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Dugong (*Dugong dugon*) movements and habitat use in a coral reef lagoonal ecosystem

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ABSTRACT: Little is known about how the Vulnerable dugong *Dugong dugon* uses coral reef lagoons despite the importance of these habitats throughout much of its vast range. We used GPS satellite tracking systems to explore the space use of 12 dugongs at 3 locations in the coral reef lagoons of the main island of New Caledonia in the southwest Pacific: Cap Goulvain, Ouano and Nouméa. The movements of the tracked dugongs varied among individuals and all except one animal undertook large-scale movements (>15 km; mean [±SE] 37.7 ± 5.2 km) from their capture location (maximum waterway distance range: 13.8 to 72.9 km). The straight-line distances between the furthest GPS locations during each animal's tracking period ranged from 21.3 to 74.5 km. We identified areas used intensively by dugongs in all 3 study areas, some of which were areas where seagrass presence has not been verified, or where dugongs have not been observed during past aerial surveys. Dugongs spent most of their tracking time within the lagoons, with 99.4 % of GPS locations found inside the barrier reef. Nonetheless, where the lagoon was narrow and confined, 3 tracked dugongs used the fore reef shelf outside the barrier reef in the open ocean to commute between bays. Our findings can inform conservation and management initiatives in New Caledonia as well as other countries within the dugong's range which have similar habitat geomorphology but where dugongs occur in numbers too low to be tracked and are considered Critically Endangered.

KEY WORDS: Dugong · Movement · Coral reef lagoons · GPS satellite technology · Conservation

1. INTRODUCTION

Information on the space use of wildlife can help their conservation (Cooke 2008, Fraser et al. 2018). Critical habitats and space use tend to vary with the spatial structure of the landscape or seascape (Boyce et al. 2003, Mayor et al. 2007). Thus, it is important to study how wildlife, particularly species with vast distribution ranges, use the various habitats within their range (Mayor et al. 2009).

The dugong *Dugong dugon*, the only surviving member of the family Dugongidae, is a broadly distributed species that occurs in tropical and subtropical coastal and island waters of some 40 countries from East Africa to Vanuatu. As the only strictly marine herbivorous mammal and a seagrass community specialist, the dugong is of high biodiversity value (Marsh et al. 2011). The dugong is listed as Vulnerable to extinction at a global scale by the International Union for Conservation of Nature (Marsh & Sobtzick 2019). However, its conservation prospects are variable across its vast distribution range. Marsh et al. (2011) consider the species to be at high risk of local extinction in multiple parts of its range, including several island groups with fringing coral reefs, such as Palau and the Nansei Islands south of Japan.

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Marsh & Rathbun (1990) pioneered the use of satellite tracking for dugongs to document their movements and habitat use in North Queensland, Australia. That study and many others which followed have shown that dugong movements in Australia are individualistic (e.g. Holley 2006, Sheppard et al. 2006, Gredzens et al. 2014, Cleguer et al. 2015a, 2016a, Bayliss & Hutton 2017). For example, Sheppard et al. (2006) found that while some of the 70 animals they tracked were sedentary (37% moved less than 15 km from their capture sites), others undertook large scale movements (40% moved 15–100 km and 20% moved >100 km).

How dugongs use space has mostly been studied in Australia where the continental shelf is wide. In other parts of the dugong's range such as Okinawa (Japan), Palau, Mayotte, Madagascar and New Caledonia, small populations of dugongs often use narrow coral reef lagoons ranging in width from a few to tens of kilometers. However, with the exception of a study by De Iongh et al. (1998) in Indonesia, there is a lack of understanding of how dugongs use these coral reef lagoons. In some regions the width of the lagoons and the tides may substantially restrict access to seagrass habitats, especially those distributed over shallow patch reefs and reef flats.

New Caledonia, a French archipelago located at the eastern edge of the dugong's range in the southwest Pacific, supports a globally important dugong population (Garrigue et al. 2008, Cleguer et al. 2017). A single baseline aerial survey of dugongs in 2003 estimated a population of 2026 ± 553 (mean ± SE) individuals (Garrigue et al. 2008). Similar surveys conducted between 2008 and 2012 produced lower estimates ranging between 426 ± 134 and 717 ± 171 individuals (Cleguer et al. 2017, Hagihara et al. 2018). It is impossible to determine whether the decline in estimates between 2003 and 2008 is due to a real decline in the population or is the result of confounding effects of variation in environmental conditions, animal behaviour and sampling biases.

Using data collected from the aerial survey time series, Cleguer et al. (2015b) identified areas of consistently high dugong density around the main island of New Caledonia. Most of these areas are not designated as Marine Protected Areas, which restrict anthropogenic activities (Cleguer et al. 2015a). The main threats to dugongs in New Caledonia include illegal take, bycatch in fishing gear, collisions with vessels and degradation of seagrass habitats (Cleguer et al. 2017).

We explored the space use of dugongs in the coral reef lagoons of New Caledonia by deploying GPS satellite tracking devices on 12 adult dugongs. We aimed to document the movement ecology of dugongs in this environment to inform local management initiatives and provide insight into how dugongs might use similar environments in other parts of their range.

2. MATERIALS AND METHODS

2.1. Study sites

New Caledonia is located in the southwest Pacific Ocean, some 1200 km east of Australia. The archipelago has a subtropical climate moderated by the south-easterly trade winds. The warm season is from October to March, when tropical depressions and cyclones occur. After a brief transition, the cool season (April to October), features cold fronts associated with polar low-pressure areas. The mean water temperature in the lagoons during this study was 26.3°C (range: 19.9–30.5°C; Varillon et al. 2020). The tides are semi-diurnal and the tidal range, which reaches up to 1.8 m, does not vary substantially diurnally or seasonally (Bonvallot et al. 2012).

The lagoons that surround the main island of New Caledonia sit on a shallow oceanic shelf ringed by a barrier reef 1600 km long (Andréfouët et al. 2009), one of the most diverse reef systems in the world (Andréfouët et al. 2004). At their widest, these lagoons are up to 50 km wide, but they narrow to only 4 km wide on the mid-west coast. The lagoons vary from very shallow (<5 m on the mid-west coast) to deep (>40 m) and channels can reach 80 m in depth at the reef passes near the barrier reef.

Reef diversity and known seagrass presence and extent is heterogeneous around the main island. A fore reef shelf stretches most of the length of the barrier reef to the west of the main island and is generally composed of spur and groove coral reef formations (Andréfouët et al. 2004). Eleven species of seagrass from 6 genera belonging to the families Cymodoceaceae (*Cymodocea, Halodule* and *Syringodium*) and Hydrocharitaceae (*Enhalus, Halophila* and *Thalassia*) have been recorded (Hily et al. 2010). Georeferenced information on seagrass distribution available at the spatial scale of our study is limited to the maximum extent of shallow seagrasses (<5 m) generated from Landsat imagery (Andréfouët et al. 2010). Diffuse seagrasses are relatively abundant in the intertidal zones of the west coast of the main island (S. Andréfouët pers. comm.). In the southwestern lagoon, a deeper association of seagrass meadows (mean depth 11.2 m) represented a biomass of 31g ash-free dry weight m^{-2} (Garrigue 1995).

