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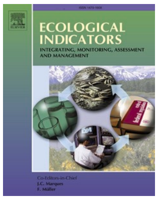

Original Articles

Sparse seagrass meadows are critical dugong habitat: A novel rapid assessment of habitat-wildlife associations using paired drone and in-water surveys

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ABSTRACT

Understanding the fine-scale behavioural and feeding ecology of marine megafauna is imperative for effective management of their habitat areas; however, obtaining the relevant data can be both costly and challenging. Here we integrate the use of small drones for dugong surveys with underwater benthic habitat assessment techniques at the local spatial scale (~30 km^2), to determine the drivers of dugong (*Dugong dugon*) distribution across three locations in the Pilbara, Western Australia. Paired assessment data was collected three times over two years. Benthic habitat (percent cover), seagrass nutritional quality and environmental parameters (temperature, water clarity, water current, water depth) were tested as predictor variables using generalised linear models, to examine drivers of both dugong presence/absence and abundance. We found that low cover (typical for this region; 2–10 %) of colonising seagrass is a key driver of the presence and abundance of dugongs. *Halophila ovalis* and *Halodule uninervis* were the main predictors of dugong presence and abundance across the three locations surveyed. Where both seagrass species simultaneously occurred, the likelihood of dugongs being present increased by over 60 times. The presence of *H. uninervis* alone was predicted to increase the abundance of dugongs by 1.4 times across all locations and by 6.8 times in one location, Exmouth Gulf, compared to when no seagrass was present. This study provided evidence of critical seagrass habitat, which is important knowledge for the protection and conservation of dugongs and their foraging habitat. The methods developed in this study could be employed in environmental impact assessments to predict and confirm potential seagrass forage habitat.

1. Introduction

Forecasting the response of wildlife to direct and indirect effects of anthropogenic activities is one of the most pressing challenges for environmental management agencies this century (Brook et al., 2008). Marine megafauna play significant roles in shaping ecosystems (Atwood et al., 2015; Marsh et al., 2018), and are considered valuable indicators of marine habitat condition as their presence or absence is typically reflective of the distribution of their preferred habitat (Hays et al., 2018; Hooker & Gerber, 2004). Monitoring marine megafauna to inform future conservation strategies requires an understanding of the links between their distribution and habitat characteristics and how megafauna use the habitat. Obtaining this understanding is difficult, particularly where there are spatial mismatches between datasets on species distribution and the underlying habitat. For example, data on marine megafauna distribution is often collected at large-spatial scales (100's-1000's km^2; Hammond et al., 2021), whilst the drivers of distribution may be better understood by investigating fine-scale habitat characteristics (1's–10's

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km^2; Johnston et al., 2005). In addition, marine megafauna are mobile species and their habitats vary over time, so investigations into the links between the two require data that are temporally synchronised (Hays et al., 2016). Small drones have been described as a promising tool for obtaining fine-scale distribution data (Christie et al., 2016; Cleguer et al., 2021) particularly if paired with fine-scale habitat assessment methods.

This study focuses on dugongs (*Dugong dugon*), a herbivorous marine mammal that is listed as Vulnerable to extinction at a global scale on the IUCN Red List, and in many regions (East Africa, India, most of South-East and East Asia) is considered Critically Endangered (Marsh et al., 2011). Here we assess how dugongs use their habitat at a fine spatial scale (10's km^2) that is ecologically meaningful to foraging dugongs, to aid in understanding what habitat characteristics are driving their distribution, and whether these characteristics can be used to predict dugong distribution, or what dugong distribution can tell us about their underlying habitat. An understanding of these links will help inform local management activities to ensure they are effective at reducing or mitigating pressures on dugong and their habitats. Further, understanding these links could assist in the design of long-term monitoring programs, environmental impact assessment and the structure or zoning of marine protected areas.

Dugongs generally occur in shallow, sheltered waters, overlapping with their preferred foraging seagrass habitat (Gales et al., 2004). Previous research suggests that dugongs select their habitat based on factors such as, seagrass species composition, biomass and nutritional content as well as other environmental influences such as tidal movement (Gales et al., 2004; Nowicki et al., 2019). The factors influencing dugong habitat use vary depending on the location, season or episodic events (Green & Short, 2003; Marsh et al., 2018). For instance, studies conducted in Queensland, Australia, inferred that dugongs favour colonising seagrass genera with low biomass, such as *Halophila ovalis* and *Halodule uninervis* (Aragones et al., 2012; Preen & Marsh, 1995; Sheppard et al., 2010), over larger persistent seagrasses. However, there are examples that contradict this trend, such as in the Torres Strait, where dugong populations target *Thalassia hemprichii*, a persistent seagrass species with high biomass (André et al., 2005; Johnstone & Hudson, 1981; Marsh et al., 2011). The nutritional requirements of dugongs remain largely unknown, though the nutritional quality of seagrasses may influence foraging selection (Sheppard et al., 2010). Research in Shark Bay demonstrated that dugong diet varies seasonally, with dugongs feeding on *H. uninervis* in shallow waters during summer months and shifting their home range to warmer temperatures in deeper water during winter months where *Amphibolis antarctica* and *Halophila spinulosa* are the predominant food source (Anderson, 1994; Holley et al., 2006). Other environmental factors, such as tidal currents and temperature, can influence dugong movements between foraging and resting sites (Cleguer et al., 2015; Preen & Marsh, 1995; Zeh et al., 2018).

Many factors can influence how dugongs select and use their habitat at any given time and location, but quantifying the factors that influence dugong habitat selectivity and use requires complementary data on habitat characteristics at the same spatial scale. Until recently, the most common method for assessing dugong distribution and abundance was observer-based aerial surveys, which are conducted over large spatial scales (e.g., Cleguer et al., 2015; Gales et al., 2004; Marsh & Sinclair, 1989), meaning they are not suitable for fine-scale assessments of wildlife-habitat associations. Insight into the fine-scale habitat use of dugongs has previously been obtained through animal-borne telemetry tracking devices (see Preen, 1992; Sheppard et al., 2007, Sheppard et al., 2010; Wirsing et al., 2007). However, this technique is typically limited to only a few tracked dugongs making it difficult to infer meaningful patterns between dugong populations and the habitat. Further, where both dugong distribution and environmental characteristics have been assessed, there is often a temporal mismatch in the data (i.e., the habitat data is often collected at a different time to the animal distribution data e.g., Cleguer et al., 2020). Thus, paired, rapid assessment techniques that align the collection of habitat data with animal distribution data would greatly assist in understanding fine-scale habitat use. This is particularly important for species like dugongs that rely on seagrass habitat that is highly dynamic and can change over short temporal scales such as over seasons or in response to disturbance events (Loneragan et al., 2013).

