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Local Variation in Feeding Ground Utilization of Dugongs (*Dugong dugon*) Across Two Intertidal Seagrass Beds in Talibong Island, Thailand

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Abstract

In this study, we describe the population characteristics and residency patterns of dugongs (*Dugong dugon*) across two intertidal seagrass beds in Talibong Island, Thailand: Site A, covering an area of 2.0×10^5 m^2, and Site B, covering an area of 2.8×10^5 m^2. Transect and individual identification surveys were conducted under clear water conditions using drones: 16 separate days over 11 months at Site A and 10 separate days over 3 months at Site B. Sixty-four individuals were identified from 180 videography sessions. The results confirmed at least two distinct patterns of seagrass habitat utilization among sites located approximately 5 km apart. Site A was characterized by a lower population density, higher year-round site fidelity, occupancy by relatively large individuals, and an absence of feeding aggregations. In contrast, Site B was characterized by a higher population density, lower site fidelity, occupancy by individuals with a wider range of body lengths, and the presence of feeding aggregations. The average population density at Site B was three to five times higher than that at Site A. Site A had a median nearest neighbor distance of 320 m with no significant bias in its distribution, whereas Site B had a median of 20 m with a significant bias. The mean site fidelity index for Site A (0.62 ± 0.08; $n = 16$) was significantly higher than that for Site B (0.39 ± 0.14; $n = 10$). Dugongs at Site A might have monopolized this site to some extent, while those at Site B might have benefited from increased opportunities for social interaction provided by aggregations. These findings highlight the importance of fine-scale monitoring of feeding ground utilization by dugongs, taking into consideration individual-specific details such as body lengths and resighting rates for a better understanding of their spatial distribution.

Key Words: habitat use, feeding, drone, dugong, *Dugong dugon*, population characteristics, photo identification

Introduction

A thorough understanding of wildlife habitat use and its relationship with underlying resources is fundamental for effective habitat conservation and management (Southwood, 1977; Gaillard et al., 2010). The optimal habitat use strategies of animals are often influenced by individual-specific factors such as age, sex, and body condition (Lesmerises & St-Laurent, 2017; Muff et al., 2020). If variations in habitat use strategies are confirmed within a population, successful population conservation might require differential strategies targeting specific threats to each habitat use strategy. Thus, understanding intraspecies variation in habitat use is a key step in developing conservation and management measures.

The dugong (*Dugong dugon*) is the only fully herbivorous marine mammal broadly distributed across tropical and subtropical regions (Marsh et al., 2011). Due to their herbivorous diet, they are restricted to inhabiting shallow coastal waters with seagrass beds, which makes them particularly vulnerable to anthropogenic threats, including coastal fisheries (Marsh et al., 2011). Globally, they are listed as vulnerable to extinction by the International Union for the Conservation of Nature (Marsh & Sobtzick, 2019).

Dugongs are typically solitary animals, with the exception of mother-calf pairs (O'Shea et al., 2022). After a gestational period of approximately 14 mo, calves become independent from their mothers by the age of 18 mo (Marsh et al., 2011). Transient groups of individuals form over resources, including seagrass beds and warm water refuges (Hodgson, 2004; Preen, 2004).

Multiple studies support that the habitat use of dugongs is heterogeneous and that they exhibit site fidelity at both the individual and group levels (Deutsch et al., 2022). Telemetry studies have shown that dugong movements are highly individualistic (De Iongh et al., 1998; Sheppard et al., 2006; Gredzens et al., 2014; Zeh et al., 2016; Cleguer et al., 2020). For instance, in the Northern Territory and Queensland, Australia, 44 of the 70 dugongs tracked over periods ranging from 15 to 551 d made large-scale movements exceeding 15 km, while 26 did not (Sheppard et al., 2006). There has been no evidence to suggest that sex and body size significantly influence the likelihood of a dugong engaging in long-distance movement nor the scale of such movements (Sheppard et al., 2006; Zeh et al., 2018). However, their primary habitat might shift based on their growth stages or other individual-specific factors given that mother-calf pairs of dugongs and manatees in certain regions have been consistently observed in the same area (Hines et al., 2005; Gannon et al., 2007; Ichikawa et al., 2012). In New Caledonia, 11 of the 12 tracked dugongs returned to their capture locations after undertaking trips across lagoons, suggesting site fidelity (Cleguer et al., 2020). In Moreton Bay (Queensland, Australia), situated at the high latitudinal limit of the dugong range, dugongs travel out of the bay in response to winter water temperatures, with all 21 tracked individuals making one or more return trips (Zeh et al., 2018). Aerial and in-water observations from several regions, such as Okinawa (Japan), Andaman Nicobar Islands (India), and Queensland (Australia), have reported that the same, or those presumed to be the same, individuals have been consistently observed over the specific seagrass beds (Lanyon, 2003; D'Souza et al., 2015; Kayanne et al., 2022). Large aggregations of dugongs have consistently been found in the same areas during aerial surveys conducted over several years in New Caledonia (Garrigue et al., 2008; Cleguer et al., 2017), the Arabian Gulf (Preen, 2004; Marshall et al., 2018; Khamis et al., 2023), Queensland (Lanyon, 2003), and the Northern Territory of Australia (CARDNO, 2014).

Large-scale spatial variations in habitat use have been reported in telemetric studies. In the coral reef lagoons of New Caledonia, the intensity of use across shallow waters, deep lagoon waters, and the fore-reef shelf varies among ecoregions, covering an area of approximately 130 to 440 km^2. These ecoregions were classified based on the geographic and topographic characteristics of the lagoons (Derville et al., 2022). Derville et al. (2022) noted that the nature and intensity of anthropogenic activities may explain some geographical variations in intensity. Dugong habitat use may also change across the latitudinal gradients. Large-scale migrations, associated with seasonal drops in water temperature, have been documented at the high latitudinal limits of their range, such as on the eastern and western coasts of Australia (Holley, 2006; Sheppard et al., 2006; Zeh et al., 2018).