We selected 3 sites on the west coast of the main island of New Caledonia: Cap Goulvain, Ouano and Nouméa (Fig. 1). These sites were chosen because (1) they support consistently high dugong densities across seasons (Cleguer et al. 2015b) and thus provided the best chances to capture dugongs, and (2) we wanted to investigate how dugongs use space in a range of environments. The central western sector, which includes 2 of our sites (Cap Goulvain and Ouano) is characterized by wide coastal barrier reefs with large shallow sedimentary terraces (Andréfouët et al. 2004). The lagoon at Cap Goulvain, 200 km north of Nouméa and the most remote of the 3 study sites, is narrow (<4 km wide) and includes shallow areas (<10 m deep) with reticulated reefs, deeper channels (>10 m deep) and inshore intertidal seagrass meadows (including one of the largest seagrass meadows in New Caledonia, at 17 km^2). Ouano is located approximately halfway between Cap Goulvain and Nouméa. At this site, the lagoon is up to 10 km wide and ranges in depth from <5 m in the north to >10 m further south. Nouméa, the urban centre and capital of New Caledonia, is located on the southwestern lagoon. This region is characterized by numerous fringing and patch reef systems with varying hydrodynamic exposure (Andréfouët et al. 2004). The Nouméa lagoon is funnel shaped, varying in width from 40 km in the southeast to about 5 km in the northwest, and has a mean depth of approximately 17.5 m.

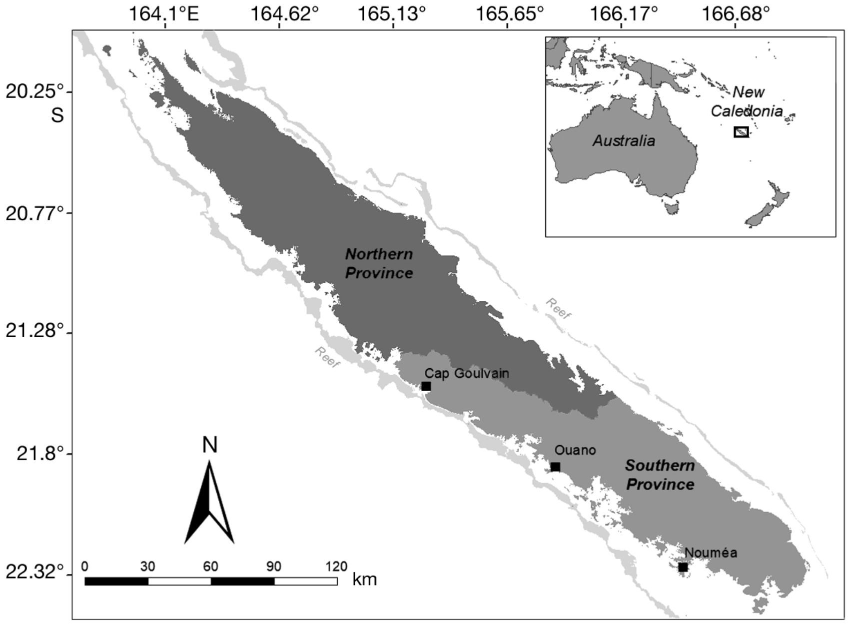

Fig. 1. Location of the 3 dugong satellite tagging sites (black squares) in New Caledonia: Cap Goulvain (n = 7 dugongs), Ouano (n = 2) and Nouméa (n = 3)

2.2. Dugong capture and tracking unit deployments

We used the rodeo technique developed by Marsh & Rathbun (1990) as detailed by Lanyon et al. (2006) to capture the dugongs. This technique requires a close pursuit of an individual dugong, preferably in clear, shallow waters to increase the likelihood of following it as it moves through the water column.

In Cap Goulvain and Ouano, the dugongs we spotted were located over shallow coral reef flats, precluding the close pursuit of individuals using a standard outboard-powered vessel. Thus, we used a 2-seater personal watercraft to enhance maneuverability and safety during the pursuit (Cleguer et al. 2016b). Once captured, the dugongs were secured in a stretcher on the side of the processing boat for tagging and measuring. The dugong monitoring and restraint protocols followed Lanyon et al. (2006) and the veterinary protocol developed by Dr Mark Flint and made available in Cleguer (2015) to ensure that the targeted animals were in good condition before, during and after tagging.

We equipped the dugongs with TMT-462-3 GPS/Argos transmitters (Telonics), hereafter GPS satellite tags. The tag was attached to the animal's peduncle near the tail via a 3 m long flexible tether fitted with a padded belt, the standard attachment apparatus developed for dugongs (e.g. Marsh & Rathbun 1990, Sheppard et al. 2006, Gredzens et al. 2014). The apparatus incorporates (1) a weak link at the peduncle end of the tether, which is intended to break if the animal becomes entangled in corals or mangroves, and (2) a corroding link comprising a zinc bolt in a stainless steel shackle (e.g. Gredzens et al. 2014, Zeh et al. 2016). Details of each tagged dugong's identification number, capture and tagging are in Table 1.

The tags were linked to the Argos location and data collection system. GPS position accuracy is typically 2–10 m (see Table S1 in the Supplement at www.int-res.com/articles/suppl/n043p167_supp.pdf). The units employed fast acquisition GPS tracking technology (Quick Fix Pseudoranging technology or QFP) developed for marine mammals that surface only briefly. The QFP technology obtains locations with as little as 3 s surfacing time to an accuracy of within 10 m (for details see the

Table 1. Dugong identification numbers and capture and tagging details

Study site	Transmitter no.	Individual ID	Sex	Length (m)	Capture location (lat (°S) / lon (°E))	Date tagged	Restraint period (min:s)	Tracking period (d)
Ouano	638703A	A	Male	2.70	21.823 / 165.799	2 Mar 2012	20:00	26
	638706	B	Female	2.33	21.783 / 165.657	3 Mar 2012	12:00	21
Nouméa	668681	C	Male	2.47	22.289 / 166.467	24 Sept 2013	10:00	3
	668682	D	Female	2.77	22.316 / 166.366	27 Sept 2013	09:00	13
	668683	E	Female	2.60	22.327 / 166.379	28 Sept 2013	04:00	40
Cap Goulvain	668680	F	Female	2.71	21.516 / 165.197	1 Oct 2013	10:00	12
	638703B	G	Female	2.90	21.510 / 165.179	2 Oct 2013	07:39	7
	668686	H	Female	2.27	21.508 / 165.173	2 Oct 2013	08:03	20
	668684	I	Male	2.15	21.520 / 165.215	3 Oct 2013	04:57	16
	668675	J	Male	2.40	21.513 / 165.205	3 Oct 2013	05:40	76
	668687	K	Female	2.69	21.529 / 165.192	3 Oct 2013	06:35	5
	668685	L	Male	2.26	21.528 / 165.215	4 Oct 2013	07:04	192

manufacturer's manual at https://www.telonics.com). Argos data (less accurate than GPS-QFP data) could also be retrieved but we used only high accuracy GPS-QFP data because we were interested in the fine scale movements of the tracked dugongs. The Argos uplink repetition period was set to 60 s ± 10% when satellites were in view, the GPS fix timeout to 180 s, and the GPS schedule update period to 1 h.

