The island hoppers: how foraging influences green turtle *Chelonia mydas* abundance over space and time in the Lakshadweep Archipelago, India

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ABSTRACT: Adult green turtles are known to display either preference in their foraging habits or fidelity to their foraging sites which, in turn, influences their migrations and the availability of forage. With an abundant supply of seagrass and algae, the lagoons of the Lakshadweep Archipelago off the Indian west coast serve as significant feeding grounds for green turtles. In the last 2 decades, the numbers of foraging green turtles have varied across islands, leading to speculation about their foraging patterns and movements. We collated secondary data and conducted periodic surveys between 2013 and 2019 to record trends in green turtle abundance and seagrass characteristics and investigate relationships between them. Over the last decade, green turtle abundances have fluctuated widely with increases followed by sharp declines within different lagoons. Our results also show that a reduction in seagrass density, particularly *Thalassia* sp. and *Cymodocea* sp., coincided with the decline in green turtle abundance. Moreover, turtle presence was observed at sites with higher seagrass density and canopy height. Our findings indicate that green turtles appeared to forage in particular lagoons until their preferred resources declined, before moving to other islands within the Archipelago or other unknown locations. Therefore, to devise effective management strategies, it is crucial to understand how this green turtle population will adapt to the decline in foraging resources. The declining seagrass populations also suggest the need for an ecosystem approach towards green turtle conservation.

KEY WORDS: Green turtle · Seagrass · Lakshadweep · Foraging · Abundance · Movement

1. INTRODUCTION

Optimal foraging theory suggests that organisms select the most profitable food resources to maximize energy intake and limit time and energy expended in searching to ensure growth, reproductive success and survival (MacArthur & Pianka 1966). These foraging requirements often result in animals altering their movements or preferences depending on various conditions. Abiotic and biotic factors further influence animal distributions across foraging areas, and sites with abundant forage, high nutritional

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capacity and lower risk of predation tend to show high aggregates of consumers (Stephens & Krebs 1986). Over time, the foraging capacity and behaviour of a consumer can change the structure and distribution of its forage through persistent feeding (Micheli 1997). This is especially true for megaherbivores that, owing to their large sizes, can alter and influence the productivity of their habitats (Owen-Smith 1988). Conversely, forage distribution, quality and abundance play an important role in influencing herbivore movements (Fryxell et al. 2004, Bjørneraas et al. 2012).

Marine grazers such as green turtles *Chelonia mydas*, dugongs *Dugong dugon*, manatees *Trichechus* sp. and various fish species can influence the structure and biomass of seagrasses (Burkholder et al. 2012). Their grazing has been shown to have different impacts through controlling competition between plants, altering nutrient dynamics and reducing plant biomass. For example, green turtle grazing can increase the decomposition rate of seagrass (Thayer et al. 1982) and improve its forage quality through the growth of new shoots rich in nutrients (Bjorndal 1980). On the other hand, persistent grazing can reduce the seagrass canopy and affect sediment by altering irradiance levels and retention rates (Gacia et al. 1999).

Green turtles show a predominantly herbivorous diet, with a distribution spanning the shallow tropical and temperate waters across the world (Bjorndal 1997). As they develop, green turtles change their habitat as they move from an oceanic phase to a neritic phase (Arthur et al. 2008). This habitat change is accompanied by a switch in diet as they undergo a drastic ontogenetic shift from omnivory and carnivory to mainly herbivory (Arthur et al. 2008). Upon reaching adulthood, their diet mostly comprises seagrasses, macroalgae and invertebrates (Bjorndal 1997, Seminoff et al. 2002, Burkholder et al. 2011), with preferences dependent on resource availability and quality (Arthur & Balazs 2008). Some populations exhibit fidelity towards their neritic feeding sites, returning to the same sites after long migrations (Broderick et al. 2007, Shimada et al. 2020). However, if their preferred resource is depleted, green turtles can exhibit behavioural plasticity by altering their food preferences or changing feeding sites (Arthur & Balazs 2008). Some green turtles have also been observed to maintain a mixed diet of seagrass and algae (André et al. 2005), which can help them adjust to changes in abundance of either resource.

In the past few decades, there have been widespread conservation efforts to protect green turtle popula-

tions across the world. Consequently, as their numbers and biomass have increased, seagrass meadows have been overgrazed in some areas such as Bermuda and Indonesia (Fourqurean et al. 2010, Christianen et al. 2014). Within these sites, green turtle overgrazing has adversely affected seagrass structure and function by reducing biomass, canopy height and leaf width and density as well as altering species composition, resulting in phase shifts in meadows (Thayer et al. 1984, Fourqurean et al. 2010, Burkholder et al. 2012). Consequently, the overall quantity and quality of seagrass available to the turtles has diminished.

Similarly, studies in India have shown that green turtle grazing has significantly altered the seagrass meadow structure and function in the Lakshadweep Archipelago (Lal et al. 2010, Kelkar et al. 2013b). In this location, it was observed that green turtles could consume an average of almost 60% of the total seagrass produced in the water around the islands, thereby causing significant changes in seagrass dynamics (Kelkar et al. 2013a). Not only did overgrazing alter seagrass meadows, but it also affected the populations of associated lagoon fish species that use seagrass habitats for feeding, breeding and protection (Arthur et al. 2013). While the effects of turtle overgrazing on seagrass and associated fish communities are still being documented, collectively they highlight the need to examine green turtle and seagrass conservation together.

In India, although several studies have focused on seagrass, these have not addressed the implications of spatial and temporal variation in green turtle abundance within the Archipelago. Therefore, we compiled secondary data and conducted primary surveys between 2013 and 2019 to monitor changes in green turtle density in island lagoons across years. We simultaneously assessed changes in seagrass abundance and characteristics over time. Finally, we examined the relationship between green turtle density and seagrass characteristics (shoot density and canopy height) in the different lagoons and explored implications for the conservation of green turtles and seagrass.

2. MATERIALS AND METHODS

2.1. Study site

The Lakshadweep Archipelago is located between 8–12° N and 71–74° E, approximately 200 km from the west coast of mainland India in the Arabian Sea. The Archipelago comprises 12 atolls and 5 sub-

merged banks with 36 islands (Saigal 1990). Many of these islands are characterized by low-lying lagoons on the western side that host multi-specific seagrass communities, algae, sea turtles, fishes, coral colonies, etc. The seagrass species found in the island group include *Halophila decipiens*, *Thalassia hemprichii*, *Cymodocea rotundata*, *C. serrulata*, *Syringodium isoetifolium*, *Halodule uninervis* and *Halodule pinifolia* (Jagtap 1998). The seagrass beds serve as suitable habitats for various marine fauna, including different life stages of green turtles that utilize these meadows for foraging and resting (Tripathy et al. 2006). Past studies have determined that green turtles feed mainly on *T. hemprichii* and *C. rotundata* in the lagoons (Kelkar et al. 2013b, Kale et al. 2021).