The relatively recent and rapid advances in imaging technology and the emergence of drones has provided the opportunity to develop repeatable small-scale wildlife surveys that are relatively affordable and easy to conduct (Cleguer et al., 2021). This study used a combination of drone surveys and in-water sampling methods to test for associations between dugong presence and key habitat characteristics, as well as to identify preferred dugong habitat in the Pilbara region of Western Australia. Currently, conservation of dugongs in this region is informed by broadscale distribution of the species, with little understanding of how variability in critical habitat might impact dugongs at a fine spatial scale. The need to understand fine-scale habitat preferences for dugongs is exacerbated by rapid, cumulative and sustained coastal development in the Pilbara region, which has the potential to disturb dugong populations both directly (e.g., coastal development, vessel strikes) and indirectly (e.g., seagrass loss). Furthermore, the Pilbara region is prone to storms, cyclones and heating events (Loneragan et al., 2013; McMahon et al., 2020), where cataclysmic weather events have previously resulted in large fluctuations in seagrass meadows which have in turn been associated with large scale changes to the distribution of dugongs throughout the area (Gales et al., 2004; Prince, 2001). The purpose of this research was to (1) develop a rapid assessment method integrating drone surveys at a fine spatial scale with habitat assessment and (2) identify environmental drivers that could be predictors for dugong presence or abundance in the Pilbara region, Western Australia.

2. Methods

2.1. Study area and species

The Pilbara region is in remote Western Australia, approximately 1400 km north of the State's capital city, Perth (Fig. 1). It has a tropical to subtropical climate, and is a highly disturbed system, characterised by low and episodic summer rainfall driven by frequent cyclonic activity (Lough, 1998). Disturbance from cyclones is one of the major drivers of the regional marine ecosystem dynamics, including seagrass habitat (Loneragan et al., 2013; Zinke et al., 2018). The shallow subtidal seagrass habitats of the western Pilbara (Exmouth to Port Headland) are dominated by small, fast-growing species, which support iconic marine megafauna, including dugongs (McMahon et al., 2017a; Waycott et al., 2004). The seagrass in this region is variable in abundance, composition and condition over time (Loneragan et al., 2013). Meadows in this region are generally low in cover (<20 %). Although seagrass cover of up to 60 % has been observed locally, this is usually only for a short period of time (e.g. 1 (Feb 2015) out of 12 time points over a six-year monitoring period in Exmouth Gulf, where one seagrass species, *H. spinulosa,* exhibited a boom/bust cycle; McMahon et al., 2020). Therefore in a global context, the seagrass meadows in this region are sparse. This study was conducted across three locations: Exmouth Gulf, Mangrove Passage, and Regnard Island (Fig. 1). Dugongs in the Exmouth Gulf were last estimated in 2018 at 4831 ± 1,965 dugongs as part of a long-term data series, based on aerial surveys conducted in the region every five years since the 1980s (Bayliss et al., 2018). These surveys have identified consistent hotspots within the eastern parts of the Exmouth Gulf, which is a wide and semi-enclosed embayment (~4000 km^2) and was recently listed as an "Important Marine Mammal Area" (IUCN, 2022). Multiple aerial surveys conducted throughout 2012–2015 (Sobtzick et al., 2015) showed Mangrove Passage (herein 'Mangrove'), a shallow, relatively open passage along the mainland ~ 100 km north of Exmouth, to be frequently used by dugongs. The area around Regnard Island (herein 'Regnard'), is the most northern location and is adjacent

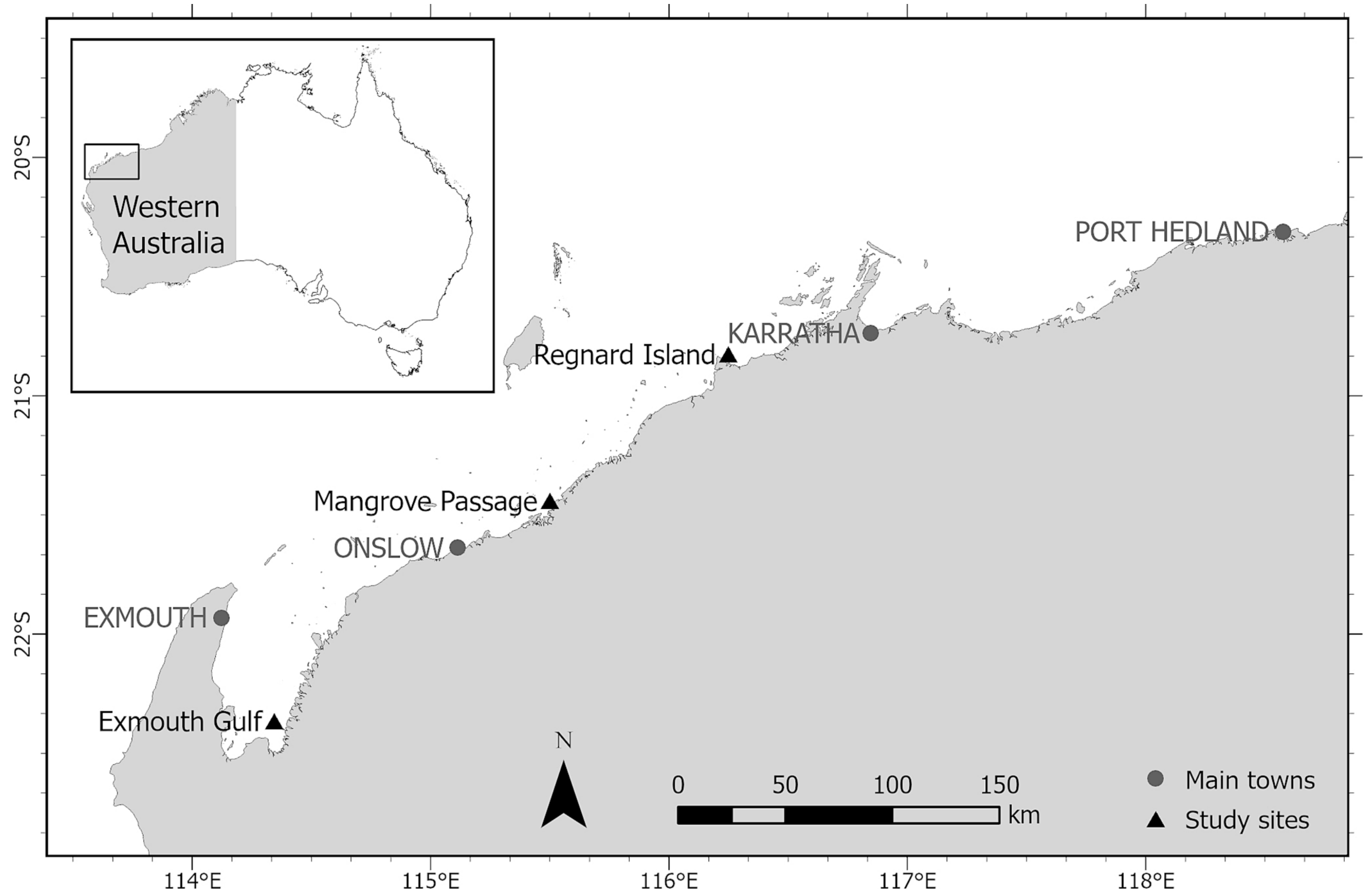


Fig. 1. The three study locations within the Pilbara region of Western Australia where drone surveys for dugong distribution were combined with biological and environmental characterisation to assess the drivers of fine-scale dugong occurrence and distribution.

to a port development at Cape Preston. Regnard, is slightly south of Dampier Archipelago, which has been recognised as an area for establishment of a marine conservation reserve, but is yet to be gazetted (CALM, 2005).