2.3. Data processing

Data from the 12 tracked dugongs were used to analyse the duration of satellite tag deployment and to explore the movement patterns of the tracked individuals. The data from 3 dugongs (C, G and K; Table 1) were removed from the analysis of utilisation distributions and subsequent analyses because their GPS transmitters detached after a week or less, which was too short a tracking period to be meaningful.

GPS data were retrieved from the Argos website and from the 10 retrieved tags (2 of the deployed tags were lost). Tags were retrieved when the data displayed clear surface drifting patterns without any dive, indicating that the tags had detached from the animals. Tags were decoded using the Telonics Data Converter software supplied by Telonics. We selected dugong location data with the highest quality indicators: GPS and QFP resolved locations (between approx. 2 and <10 m error). The data were then filtered using the SDLfilter package (Shimada et al. 2012) in R (R Core Team 2013). This filter removes location points that are temporally duplicated, or that are unrealistic given the individual's travel speed and turning angle. For example, over-speed errors were removed by identifying the distance and time between successive fixes necessitating speeds beyond the maximum sustained swimming speed for dugongs of 10 km h^{-1} (Gredzens et al. 2014). Location points found over land but which did not exceed the speed filter and were within 100 m of the shoreline were retained for the analysis.

2.4. Space use

The maximum distance each dugong swam from its capture location was determined using the 'least-cost path analysis' tool in ArcGIS 10.2 (ESRI 2013) and using a land layer with a 20 × 20 m cell size resolution (Andréfouët et al. 2004) as a cost raster. Insufficient information on the 'cost' of habitat variables such as bathymetry and/or coral reefs to the movement capabilities of dugongs precluded their inclusion in the analysis. The location point furthest from the capture location via waterway distance was selected visually. All paths were visually checked before the estimated distances were validated. The mean (±SD), minimum and maximum straight-line distances from the nearest land were determined for each tracked dugong using the 'near' tool in ArcGIS 10.2. A dugong returning within 1 km of its capture location after taking a trip beyond 1 km was considered to be a 'returned' animal (Table 2).

Data exploration focused on investigating the dugongs' movements and core areas of use during their tracking periods rather than generating estimates of home range because the data were not collected for long enough to calculate meaningful home range statistics. The tracked dugongs' space use was measured using a fixed kernel density estimation

Table 2. Distance analysis and movement attributes of the 12 dugongs tracked in New Caledonia. Individual range was calculated as the Euclidean distance between the 2 furthest locations for each tracked animal

Study site	Individual ID	Distance from capture location (km)			Distance to any land (km)			Individual range (km)	Returned to <1 km of capture location
		Min	Max	Mean (±SD)	Min	Max	Mean (±SD)		
Ouano	A	0.21	21.53	7.27 (6.80)	0.02	3.9	0.89 (0.60)	27.89	Yes
	B	0.20	37.11	11.35 (10.24)	0.01	6.25	1.59 (1.47)	45.79	Yes
Nouméa	C	0.77	23.19	12.32 (7.24)	0.04	2.59	0.53 (0.53)	22.69	No
	D	0.91	31.12	15.56 (9.82)	0.09	6.77	1.81 (1.51)	50.92	Yes
	E	0.81	66.25	47.22 (20.72)	0	5.12	1.21 (1.09)	74.65	Yes
Cap Goulvain	F	0.53	46.62	18.27 (14.67)	0.07	6.35	2.74 (1.42)	51.95	Yes
	G	1.68	38.39	9.87 (8.22)	0.07	5.44	2.25 (1.33)	54.80	Yes
	H	0.82	13.67	6.76 (2.74)	0.03	5.49	1.74 (1.31)	21.30	Yes
	I	0.29	66.75	11.65 (22.20)	0.05	7.78	1.13 (1.65)	67.24	Yes
	J	0.03	18.00	1.82 (1.53)	0.07	5.16	1.06 (0.61)	22.70	Yes
	K	0.52	30.46	7.19 (0.68)	0.68	5.6	2.28 (0.90)	32.61	Yes
	L	0.62	29.33	4.26 (3.04)	0	4.56	0.49 (0.44)	39.31	Yes

analysis in the Geospatial Modelling Environment software (Beyer 2012). A resolution of 30 m ensured that all filtered fast-acquisition GPS locations were included. The likelihood cross-validation (CVh) smoothing parameter (sensu Horne & Garton 2006) was chosen as the most biologically relevant for the dataset. (The least squares cross-validation was tested but tended to under-smooth the data, an issue highlighted by Horne & Garton 2006.) The tracked dugongs' space use was represented by 95 and 50% utilisation distributions (UDs). The 95% UDs represent the extent of movements whereas the 50% UDs delineated core areas of use. This approach is consistent with other analyses of activity spaces for dugongs and green turtles (Gredzens et al. 2014, Cleguer et al. 2015b, Shimada 2015, Zeh et al. 2015) and other marine megafauna species (e.g. sharks; Heupel et al. 2004, 2012).

UDs were calculated for the combined ranges of all tracked dugongs by summing the UDs of each tracked animal within each region using the raster calculator tool in ArcGIS 10.2. The output rasters representing the combined UDs were then converted into polygons. The combined UDs were not weighted for the tracking period of each tracked dugong because our aim was to provide an overview of the combined area used by dugongs in a region. Any area of a UD overlapping land was removed to calculate the 'true' area of each UD polygon (Table 3).

2.5. Space use in relation to bathymetry, seagrass and aerial survey data

A bathymetric model with a resolution of 100 m (J. Lefevre et al. unpubl.) was used to determine the depth zones used by each tracked animal. Each layer was stored in raster format, reclassified into 5 m depth zones and converted to vector format. Both 95 and 50% UDs for each animal were then superimposed on the reclassified bathymetry layer and the total area over each depth zone calculated for each individual.

We identified areas of known or unverified seagrass presence used by the tracked dugongs by overlaying the 95 and 50% UDs of the combined tracks of

Table 3. Details of the tracking period and space use (utilisation distributions; UDs) of each tracked dugong. NA: not available; the 95 and 50% UDs were not calculated for dugongs with short tracking periods (i.e. <7 d)

Study site	Individual ID	No. of filtered location points (% of locations lost in the filtering process)	Mean no. of filtered location points per day	95% UD (km^2)	50% UD (km^2)
Ouano	A	535 (5)	20.6	45.6	5.0
	B	356 (15)	16.0	117.4	17.4
Nouméa	C	33 (3)	11.0	NA	NA
	D	156 (4)	12.0	455.8	47.2
	E	505 (11)	12.6	250.3	12.3
Cap Goulvain	F	137 (6)	11.4	206.0	42.6
	G	67 (1)	9.6	NA	NA
	H	261 (5)	13.1	74.1	12.6
	I	191 (2)	13.0	82.1	3.9
	J	1223 (1)	18.0	12.8	1.0
	K	57 (0)	11.4	NA	NA
	L	2720 (1)	16	12.40	2.30

animals onto the layer of maximum extent of shallow seagrasses (<5 m) generated from Landsat imagery (Andréfouët et al. 2010). We then calculated the proportion of 95 and 50% UDs over this seagrass layer. Any core area use overlaying areas of unverified seagrass presence could then be interpreted as requiring further investigation of benthic habitat (beyond the scope of this study).