Based on reports of green turtle presence and foraging from past studies and local observations (Lal et al. 2010, Kelkar et al. 2013b), we chose to survey the island lagoons of Agatti (area: 16.8 km^2), Kadmat (area: 20.9 km^2), and Kalpeni (area: 26 km^2) in the Archipelago (Fig. 1). Green turtle and seagrass surveys were carried out once per year in 2013, 2016, 2018 and 2019 in the pre-monsoon months from January to April. All surveys were carried out in the daytime between 07:00 and 15:00 h using a diesel-powered fishing boat; transects and sampling locations were located using a hand-held GPS.
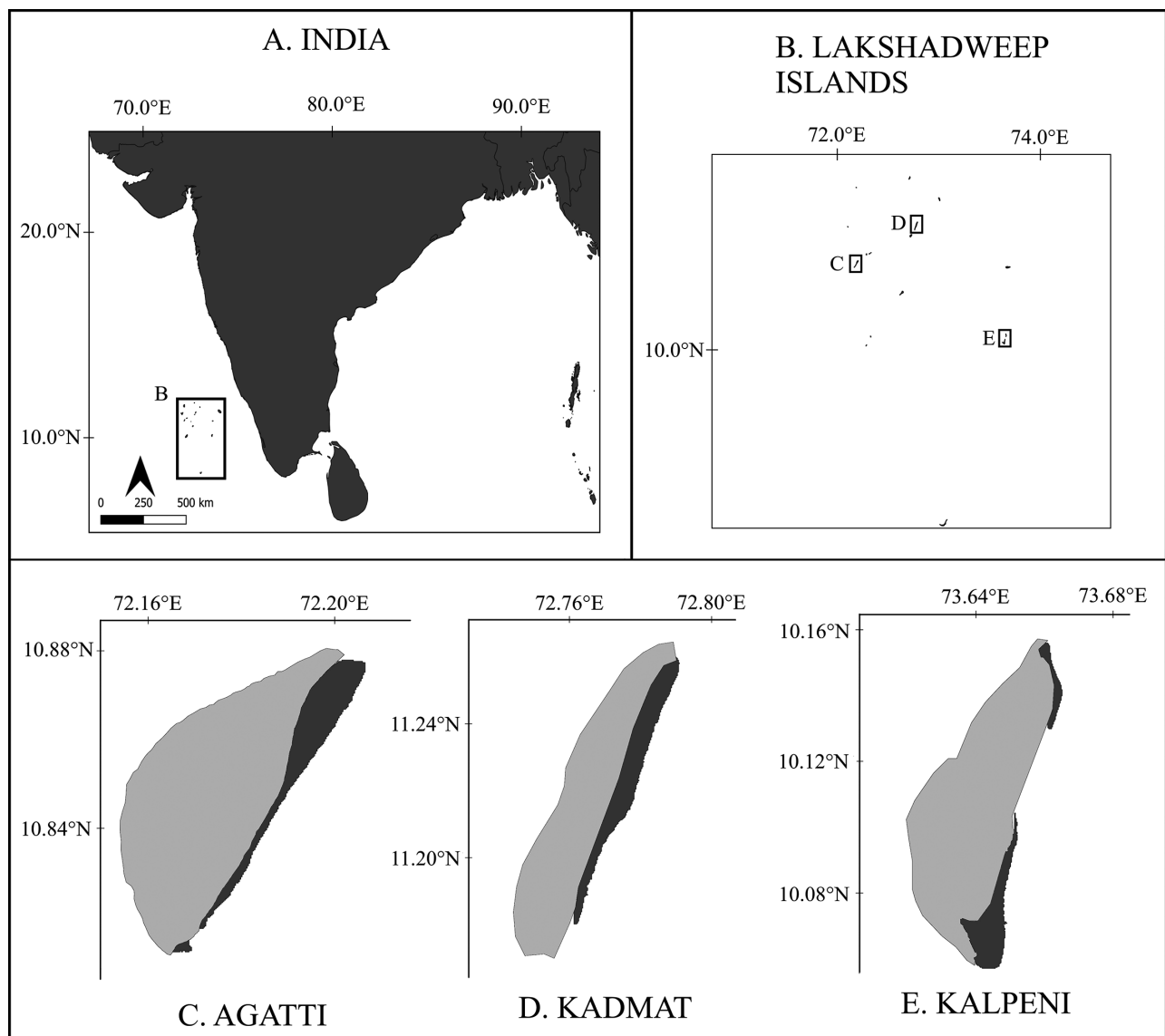

Fig. 1. (A) India, with inset rectangle highlighting the location of (B) the Lakshadweep islands with the 3 study sites (C) Agatti, (D) Kadmat and (E) Kalpeni and their adjoining lagoon boundaries

2.2. Sea turtle monitoring

We conducted green turtle surveys in 2013, 2016, 2018 and 2019. Sampling was designed to cover the northern, central and southern zones of the lagoons as well as different strata such as reef, mid-lagoon and near-shore regions. In 2013, we conducted sea turtle surveys in conjunction with seagrass surveys by dividing the lagoon into grids of 500 × 500 m. From these, survey grids were randomly chosen and sub-divided into plots of 100 × 100 m, of which 36 plots in Agatti and 43 plots in Kadmat were surveyed. In each plot, the boat was anchored at the centre and the number of turtles that surfaced in the plot was counted for 10 min by a single observer. In 2016, 2018 and 2019, we conducted 1 × 0.01 km belt transects using a boat to record sea turtles in each lagoon (Fig. 2B). A single observer stood at the bow of a boat surveying a belt of 5 m on either side as the boat travelled at a constant speed of 8 km h^{-1} along the length of the transect. The transects were laid in different zones and strata of the lagoons, with 9 transects in Agatti, 12 in Kadmat and 12 in Kalpeni (Kadmat was not surveyed in 2016).

2.3. Seagrass monitoring and substrate cover

Seagrass characteristics such as seagrass cover, species composition, shoot density and canopy height were measured. For all years, the lagoon area was first divided into 500 × 500 m grids (Fig. 2A). Using QGIS, seagrass sampling locations were then randomly selected within the grids while ensuring representation of different sections of the lagoon. Sampling locations were the origin points within each grid from which point counts (2013) or 4 transects (2016, 2018 and 2019) were initiated. We surveyed a total of 79 (Agatti: 36; Kadmat: 43), 77 (Agatti: 52; Kalpeni: 25), 84 (28 locations/island in Agatti, Kadmat and Kalpeni) and again 84 (28 locations/island in Agatti, Kadmat and Kalpeni) sampling locations across islands in 2013, 2016, 2018 and 2019 respectively. Some locations had to be altered in the field owing to proximity to the nearby reef region where it was unsafe to survey.

In 2013, at each seagrass sampling location, the observer recorded a total of 40 quadrat points after every 10 fin strokes while snorkelling randomly within the 500 × 500 m grid. At each point, the observer noted substrate type and seagrass characteristics within a 0.25 m^2 quadrat. In 2016, 2018 and 2019, 40 quadrat points were recorded along transects in 4 directions (north, south, east and west) from the point of origin, with 10 quadrats each. Each transect roughly spanned 25 m in length, and the observer recorded 1 quadrat after every 8 fin strokes to collect substrate and seagrass data. Different substrate types such as sand, algae, algae on coral rubble, coral rubble, live coral, dead coral and seagrass were visually estimated (as percent cover) by placing a 0.25 m^2 quadrat. From these estimations, the total cover for different substrate types was calculated for each of the islands.

