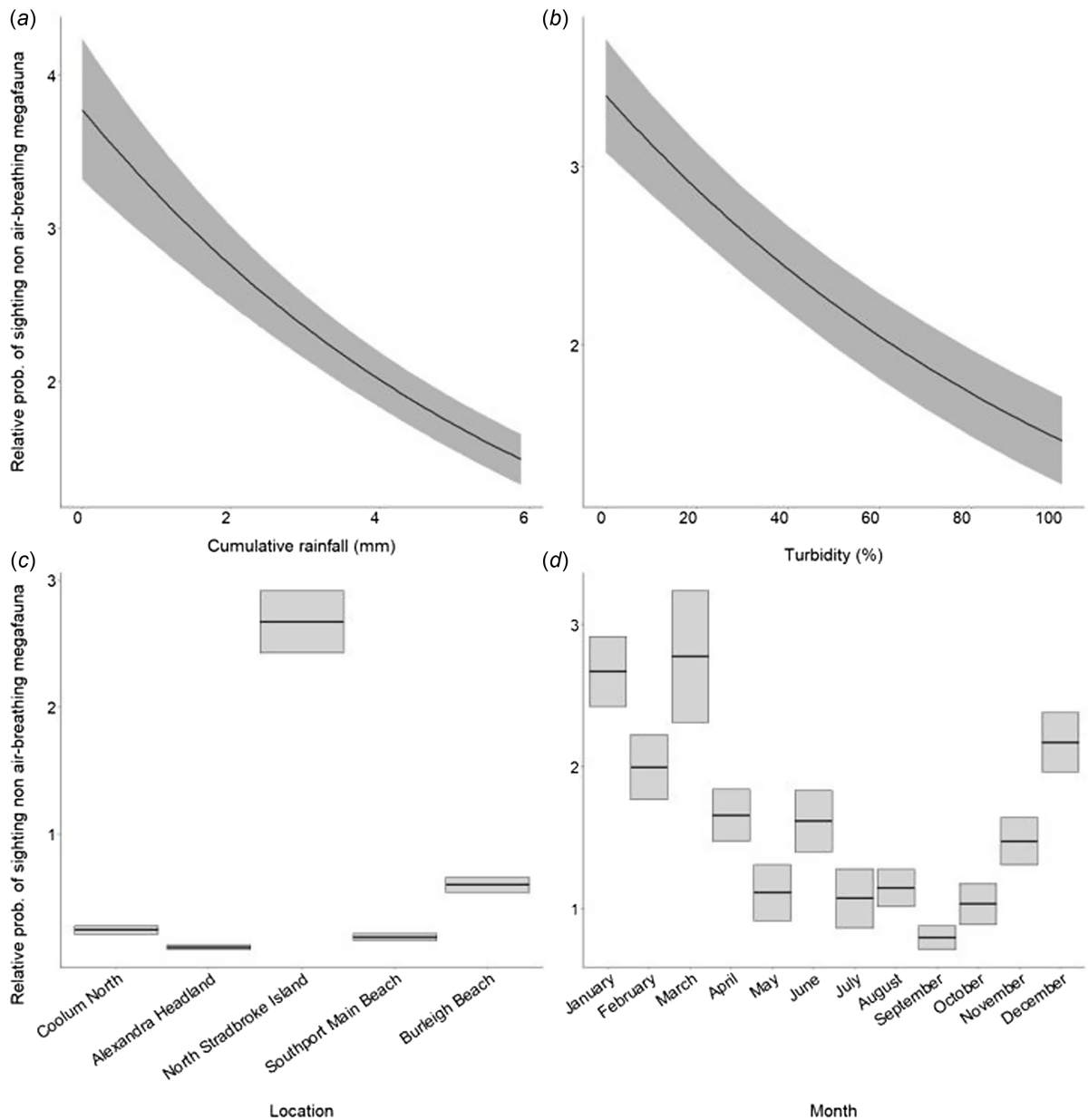


Fig. 7. Influence of predictor variables on the sightability of non-air-breathing marine megafauna: (a) rainfall, (b) turbidity, (c) location and (d) month. Solid black lines indicate model fitted values. Grey shaded areas indicate 95% confidence intervals.