Relatively little is known about whether variations in dugong habitat use can occur across habitats with similar environments, where populations are more likely to overlap. Despite the highly individualistic nature of their movement ranges, most dugongs are likely to travel at least a few kilometers daily (De Iongh et al., 1998; Holley, 2006; Sheppard et al., 2006). However, to date, few studies have documented variation in dugong habitat use at this scale (< 10 km). Recent studies have indicated possible local variations in the socializing grounds. Passive acoustic monitoring on a 2 km grid around Talibong Island, Thailand, revealed spatiotemporal heterogeneity in the detection rate of dugong vocalizations (Tanaka et al., 2023a, 2023b). Because their vocalizations function to exchange information and determine the distance between individuals (Ichikawa et al., 2011), areas with high detection rates are considered key socializing grounds. This observation suggests potential local variations in other aspects of habitat use such as feeding ground utilization. Given that dugongs spend considerable time feeding due to their herbivorous diet, understanding the local variation in feeding ground utilization is important. However, this aspect has not yet been fully explored.

Few studies have investigated the fine-scale heterogeneity in habitat use associated with individual-specific details. Research on local variations in feeding ground utilization has been limited because of the challenges in collecting individual-specific details of any individual within a specific area. While aerial surveys are the gold standard for censusing any individual within feeding grounds, the reconciliation of identifying and locating individuals has posed challenges, often owing to time and resource constraints. Consequently, traditional aerial surveys have typically categorized dugongs as either "mother-calf pairs" or "solitary individuals" (Hines et al., 2005; Garrigue et al., 2008; Ichikawa et al., 2012; Marshall et al., 2018). Advancements in drone technology have paved the way for swift individual identification and body length estimation in other sirenian species in recent years (Landeo-Yauri et al., 2020, 2021; Ramos et al., 2022). The body length of dugongs serves as an indicator of their growth stage because they are born, weaned, and reach sexual maturity within distinct body length ranges (Marsh, 1980; Marsh et al., 1984; Kwan, 2002). Therefore, incorporating body length and sighting history into location data could provide insights into the factors influencing local variations in feeding ground utilization.

The aim of this study was to reveal local variations in the feeding ground utilization of dugongs across two intertidal seagrass beds on Talibong Island, Thailand. We examined the variations in site fidelity and body length frequency distribution. Population density and inter-individual distances were also investigated as indicators of the presence or absence of feeding aggregation. This study has significant implications for optimizing the monitoring parameters to better understand dugong habitat use. Accounting for local variations may help develop monitoring strategies for dugong conservation, enabling the identification of key feeding grounds at a local scale.

Methods

Field Data Collection

Field surveys were conducted in the intertidal seagrass beds on Talibong Island, Trang Province, Thailand (Figure 1). Previous surveys estimated a minimum population of approximately 120 dugongs around this island, representing the largest population in Thailand (Hines et al., 2005). Two observation areas were established within intertidal seagrass beds. Site A was where solitary individuals were observed, whereas Site B was where the largest herd and mother-calf pairs were previously detected through aerial surveys (Hines et al., 2005; Ichikawa et al., 2012; Kittiwattanawong, pers. comm., 20 February 2020), suggesting that their habitat use might vary based on individual-specific factors across these sites. For Site A, surveys were conducted from 27 January to 2 March, from 24 April to 28 May, from 21 September to 18 October, and from 20 November to 15 December 2022. Meanwhile, Site B was surveyed during the latter two periods: from 21 September to 18 October and from 20 November to 15 December 2022 (Table 1). The survey area has two seasons: (1) a rainy season from approximately May to October and (2) a dry season from November to April (Isa et al., 2020). The tidal ranges at Sites A and B were approximately 0.0 to 2.3 m and 0.0 to 2.8 m, respectively. At both sites, *Halophila ovalis* was the most dominant seagrass species. Seagrass coverage was generally higher at Site A than at Site B (Yamato et al., under review). The annual mean seagrass coverage, observed at 3 mo intervals, was 10.1 ± 12.6% (observed at 11 points) for Site A and 3.5 ± 4.3% (observed at 12 points) for Site B. Seagrass coverage in patches that included dugong feeding trails was 6.5 ± 9.2% (n = 37) at Site A and 34.0 ± 10.7% (n = 6) at Site B.

This study was approved by the Animal Experimentation Committee of the Graduate School of Informatics, Kyoto University (Approval Number Inf-K22004). All aerial observations were conducted according to the regulations of the Announcement of the Ministry of Transport on Rules to Apply for Permission and Conditions to Control and Launch Unmanned Aircraft in the Category of Remotely Piloted Aircraft B.E. 2558, published in 2015, with permission from the National Broadcasting and Telecommunications Commission (Registration Numbers 30650101209, 30650101214, 30651001094, and 30651100124).

Data were collected using a transect survey followed by an individual identification survey. Surveys were conducted 27 times and 16 times at Sites A and B, respectively (Table 1). A transect survey was designed to grasp the number and location of individuals within the observation area, facilitating more efficient data collection for subsequent individual identification surveys. Data from the transect survey were utilized to analyze population density and inter-individual distances. In contrast, data from the individual identification survey were used to examine the body length frequency distribution and resighting rate. In the study area, the underwater visibility and detectability of dugongs decreased significantly for at least a few days following heavy precipitation (Yamato, pers. obs.). Therefore, only data from days with clear visibility, when the seafloor was visible and all dugongs within the observation area could be detected, were used for subsequent analyses (Table 1). When surveys were conducted twice daily, only data from the first survey were used for the analysis. The drones were equipped with circular polarizer/linear (CPL) filters to reduce the effects of sun glitter when sunlight was intense. The same pilot conducted all surveys throughout the study.