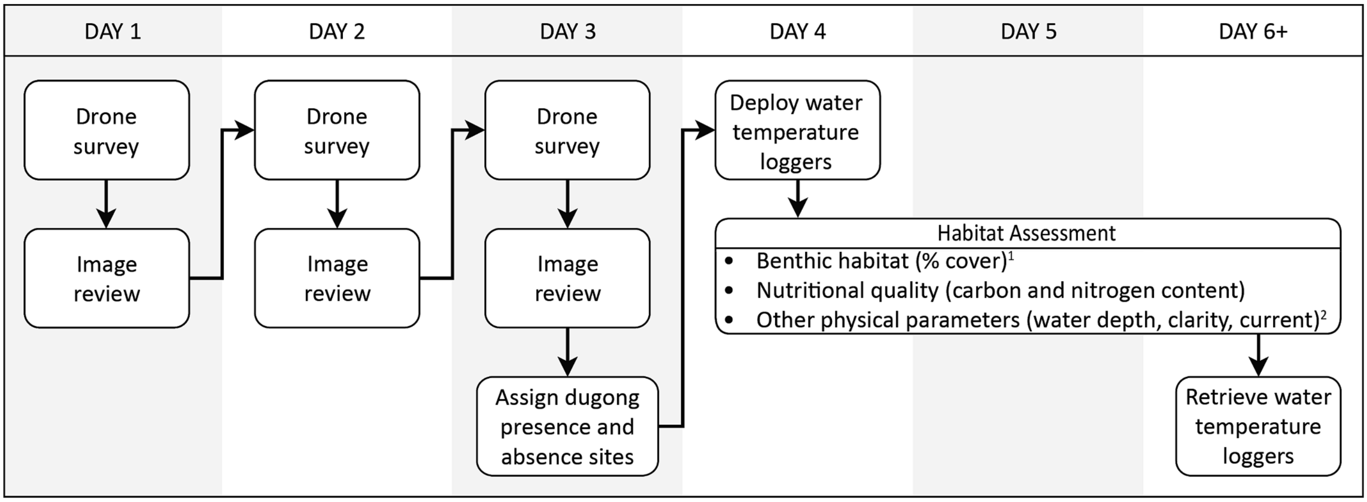
2.2. Study design

Dugongs were locally surveyed using small drones at the three study locations (Exmouth Gulf, Mangrove and Regnard; Fig. 1). A standard area (~30 km^2) was repeatedly surveyed two times in each location in May 2018 and November 2018, and a third time in June 2019 for Exmouth Gulf only, using either a standard line transect survey, or a gridded randomised approach (surveys are described in more detail below in Section 2.3). During each survey, an *in situ* rapid assessment (3-days of drone surveying) was performed to identify dugong presence or absence sites (n = 6–12) within each location and field time (month/year). Where dugongs were present, these sites are named 'presence', and where absent, these sites are named 'absence'. The number of sites varied depending on the abundance and distribution of dugongs (particularly the number of 'presence' sites) and the time available to perform aerial surveys, which was weather-dependent. Proportionally, based on drone surveys there were less dugong presence sites than absence sites, however, within the timeframe available it was not possible to sample all absence and presence sites in the same proportion. Therefore to best predict the drivers of dugong presence, at any one time, typically half of the sites within an area (n = 6–12 sites total) were defined as 'presence' (n = 3–6) and the other half as 'absence' (n = 3–6). Exceptions to this was in May 2018 at Exmouth, when four 'presence' sites were identified and only two 'absence' sites, and at Mangrove in May 2018 there were no dugong sightings and hence no sites could be assigned to assess dugong presence (limitation of one time point for Mangrove location). On a few occasions, opportunistic visual sightings of dugongs from the research vessel and the presence of dugong feeding trails in the benthic substrate/sediment detected during SCUBA diving for a concurrent project (assessing seagrass species and cover over time) were used to inform the selection of dugong presence sites (Mangrove and Regnard, November 2018; S1).

Each of the 'presence' and 'absence' sites (200 m^2) were then surveyed using an underwater camera system and environmental loggers to characterise the benthic habitat, nutritional quality and environmental features that could influence the presence or absence of dugongs (See Section 2.5). Surveys typically occurred over a 5 to 6-day period with a typical sequence of events demonstrated in Fig. 2. The exception to this was June 2019, where Exmouth Gulf was surveyed for a longer period (10 days) in order to collect more detailed dugong distribution and environmental data, as Exmouth Gulf had the highest dugong density (S1). These datasets were analysed using generalised linear models (GLM's) to predict the drivers of dugong occurrence and distribution at a fine-scale (~30 km^2).

2.3. Unmanned aerial surveying and mapping

Most dugong aerial surveys employed a grid sampling design, where two Phantom 4 Pro (DJI Technology Co., Ltd) drones were flown simultaneously. Surveys were conducted from a vessel under standard operating conditions set by the Australian Civil Aviation Authority (CASA; i.e., within visual line of sight flight and not above 400 ft above ground level). This novel approach was developed for this project and is described in Cleguer et al. (2021). This approach allows for reasonable sized survey areas (10's km^2), despite aviation regulation constraints and



Notes:

1. Benthic habitat was assessed using an underwater towed camera system.
2. Other physical parameters (water depth, water clarity, and current speed) were assessed in lieu of nutritional quality in June 2019 at Exmouth.

Fig. 2. Conceptualisation of paired drone dugong survey and in water habitat assessment conducted at Exmouth Gulf, Mangrove and Regnard locations from 2018 to 2019.

the limited flying capabilities of small, multirotor drones. The grid cells (700 × 700 m) were sampled in random order one or more times and the sample rate was 100 % (i.e., each grid cell was completely covered in the imagery).

As an alternative, a hybrid fixed-wing drone using a traditional line transect survey approach was also utilised. As a result of: (1) obtaining permission to fly beyond visual line of sight and up to 800 ft above ground level (i.e., outside the Australian standard operating conditions), and (2) the greater range, endurance and sensor capabilities of this drone, the surveys could be conducted at larger spatial scales (50–100 km^2) than the small multirotor (Cleguer et al., 2021). This approach allowed for locations to be sampled in a similar way to traditional dugong population surveys that use planes (Marsh & Sinclair, 1989), i.e., the survey 'blocks' (3 × 3 km edge size) were partially covered in the imagery (the sample rate was 25–38 % for surveys flown at altitudes of 160 and 240 m respectively) to optimise the spatial extent of the surveyed area rather than obtaining full imagery cover of a block. Drone specifications and survey design are shown in Supplementary 2.

All the images collected during the surveys were manually reviewed post flight by trained observers using the first iteration of WISDAM, a customised image review program written in Python 3.7, standardising the manual processing method (©Martin Wieser; Cleguer et al., 2021). Each image was analysed by one observer and if dugongs were detected, the identification was confirmed by a dugong expert. The position of each dugong sighting was mapped in GIS. Only the dugong sightings qualified as 'certain' were retained for mapping and analyses.