In all years, upon encountering seagrass, we used a 0.25 m^2 gridded square PVC frame to collect data on seagrass composition, density and canopy height. For seagrass composition, we recorded the different species present in each lagoon. Shoot density was measured as the total number of shoots observed within the placed quadrats; the lengths of the 3 longest shoots were measured and the average was recorded as the canopy height.
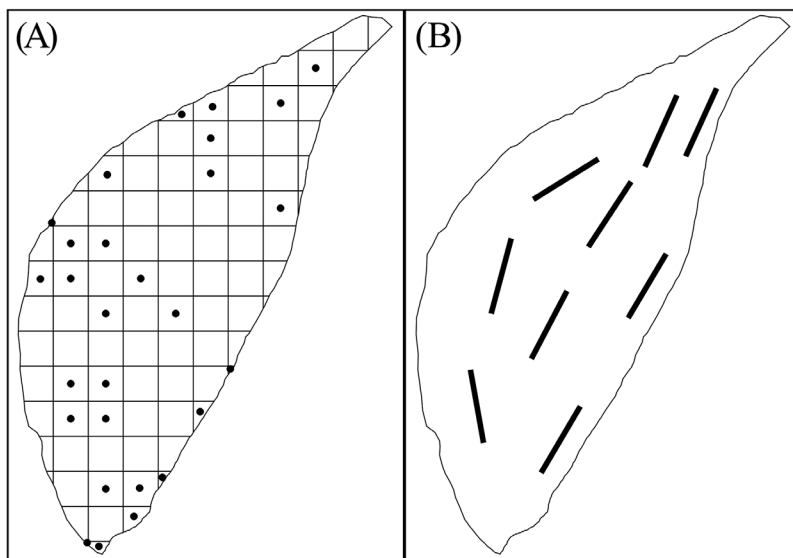

Fig. 2. (A) Sampling locations and (B) transects in the Agatti lagoon used to measure seagrass and sea turtle abundances, respectively, for the different years. In 2013, sampling locations were used to measure both seagrass and sea turtle abundances, whereas belt transects were used in 2016, 2018 and 2019 to measure turtle abundance

2.4. Data analyses

First, we examined spatial and temporal variation in green turtle abun-

dance from each island over the study period (2013–2019). For this, we calculated green turtle density (per km^2) at each transect (2016, 2018 and 2019) and plot (2013) (number of turtles sighted on transect or plot/area of the belt transect or plot) as well as density per island (average density across all transects/plots). Using transect or plot density values (hereafter transect density), we tested the difference in densities of green turtles among the 3 islands and across years using a non-parametric Kruskal-Wallis (KW) test and a post hoc Dunn's test, with p-values adjusted using the Holm method for multiple comparison. We used the green turtle densities per island (average of all transects for each island for a particular year) from our study to compare with densities recorded in other studies and highlight changes in the last 2 decades.

Second, we examined patterns in seagrass cover, density and height; quadrat data were averaged for each sampling location, which was the unit of further analysis. We compared total and species-specific seagrass cover and tested year- and island-wide differences using a KW test and a Dunn's test, with p-values adjusted using the Holm method. Similarly, we examined year and island-wide changes in seagrass density (aggregate and by species) and canopy height (aggregate) using a KW test followed by a Dunn's test, and an ANOVA with a Tukey's test to compare canopy heights by species. Additionally, we collated information on seagrass densities from secondary data to document changes in the last 2 decades. Lastly, the relationship between seagrass density and canopy height was examined using Pearson's correlation at the aggregate level and for individual species.

We also used Pearson's correlations to understand univariate relationships between sea turtle density and seagrass characteristics, i.e. density and canopy height at the aggregate level, by using averages for each island for a particular year as independent data points. To identify specific factors that may influence sea turtle presence and density in a lagoon, a generalized linear model (GLM) was run by pooling data from all years. The turtle transects and seagrass sampling locations were overlaid to check for spatial overlap or proximity (within the 500 × 500 m grid in 2016–2019) to create a matrix of response (turtle presence/absence and turtle transect density) and predictor variables. Independent predictor variables included different lagoon strata where a turtle was sighted (near-shore, mid-lagoon and reef) and the island location (Agatti, Kadmat and Kalpeni). In addition, using the seagrass sampling locations, we

treated seagrass species (*Thalassia*, *Cymodocea*, *Halophila* and *Syringodium* sp.) present at or near the sea turtle transect as a predictor variable; if multiple species were present at a sampling location, each species was treated as an independent variable. We fitted models with a binomial distribution for sea turtle presence and a quasi-Poisson distribution for turtle density.

Finally, we analysed the quadrat data to estimate the cover of other substrates such as sand, algae, algae on coral rubble, live coral, dead coral and coral rubble on the lagoon floor. The data were averaged and converted to percentages to derive individual cover for each lagoon across years.

Before conducting the analysis, all data were checked for normality using the Shapiro-Wilk test and homogeneity of variances using the Levene test. All statistical analyses were performed using R version 4.0.2 and Microsoft$^©$ Excel.

3. RESULTS

3.1. Sea turtle abundance

Sea turtle densities varied across all islands, with sudden increases followed by declines until 2019 (Table 1). In our study, significant differences in green turtle densities (Table S1 in the Supplement at www.int-res.com/articles/suppl/n048p001_supp.pdf) were observed only in Kadmat (KW = 21.26, p < 0.001), specifically between 2013 and 2018 (p = 0.004) and 2013 and 2019 (p < 0.001) (Table S1). For individual years, 2013 showed significant differences in densities between the 2 islands that were surveyed (i.e. Agatti and Kadmat; KW= 9.92, p = 0.002). On the other hand, in 2018 (KW = 11.51, p = 0.003) and 2019 (KW = 7.63, p = 0.021), significant differences were observed only between Kadmat and Kalpeni (p = 0.003 in 2018, p = 0.018 in 2019) (Table S1).