Transect Survey

Transect survey flights were conducted using one of the two commercial drones—Mavic 2 PRO and Phantom4 PRO V2.0 (Da-Jiang Innovations Science and Technology Co., Ltd., Shenzhen, China). The flight courses for collecting aerial photographs were programmed using commercial software (*UgCS*, Version 4.1; SPH Engineering Co., Ltd., Riga, Latvia). The overlap between lines was set to 0% to ensure that all individuals within the observation area were located, thereby facilitating more efficient data collection in subsequent individual identification surveys. We conducted the surveys as swiftly as possible to minimize the risk of overcounting individuals across lines while ensuring reliable detection of dugongs. Therefore, we set the flight speed to 10 m/s after several trials.

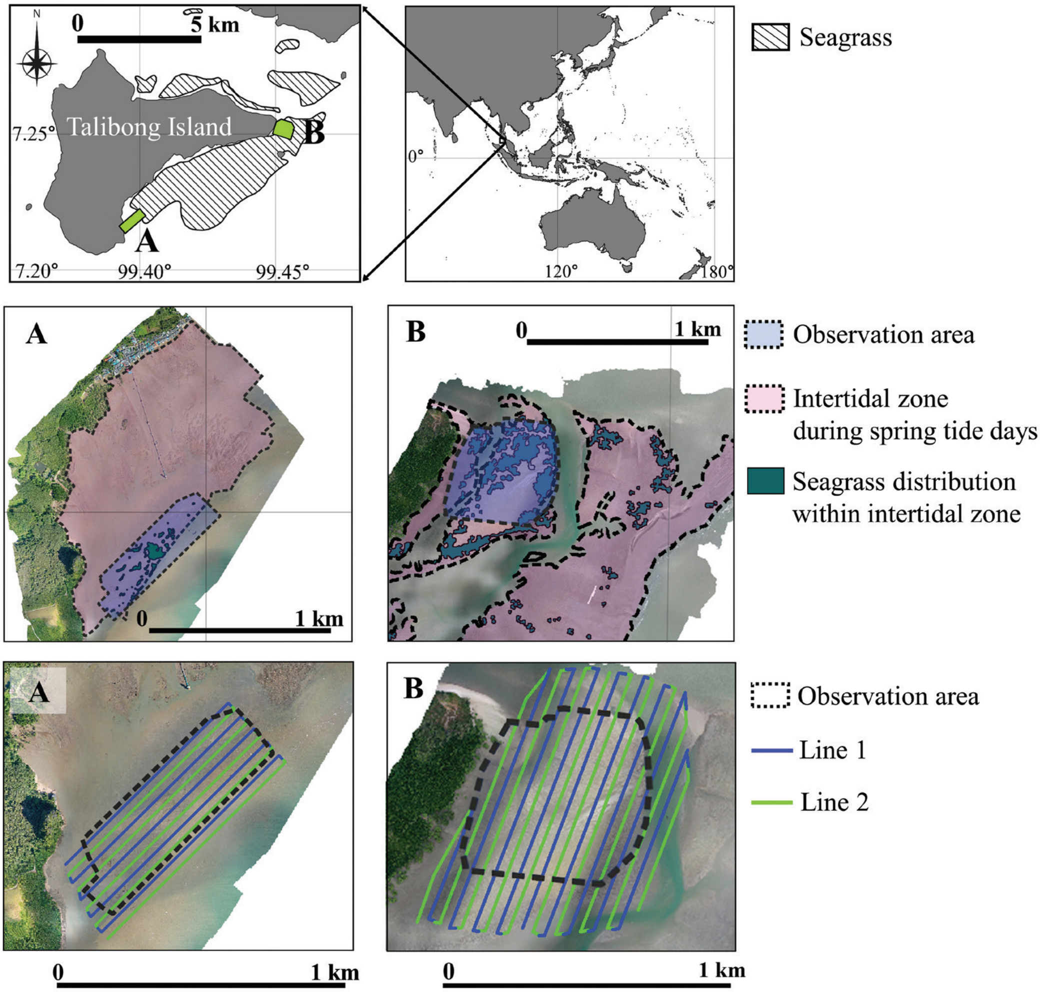

Figure 1. Map of the survey area. Striped area in the upper inset indicates the seagrass distribution (Kittiwattanawong, pers. comm., 20 February 2020). The lower inset's blue and green lines represent the flight courses for the transect survey. Overlap between lines is set to 0% to ensure all individuals within the observation area are located, facilitating more efficient data collection in the subsequent individual identification surveys. In the following population density analysis, individuals observed along the blue and green lines were analyzed separately to reduce the potential for overcounting.

The forward overlap rate, defined as the overlap rate between successive images along the transect line, was 80%. For Site A, the flight time was 17 min for a single flight; whereas for Site B, it took 30 min and involved two flights. The drones flew at a flight height of 39 m, yielding a ground sampling distance of 1 cm per pixel. This resolution was well within the standards shown to be sufficient for detecting dugongs (Hodgson et al., 2013; Cleguer et al., 2021).

Individual Identification Survey

After the transect survey, videos of dugongs observed within the observation area were collected using a drone, either the Mavic 2 PRO in February or the Mavic 3 in other periods. The drone was first launched at an altitude of 80 to 100 m, and the search for dugongs was performed manually. When a dugong was found, it descended vertically above its position, and a video of one to three dive cycles (approximately 1 to 6 min) was recorded. The videos were captured at an altitude of 30 or 40 m with a 7x zoom when using the Mavic 3 (in most cases) or at 10 m when using the Mavic 2 PRO (on 25 and 28 February). Disturbances from the drone were not apparent. The dugongs did not flee and were either feeding, resting, or moving inactively

Table 1. Overview of transect and individual identification surveys. The observation effort for identification (h/animal) was defined as the total time required for individual identification surveys (from the take-off of the first flight to the landing of the last flight) divided by the number of individuals identified on the day.