Large-scale aerial surveys provide a snapshot of the distribution and density of dugongs, which can be relatively mobile animals (Sheppard et al. 2006). We explored the space use of the tracked dugongs in relation to a spatially explicit model of dugong density developed from data collected during aerial surveys conducted in New Caledonia in 2003, 2008, 2011 and 2012 (Cleguer et al. 2015b). We focused on identifying areas used by the tracked dugongs not detected by the aerial surveys. Cleguer et al. (2015b) binned dugong relative density values into 4 categories: low density (0 dugongs km^{-2}), medium density (0–0.10 dugongs km^{-2}), high density (0.10–0.5 dugongs km^{-2}) and very high density (>0.5 dugongs km^{-2}). We superimposed the polygon layers of the UDs for the tracked dugongs on the polygon layers of dugong densities from the aerial surveys (Cleguer et al. 2015b) and calculated the proportion of the 95 and 50% UDs which overlapped with areas classified as low dugong density by the aerial survey data.

3. RESULTS

3.1. Information about the tracked dugongs

We caught and satellite tagged 12 adult dugongs: 7 at Cap Goulvain in October 2013, 2 at Ouano in March 2012 and 3 at Nouméa in September 2013. The time from onset of pursuit to capture could not exceed 10 min (as this was the cut off time set to abandon a pursuit) and the duration of restraint (i.e. capture to release) was between 4 and 12 min (mean = 8 min 45 s; Table 1). Seven of the captured dugongs were females and 5 were males. Dugongs ranged in body length from 2.15 to 2.90 m with a mean (±SE) of 2.52 ± 0.07 m (Table 1). The mean body lengths of males and females were similar (independent *t*-test: p = 0.13, *t* = 0.89, df = 10). Individual dugongs were tracked between 3 and 192 d (mean (±SE) = 35.9 ± 15.3 d, median = 18 d). Ten of the 12 tags were retrieved. From the retrieved tags we determined that the short tracking durations resulted from the tethers of the towed tags tangling with marine obstructions (likely coral reefs or mangrove trees), breaking the tether at the weak link as was designed to occur. GPS fix success was 59.6%, indicating that there may have been some bias against areas used for traveling (which pulls the tag underwater) and deep-water activities (e.g. bottom resting in waters deeper than 3 m, which is the length of the tether).

3.2. Extent and heterogeneity of movements

The dugongs did not show a preferred direction after release and made use of the width of the lagoons (Figs. 2 & 3). Three of the 7 dugongs tagged in Cap Goulvain (J, K and L) swam outside the coral reef lagoon and used the fore reef shelf to commute to another bay some 20 km south near Bourail (the mean percentage of GPS locations outside the lagoon for those 3 individuals was 6.9%).

All except one of the tracked dugongs (individual C, only tracked for 3 d) returned to their capture site after undertaking a trip. All except one animal (individual H) undertook large-scale movements (>15 km; mean (±SE): 37.7 ± 5.2 km) from their capture location (maximum waterway distance range: 13.8 to 72.9 km). The mean Euclidean distance of GPS locations from capture site for the 12 animals was 12.8 km (range of individual means: 1.8 to 47.2 km). There was no significant relationship between the maximum distance the dugongs moved from their capture location and tracking period (Pearson's correlation coefficient = −0.14, p = 0.68, df = 11). The Euclidean distance between the 2 furthest locations provides a linear measure of each individual's range. These distances ranged between 21.3 and 74.5 km for the 12 tracked dugongs (Table 2). Individual I ranged further from its capture location than any other tracked dugong (Fig. 2A, Table 2), undertaking a 7 d trip 66.75 km north from Cap Goulvain to the Konième coral reef-seagrass plateau before swimming back to its capture location. Individual H moved the shortest distance away from its capture location (14 km) between Cap Goulvain and the Poya Pass (Fig. 2B, Table 2).

We could not distinguish any general patterns in movement behaviour between the sexes. The mean and maximum distances from capture location did not significantly differ between males (mean (±SE) = 7.4 ± 2.04 km, max = 66.7 km) and females (16.6 ± 5.3 km, max = 66.2 km), (*t*-test of 2 samples for mean distances assuming equal variance, *t* = −1.38, df = 10, p = 0.19). Similarly, there was no significant difference in linear range between males (35.7 ± 7.5 km)