We compiled green turtle densities using secondary data and compared them with primary data from our study to understand changes that have occurred over the last 20 yr (Table 1). Turtle densities were initially low in the mid-2000s, but increased significantly in different lagoons in different years. By 2019, densities had returned to moderate to low levels in the lagoons surveyed. Agatti, which has been consistently monitored over the years, recorded the highest densities in 2008 (~300 turtles km^{-2}) but this declined by 2012. Since 2013, the turtle density has varied. Similarly, turtle densities also fluctuated at Kadmat, with a dramatic increase in 2013 and a

Table 1. Green turtle densities/sighting indices across the 3 islands from different studies between 2001 and 2019. Densities fluctuated greatly, both between islands and across years at each island. NA: not surveyed

Year	Green turtle density			Source
	Agatti	Kadmat	Kalpeni	
2001	1.18[a]	0.71[a]	NA	Tripathy et al. (2006)
2005	32.8 turtles km^{-2}	NA	NA	Kelkar et al. (2014)
2007	10.9 turtles km^{-2}	NA	NA	Kelkar et al. (2014)
2008	~300 turtles km^{-2}	NA	NA	Lal et al. (2010)
2010	27.6 turtles km^{-2}	3.2 turtles km^{-2}	NA	Arthur et al. (2013), Kelkar et al. (2014)
2011	30.8 turtles km^{-2}	3.9 turtles km^{-2}	1.2 turtles km^{-2}	Arthur et al. (2013), Kelkar et al. (2014)
2012	8 turtles km^{-2}	2.6 turtles km^{-2}	NA	Kelkar et al. (2014)
2013	~155.5 turtles km^{-2}	~485 turtles km^{-2}	NA	Current study
2014	4.5 turtles km^{-2}	NA	14.1 turtles km^{-2}	Kelkar et al. (2014)
2016	~166.6 turtles km^{-2}	NA	~1516.6 turtles km^{-2}	Current study
2018	~100 turtles km^{-2}	41.6 turtles km^{-2}	~400 turtles km^{-2}	Current study
2019	33.3 turtles km^{-2}	0 turtles km^{-2}	91.6 turtles km^{-2}	Current study

[a]Sighting index used by Tripathy et al. (2006)

subsequent decline. By 2018, green turtle density increased again; there were no turtles recorded at this site in 2019. On the other hand, green turtle densities in Kalpeni were consistent until increasing dramatically in 2016 (~1500 turtles km^{-2}) and then declining over the next 3 yr (Table 1, Fig. 3).

3.2. Seagrass characteristics

Our data from Agatti showed the presence of multiple seagrass species, namely *Thalassia hemprichii*,

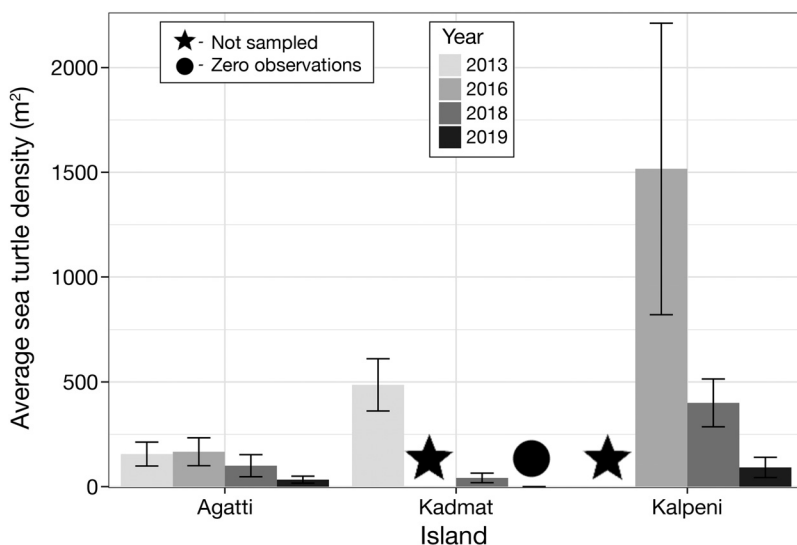
Fig. 3. Changes in average (±SE) green turtle densities. Green turtle density varied over time in different lagoons; Kadmat showed high green turtle density in 2013 and Kalpeni recorded its highest density in 2016
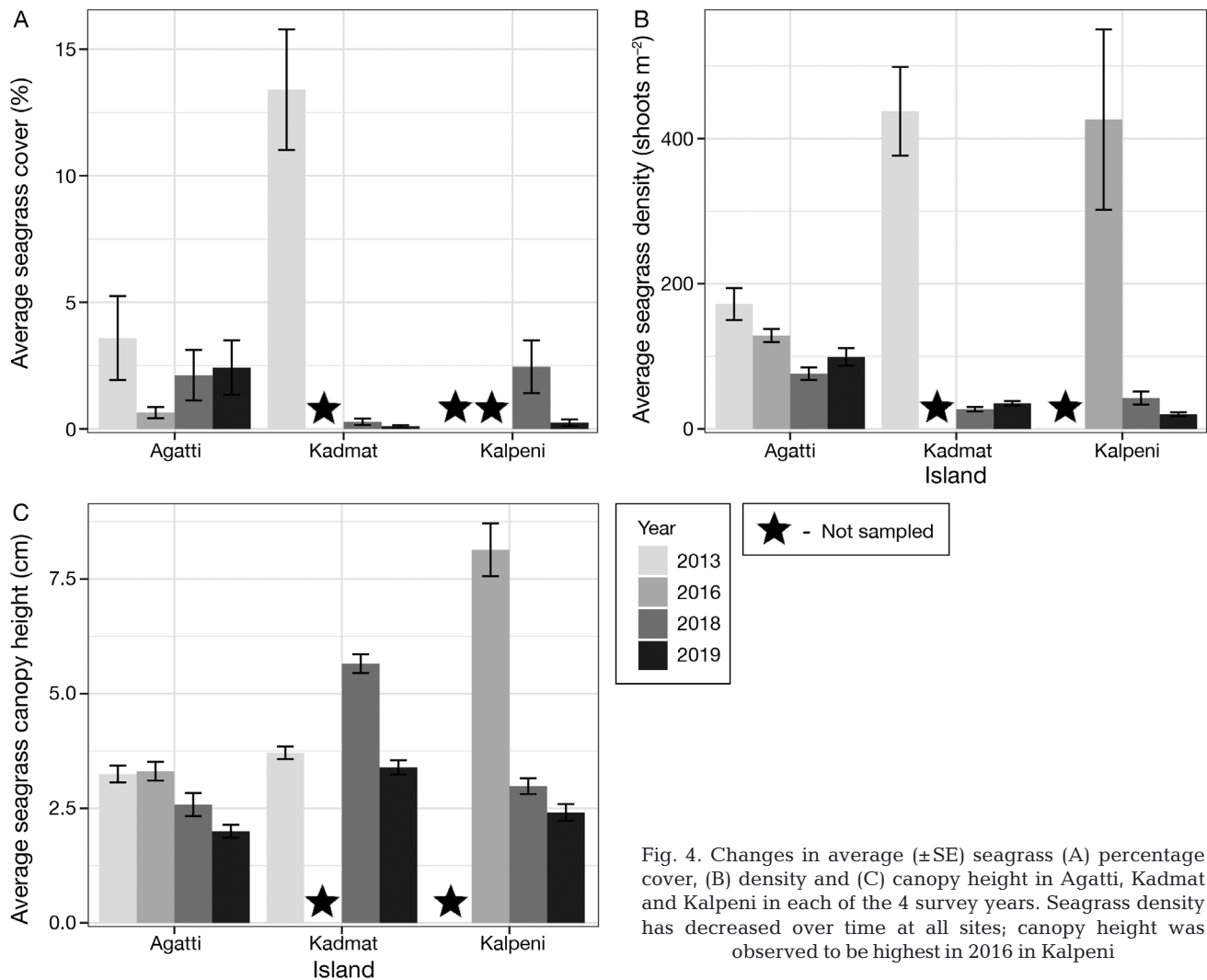
Cymodocea rotundata, *Halophila decipiens* and *Syringodium isoetifolium*. Only *Thalassia* and *Cymodocea* were observed in Kadmat, and in addition to these two, *Syringodium* was also found in Kalpeni (see Table S3). Seagrass cover was extremely sparse (under 10%) across the years in all lagoons except Kadmat in 2013, when total seagrass cover was marginally higher at 13% (Fig. 4A). Overall, there was a significant difference in total seagrass cover between different islands across years (KW = 40.949, p < 0.001). For different islands, Agatti and Kalpeni showed no difference in seagrass cover over the years, while Kadmat showed significant differences between 2013 and 2018 (p < 0.01) and 2013 and 2019 (p < 0.01). In terms of species-specific seagrass cover, *Thalassia* cover declined across Agatti and Kadmat. While *Cymodocea* cover in both islands showed a reduction until 2018, it increased in 2019. *Halophila* cover, on the other hand, increased until 2018, with a dip observed in 2019 (Fig. S1).