Site A					Site B			
Month	Date	Trial	Number of individuals identified	Observation effort for identification (h/animal)	Month	Date	Number of individuals identified	Observation effort for identification (h/individual)
Feb	14*				Sep	26[§]	2[§]	0.13[§]
	19*				Oct	3[§]	1[§]	0.95[§]
	20*					5	11	0.21
	21*					6	6	0.35
	22*					7	10	0.20
	24*					8	5	0.27
	25	1	2	0.09		15	6	0.51
		2[†]	2[†]	0.18[†]	Nov	21	12	0.26
	28		2	0.48		22	8	0.09
April	25	1	2	0.34		23[§]	7[§]	0.22[§]
		2[†]	2[†]	0.11[†]		24[§]	2[§]	0.35[§]
	26		1	0.17		29	5	0.39
	27		1	0.08		30[§]	3[§]	0.36[§]
May	1	1	2	0.17	Dec	5	8	0.13
		2†	3[†]	0.08[†]		6[§]	1[§]	0.16[§]
	2	1	1	0.07		8	5	0.10
		2[†]	1[†]	0.12†				
	4		3	0.24				
	6		2	0.23				
Oct	12		2	0.30				
	13		1	0.15				
	14		3	0.21				
Nov	29		1	0.25				
Dec	1[P]							
	5		2	0.22				
	6		1	0.12				
	7		3	0.17				
Average ± SD			1.8 ± 0.8 (*n* = 16)	0.20 ± 0.11 (*n* = 16)	Average ± SD		6.8 ± 3.0 (*n* = 10)	0.26 ± 0.12 (*n* = 10)

*Only data from the transect survey were utilized. Data from the individual identification survey were excluded due to the inadequate quality of photographs for individual identification.

[§]Data were not used because of poor water visibility (i.e., the seafloor was not visible).

[†]Excluded data from the second survey of a day.

[P]Only transect survey was conducted.

(occasionally stroking their fluke). Individual identification surveys were conducted until new individuals became difficult to identify.

The most distinctive images of the surfacing dugong were extracted from each video for individual identification using the video-editing application *Films & TV*, Version 10.22091.10031.0 (Microsoft Corporation, Redmond, WA, USA). The scarring pattern of dugongs has been used as a marker for individual identification (Anderson, 1995). A catalog of the dugongs was initiated by matching their body scarring patterns on the dorsal side. Only the images in which an individual linear and/or spotted scar was visible on the ventral side were used. However, two individuals observed on 30 November at Site B could not be identified due to the absence of identifiers. Data from that day were excluded because of poor water visibility (Table 1).

Data Analysis

Population Density—Population density was defined as the number of individuals per survey area. Even with a 0% overlapping rate between lines, there remained the possibility of double counting between transect lines as a dugong might cross adjacent transect lines while a drone passes along the same lines. To further mitigate the risk of double counting, we established two groups of transect lines spaced apart, and counted the number of individuals in each group separately (Figure 1). Resights due to forward overlap (most individuals were visible across several consecutive images) were manually removed.

Nearest Neighbor Distance—The distance, a measure of animal aggregation (Clark & Evans, 1954), was determined using data from the transect survey. First, the coordinates for each individual were determined. Because most individuals were visible across several consecutive images due to forward overlap, a single image was assigned to each individual. To mitigate the effects of aerial image distortion, the image in which the individual was most centrally positioned within the frame was selected.

The coordinates of the snout were determined based on its position relative to the center of the image. The coordinates at the center of the image were defined as the location of the drone when the image was captured. The snout coordinates were calculated based on the location and yaw direction of the drone at the time of capture, both of which were extracted from the EXIF metadata of the images. The distance between the image center and snout was scaled based on the flight height, image size (in pixels), camera sensor width, and focal distance of the drone (Ramos et al., 2022). The software *MATLAB R2023a* (MathWorks Inc., Natick, MA, USA) was used for the analysis.

The nearest neighbor distance for Site A was calculated among the individuals found along all transect lines as no dugongs were observed within the same transect line. For Site A, we considered the risk of double counting to be low, even if we used all transect lines. This is because a few individuals (1.7 ± 0.7 animals on 16 separate days) were observed during the transect survey at Site A, and the same number of different individuals were observed during the subsequent individual identification survey. For Site B, the nearest neighbor distance was calculated among individuals observed within the same transect line to prevent double counting between transect lines.

Subsequently, Pearson's chi-squared test with Yates' continuity correction was used to determine whether there was a significant bias in the distribution of the nearest neighbor distances at each site. Yates' continuity correction was applied because several expected frequencies were nearly zero. A class width was defined as the average body length of adult dugongs (2.5 m), reported by Marsh (1980), to simplify the analysis. The individual body length served as a unit for nearest neighbor distances in a previous study by Hodgson (2004).

Site Fidelity—The proportion of individuals with strong site fidelity was compared between the sites. First, each individual was assigned a single site fidelity index. The site fidelity index is defined as the ratio of the number of resights for each animal to the number of survey days from an individual's first to last sighting (Simpfendorfer et al., 2011; Daly et al., 2014; Zanardo et al., 2016; Mintzer et al., 2023). A site fidelity index value of one indicates that the individual was sighted on all survey days from its first sighting to its last sighting, and a value of zero indicates that it was never resighted after its first sighting. We then calculated the average site fidelity index of the individuals sighted on each survey day. A high average site fidelity index indicates a high proportion of individuals with strong site fidelity. An independent sample t test with unequal variances (Welch's t test) was conducted to compare the average site fidelity indices between the two sites.