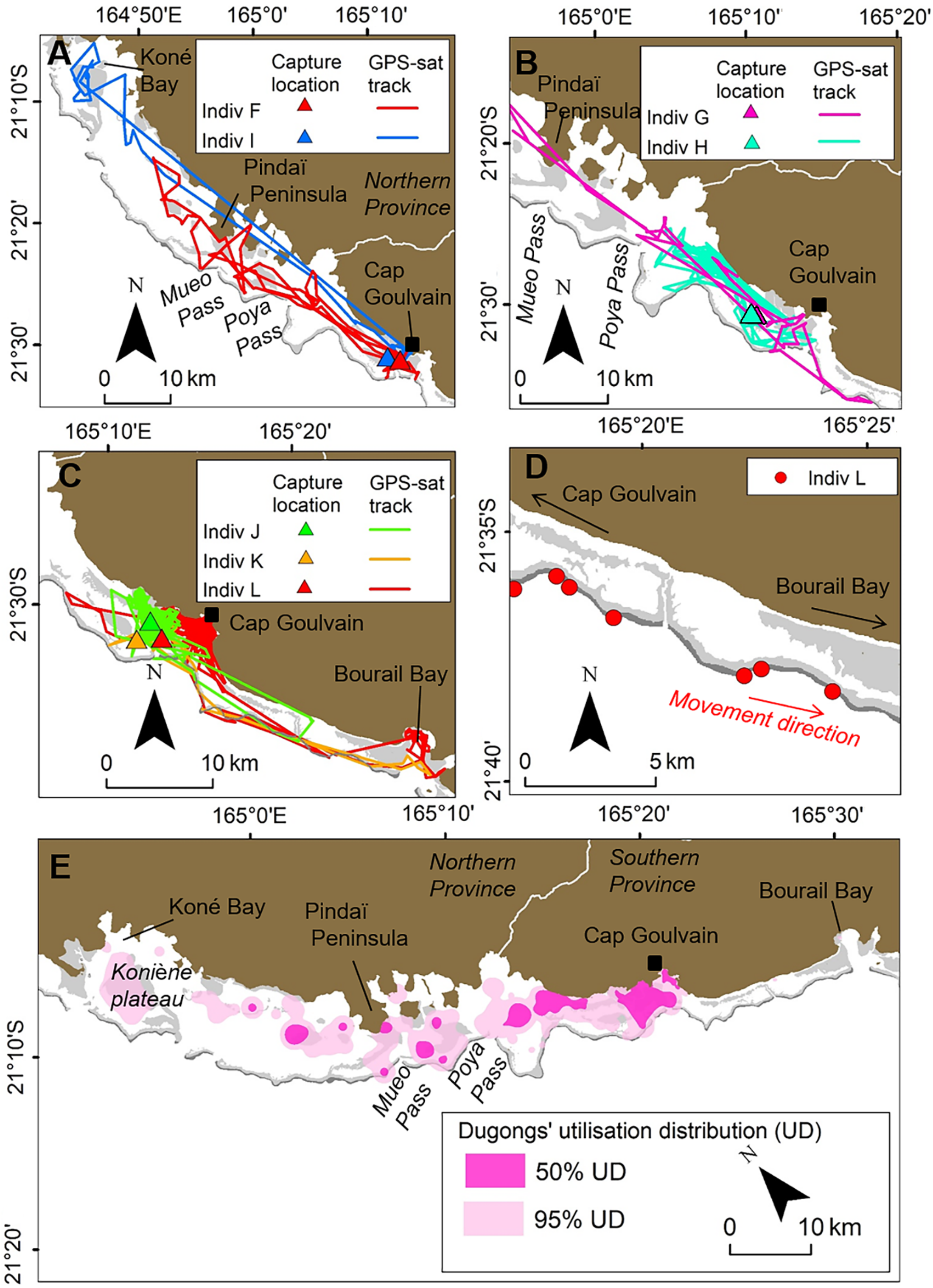

Fig. 2. Movement tracks and space use of dugongs captured in Cap Goulvain based on the total tracking period of each individual. (A–C) The movement tracks of the 7 dugongs tracked in the Cap Goulvain region. (D) An example of a tracked dugong travelling through oceanic waters and using the fore reef shelf outside the lagoon to go from Cap Goulvain to Bourail Bay. (E) The combined utilisation distributions (UDs) of the 7 dugongs captured in Cap Goulvain. UDs were not weighted by tracking period because the aim was to provide an indication of the combined area used by dugongs. Brown represents land, dark grey represents barrier reef and light grey represents the reefs inside the lagoons

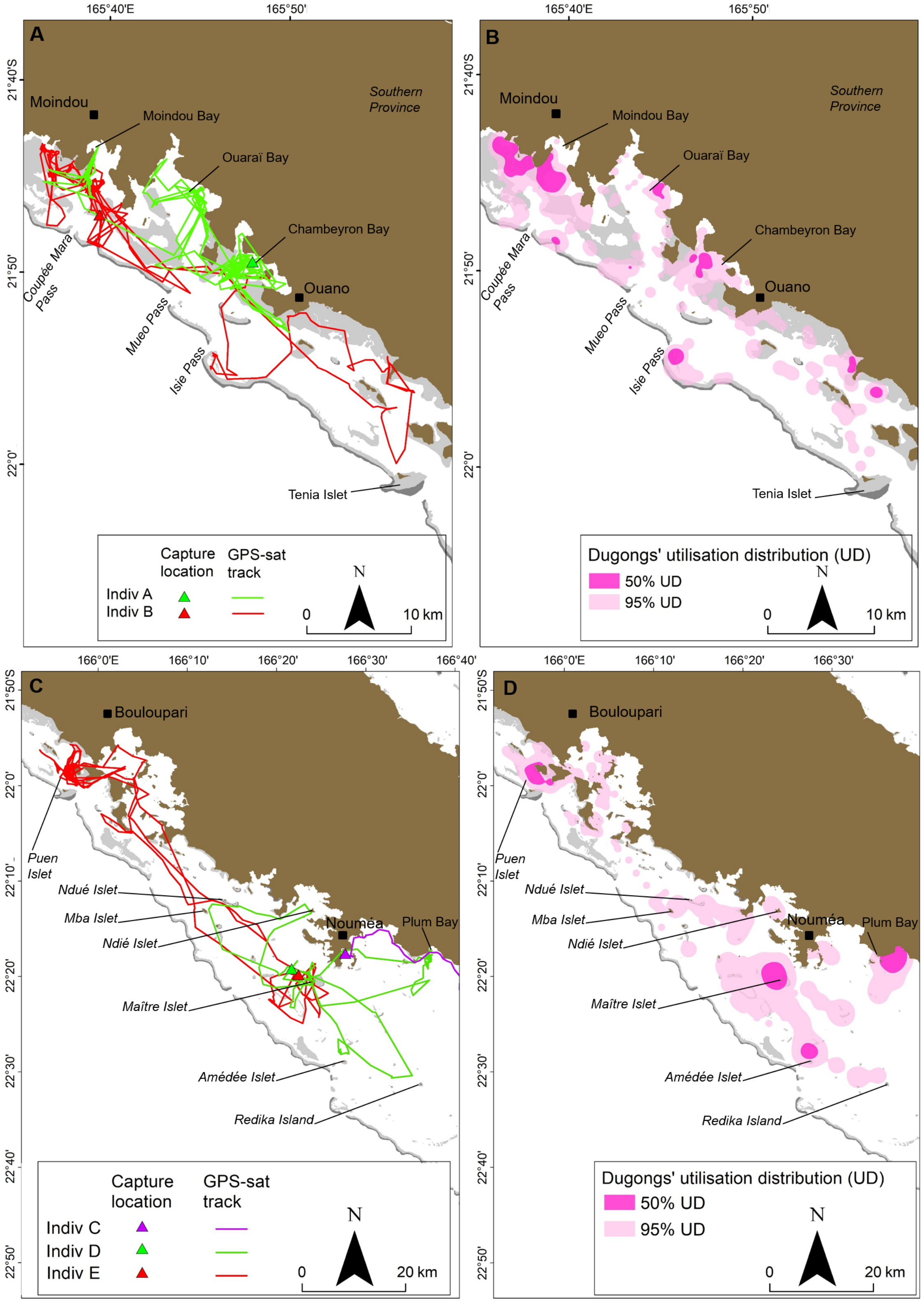

Fig. 3. Movement patterns of the dugongs captured in (A) Ouano and (C) Nouméa based on the total tracking period of each individual; and combined utilisation distributions (UDs) of dugongs captured in (B) Ouano and (D) Nouméa. UDs were not weighted by tracking period because the aim was to provide an indication of the combined area used by dugongs. Brown represents land, dark grey represents barrier reef, and light grey represents the reefs inside the lagoons

and females (47.4 ± 5.9 km), (*t*-test of 2 samples assuming equal variance, $t = -1.10$, df = 10, $p = 0.29$).

The tracked dugongs displayed individual use of space and scales of movements, regardless of capture location. For example, some dugongs (F, H and I) only made use of the areas north of Cap Goulvain (Fig. 2A,B) while others (J, K and L) caught at that site spent some of their tracking time moving towards Bourail Bay, approximately 20 km to the south (Fig. 2C). The 2 dugongs captured at Ouano were also individualistic. Dugong A mainly used a small area in 3 adjacent bays (Fig. 3A), whereas dugong B was more mobile, making brief daily return excursions to the reef complexes, adjacent to the back reef (Fig. 3A).