Aggregated seagrass densities from this study showed significant differences in surveyed islands across years (KW = 78.73, p < 0.001) (Fig. 4B). Analogous to sea turtle densities, seagrass densities recorded over the last 2 decades also showed that Agatti had the highest recorded density in 2008 (1281 shoots m^{-2}), which varied over time (Table 2). Following Agatti, Kadmat

Fig. 4. Changes in average (±SE) seagrass (A) percentage cover, (B) density and (C) canopy height in Agatti, Kadmat and Kalpeni in each of the 4 survey years. Seagrass density has decreased over time at all sites; canopy height was observed to be highest in 2016 in Kalpeni

had high densities in 2012 (~600 shoots m^{-2}) followed by a decline over the next 7 yr. However, Kadmat had low seagrass density in 2001 (52 shoots m^{-2}), as observed in 2018−2019 (~30 shoots m^{-2}). In 2016, Kalpeni recorded high seagrass densities that declined drastically over the following years (Fig. 4B).

Differences in aggregate densities for individual islands were seen in Kadmat between 2013 and 2018 (p < 0.001) and 2013 and 2019 (p = 0.007); and in Kalpeni between 2016 and 2018 (p = 0.007) and 2016 and 2019 (p = 0.018) (Table S2). Furthermore, species-level changes in seagrass densities were found in the island lagoons for the years surveyed (KW = 13.443, p = 0.003) (Table S3). *Cymodocea* spp. density differed between 2013 and

2016 in Agatti (p = 0.013) following which it showed lower densities (Table S3), whereas *Thalassia* density significantly differed in Kadmat between 2013 and

Table 2. Seagrass densities recorded in Lakshadweep islands by different studies over the last 2 decades. Densities fluctuated widely between islands and years. NA: not surveyed

| Year | Seagrass density (shoots m^{-2}) | | | Source |
	Agatti	Kadmat	Kalpeni	
2001	45	52	NA	Tripathy et al. (2006)
2008	1281−963	NA	NA	Lal et al. (2010)
2012	*T. hemprichii*: 16 *C. rotundata*: 424.53	*T. hemprichii*: 630.4 *C. rotundata*: 692.3	NA	Kelkar et al. (2013b)
2013	171.99	437.48	NA	Current study
2016	128.59	NA	426.16	Current study
2018	76.03	27.01	42.47	Current study
2019	99.09	35.25	20.11	Current study

2018 (p < 0.001) and 2013 and 2019 (p = 0.0017). Kalpeni also recorded a significant reduction in *Thalassia* density between 2016 and 2018 (p < 0.001), after which it remained low.

The highest average canopy height across species was observed in Kalpeni in 2016 (~8 cm) and the shortest in Agatti in 2019 (1.9 cm) (Fig. 4C). The short canopy height in Agatti can be attributed to the dominance of short *Halophila* species found in the lagoon. Moreover, there was a significant difference in canopy heights across different years for each island (KW = 63.504, p < 0.001). *Cymodocea* in Agatti and Kadmat showed comparable canopy heights across surveyed years that suggest small growth and subsequent

Table 3. Average (±SE) canopy height (cm) of different species recorded across different years in the 3 study islands. NO: not observed; NA: not surveyed

| Year	Seagrass species	Agatti	Kadmat	Kalpeni
2013	*Cymodocea*	3.68 ± 1.07	3.72 ± 1.28	NA
	Halophila	NA	NO	NA
	Syringodium	NA	NO	NA
	Thalassia	3.15 ± 1.51	3.72 ± 0.96	NA
2016	*Cymodocea*	5.09 ± 1.38	NA	5.95 ± 0.80
	Halophila	1.53 ± 0.25	NA	1.02 ± 0.32
	Syringodium	NO	NA	12.35 ± 0.35
	Thalassia	NO	NA	9.32 ± 2.08
2018	*Cymodocea*	3.87 ± 1.19	4.75 ± 0.97	NO
	Halophila	1.67 ± 0.26	NO	NO
	Syringodium	2.41 ± 0	NO	4.99 ± 0
	Thalassia	NO	5.92 ± 0.95	2.78 ± 0.67
2019	*Cymodocea*	2.42 ± 0.59	3.42 ± 1.53	NO
	Halophila	1.39 ± 0.23	NO	NO
	Syringodium	3.62 ± 0.48	NO	4.25 ± 0
	Thalassia	NO	3.43 ± 0.71	2.02 ± 0.44
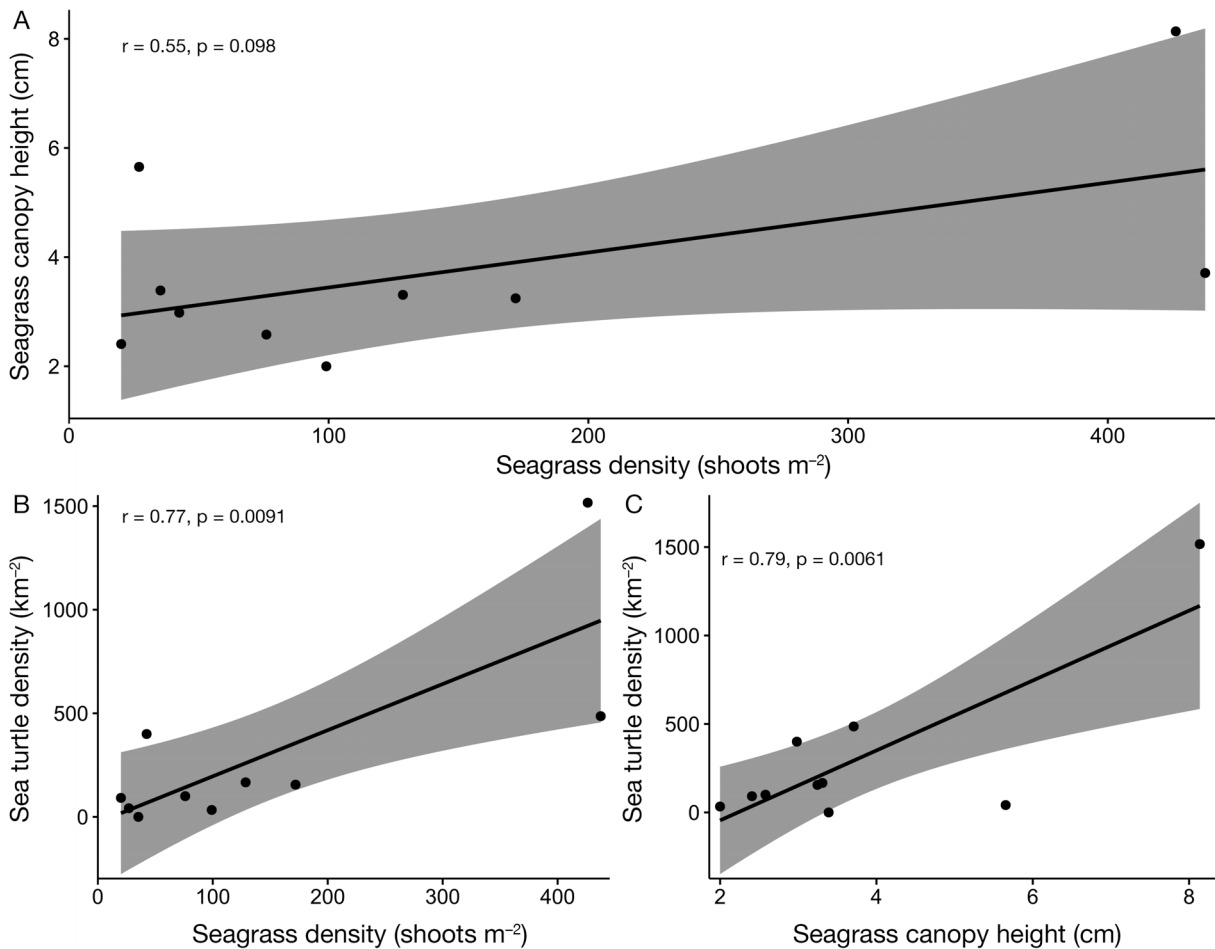
Fig. 5. Association between (A) aggregated seagrass density and canopy height, showing a weak relationship for different years; strong correlations between (B) sea turtle density and seagrass density and (C) sea turtle density and canopy height. Each data point represents an island in a particular year. Black line: 'line of best fit' or linear relation between the points; grey shaded area: 95% confidence interval around the line of best fit