2.4. Selecting dugong presence and absence sites

The dugong distribution maps were assessed to identify the distribution of dugongs over the survey area. The process of selecting and defining 'presence' and 'absence' sites varied depending on the number of dugongs detected from the drone surveys or visual sightings. Priority was given to 'presence' sites with the highest count of dugongs identified within a block (WingtraOne surveys) or grid cell (P4Pro surveys), ranging from 1 to 11 dugongs (S1). If there was only a single dugong sighting, the position of that sighting was used as the centroid of the 'presence' site. If multiple dugongs were observed in a cell, we prioritised the centroid of the 'presence' site to where the maximum number of dugongs were observed together. If dugongs were not observed together in a block or grid cell, then we randomly selected one of the sighting positions as the centroid of the 'presence' site. Where there were more than 6 dugongs per cell, which occurred in May 2018 in Exmouth Gulf, a kernel density analysis (using the Spatial Analyst tool in ArcGIS version 10.4.1, Esri® 2016) was used to identify 'presence' sites with a 200 × 200 m square prediction grid. In this case we selected four 'presence' sites that ranged from 2 to 11 dugongs per cell (S1).

For all locations and field seasons, 'absence' sites were randomly chosen among the cells that had been surveyed with no dugong sightings. On three occasions, grids that had been defined as 'absence' sites were resampled, and none of these sites subsequently had dugong sightings (S1). On six occasions, grids that had been defined as 'presence' sites were resampled and half of these still had dugong sightings (S1). For the purposes of this study, they remained as 'presence' sites based on dugongs being sighted in the initial surveys of these sites. Where 'presence' sites still had dugongs present, only dugong counts from the first survey time period were used for analysis. A 'presence' site does not imply that a dugong was feeding in that area; it may have been feeding, resting or transiting. On some occasions there was clear evidence of feeding when a feeding plume was visible near a surfacing animal, however, it was not always possible from the aerial imagery to determine if a dugong was feeding. An 'absence' site was defined as an area where dugongs were not detected during the period of the survey. However, there may have been dugongs present but 'unavailable' (submerged too deep/in turbid waters) for detection during the surveys. It is important to note that an 'absence' site identified during drone surveys does not necessarily mean dugongs never use these areas. Once the sites were selected, they were assessed to characterise the benthic habitat and environmental features that could explain the distribution of dugongs.

2.5. Environmental variables to assess dugong distribution

A range of variables were collected at each of the 'presence' and 'absence' sites. The composition of the benthic habitat (percent cover) and the water temperature were recorded at all sites and on all occasions (S3). Benthic nutritional quality based on the carbon and nitrogen content was assessed in May and November 2018 for all locations (except Mangrove in May 2018). In June 2019, when only Exmouth Gulf was sampled, additional environmental variables that could potentially explain the distribution of dugongs were measured: water depth, water clarity and water current speed at the time of drone sampling and dugong detection.

To assess the benthos composition and percent cover, an underwater camera system (Deep blue HD- Ocean Systems™) was used to survey 3 × 100 m transects in a 200 m^2 area to assess potential for continuous habitat including seagrass meadows. The start of each transect was selected using a randomly generated bearing and distance from the centroid of the site. The GPS track was recorded along the transect and the underwater camera system towed behind the vessel at 0.5–1 km hr^{-1}. The camera angle was partially forward facing, and therefore the entire area surveyed in each transect was ∼1 m wide and 100 m long. Real time footage was streamed to the surface and every 5 m the percent cover of seagrass species and algae phyla were visually assessed on the live stream by the same person, resulting in 20 data points per transect. Seagrass species recorded were *Halophila ovalis*, *Halodule uninervis*, *Syringodium isoetifolium*, *Cymodocea serrulata*, *Halophila spinulosa*, and additional categories of green algae and brown algae. The data recorded in the field were confirmed by checking the recorded video footage on return to the laboratory post field trip.

Samples for the nutritional quality of macrophytes (seagrass and algae) were collected to assess their carbon and nitrogen content. Five samples of each dominant macrophyte species (determined from towed video analysis) were collected at each site and frozen at −20 °C. Each macrophyte species was not always represented in samples collected at each site and time, therefore, to ensure there was enough sample to conduct the analysis, samples were pooled within each site at each time. However, not all ‘absence’ sites contained all species, so for some locations and field times, there were no samples for benthic habitat nutritional quality. Only the seagrass species *H. uninervis* and *H. ovalis* which from preliminary analyses were shown to be important predictors for explaining dugong distribution based on percent cover data were analysed for nutritional quality. In the laboratory the samples were defrosted and rinsed briefly in freshwater. Whole seagrass plants comprising above and below-ground material consisting of at least 3 nodes with leaf pairs/shoots were extracted and dried at 60 °C for 48 h, then ground with a mill-ball grinder. Above- and below-ground material was pooled for analysis, as dugongs commonly feed on whole plants when they furrow through seagrass meadows. The samples were analysed for %N and %C using a continuous flow system Delta V Plus mass spectrometer connected to a Thermo Flush 1112 via Conflo IV (Thermo-Finnigan/Germany) (Coplen et al., 2006; Skrzypek, 2013; Skrzypek & Paul, 2006). C (%), N (%) and the C:N ratio values were extracted. As samples were pooled, there was only one measurement per site and time for each variable.

At each site, HOBO temperature loggers (range −20 to 50 °C, accuracy 0.47 °C) were deployed at both the bottom (∼0.1 m above bottom) and top (∼0.5 m below surface) of the water column at the centroid of the site. Temperature loggers were programmed to record every 15 min and were deployed for 2–5 days. Once loggers were retrieved, the data for all sites at each location and time were compared and a 24-hour time period that overlapped for all sites was selected (except 4 sites in June 2019 where no data were collected).

At Exmouth Gulf in June 2019, additional environmental data (water depth, water clarity and water current velocity) were collected during each drone survey, to capture real-time environmental conditions. These measurements were taken at the centroid of the drone survey area. Water clarity was measured with a Secchi disk (m) and water depth was measured using a depth sounder. A standardised measure of water transparency was calculated by dividing the Secchi disk measurement by the water depth, as on many occasions the Secchi disk was visible on the bottom. Ocean current speed (m/s) was assessed at the surface (0.1 m deep) and mid-water column using a drogue. On some occasions we were not able to collect water and Secchi depth (two drone survey sites) or current speed (three drone survey sites).

2.6. Statistical modelling

The dugong distribution was described in two ways; as a binomial outcome, i.e., ‘presence’/‘absence’ of dugongs, or as the number (abundance) of dugongs recorded from each site from the original survey period. Two generalised linear models (GLM’s), 1) logistic binomial regression for the dugong ‘presence’/‘absence’ data, and 2) negative binomial regression for the count data, were used to assess the relationship between dugong distribution and the biological and physical variables. Of all the independent or predictor variables, only benthic habitat and water temperature data were collected at all locations (Exmouth Gulf, Mangrove and Regnard) and field times (May-18, Nov-18, Jun-19). The additional nutritional quality data were collected in two field times (May-18, Nov-2018) and the additional water depth, clarity and current data were only collected at Exmouth Gulf in June 2019. Therefore, matching subsets of dugong data were used to model the association with these sets of variables as outlined in Table 1, resulting in a set of six models.

Table 1

A summary of models tested with two different dependent variables (‘presence’/‘absence’ of dugongs (+/-) or the count of dugongs), and the predictor variables that were assessed in each of the six GLM’s data subsets. Refer to S3 for the full list of the predictor variables. Location had three categories (Exmouth Gulf, Mangrove, Regnard), Time (month/year) had three categories (May 2018, November 2018, June 2019), and the number of sites varied depending on Location/Time. # of predictor variables refers to those after correlated variables were removed (S4).