Body Length Frequency Distribution—We determined the body length frequency distribution of individuals visiting each site. The body lengths of the individuals were estimated from videos captured during individual identification surveys. The most representative frames were extracted from each video. A "same video" was defined as videos taken during a single flight. Frames were categorized as either "available" or "not available" based on whether the dugong was flat, horizontal, or straight (neither twisted nor inclined) and whether its extremities were distinct. These criteria are commonly used to estimate the body length of whales (Koski et al., 2006; Christiansen et al., 2018). Examples of rated photographs are provided in Figure 2. The length of the straight-line from the tip of the snout to the medial notch of the fluke was measured. The body length of the dugong was scaled using flight altitude data, image size, camera sensor width, and the focal distance of the drones (Ramos et al., 2022).

Videography was conducted 180 times, and "available" images were obtained on 104 occasions (57%). A total of 64 individuals were identified, with one to 14 videos collected for each individual. Each individual was assigned a length value. The mean values of measurements were used for individuals observed multiple times. Six individuals were measured three to 14 times. For these individuals, the interquartile range of body length difference between different videography sessions was 0.20 ± 0.15 m (n = 6; range: 0.09 to 0.45 m).

Of the 64 individuals, four were also measured using an alternative method when they were opportunistically photographed alongside objects of known length such as seagrass patches or feeding trails. Measurements for these objects were obtained from orthophotos of the seagrass bed with a resolution of 1 cm/pixel (refer to Supplemental Material S1 [which includes Figure S1 & Tables S1-S3] for detailed methodology; supplemental materials for this article are available on the *Aquatic Mammals* website). Each individual was measured one to three times using this method. The median value of body length obtained from this method differed from the one measured without utilizing orthophotos by an average absolute value of 0.21 ± 0.09 m (n = 4; range: 0.15 to 0.35 m; Table S2).

The body length frequency distribution for each site was created by pooling the body lengths of the individuals sighted during the individual identification survey. For example, if a dugong was sighted on two separate days, its body length was included twice in the pooled data.

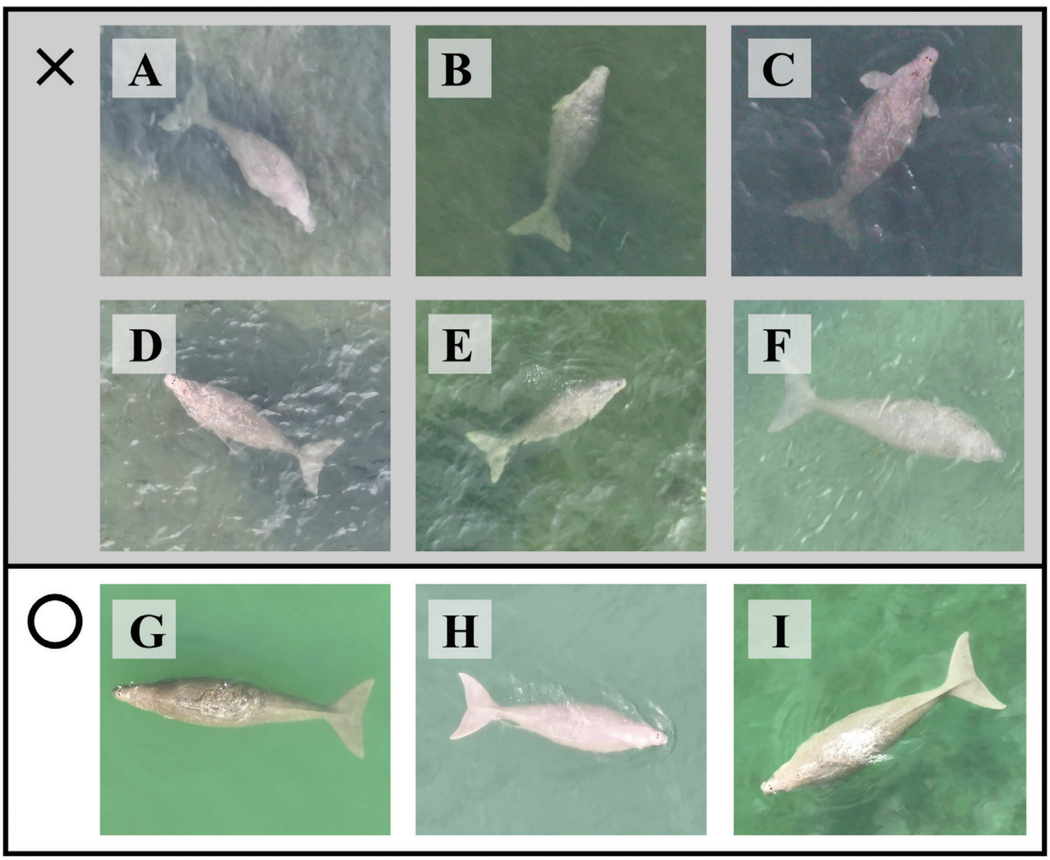

Figure 2. Examples of rated photographs: photographs A through F were categorized as "not available" either because the dugong was not flat, horizontal, or straight or its extremities were not distinct; and photographs G through I were categorized as "available." (Photos provided by Chiaki Yamato)

Results

Population Density

The average population density at Site B was approximately three to five times higher than that of Site A (Table 2). Sites A and B were occupied with an average of 1.6 ± 0.7 individuals (n = 23) and 9.8 ± 3.6 (n = 10) individuals, respectively.

Nearest Neighbor Distance

The median value of the nearest neighbor distance at Site A was 320 m (interquartile range: 210 to 493 m; range: 117 to 786 m; n = 27) and 20 m at Site B (interquartile range: 7 to 47 m; range: 2 to 384 m; n = 56). No significant bias was observed in the distribution of nearest neighbor distances at Site A ((311) = 49.9; p = 1.0; Figure 3). In contrast, there was a significant bias in the distribution at Site B ((311) = 4,754.2; $p < 0.01$).