cropping (Table 3). Data also showed that the *Thalassia* and *Syringodium* canopy has declined in Kalpeni since 2016.

Lastly, the correlation between seagrass density and canopy height (Fig. 5A) was found to be weak (Pearson's r = 0.55, p = 0.098). This indicates that not all lagoons with a high density of seagrass have shoots with greater length, and these seagrasses may be affected by threats other than grazing. At the species level, *Thalassia* (Pearson's r = 0.77, p = 0.044) and *Syringodium* (Pearson's r = 0.9, p = 0.039) showed a positive correlation between density and canopy height (Fig. S2c,d).

3.3. Sea turtles and seagrass

Finally, we investigated the relationship between turtle density and different seagrass characteristics such as shoot density and canopy height. At an island level, a higher density of turtles was encountered in lagoons where seagrass density was high (Pearson's r = 0.77, p = 0.009; Fig. 5B) and seagrass heights were greater (Pearson's r = 0.79, p = 0.0061; Fig. 5C).

We also checked if independent variables such as individual seagrass species, lagoon stratum and/or island influenced turtle presence or absence within a lagoon by running a GLM. As the predictor 'island' did not show any difference in green turtle presence or absence, we removed it and ran the model with only seagrass species and lagoon strata. The results showed that the presence of *Thalassia* sp. (GLM: z = 0.5592, p < 0.001) and reef (GLM: z = −2.090, p = 0.053) and near-shore (GLM: z = −2.455, p = 0.014) strata were significant predictors of the presence of turtles within the lagoons. Similarly, the results showed that *Thalassia* sp. (GLM: t = −2.419, p = 0.017) and Kalpeni (GLM: t = 3.324, p = 0.001) had a significant effect on turtle density during the study years.

3.4. Substrate cover

Substrate type was noted at each sampling location and categorised as sand, algae, algae on coral rubble, coral rubble, live coral, dead coral and seagrass. Apart from seagrass (under 10%; Fig. 4A), cover for the other substrate types was also calculated as a percentage for each island over the sampled years. The lagoon floor in all the islands mainly comprised sand (19.72–76.18%, highest in Agatti in 2018; Fig. 6A) followed by algae (5.56–24.03%, highest in

Agatti in 2013; Fig. 6B) and coral rubble (3.55–23.35%, highest in Kadmat in 2013; Fig. 6F). On the other hand, the 2 coral categories (live and dead coral) and algae on coral rubble showed very little cover across years.

4. DISCUSSION

Green turtles are known to show plasticity in their foraging behaviour, which makes it important to assess the influence of various biotic and abiotic factors and determine behavioural patterns at individual and population levels. By monitoring green turtles and their primary dietary resource, we showed that foraging is likely to have resulted in changes in the abundance of their preferred seagrasses i.e. *Thalassia hemprichii* and *Cymodocea rotundata* and, in turn, their own distribution and abundance. Changes in the availability of forage may have prompted green turtles to alter their foraging sites over time between the lagoons of the Lakshadweep Archipelago and other possible locations. Therefore, changes in their abundance provide clues to the behaviour of this green turtle population with implications for the management of green turtles and seagrass meadows in the Lakshadweep Archipelago.