3.3. Space use in relation to seagrass habitats, bathymetry and aerial survey data

The tracked dugongs' core areas of use (50 % UDs) varied across the 3 study sites (Figs. 2E & 3B,D). In Nouméa, these areas were located at their capture site (Maître Islet), in Plum Bay, and adjacent to Puen Islet, approximately 60 km north of Nouméa (Fig. 3D). In Ouano, the tracked dugongs mostly used coastal waters near Moindou, Ouaraï and Chambeyron Bays and near the barrier reef between Coupée Mara Pass and Ouaraï Pass and adjacent to Isié Pass. Although the dugongs tracked in Cap Goulvain ranged over larger areas, their core activities were concentrated in the bay near Cap Goulvain and another inshore area less than 10 km north (Fig. 2E). The mean (±SD) of individual mean distance to land was 1.5 ± 0.7 km (range = 0.5–2.7 km) and the maximum distance to land varied between 3.9 and 6.8 km (Table 2).

The depth uses of dugongs tracked in Cap Goulvain and Ouano were similar (Fig. 4). Over 70 % of the combined 95 and 50 % UDs of the tracked dugongs in Cap Goulvain and Ouano were in shallow waters (<5 m), whereas the dugongs tracked in Noumea used deeper waters (Fig. 4).

We identified some shallow areas with known seagrass patches that were intensively used by the tracked dugongs, including the shallow seagrass meadows surrounding Maître Islet in Nouméa, in Moindou Bay north of Ouano and in the bay near Cap Goulvain. Nonetheless, a large proportion of the dugongs' ranges occurred over deeper areas where the presence of seagrass has not been verified (Fig. 5A–C). Over 90 % of the 95 % UDs and over 85 % of the 50 % UDs of the dugongs captured in Nouméa were located in such areas (Fig. 5C). Similar patterns were observed at Cap Goulvain and Ouano, where there were 4 core areas in each of the Cap Goulvain and Ouano regions that did not overlap with confirmed shallow seagrass beds (Fig. 5A,B).

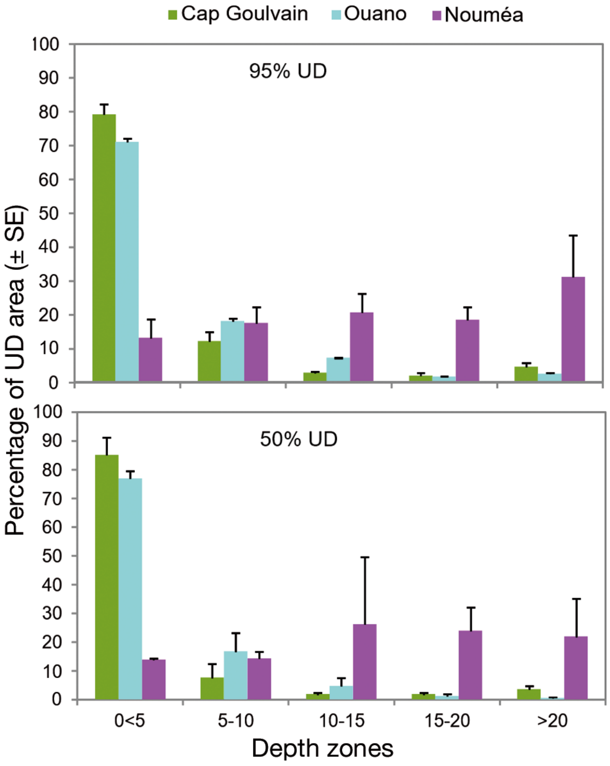

Fig. 4. Mean proportion of the 95 and 50 % utilisation distribution (UDs) of dugongs across depth zones at 3 sites in New Caledonia

In all 3 study regions, we identified areas intensively used by the tracked dugongs where no dugongs had been sighted during aerial surveys (Fig. 6A–C). The proportion of the 95 and 50 % UDs located over areas where no dugongs were detected during the aerial surveys ranged from 26.7 to 43.7 % for 95 % UDs and from 25.1 to 28.9 % for 50 % UDs (see Table S2 in the Supplement). The highest proportion of areas intensively used by tracked dugongs but undetected in aerial surveys was located near Cap Goulvain (29 %; Fig. 6A & Table S2).

4. DISCUSSION

Tracking dugongs in New Caledonia provided significant new insights into the species' space use in this coral reef lagoon environment. Dugongs used the full width of the reef lagoons, from close to shore all the way out to the back reef. Eleven of the 12