Resighting Rate

In total, five and 59 individuals were identified at Sites A and B, respectively. No individuals were observed at both sites. At Site A, one individual was observed only once, whereas the remaining four individuals were observed on more than three separate days. These four individuals consistently appeared across the seasons (Table 3). At Site B, 62.7% (37 individuals) were sighted only once, while 18.6% (11 individuals) were encountered twice, and 18.6% (11 individuals) were sighted three or more times (Table S3).

The mean fidelity index for Site A (0.62 ± 0.08; n = 16) was higher than that for Site B (0.39 ± 0.14; n = 10). There was a significant difference in the mean site fidelity indices between the two sites: t (13) = 2.16, $p < 0.01$ (two-tailed).

Length Frequency Distribution

At Site A, only relatively large individuals (2.1 to 2.9 m) were observed; while at Site B, individuals with a wider range of body lengths (1.1 to 2.9 m) were observed (Figure 4). The median value of body length was 2.5 at Site A (interquartile range: 2.5 to 2.6 m; n = 36) and 2.0 m (interquartile range: 1.7 to 2.6 m; n = 78) at Site B.

Discussion

Site A was frequently occupied by fewer individuals with higher resighting rates than Site B. Only relatively large individuals were observed at Site A, whereas individuals with a wide range of body lengths were observed at Site B. The nearest neighbor distance for Site A was longer than that for Site B. It is likely that there were at least two distinct patterns of feeding ground utilization across these sites.

Body Length Frequency Distribution

Based on the carcass analysis of 108 dugongs from North Queensland, Australia, Marsh et al. (1984) established three size/maturity classes for dugongs: (1) juveniles (2.2 m body length), likely to be reproductively immature; (2) subadults (2.2 to 2.49 m body length) with uncertain reproductive status; and (3) adults (2.5 m body length). The size/maturity classes of dugongs in Moreton Bay, Queensland, confirmed by reproductive hormone levels, were calves (straight body length: 2 m), subadults (male: 2.2 to 2.39 m; female: 2.2 to 2.49 m), and adults (male: 2.4 m; female: 2.5 m) (Burgess et al., 2012a, 2012b; Lanyon et al., 2021). The average lengths of mature males and females in Thailand were 2.58 ± 0.18 m (n = 12) and 2.55 ± 0.17 m (n = 23), respectively (Adulyanukosol et al., 2011). The body length of calves in Thailand ranges from 0.97 to 1.31 m (n = 14) (Adulyanukosol et al., 2011). According to the classification of Lanyon et al. (2021), the individuals observed at Site B were likely calves, juveniles, subadults, and adults. In contrast, Site A was occupied by subadults and adults only. The smallest individual, with an estimated body length of 1.2 m observed at Site B, may have been a calf. It swam approximately 2 to 3 m from a larger individual

Table 2. Population density of individuals. The total observation areas of Sites A and B were 2.0×10^5 m^2 and 2.8×10^5 m^2, respectively. Transect surveys for Lines 1 and 2 were conducted simultaneously, while individuals observed along Lines 1 and 2 were counted separately to reduce the potential for overcounting.

	Site A (n = 23)		Site B (n = 10)	
	Line 1	Line 2	Line 1	Line 2
Observation area (m^2)	1.0×10^5	1.0×10^5	1.4×10^5	1.4×10^5
Number of individuals (range)	0.9 ± 1.0 (1-2)	0.6 ± 0.8 (1-2)	4.3 ± 1.1 (3-6)	4.5 ± 2.8 (3-11)
Population density (individuals/m^2)	$2.2 \pm 2.5 \times 10^{-6}$ ($2.5\text{-}5.0 \times 10^{-6}$)	$1.5 \pm 2.0 \times 10^{-6}$ ($2.5\text{-}5.0 \times 10^{-6}$)	$7.7 \pm 2.0 \times 10^{-6}$ ($5.4\text{-}10.8 \times 10^{-6}$)	$8.1 \pm 5.0 \times 10^{-6}$ ($5.4\text{-}19.8 \times 10^{-6}$)

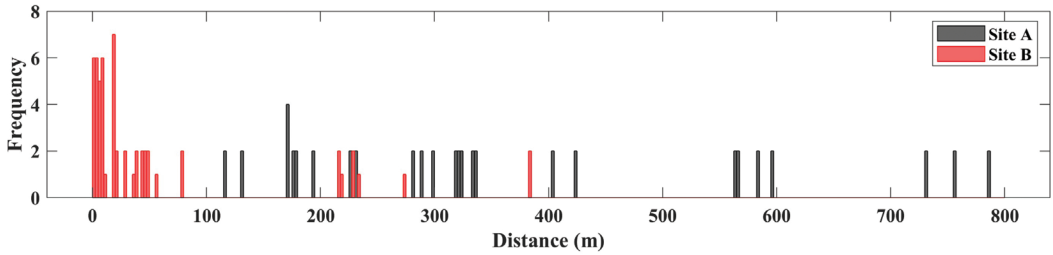

Figure 3. The nearest neighbor distances among individuals observed during the transect survey. The class width of the histogram is set to 2.5 m.

Table 3. Resighting record of individuals at Site A. The checkmarks indicate the presence of dugongs (*Dugong dugon*), while hyphens indicate their absence. ID = Identifier names of encountered dugongs.