4.1. Green turtle abundance trends

Monitoring changes in green turtle abundance is essential to assess population trends and potential risks of collapse (Roos et al. 2005). This study, in conjunction with secondary data, shows that green turtle abundances within the Lakshadweep lagoons have fluctuated over the last 20 yr. According to Bhaskar (1978), local community members reported that turtle numbers in the Archipelago were dwindling in the 1970s due to hunting. However, a steep rise in their numbers was first observed in Agatti in the mid-2000s, followed by Kadmat and more recently in Kalpeni. This increase could be a consequence of the strict implementation of a wildlife hunting ban on green turtles (Kelkar et al. 2013b). Previously, green turtles were commonly hunted to make oil from their fat which was used to caulk wooden boats. Turtle eggs were also consumed by the island community in the past when food resources were scarce (Anon pers. comm.). A shift in the material used for constructing boats (wooden to fibre) and an increased food supply from the mainland, along with protection, eventually led to the cessation of turtle hunting
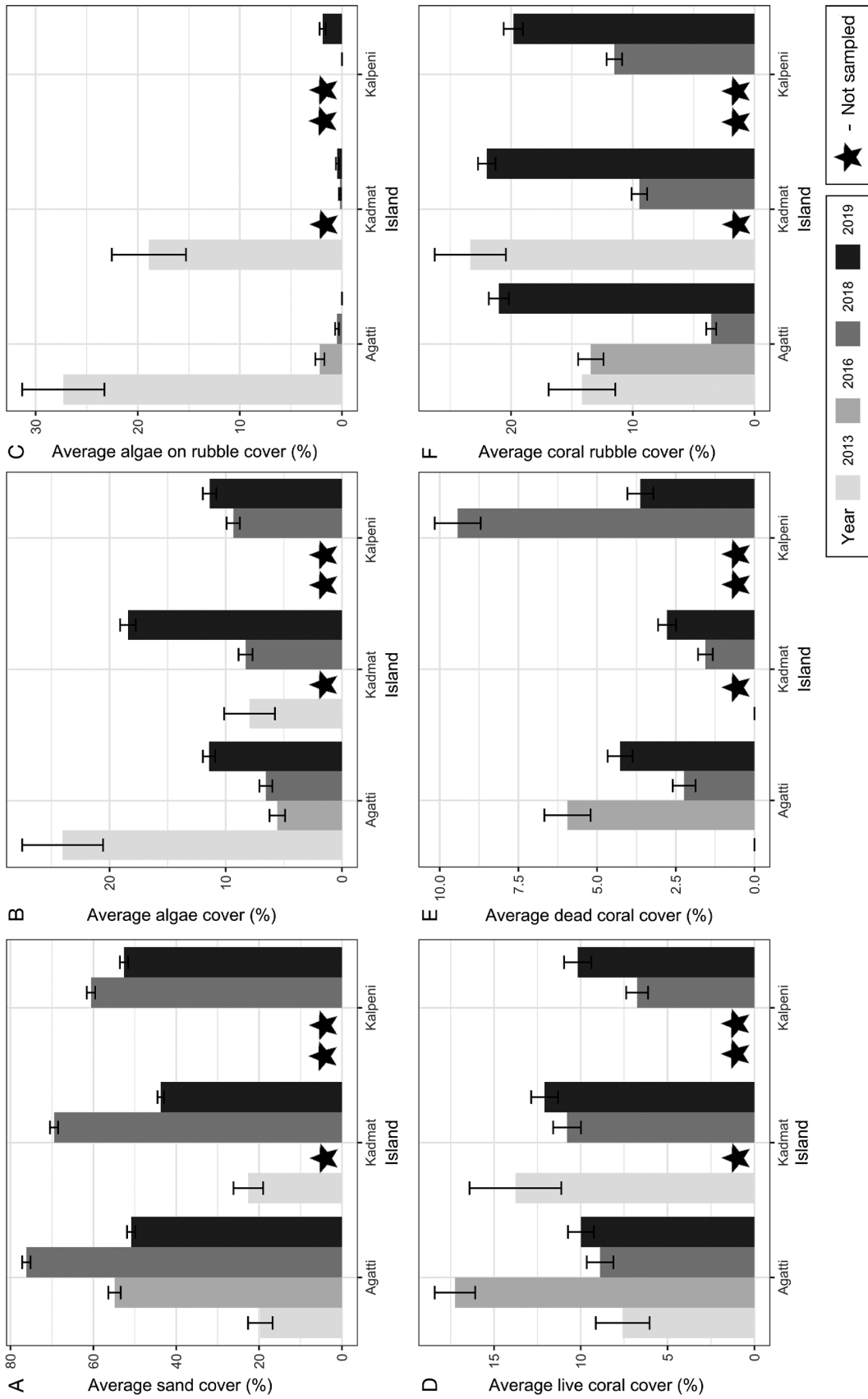
Fig. 6. Lagoon substrates showing (A) sand, (B) algae, (C) algae on coral rubble, (D) live coral, (E) dead coral and (F) coral rubble cover on all 3 islands. Sand dominated the lagoon-scape across years and had maximum cover until 2018 before declining slightly in 2019. Other substrates showed varying cover over the years, with algae on coral rubble showing the least cover overall

and turtle product use. Furthermore, the ample resource supply in the lagoons could have enhanced the habitat quality for foraging green turtles (e.g. Bermuda, see Fourqurean et al. 2010). Overfishing of predators such as tiger sharks *Galeocerdo cuvier* could have also allowed green turtle abundances to increase through lowered predation risk (Kelkar et al. 2013b). The increase could also be attributed to individuals immigrating from nearby locations such as Sri Lanka, where conservation programmes have been active since the early 1990s and have resulted in increased recruitment (Richardson et al. 2013).

Our surveys and previous secondary data showed that increases in abundance of green turtle numbers were followed by declines in the 3 lagoons. The decline could be a result of loss in seagrass resources, as changes in turtle numbers corresponded with changes in seagrass density and canopy height, especially that of *Thalassia* as seen from our GLM results. Our GLM results also showed that some lagoon strata influenced turtle presence in the lagoons, specifically the reef and the region close to shore. Green turtles belonging to different size classes have been observed occupying these habitats for either foraging or resting. While seagrass found in shallow, near-shore waters provides forage for adult green turtles, the reef region provides food such as invertebrates and algae for immature turtles (Limpus 2008). This presence in the near-shore region and reef could also be influenced by tides, with turtles preferring shore areas for foraging during high tide and the reef as the tide recedes (Pillans et al. 2021, N. Kale pers. obs.). However, the habitat utilization patterns of different size classes of green turtles need to be studied to determine differences in habitat use.

4.2. Seagrass abundance trends

Seagrass densities have changed considerably from 2008 in Agatti, 2012 in Kadmat and 2016 in Kalpeni. Of the different species found in the Lakshadweep islands, drastic reductions were observed mainly for *Thalassia* and *Cymodocea* species (Table S3). Following the high grazing levels in the late 2000s (Lal et al. 2010), we did not observe *Thalassia* in Agatti from 2016 onward (Table S3), which could be due to its slow-growing nature (Duarte 1991), grazing and other disturbances. Our data showed that at Kadmat and Kalpeni, *Thalassia* declined drastically between 2013–2018 and 2016–2018 respectively. While *Syringodium* species showed minimal difference in density, the fast-growing *Halophila* shoots had fluctuating

densities in Agatti lagoon but continued to show higher densities in comparison to other species. Previously, *T. hemprichii* and *C. rotundata* were documented to co-dominate the seagrass meadows of Agatti island (Jagtap 1998), which later shifted to *Cymodocea* dominating the meadows alone as green turtle grazing intensified (Lal et al. 2010, Kelkar et al. 2013b).

Our findings indicate that a complete loss of *Thalassia* and continued foraging on *Cymodocea* may lead to pioneer and fast-growing species like *Halophila* potentially dominating the Agatti lagoon (Table S3). Such shifts in seagrass species composition have been reported at various foraging grounds across the world, where faster growing species take over after the dominant species is removed by megaherbivores (Kelkar et al. 2013b, Molina Hernández & van Tussenbroek 2014). Therefore, the change in densities and cover of *Thalassia* and *Cymodocea* (Table S3, Fig. S1) over time in Agatti and Kadmat indicates that preferential grazing by green turtles could impact seagrass composition and cause a shift in species dominance in some lagoons of the Lakshadweep islands (Kelkar et al. 2013b).