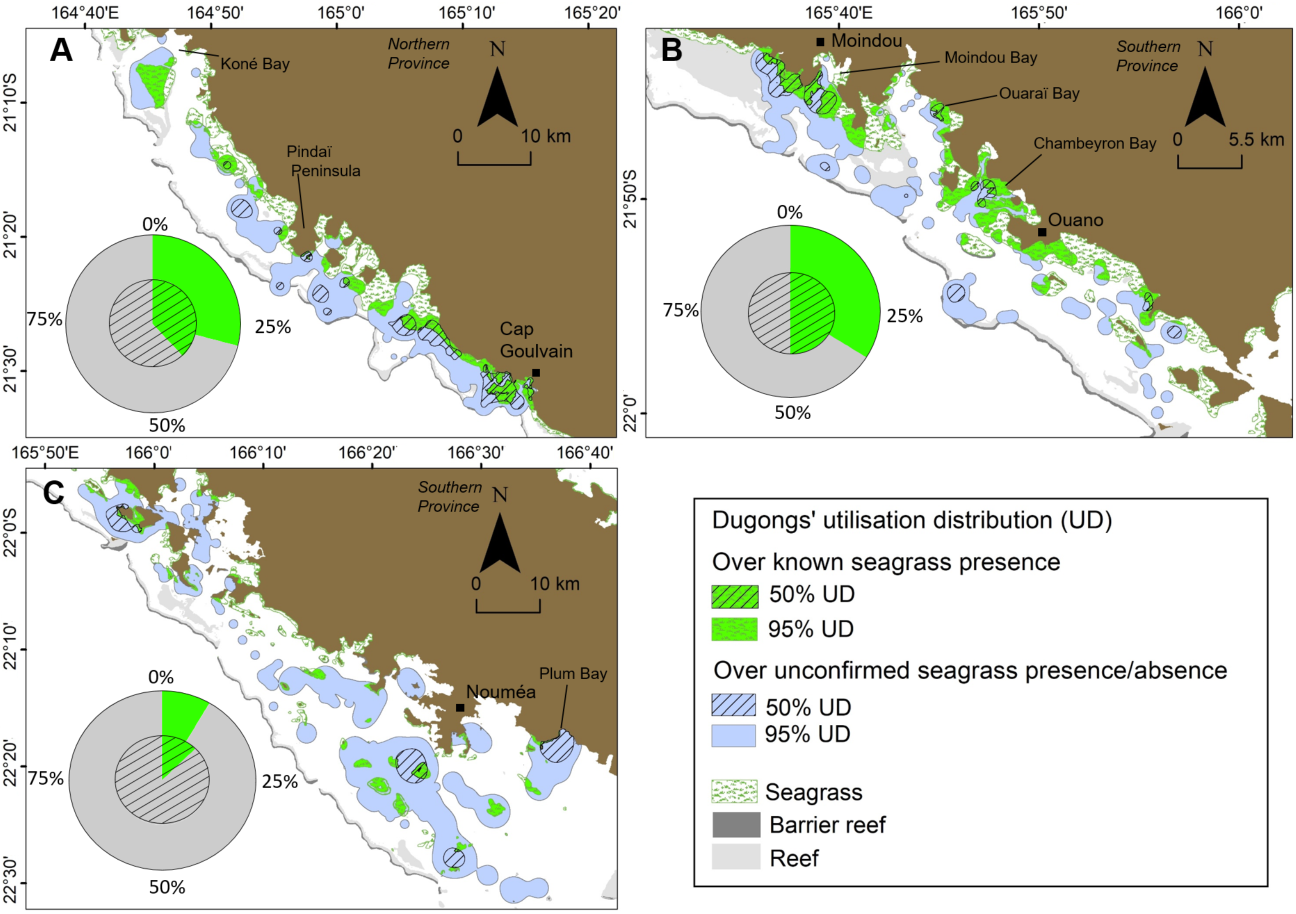

Fig. 5. Relationship between the space use of dugongs captured in (A) Cap Goulvain, (B) Ouano and (C) Nouméa and the known shallow seagrass habitats (Andréfouët et al. 2010). Panels show the combined 95 and 50% utilisation distributions (UDs) of dugongs captured in each study region. Pie charts represent the proportions of 95% UDs (outer ring) and 50% UDs (inner ring) of dugong areas where the presence of seagrass has been confirmed (in green) or is unconfirmed (in grey)

dugongs tracked returned to their capture site after undertaking a trip, suggesting high fidelity in their use of space. We discovered intensively used habitats that were not identified in the aerial surveys conducted in New Caledonia (Cleguer et al. 2015b), and other intensively used areas where the presence of seagrass has not been verified. The dugongs displayed heterogeneous movement patterns across the 3 study regions, consistent with results from other regions (e.g. De Iongh et al. 1998, Holley 2006, Sheppard et al. 2006, Gredzens et al. 2014, Cleguer et al. 2015b, 2016a, Bayliss & Hutton 2017). Surprisingly, 3 of the 7 dugongs tagged in Cap Goulvain used the fore reef shelf outside the coral reef lagoon, an oceanic habitat that has not been recorded as being used by dugongs before.

Some of the movement of the tracked dugongs may be attributable to flight responses. For example, individuals K and I (captured in the Cap Goulvain region) undertook large-scale movements less than a day after they were captured. In contrast, individual L swam from Cap Goulvain to Bourail Bay using the fore reef shelf 110 d after it was captured, suggesting that not all large-scale movements can be explained by flight responses.

4.1. Use of the lagoons

The use of the coral reef lagoons by the dugongs reflected each lagoon's size and depth. Dugongs spent most of their tracked time within the lagoons, with 99.4% of GPS fixes located inside the barrier reef. In Nouméa, dugongs ranged over large areas and used the water depth gradient of the lagoon evenly. This pattern can be explained by the distribution of the seagrass, which is known to be mainly subtidal in this region, although it has not been

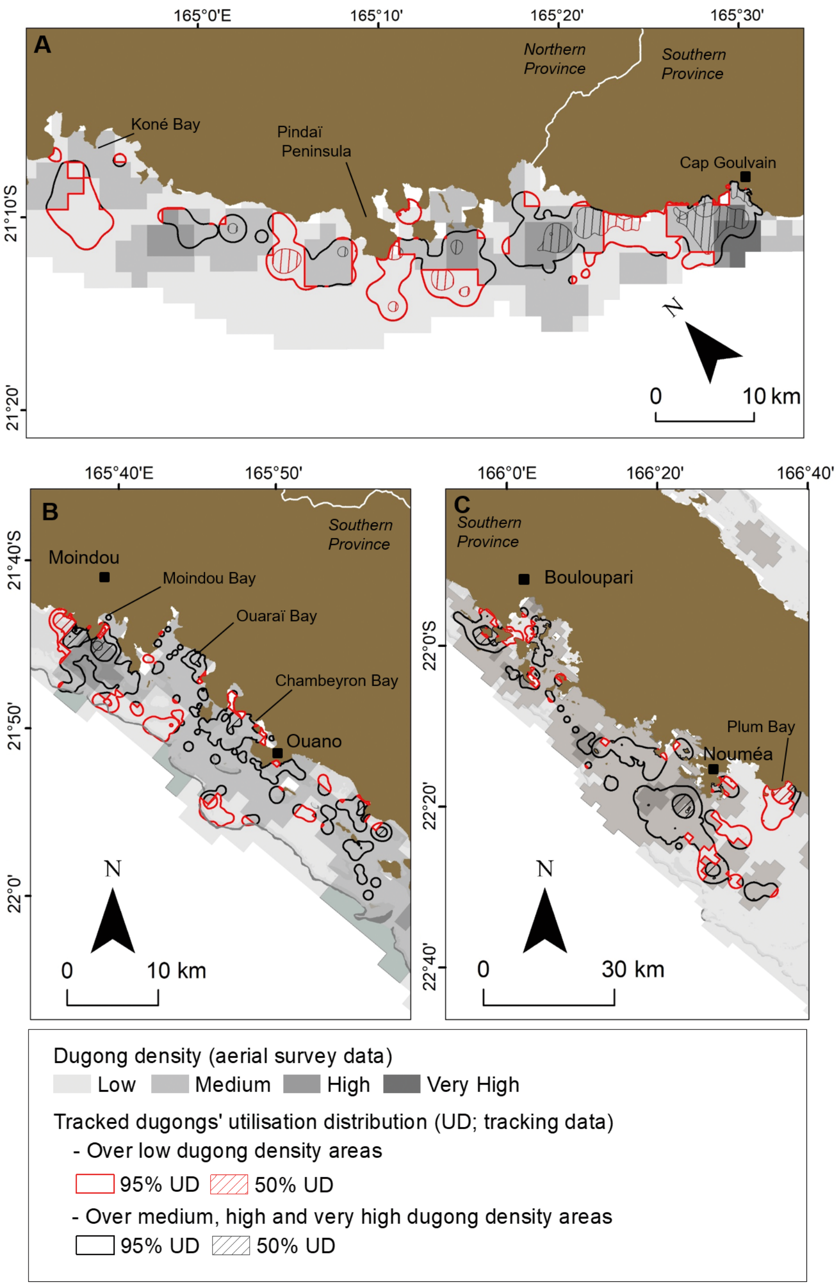

Fig. 6. Relationship between the tracked dugongs' space use (this study) and data on dugong densities collected from large-scale aerial surveys conducted in New Caledonia (Cleguer et al. 2015b) in (A) Cap Goulvain, (B) Ouano and (C) Nouméa

mapped recently (Garrigue 1995). In Cap Goulvain and Ouano, the lagoons are narrower and seagrasses are distributed over shallower inshore areas, hence the use of smaller and shallower areas by dugongs at these 2 sites. Similar regional differences in dugong range sizes and water depth use have been observed in Australia. For example, the range of tracked dugongs was substantially larger in Torres Strait (median range = 942.6 km^2) than in Shoalwater Bay, a much smaller and shallower habitat (median range = 60 km^2; Gredzens et al. 2014). Collectively, these findings suggest that dugongs are well adapted to a range of geomorphological settings, giving them an adaptive advantage that might enable their widespread distribution.