🌱 Benthic habitat 🌡 Water temperature C:N Benthic quality 🌀 Other physical parameters

Data subset #	Dependent variable	# of observations	Location/Time/Number of Sites						# of predictor variables	# of significant predictor variables
			Exmouth Gulf			Mangrove	Regnard			
			May-18	Nov-18	Jun-19	Nov-18	May-18	Nov-18		
			6	8	12	6	8	6		
1	+/-	46	🌱 🌡	🌱 🌡	🌱 🌡	🌱 🌡	🌱 🌡	🌱 🌡	8	2
2	Count	46	🌱 🌡	🌱 🌡	🌱 🌡	🌱 🌡	🌱 🌡	🌱 🌡	8	2
3	+/-	34	🌱 🌡 C:N	🌱 🌡 C:N		🌱 🌡 C:N	🌱 🌡 C:N	🌱 🌡 C:N	15	4
4	Count	34	🌱 🌡 C:N	🌱 🌡 C:N		🌱 🌡 C:N	🌱 🌡 C:N	🌱 🌡 C:N	15	7
5	+/-	12			🌱 🌡 🌀				13	1
6	Count	12			🌱 🌡 🌀				13	3

Before input into models, variable selection was undertaken by assessing co-correlation, individual variable GLM, and log likelihood ratio tests. If variables were identified as being correlated (>0.7), then only one was used during variable selection. Correlated variables were total seagrass cover with seagrass species cover, total algae with algae genera, water temperature across the water column and water current across the water column. For benthic habitat variables the individual seagrass species and algae genera were retained, and for environmental parameters the average bottom water temperature, and mid-surface current (where dugongs are likely to spend more time) were retained. For each data set identified in Table 1, a GLM was performed for each individual covariate including the factors of Location and Time for models 1–4. If a particular covariate significantly ($p < 0.05$) explained differences between presence and absence sites, then it was selected to be included in the initial GLM. Secondly, a log likelihood ratio test was performed against the null model for each covariate, and if this significantly explained the differences between the 'presence' and 'absence' sites this variable was also included in the model. The factors Location and Time (month/year) were also included in the final models, except models 5 and 6 where predictor variables were only sampled at one Location and Time.

The GLM's were performed in R (version 3.6.1) for each data set identified in Table 1, using the glm() function in the package MASS, and the lrtest() function in package lmtest (Zeileis and Hothorn 2002). For datasets with missing values, where possible the average of the variable across sites (within a Location and Time) was used, and in some cases where there was one value for benthic habitat quality data, this value was used to represent sites within a survey. To adjust for low sample size the Akaike Information Criterion Correction (AICc) was calculated to compare models (Burnham & Anderson, 2004). The stepwise function was used with all appropriate predictor variables and their interactions, as well as the factors Location and Time were tested, and the most parsimonious model selected based on the lowest AICc within 2 units (Burnham & Anderson, 2004). Final models, including interactions terms can be seen in Table 2. For the predictor variables that significantly explained the dependent variable, their odds ratios (ORs; for binomial regression model) or incidence rate ratios (IRRs; for negative-binomial regression model) and the corresponding confidence interval (CIs) were calculated. Where the factors Location or Time were identified as predictors in the supported model, the levels in each model were tested to identify which Locations or Times were best supported and the ORs or IRRs calculated on these.

3. Results

3.1. Benthic habitat and temperature variables

Section 3.1 assesses data subsets 1 and 2 (Table 1, S4), which incorporates benthic habitat variables (*H. ovalis, H. uninervis, C. serrulata, S. isoetifolium, H. spinulosa*, green algae, brown algae) and water temperature at all locations and time points.

Generalised linear modelling identified the optimal model for predicting dugong presence across all locations and times included *H. ovalis* (Ho) and *H. uninervis* (Hu) (subset 1; Table 2). The interaction of the two variables was significant in explaining dugong presence ($p < 0.039$) and increased the odds of dugongs being present by 60 times (OR, 95 % CI 1.2–3009) (Table 2, Fig. 3a). *Halophila ovalis* and *H. uninervis* were generally the dominant seagrass species at the dugong 'presence' sites across all locations and times, with the average mean cover of the two species combined being 2–10 % at the dugong 'presence' sites, compared to 0.1–2 % at the dugong 'absence' sites. Total seagrass cover of all species at the dugong 'presence' sites ranged from 4 ± 2 to 11 ± 7 %, higher than at the dugong 'absence' sites (0.1 ± 0.2 to 4 ± 5 %, respectively; S5).

The optimal model for predicting dugong abundance across all locations and times was *H. uninervis* (subset 2; Table 2). Generally, when there was a higher cover of *H. uninervis* within a location or time there was a greater number of dugongs, with the potential to increase the incidence of dugongs by 1.35 times (IRR, 95 % CI 1.1–1.6).

3.2. Benthic habitat, temperature and nutritional quality variables

Section 3.2 assesses data subsets 3 and 4 (Table 1, S4), which incorporates benthic habitat variables (*H. ovalis, H. uninervis, C. serrulata, S. isoetifolium, H. spinulosa*, green algae, brown algae), water temperature, and nutritional quality (Ho %N, Ho %C, Ho %C:N, Hu %C, Hu %N, Hu %C:N) at all locations and time points, except Exmouth in June 2019.

When nutritional quality was added as an additional predictor (to benthic cover of species and water temperature), across all locations the optimal predictive model for dugong presence included *H. ovalis* cover, the C:N ratio of *H. uninervis* (Hu C/N), and Time (subset 3; Table 2). The C:N ratio of *H. uninervis* was significant, with a higher C:N ratio associated with dugong presence sites (OR, 1.14 % CI 1–1.3), which was most obvious in Nov-18 (Fig. 3b). Generally, across most locations and times the %N values were low (<1 %), however *H. uninervis* plants at 'absence' sites tended to have a slightly higher %N (although not significant) than at 'presence' sites (0.86 ± 0.19 % vs. 0.65 ± 0.24 % DW; S6). The 'presence' sites had a higher C:N ratio compared to the 'absence' sites, 67.6 ± 21 % DW and 47.7 ± 16.3 % DW, respectively. Although *H. ovalis* (Fig. 3c) was not a significant predictor, it was included as a factor within the most parsimonious model and had a higher odds ratio than nutritional quality C:N ratio of *H. uninervis*, 9.4 (IRR 95 % CI 0.8–113), and 1.14 (IRR 95 % CI 1–1.3), respectively.

For dugong abundance, the optimal model included the same variables as the 'presence/absence' GLM (Ho, Hu C/N, Time), as well as additional variables *Syringodium isoetifolium* (Si), Green algae and Location (Subset 4; Table 2). Cover of seagrass species as well as Location and Time significantly improved the model fit. Greater *S. isoetifolium* and *H. ovalis* cover increased the likelihood of dugongs being present by 2.6 (IRR 95 % CI 1.5–4.6) and 1.15 (IRR 95 % CI 1–1.3) times, respectively. The effects of Location and Time are based on the higher dugong counts at Exmouth Gulf compared to the other two locations, and the lower number of dugongs in November 2018 compared to other times.