We also found that the *T. hemprichii* canopy was reduced in Kalpeni from 2016–2019 (Table 3). This decrease coincided with a decrease in its density (Table S3) and in green turtle densities (Fig. 3), indicating that the reduction may be a consequence of green turtle overgrazing. Short canopy height suggests constant grazing, as green turtles prefer eating the lower part of the leaf blade, resulting in a cropped patch of seagrass (Bjorndal 1980). For associated species such as small fish, habitat functions such as foraging and breeding sites or protection from predators could be affected by a low canopy (Connolly 1994, Guidetti & Bussotti 2002).

The varying densities and heights of all seagrass species also suggest that other disturbances may affect meadow health in these lagoons. While *Thalassia* and *Cymodocea* densities were mainly affected by green turtle grazing (Kelkar et al. 2013b), seagrasses such as *Halophila* and *Syringodium* could have been impacted by other threats. Seagrass habitats across the world face high levels of pressure due to natural events such as storm surges and anthropogenic activities like the construction of jetties, regular dredging, pollution, fishing and boat activities. Moreover, warming seawater temperatures can also contribute to declines in seagrass meadows (Strydom et al. 2020). These stressors occur in the Lakshadweep lagoons and, along with green turtle herbivory, could contribute towards the reduction of seagrass in the Archipelago (Nobi & Thangaradjou 2012).

4.3. Green turtle foraging behaviour

Our study further confirmed previous findings that the green turtle foraging population in the Lakshadweep islands shows a preference for *Thalassia* and *Cymodocea* (Kelkar et al. 2013a,b, Kale et al. 2021). Annual declines in *T. hemprichii* and *C. rotundata* were observed to be 17 and 10 % respectively due to grazing (Kelkar et al. 2013b). In Lakshadweep, green turtles' preference could have been influenced by the availability of the forage, as high densities of *Thalassia* and *Cymodocea* were recorded prior to turtle foraging (Jagtap 1998, Kelkar et al. 2013b). However, sea turtle diet composition is not always proportional to the amount of available forage (Brand-Gardner et al. 1999). Therefore, this preference could also be due to the high nutritional value (Bjorndal 1980) of the 2 seagrass species, which is positively correlated with the growth of an individual turtle (Hadjichristophorou & Grove 1983).

For the Lakshadweep green turtles, the long-term consequence of losing their forage could result in either modification of their diets and/or a switch to alternative foraging areas. Diminishing shoot densities and canopy cover in the lagoons seems to have resulted in inter-island movement, whereby green turtles would move to a nearby lagoon once the forage depleted. High abundances were noted in Agatti in 2008 (Lal et al. 2010), followed by Kadmat in 2013 and then Kalpeni in 2016 (this study). The changes in abundance during this period indicate that green turtles may have moved from the westernmost island eastwards within the Archipelago, potentially as a result of oceanic currents and/or forage quality/availability (Luschi et al. 2003), factors known to influence movement between foraging sites. The apparent movement from Agatti to Kadmat and finally Kalpeni suggests that green turtles may have some knowledge of how these foraging sites were spatially distributed. Further studies are required to understand how these green turtles were able to locate the isolated island lagoons within the Archipelago.

The inter-island movements also indicate that once *Thalassia* seagrass declines in Kalpeni, green turtles may move to another seagrass-rich lagoon within the Lakshadweep islands or to another nearby site rich in their preferred seagrasses in case there is no shift in their dietary choice (see Burgett et al. 2018). Habitat-driven shifts in herbivores have been seen in Shark Bay, Ningaloo and Exmouth Gulf, where the loss in available forage resulted in dugongs moving to a different region (Gales et al. 2004). Similarly, these turtles could potentially move to nearby areas such as the west coast of India or the Gulf of Mannar and Palk Bay on the southeast coast of India, as well as to the offshore waters of Sri Lanka, which are known to have rich seagrass meadows.

On the other hand, green turtles are known to show strong site fidelity to their neritic foraging grounds (Reich et al. 2007, Arthur et al. 2008, Shimada et al. 2020) due to the extra costs involved in discovering and occupying new foraging sites. Therefore, if the green turtles remain at these sites, they may slowly shift their preference to other seagrass or algal species found abundantly in the Lakshadweep islands. Green turtles are capable of a shift in their gut microbiomes as they move from oceanic to neritic life stages (Price et al. 2017). However, the rate at which they can adapt to this dietary shift in order to assimilate and digest the new foraging resource is unknown. Moreover, as green turtles show individual variation in their foraging preferences, the loss of forage would mainly impact individuals that are specialists (Thomson et al. 2018). Analysis of faecal samples collected from the different islands revealed the presence of algae in the faeces of a few individuals but not others (Kale et al. 2021). This indicates that while some individuals may be affected by the loss in seagrass resources, others may not be impacted. Algae could be substituted as a major constituent of their diet, or they may have a mixed diet of algae and seagrass, enabling them to switch between the two (André et al. 2005). This highlights the need to study individual specialization to understand their responses to loss in forage (Burkholder et al. 2011). As individuals from the same foraging population tend to display varied foraging habits and residency patterns (Thomson et al. 2018), tools such as stable isotope analysis can shed light on the dietary choices and habitats occupied by individual turtles (e.g. Reich et al. 2010).

4.4. Substrate cover

Our results showed that sand is the dominant substrate in the lagoons, followed by algae and coral rubble in islands like Kadmat and Kalpeni as a consequence of green turtle herbivory (Fig. 6). Newly available space caused by turtle grazing could allow macroalgal communities to increase, resulting in succession that alters primary productivity and ecosystem function (McGlathery 2001). As seagrass cover further declines, it could have adverse effects on services such as nutrient filtering, protection from erosion, fisheries etc. (Gangal et al. 2021). Past studies have al-

ready shown that green turtle overgrazing has caused a considerable reduction in seagrass-associated fish species (Kelkar et al. 2013a). This could also affect the livelihoods of local fishers who utilize seagrass-associated fish species for consumption, sale and as bait. This association has resulted in an increase in fisher–turtle conflict in some of these islands in the past (Arthur et al. 2013) and may be detrimental to the green turtle populations in these islands.

4.5. Conclusions

As foraging grounds generally host turtles from different breeding grounds, these seagrass beds form vital foraging habitats for green turtles that nest in different countries in the region. Our results show that as the seagrass resources declined, turtle abundance reduced simultaneously. This indicates that green turtles may change foraging sites, causing them to expend extra energy in search of appropriate seagrass meadows elsewhere in the Arabian Sea. The energy spent in search of new foraging grounds could have a direct impact on green turtle growth and health.

Our study provides insights into the impacts of foraging on seagrass and green turtle abundances and consequent movement within the Lakshadweep Archipelago. It confirms that the shallow lagoons of the Lakshadweep islands serve as important foraging sites for this population. Going forward, we emphasize the need for satellite telemetry to track the turtles' movements across their foraging grounds. A further understanding of foraging habits and preferences, using methods such as stable isotope analysis, will help direct conservation and management plans for this foraging population and its habitat and, in turn, safeguard different breeding populations in the region. Despite their global status as endangered, high densities of green turtles and evidence of overgrazing indicate that green turtle populations may have increased in the seagrass-rich lagoons of the Lakshadweep islands. Our study thus highlights the need to include habitat quality and ecosystem function in future conservation planning.

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