Current (EAC) and colder oceanic currents (Armstrong *et al.* 2020). The convergence of these currents provides essential biophysical conditions, as well as periodic nutrient enrichment through upwellings, to support high concentrations of megafauna (Sleeman *et al.* 2007; Jaine *et al.* 2014). Key species including manta rays (Couturier *et al.* 2011), turtles (Limpus and Coffee 2019) and whales (Bolin *et al.* 2020) are known to use the EAC to facilitate their migrations to the southern Great Barrier Reef.

High sighting rates of megafauna also occurred at Burleigh Beach on the Gold Coast, which may be due to the close proximity to a productive river estuary, Tallebudgera Creek.

The substantial contributions of nutrients and organic materials provided by estuarine plumes promotes primary and secondary production in nearby ecosystems, including sandy beaches (Connolly *et al.* 2009). These inputs and resulting enhanced biological activity may increase prey availability for megafauna (Loneragan 1999). Elasmobranchs were the most dominant group sighted off this location, with their movements possibly driven by factors associated with foraging (DiGiacomo *et al.* 2020), reproduction (Yokota and Lessa 2006; Schluessel *et al.* 2010) and anti-predatory strategies (Schlaff *et al.* 2014). Specifically, proximity to nearby rivers may explain the high occurrence of cownose

rays off Gold Coast locations. This result is similar to the findings from the New South Wales trial, which identified that the beach adjacent to a river mouth had the highest abundance of cownose rays (Kelaher *et al.* 2020; Tagliafico *et al.* 2020).

Excluding turtles, the low probability of sighting large marine animals off Sunshine Coast locations may be due to the distance to the continental shelf (>53 km), and less suitable habitat (refer to Table 1 for location characteristics). In contrast, turtles are known to nest in small densities on Sunshine Coast beaches (Limpus 1993) and show site fidelity to these zones (Limpus *et al.* 1994).

Assessing the temporal variation of megafauna

The abundance of most megafauna groups peaked in austral spring–summer (September–February). This was possibly due to the increase in water temperature and related productivity (Meynecke *et al.* 2006), although chlorophyll concentrations and surface temperature could not be included in our analyses because of restrictions with data. In SEQ, dramatic increases in phytoplankton biomass have been reported to occur each spring, with little inter-annual variability; thus, these regular spring blooms may attract large marine animals (Lee *et al.* 2018). Furthermore, as most elasmobranchs are ectothermic (excluding lamnid sharks), the energy requirements of thermoregulation would be reduced by remaining within their thermal preference (Lee *et al.* 2018; Elston *et al.* 2022). Owing to similar morphologies within some taxonomic groups of elasmobranchs, the ability to identify to a species level was limited; thus, analysis of temporal variation was restricted to more generalised taxa.

Manta rays and leopard sharks exhibited strong temporal variation, with high detections in September and December respectively. These results are consistent with those of Couturier *et al.* (2011) and Dudgeon *et al.* (2008, 2013), who reported strong seasonal aggregations over the austral spring and summer in SEQ from photo-identification surveys and acoustic tracking. It is apparent that these species show the same temporal preference in the photo-ID work and acoustic tracking as they do in drone sightings, providing valid resolution for seasonal comparisons. Given the congruence of the leopard shark and manta ray data, this provides support for temporal patterns shown in the drone data for other species.

Indo-Pacific bottlenose dolphins are resident to North Stradbroke Island (Chilvers and Corkeron 2003) and, therefore, the increased sightings in spring–summer may be associated with mother–calf pods, because an increase in calving generally occurs at this time of year (Hawkins and Gartside 2008). Additionally, the variation (composition, size, movement) of dolphin pods may change routinely depending on the availability of prey, habitat type, reproductive state, behaviour and time of day (Chilvers and Corkeron 2003; Kelaher *et al.* 2020).