3.3. Benthic habitat and physical parameter variables in Exmouth Gulf

Section 3.3 assesses data subsets 5 and 6 (Table 1, S4), which incorporates benthic habitat variables (*H. ovalis, H. uninervis, C. serrulata, S. isoetifolium, H. spinulosa*, green algae, brown algae), water temperature, water current, water depth, and water transparency at Exmouth in June 2019.

When assessing dugong 'presence' and 'absence' in Exmouth Gulf the optimal model included only *H. uninervis* cover (subset 5, Table 2, Fig. 4a). *Halodule uninervis* cover was 10-fold greater at dugong presence sites (2 ± 2 compared to 0.2 ± 0.5), with the odds of dugongs being present 6.8 times (OR 95 % CI 0.7–10.6) greater with increased *H. uninervis*.

When assessing the abundance of dugongs, the optimal model only included the variable mid-surface current speed (subset 6, Table 2). More dugongs were present where the mid-surface current speed was lower (Fig. 4b). Although this was significant, the current speed increased the dugong counts by a minute factor (0.000008 to 0.04 based on the upper limit of the 95 % CI).

4. Discussion

This study has successfully developed a new method to assess paired fauna and habitat data in real-time to produce more ecologically relevant data on how megafauna use their habitat, which could be employed across both marine and terrestrial habitats. Combining highly accurate fine-scale drone surveys with spatially and temporally matched *in-situ*

Table 2
GLM modelling showing the best supported models based on AICc for benthic habitat, nutritional quality and environmental parameters to explain dugong presence and density. n: number of independent observations, ‘x’ within model means variables had an interaction. Where Location and Time were predictors in the model, the variable significance determined where the differences within these factors were. Abbreviations: *Halophila ovalis* (Ho), *Halodule uninervis* (Hu), %Carbon:%Nitrogen (C:N), *Syringodium isoetifolium* (Si).

Data subset	GLM type	n	Model	AIC	AICc	Variable	P	OR/IRR (95 % CI)
1	Dugong presence: logistic binomial regression	46	Null	65.7	65.8	$\sim$1		
			Ho + Hu + Ho × Hu	44.11	45.1	Ho	0.75	1.21 (0.4–0.8)
						Hu	0.94	1.03 (0.5–2.4)
						Ho × Hu	**0.039**	60.6 (1.2–3009)
2	Dugong abundance: negative binomial regression	46	Null	158	158.3	$\sim$1		
			Hu	150.4	151.1	Hu	**0.0011**	1.35 (1.1–1.6)
3	Dugong presence: logistic binomial regression	34	Null	49.1	49.1	$\sim$1		
			Ho + Hu C:N + Time	27.4	28.9	Ho	0.0776	9.4 (0.8–113)
						Hu C:N	**0.0261**	1.14 (1–1.3)
						Time Nov-18	0.1042	0.02 (<0.01–2.2)
4	Dugong abundance: negative binomial regression	34	Null	113.2	113.6	$\sim$1		
			Ho + Si + Hu C:N + Green algae + Location + Time	94.7	102.2	Ho	**0.0024**	1.15 (1–1.3)
						Si	**0.0008**	2.6 (1.5–4.6)
						Hu C:N	0.137	1 (0.99–1)
						Green algae	0.132	0.84 (0.7–1)
						Location Exmouth Gulf	**0.032**	1.9 (1–7.9)
						Location Mangrove	0.471	1.6 (0.5–5.6)
						Time Nov-18	**0.00003**	0.18 (0.1–0.4)
5	Dugong presence: logistic binomial regression	12	Null	18.64	19.1	$\sim$1		
			Hu	13.92	15.3	Hu	0.11	6.8 (0.7–10.6)
6	Dugong abundance: negative binomial regression	12	Null	48.39	49.7	$\sim$1		
			Current mid-surface	44.74	47.7	Current mid-surface	**0.008**	<0.01 (<0.01)

physical and biological habitat characterisation has enabled us to identify drivers of habitat use by a marine megafauna species of high conservation value, the dugong. Of the variables assessed in this study, we found that seagrass is the only variable that can be used as a proxy to predict dugong distribution. Specifically, we found that *H. ovalis* and *H. uninervis* and the relative abundance of these two species (2–10 %), and in some cases, the nutritional content of these small colonising seagrass species (*H. uninervis)* best predicted localised-presence or abundance of dugongs across multiple locations and times in the Pilbara region. This study has provided evidence of critical seagrass habitat, which is important knowledge for the protection and conservation of dugongs and their key foraging habitat across the Pilbara, and potentially other locations, where coastal development and industry are on the rise.

4.1. Ecological insights

This study demonstrates the value of low cover seagrass meadows for predicting dugong distribution. It is clear from our findings that sparse meadows (2–10 % of *H. ovalis* and *H. uninervis* cover or 4–11 % of total seagrass cover) serve an important role as habitat for dugongs, a fact not intuitively recognised in assessments of the relative importance of seagrass meadows. Sparse seagrass meadows are typical in the Pilbara region, with seagrass monitoring areas surveyed typically having a total seagrass cover of 5–14 % cover (McMahon et al., 2020), and therefore, the values of seagrass cover used in our analysis are likely representative of the region. At larger spatial scales (than our study), there is no clear trend linking seagrass cover to dugong density due to the lack of data available at these spatial scales (Table 3), although in most cases it seems that where dugong populations have been associated with seagrass cover, dugongs prefer lower cover seagrass area, typically of colonising or opportunistic seagrass genera (Table 3). Dugong density in Exmouth, WA (1.21; 4831 dugongs in ~4000 km^2), is comparable to that of Shark Bay, WA (1.42; 18,555 dugongs in ~13,000 km^2) (Table 3). Shark Bay is the low temperature limit of the dugongs’ range and has the most expansive seagrass meadows in the world, supporting one of the largest dugong populations in Australia. In Shark Bay, where dugongs have a choice between small, low-biomass species (i.e. *Halodule* spp. *and Halophila* spp.) and large, higher-biomass species (i.e. *Amphibolis* spp. *and Posidonia* spp.), dugongs prefer low-biomass species in summer, but in winter, shift their home range to deeper and warmer temperatures where larger species (i.e. *Amphibolis antarctica*) are the main seagrass available and becomes their predominant diet (Anderson, 1986; Holley et al., 2006). Recently, Bayliss et al. (2019) found a correlation between high density dugong areas and low seagrass cover (≤40 %) for persistent species (i.e. *Amphibolis*) in Shark Bay, suggesting that an increase in persistent seagrass species biomass does not necessarily equate to increased foraging potential for dugongs. However, there was no comparison of abundance for smaller colonising species such as *Halodule* spp. and *Halophila* spp. for this region. Conversely, dugongs in Torres Strait, northern Queensland, are often found in high seagrass cover areas with structurally larger species like *Thalassia* (Marsh et al., 2011). This reaffirms that local (fine-scale) information on dugong density and foraging habits are critical to inform management at the local scale, which is typically the level at which environmental impact assessments are conducted.