Month	Date	Trial	Encounter (ID)				
			WB	N	WBS	WF	NS
Feb	25	1	✓	-	✓	✓	-
		2	✓	✓	✓	-	-
	28		-	✓	-	✓	-
April	25	1	✓	✓	-	-	-
		2	✓	✓	-	-	-
	26		✓	-	-	-	-
	27		-	✓	-	-	-
May	1	1	✓	✓	-	-	-
		2	✓	✓	✓	-	-
	2	1	-	-	-	✓	-
		2	✓	-	-	-	-
	4		✓	-	✓	-	-
	6		✓	✓	-	-	-
Oct	12		✓	✓	-	-	-
	13		-	✓		-	-
	14		✓	✓	✓	-	-
Nov	29		✓	-	-	-	-
Dec	5		✓	-	-	-	-
	6		-	✓	-	-	-
	7		✓	✓	✓	-	-

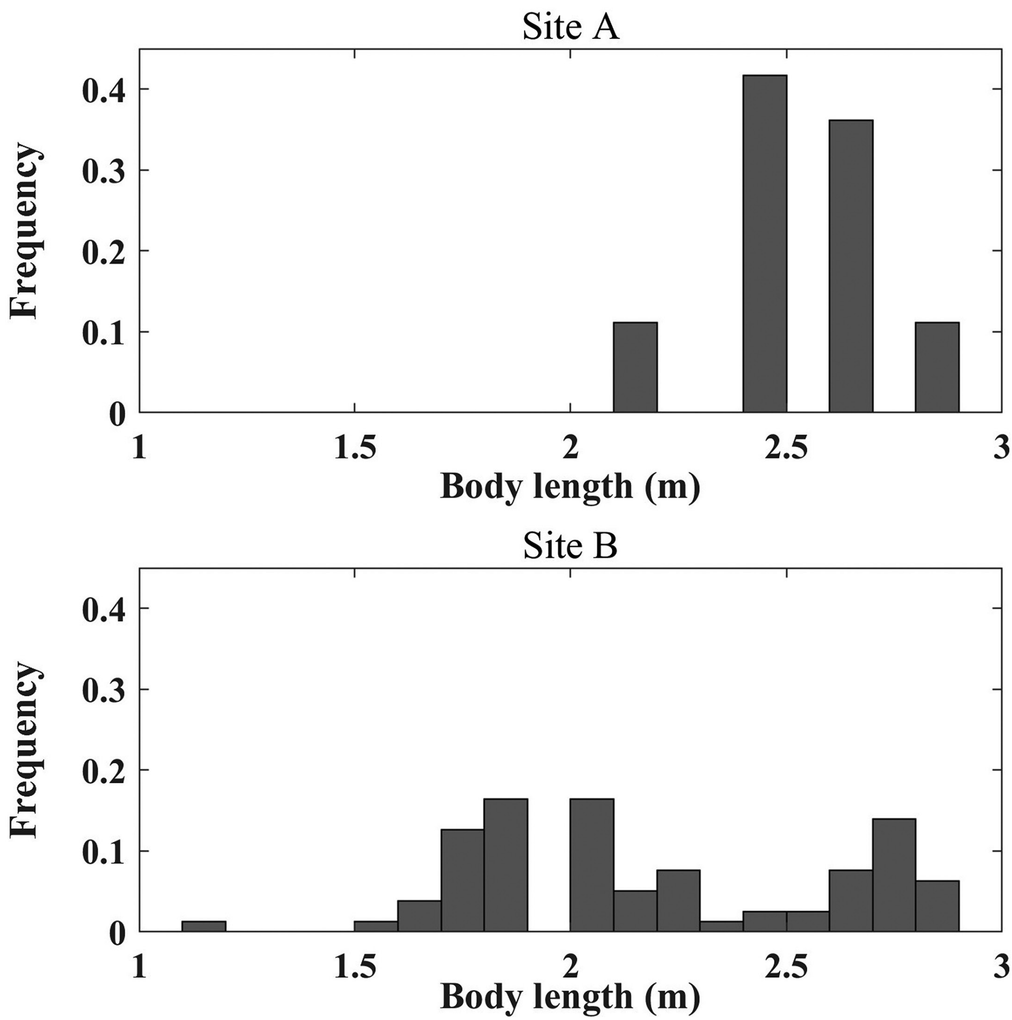

Figure 4. Length frequency distribution of dugongs identified at Site A (the upper inset) and Site B (the lower inset)

with an estimated body length of 2.2 m and exhibited synchronous breathing. Dugong calves surface synchronously with their mothers on more than 50% of their surfaces (Hodgson, 2004). Also, a possible herd of seven individuals with estimated lengths of 2.2, 2.0, 2.0, 1.8, 1.7, 1.7, and 1.5 m might have included dependent calves. They swam in the same direction and were closely accompanied by one another (less than 2 to 3 m). Other individuals smaller than 2.0 m appeared to not be fully dependent on their mothers as they were not closely (< 3 m) accompanied by larger individuals.

For a more reliable distinction between size classes, the estimation error for body length should be minimized in future studies. The largest contributor to the estimation error in this method is the inaccuracy of the flight altitude provided by the drones. Such errors can be mitigated by measuring altitude using LiDAR (Light Detection and Ranging) or a laser range finder mounted onto a drone (Dawson et al., 2017; Christiansen et al., 2018; Ramos et al., 2022). Furthermore, it is essential to accumulate further information regarding the body length of each size class in the study area.

Nearest Neighbor Distance

At Site A, the distribution of nearest neighbor distances lacked distinct peaks and biases, indicating that there was no specific inter-individual distance at this site. Furthermore, the minimum distance exceeds 100 m, suggesting that aggregation did not occur at this site. In contrast, the distribution at Site B exhibited a significant bias, particularly with a relatively higher frequency of nearest neighbor distances ranging from 2 to 20 m. Dugong calves often travel close to their mothers (less than 2 m apart) (Anderson, 1984; Adulyanukosol et al., 2007). Both single individuals and mother-calf pairs tend to be closer to each other (less than 2 to 3 m) during feeding than when exhibiting other behaviors (Hodgson, 2004). These distances were within the predominant range of the nearest neighbor distances observed at Site B. Based on these observations, feeding aggregations were present at Site B and likely not at Site A.