In general, this study found limited temporal influence on large pelagic fish assemblages off the coast of SEQ, Australia. Peaks in large fish abundance occurred in September at North Stradbroke Island. More research and ability to identify fish down to a species level is required to better understand the spatio-temporal variation in this region.

Environmental factors influencing the sightability of marine megafauna

Unless optimal conditions (e.g. calm, clear, shallow water <5 m deep) occur in all drone flights, the presence and detectability of megafauna can be influenced by environmental factors. Environmental factors including turbidity, rainfall, month and location can influence the probability of sighting marine megafauna off sandy beaches during aerial surveys (Fiori *et al.* 2017). Cumulative rainfall over the previous week can influence turbidity levels, contributing to a lag in correlation. High rainfall can lead to large plumes of organic materials from rivers and stir up bottom sediments, thus decreasing visibility into the water column. Therefore, detection probabilities of benthic organisms (e.g. rays) and fauna exhibiting diving behaviour are reduced (Hodgson *et al.* 2013). A similar result was reported in a recent New South Wales study, which indicated that turbidity had a strong negative influence on megafauna detectability (Butcher *et al.* 2019). Although rainfall had a negative relationship with megafauna sightability because of the connection with turbidity, it is known that rainfall has positive links with the coastal environment by increasing productivity (Schlacher *et al.* 2008; Connolly *et al.* 2009).

Warmer temperature and relative productivity during summer are plausible contributors to the higher detection of non-air-breathing megafauna during these months. The slightly higher sightings of air-breathing fauna during winter may be linked with annual whale migrations (Noad *et al.* 2006), and warmer ocean temperatures than in the sheltered Moreton Bay (Zeh *et al.* 2018). Temperature has been found to affect megafauna sighting rates in other drone-based studies, with higher rates being observed with an increasing temperature (Ayres *et al.* 2021; Elston *et al.* 2022). However, in the current study this did not have a significant influence on the sightability of marine megafauna. Other influencing factors include sea state, cloud cover, glare and time of day, although these effects were also not significant in this study (Hodgson *et al.* 2013; Colefax *et al.* 2018). Group size can also play a role in detecting megafauna (Dudgeon *et al.* 2018), because groups are more likely to be detected by pilots than individuals.

Future applications

Although drone technology offers new opportunities for marine megafauna detection off coastal beaches, there are a number of caveats in the data that must be acknowledged.

The inability to determine whether it is the same animal being sighted on multiple flights or different animals is a limitation in this study, because drones cannot identify individual animals. The impact of water clarity on faunal sightability is another limitation faced. Although no megafauna may be detected on days with low clarity, it is possible that these animals are still present.

Owing to the wide range of marine megafauna observed in this drone study, there is a significant opportunity to conduct further research on specific species or groups. The ability to identify temporal trends to a valid resolution with drones also provides a useful tool that can be applied globally to document spatio-temporal patterns of megafauna. Additionally, the implementation of drone image-analysis software on a global scale can provide further insights into the habitat use of threatened species. This knowledge plays an important role in the conservation of threatened species, because it can assist in population estimates, guide management decisions, contribute to citizen science and inform the designation of marine protected areas by identifying critical habitats used by marine megafauna.

Supplementary material

Supplementary material is available [online](#).

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Data availability. The corresponding author can provide the datasets used in this study upon reasonable request.

Conflicts of interest. Christine Dudgeon is an editor for *Marine and Freshwater Research* but did not at any stage have editor-level access to this manuscript while in peer review, as is the standard practice when handling manuscripts submitted by an editor to this journal. *Marine and Freshwater Research* encourages its editors to publish in the journal and they are kept totally separate from the decision-making processes for their manuscripts. The authors have no further conflicts of interest to declare.

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