The nutritional requirements of dugongs are largely unknown; however, research suggests that the nutritional quality of seagrasses may influence foraging patterns (Sheppard et al., 2010). This study found that in addition to seagrass cover, the nutritional content (C:N ratio of whole plant) of one of the colonising species, *H. uninervis,* also predicted the presence and abundance of dugongs. A number of grazers have been shown to preferentially select seagrass based on a lower C:N ratio indicating it is an important factor influencing herbivore choice of forage (Bakker et al., 2016; Heck & Valentine, 2006). Although dugongs are likely to be limited by nitrogen in their diet (Lanyon, 1991), it has not been verified as a major criterion for food selection. However, Sheppard et al. (2010) suggested that dugongs in Hervey Bay, Queensland fed more regularly in meadows with higher nitrogen and carbohydrate concentrations relative to other resources. Colonising seagrass species with a relatively high percentage of nitrogen and carbohydrates and low percentage of lignins and cellulose that are difficult to digest have been proposed as higher quality food for dugongs compared to

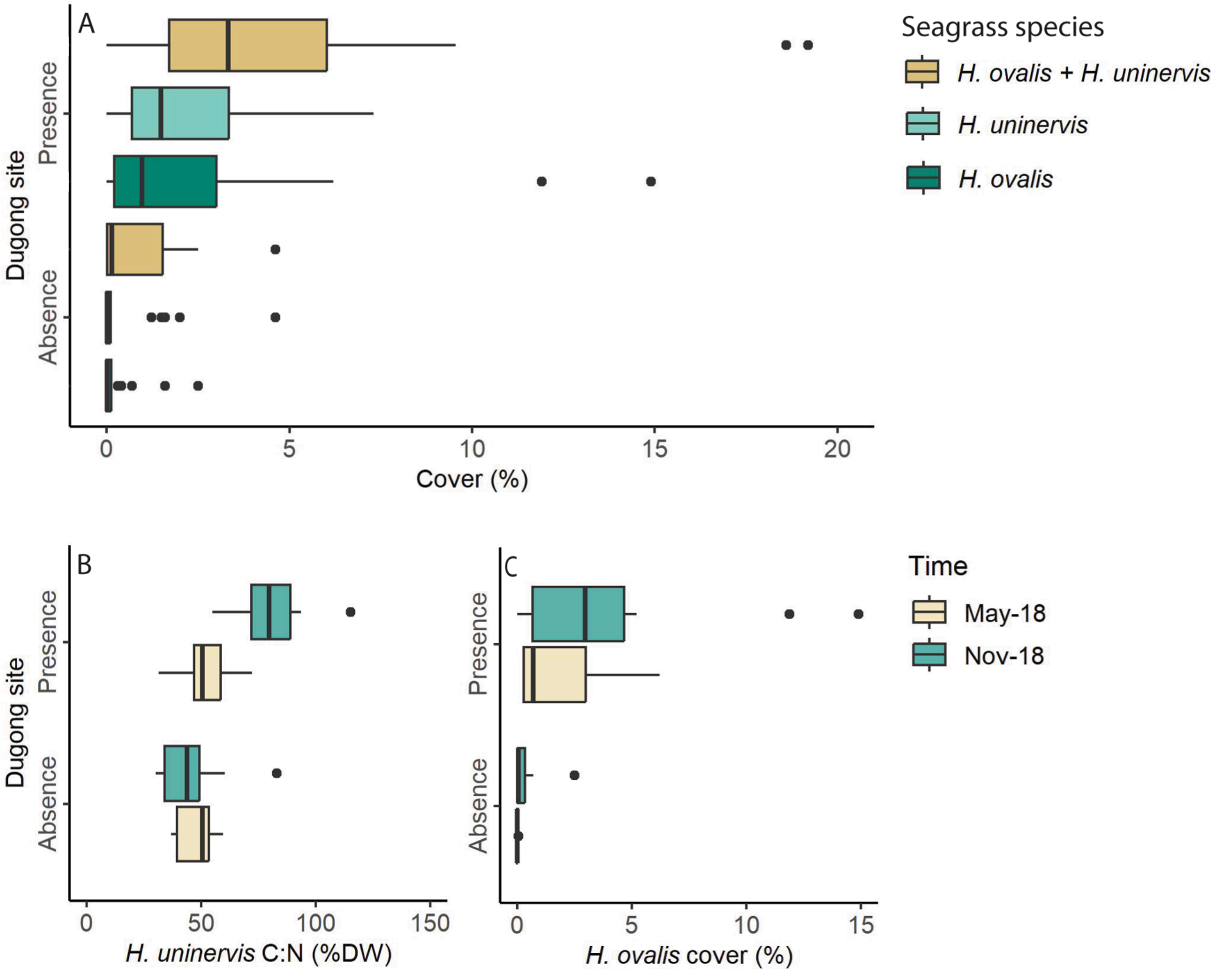


Fig. 3. Boxplots demonstrating the role of the key variables that explain the presence of dugongs in the Pilbara based on (A) Subset 1 data all locations and field seasons with benthic habitat and water temperature as potential predictors and Data subset 3 (B) *H. uninervis* C:N ratio and (C) *H. ovalis* cover, for all locations for May and November 2018 with the addition of nutritional quality predictors. Note scale differences on X-axes.

larger species (Aragones et al., 2012; Marsh et al., 2011; Sheppard et al., 2008). The meadows assessed in this study had relatively low nitrogen across all sites/locations (ranging from 0.65 ± 0.24 to 0.86 ± 0.19 for *H. uninervis*), compared to that of seagrasses targeted by the dugongs tracked in Queensland (*H. uninervis* 1.28 ± 0.05 %; Sheppard et al., 2010). Therefore, it is possible that dugongs in the Pilbara region, where nitrogen content is comparatively low across all sites/locations (compared to other regions), are selecting forage with greater carbohydrate content. Our results, combined with previous studies suggests that nutritional requirements play a role in how dugongs select their food, and this is likely to differ across locations which have varying nutritional quality or relative C:N content.

The effect of water current on the occurrence and abundance of dugongs has not been previously investigated at the fine spatial scale

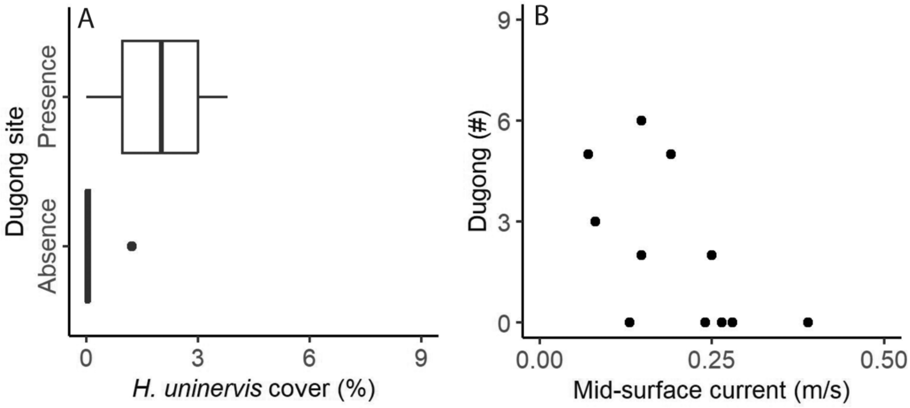


Fig. 4. Data from Exmouth Gulf, June 2019 showing a) The cover of *H. uninervis* at ‘presence’ and ‘absence’ dugong sites and b) the dugong abundance at mid-surface current.