4.2. Dugongs as indicators of unconfirmed seagrass habitats

Seagrasses play a critically important ecological role, and are among the most valuable ecosystems on earth (Costanza et al. 2014). Nevertheless, their spatial extent and distribution is unclear for much of the globe (Duarte 2017)

As seagrass community specialists, dugongs are believed to be a good indicator of seagrass presence (Hays et al. 2018). In the Torres Strait, dugong distribution data collected from aerial surveys (Marsh et al. 1997) were used to design vessel surveys that revealed a total seagrass area of ~48 500 km^2. This included the largest continuous seagrass meadow mapped in Australia (and possibly the world), totalling over 8750 km^2 of mostly deep-water (>15 m) seagrasses growing to around 30 m deep (Taylor & Rasheed 2010).

Six systematic aerial surveys conducted in New Caledonia between 2003 and 2012 resulted in the identification of areas of consistently high dugong density (Garrigue et al. 2008, Cleguer et al. 2017). Cleguer (2015) suggested that these high dugong density areas may reflect seagrass habitats that have not been identified but are important to dugongs. Using our satellite tracking data, we identified additional areas intensively used by dugongs but not detected during the aerial surveys. The combined aerial survey and dugong tracking data collected in New Caledonia should now be used to direct in-water sampling to assess the benthic habitat and to verify the presence of seagrass.

Some of the tracked dugongs used coral reef habitats but the reasons for this use require further investigation. In a recent study conducted north of Cap Goulvain, dugongs were seen feeding over the reticulated reefs (Cleguer et al. 2020). Thus, some parts of the reef may contain seagrass patches that are important to dugongs but too small and sparse for the animals to spend extended periods of time in, or to be detected by remote sensing tools (e.g. satellite imagery and even drone imagery). Rather, these small diffuse patches of seagrass may provide supplementary food resources when larger intertidal seagrass meadows are not available at low tide. In-water sampling of the benthic habitat would help to better understand the use of these areas.

4.3. Use of the fore reef shelf

This study is the first evidence of dugong use of a fore reef shelf in the open ocean as a movement corridor, an observation supported by anecdotal reports from local fishermen. Using in-water observation, Self-Sullivan et al. (2003) found that Antillean manatees were using breaks in the northern Belize barrier reef, predominantly in summer, but the movements of the animals on the reef were not studied. In non-lagoonal habitats in Australia, Zeh et al. (2016) demonstrated that tracked dugongs followed coastline features when moving from one bay to another. A combination of geomorphological characteristics, environmental factors and the risks of human disturbance and shark predation are possible reasons for the dugongs' use of the open ocean. The lagoon between Cap Goulvain and Bourail Bay is one of the narrowest (mean width = 2 km) and shallowest (<5 m) around the main island. In this region, the lagoon also supports reticulated reef formations (Andréfouët et al. 2004) that may limit the movements of large animals like dugongs, especially at low tide (Fig. 2D). Local sea-rangers (R. Laigle pers. comm.) have reported dugongs being ambushed by sharks in shallow reticulated reef areas near Cap Goulvain (see also Garrigue et al. 2008). Dugongs are likely more vulnerable to attack from sharks in shallow waters, where they have fewer escape routes. Deeper water may provide 'cover' from sharks (Heithaus et al. 2002, Hodgson 2004, Wirsing et al. 2007a,b). Hence, dugongs may choose to travel, feed or rest over relatively shallow areas with access to deeper/safer waters to increase their chances of escape from predation (Heithaus et al. 2002). Sheppard et al. (2006) found that travelling dugongs made repeated deep dives (presumably along the seafloor) and hypothesized that this may reduce their exposure to shark predation. The fore reef shelf is a relatively shallow habitat with easy access to deep waters and hence could be a safer travelling route than the shallow reticulated reefs inside the lagoon. Information on the density and movement patterns of shark species likely to attack dugongs is needed to verify this hypothesis.

4.4. Insights for the management of dugongs in small lagoonal coral reef systems

The dugongs we tracked were captured in areas of consistently high dugong density (Cleguer et al. 2017). Once released, they undertook trips across the lagoons, but eventually returned to their capture locations, suggesting site fidelity as observed in manatees (e.g. Deutsch et al. 2003) and other species of marine megafauna such as sea turtles (González Carman et al. 2016), cetaceans (Samarra et al. 2017) and sharks (Doherty et al. 2017). The tracking data therefore reinforce the ecological importance of the high dugong density areas identified during the aerial surveys (Cleguer et al. 2015b). Areas identified as consistently high dugong density have enabled the creation of marine protected areas to protect dugongs in Australia (Dobbs et al. 2008) and in Malaysia (F. Jamal pers. comm.). Given the dugong aerial survey and tracking data now available for New Caledonia, a similar process could be followed by local managers.

In New Caledonia the management agencies responsible for dugong conservation operate at provincial scales and have not yet considered animal movement in their decision making. Our study adds to the body of evidence that dugongs are not constrained by jurisdictional boundaries. Thus, the conservation management of dugongs needs to be coordinated across jurisdictions within countries as well as across range states. Unfortunately, the Dugong Memorandum of Understanding (MoU) under the Convention on the Conservation of Migratory Species of Wild Animals applies only to the latter. Thus, the need to coordinate management across jurisdictions within a range state tends to be overlooked (Miller et al. 2018).

The identification of movement corridors is important. Protecting movement corridors helps conserve mobile species as they are transiting in space in terrestrial (Walker & Craighead 1997, LaPoint et al. 2013), aerial (Davy et al. 2017) and marine habitats (Pendoley et al. 2014). We found that the fore reef shelf is occasionally used as a movement corridor by dugongs where the lagoon is covered in dense reticulated reef, presumably impeding dugong movement and potentially heightening risk from shark attack. In contrast, it was difficult to identify movement corridors within the lagoon because (1) dugongs are individualistic in their movement patterns, (2) the amount of data available to make inferences about their movement is insufficient (both in the number of animals tracked and the tracking duration) and (3) despite continuing advances in telemetry technology, success in obtaining a location fix from a tag is typically lower when a dugong is travelling and the tag is pulled underwater. Thus, it can be difficult to plot travel paths (as indicated by the many straight, long-distance tracks in the figures) and locations are biased against traveling activity. Nonetheless, further analysis of the data in relation to habitat features (bathymetry, reef configuration, seagrass meadows) could help to model movements that could identify important movement corridors.

Our study is the first to document how dugongs use coral reef lagoon environments in the Oceania island region. Our investigation identified habitats intensively used by dugongs, some of which may or may not contain seagrass and hence deserve further assessment. Together these core areas of use, the newly identified movement corridors, such as the fore reef shelf, combined with the aerial survey data can be used to inform evidence-based local management actions aimed at the conservation of dugongs and their critical habitats. Our results could also inform management in countries within the dugong range, such as the Nansei Islands south of Japan, Mayotte, Palau and much of Indonesia, which have similar habitat geomorphology but where dugongs occur in numbers too low to be tracked.

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