Feeding Ground Utilization at Site A

The higher site fidelity at Site A suggests that this seagrass bed was able to support the feeding requirements of dugongs that utilize this area, which is consistent with a report from another region with low population density (D'Souza et al., 2015). At Site A, the proportion of feeding trail coverage relative to seagrass coverage and biomass was smaller than that at Site B (Yamato et al., under review). This more abundant food resource, lower population density, and greater nearest neighbor distance at Site A compared to Site B may indicate that dugongs at Site A monopolize this site to a certain extent. Conspecific aggressions observed in this area may support this hypothesis (Yamato et al., 2023). Anderson (1997) proposed that dugongs in Shark Bay, Australia, form lek territories. In sparsely vegetated coves, he identified 19 to 22 areas frequently occupied by solitary adults for an average duration of approximately 40 to 45 d (with a maximum of 75 d). Aggressive behavior occurred at the borders of these zones; however, other than these reports, there is little evidence suggesting dugong territoriality. Furthermore, the inaccessibility of this site during low tide makes it difficult to maintain these territories (if they were indeed territories). It is necessary to record occupancy, home ranges, and the behavior of neighboring individuals using both telemetry surveys and visual observation to test this hypothesis and determine whether dugongs exclusively defend their feeding grounds.

Feeding Ground Utilization at Site B

Individuals at various growth stages used Site B due to its probable use as a calving and nursery ground. The mating behavior of solitary pairs was observed in (Yamato et al., under review) and around (Adulyanukosol et al., 2007; Infantes et al., 2020) the site. Calves have also been observed around this site during earlier aerial surveys (Hines, 2002; Ichikawa et al., 2012). After learning the resource location from their mothers, weaned juveniles may continue to use the site. Once newly independent, juveniles of Florida manatees follow the same seasonal migration patterns as their mothers (Deutsch et al., 2003). Subadults and adults may benefit from increased opportunities for social interaction, such as mating, provided by feeding aggregations (Hodgson, 2004). It is unlikely that dugongs in this study area formed herds in response to predation pressure given the absence of predators, such as the tiger shark, as reported in other regions (Preen, 1992; Wirsing et al., 2007; Wirsing & Heithaus, 2012).

The information collected in this study regarding the social functions of these seagrass beds is limited because the sex of most individuals was not determined. One of the individuals who frequently visited Site A (ID: N) was identified as male based on the genitalia observed during a drone survey. Both males and females were present at Site B because mating behavior was observed at this site during the observation period (Yamato, pers. obs.). Sexual segregation occurs on various scales in other marine mammal species (Pirotta et al., 2020). One of the common contexts for sexual segregation is that mothers and calves use different habitat areas than other age groups, presumably to avoid harassment from males (Weir et al., 2008; Fury et al., 2013; Craig et al., 2014). A similar phenomenon might be evident around these sites. Dugong mothers may provide calves with protection from aggressive adult males. Estranged calves have relatively heavy body scarring and higher fecal glucocorticoid concentrations than similar-sized dependent animals (Burgess et al., 2013; Lanyon et al., 2021).

The lower site fidelity at Site B suggests that this seagrass bed might not be capable of supporting the feeding requirements of the dugongs that utilize this site. As discussed above, the proportion of feeding trail coverage relative to seagrass coverage and biomass at Site B was greater than that at Site A (Yamato et al., under review). Dugongs utilizing this site might benefit from intensive feeding, which can promote the growth of nutritionally superior new seagrass shoots and alter species composition (Preen, 1995; Aragones et al., 2006). Given the survey effort of 3 mo for this area, the observed site fidelity might not fully represent long-term site fidelity such as that on a yearly basis. The survey period for Site B corresponded to the end of the rainy season and the beginning of the dry season. During this period, seagrass coverage at Site B was significantly lower than in February (Yamato et al., under review). In contrast, seasonal variations in seagrass coverage at Site A were not evident (Yamato et al., under review). Individuals using this site may be disadvantaged by the seasonal heterogeneity of their food resources.

Limitation of Individual Identification Survey of Dugongs Using Drones

To the best of our knowledge, this study is the first to employ drones to identify individual dugongs, apart from Yamato et al. (2023) who identified four individuals. Because individual identification of dugongs necessitates high-quality photographs from the same point, we focused on each individual until it surfaced at least once. Given this approach, the method used in our study may not have been optimized for identifying all individuals within larger and denser feeding aggregations. Furthermore, individuals without body scarring on the dorsal side may not be identifiable. In our study, there were two instances in which identification failed due to the absence of identifiers, whereas 64 individuals had distinct identifiers. Even with these constraints, the drone-based approach is poised to be the most efficient method for the noninvasive identification of dugongs with a high probability of identification. Compared with traditional identification methods that use photographs taken underwater or from boats (Anderson, 1995; Shawky et al., 2019), this approach has the advantage of capturing photographs of dugongs in a similar posture while surfacing from a consistent viewpoint, thus making the matching of identifiers easier.

Conclusions

Dugongs are typically solitary animals; however, they are not evenly distributed across feeding grounds. This study highlighted fine-scale variations in seagrass habitat utilization and observed at least two distinct patterns of feeding ground utilization across our study site. That is, population distribution, site fidelity, body size, and aggregation varied among seagrass beds located 5 km apart. These findings highlight the importance of fine-scale monitoring that incorporates body lengths and resighting rates into their locations to better understand the spatial heterogeneity of dugongs. Continuous individual identification surveys will help enhance our understanding of the causes and consequences of this variation, providing baseline data for the further development of habitat assessment.

Note: The supplemental materials for this article are available in the "Supplemental Material" section of the *Aquatic Mammals* website: https://www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=10&Itemid=147.

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