Table 3
Dugong population estimates and densities (at known hotspots) with associated seagrass extent, cover, and species type, as well as percent cover of seagrass within an area associated with dugong populations where available.

Location	Location area (km^2)	Dugong Population estimate	Dugong density (km^2)	Method to correct for perception bias	Seagrass extent (km^2)	Seagrass cover	Seagrass life history	Seagrass % cover associated with dugong populations
Exmouth, WA	~4,000	4,831[1]	1.21	Pollock	NA	5–14 %[8]	C, O	~2–11 % (S5)
Shark Bay, WA	~13,000	18,555[1]	1.42	Pollock	8,900[4]	5->40 %[1]	C, O, P	<40 %[1]
Hervey Bay, QLD	~4,900	2,055 ± 382[2]	0.42 ± 0.08	Hagihara	2,300[5]	14 %[5]	C, O	<14 % cover[5]
Moreton Bay, QLD	~1,600	601 ± 80[2]	0.38 ± 0.05	Hagihara	179[6]	10–40 %[6]	C, O	<80 %, average 35 %[9]
Torres Strait, QLD	~3, 500	102,519 ± 20,146[3]	29 ± 5.8	Hagihara	13,447[7]	5–60 %[7]	C, O, P	NA

*Seagrass species life history: Colonising = C, Opportunistic = O, Persistent = P Following Kilminster et al. (2015).
References: Bayliss et al., 2019[1], Sobtzick et al., 2017[2], Hagihara et al., 2018[3], Strydom et al., 2020[4], Sheppard et al., 2007[5], Kovacs et al., 2018[6], Carter et al., 2023[7], McMahon et al., 2020[8], McMahon, 2005[9].

reported in this study. At larger-spatial scales, dugongs have been shown to coordinate their movements with tidal flow and potentially preserve energy when swimming between their foraging grounds and other habitats such as resting areas (e.g., Lanyon, 2003; Sheppard et al., 2009; Zeh et al., 2018). If dugongs are selecting areas with lower horizontal currents this could be beneficial in reducing energy expenditure when diving and feeding. In this study we found that dugongs preferred areas with lower current speeds relative to areas where no dugongs were detected. However, this variable was only assessed at one location and time and our findings would benefit from further enquiry.

4.2. *Conservation and management*

Emerging technology, such as drones have become an important tool in marine mammal research to assess the number of individuals in populations, body condition and biometrics, behaviour patterns and for collecting blow samples (Álvarez-González et al., 2023). We have demonstrated a successful approach for rapidly assessing associations between dugong distribution and a range of potential habitat predictors at a fine-spatial scale (~30 km^2) using drone technology combined with in-situ habitat sampling. This approach is applicable in populated and remote areas and can be achieved by operating from one to two small vessels. The spatial extent of our study area was mainly limited by permit (aviation) and boat safety restrictions.

We found consistent predictors of habitat-use by dugongs across locations with different environmental conditions at a relatively fine spatial scale and in a highly dynamic tropical setting. Such understanding is a key step to predicting how a species will respond to changes in their environment (Rodríguez et al., 2007). Even though two of the three locations had relatively low densities of dugongs, consistent predictors of their presence and abundance were still identified. These predictors (cover of *H. ovalis* and/or *H. uninervis*) were not only consistent at locations separated by ~500 km, but also over time (three field time periods ~6 months apart), providing confidence that they are ecologically meaningful and reliable. At a large spatial scale, small and sparse seagrass meadows, like those in the Pilbara region, are challenging to map using aerial imagery. Large-scale aerial surveys of dugong, however, are a standard methodological approach to assessing dugong distribution and abundance. Based on the strong relationship between seagrass presence and dugong presence/abundance shown in this study, there is potential to use dugong presence as a proxy for seagrass cover and/or health. This could be achieved by mapping dugong distribution, followed by benthic survey ground-truthing to create large-scale maps of seagrass diversity and cover. Our paired fauna-habitat rapid assessment method could be improved by employing deep learning artificial intelligence models for processing the drone imagery. Such models are currently being developed for dugong detection from imagery (Jahanbakht et al., 2024; Maire et al., 2015), and could be employed in the future to improve processing times.

To effectively manage existing seagrass habitat it is important to take resilience mechanisms of a species into consideration. Small colonising seagrass species have low resistance to disturbance but the potential to recover rapidly; in a study of the same species and in the same region as our study, Vanderklift et al. (2017) estimated that small patches (~0.5 m^2) of these seagrasses recover vegetatively within 2–3 months. However, if larger areas are lost, for example through cyclone events or heatwaves, the main mechanism of recovery would likely be recruitment from seed banks or floating fragments of seagrass, and the timescales of recovery could be longer (i.e., years; Evans et al., 2020). With a changing climate and predicted increased intensity and frequency of extreme climatic events (ECE's; Oliver et al., 2018) coupled with extensive coastal industrialisation (WAMSI, 2019), the Pilbara region may be more prone to reduced seagrass resilience and/or loss of seagrass habitat. Therefore, there is a need to minimise human impacts on the existing habitat to support this critical dugong population. One way to address this need is to change the concept of "significant habitat" in this region. McMahon et al. (2017b) reviewed dredging projects in north-west of WA from 2006 to 2011 and approximately 70 % (9/13) of these projects detected sparse seagrass within and surrounding the development footprint. Only one of those nine projects recommended monitoring seagrass as part of the development management plan. Seagrass cover within that project area was variable over time, and sometimes not detected, but when it was detected, the average cover was low (2–3.5 %). Based on our data for this region, this low cover of seagrass is likely targeted by dugongs and therefore important habitat. For the other projects where seagrass was detected, but not monitored as part of the management plan, low cover seagrass was not considered significant habitat and for species with a colonising life-history strategy it was suggested that they would have a high probability of recovery and therefore any seagrass loss would be insignificant. Contradicting this prevalent view, our work has highlighted that low cover (2–10 %) of colonising seagrass species is a key predictor of the presence and abundance of dugongs, clearly demonstrating the significance of low cover seagrass meadows as dugong habitat. Therefore, low cover of seagrass is not a valid reason to ignore seagrass habitat in environmental impact assessments, but rather, should be considered as an indicator of potential dugong habitat, if dugongs are known to occur in the area. Cumulative impacts on low cover seagrass meadows also requires consideration where multiple activities are occurring in the Pilbara Region. We recommend that environmental impact assessments should use appropriate methods, such as those presented in this study, to detect and inform the management of low cover seagrass.

CRediT authorship contribution statement

Nicole E. Said: Methodology, Project administration, Investigation, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Christophe Cleguer:** Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Paul Lavery:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Conceptualization. **Amanda J. Hodgson:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Connor Gorham:** Writing – review & editing, Investigation. **Julian A. Tyne:** Investigation, Writing –

review & editing. **Ankje Frouws:** Writing – review & editing, Investigation. **Simone Strydom:** Writing – review & editing, Investigation. **Johnny Lo:** Writing – review & editing, Methodology. **Holly C. Raudino:** Writing – review & editing, Project administration. **Kelly Waples:** Writing – review & editing, Project administration. **Kathryn McMahon:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2025.113135.

Data availability

Data online ECU repository: DOI:10.25958/42sw-xp64

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