



Policy analysis

Sequential overgrazing by green turtles causes archipelago-wide functional extinctions of seagrass meadows[☆]

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ABSTRACT

After centuries of decline, green turtle (*Chelonia mydas*) populations are showing handsome localized recoveries due to dedicated conservation efforts. This calls into question how much herbivory can be sustained by seagrass meadows that these turtle populations feed on. In our study, we documented the long-term impacts of green turtle foraging on seagrass meadows in the Lakshadweep archipelago, Indian Ocean. We tracked green turtle densities and seagrass areal extent in five atolls across the archipelago since 2005. Turtle densities first grew to record levels in the seagrass meadow of the Agatti lagoon around 15 years ago. Within a few years of intense herbivory, the meadow underwent radical biomass reduction and compositional shifts, leading to functional extinction and ultimately, bare sand. This trajectory of decline was repeated in every atoll, with turtle aggregations persisting 2 to 6 years before meadows were depleted, depending on their initial size. By 2019, all large meadows had declined, and in 2020, green turtles were distributed at low densities in every meadow. The meadows were limited to small patches of early successional species, maintained in a state of protracted recovery by constant, low-level herbivory. We measured the impacts of turtles on two key ecosystem services, a habitat for fish communities and stored organic carbon. Turtle overgrazing resulted in massive declines in seagrass fish diversity, biomass, and abundance, and major reductions in sediment-stored carbon. Apart from being important conservation flagships, green turtles are strong ecosystem interactors, and can potentially cause trophic cascades or functional extinction of seagrass ecosystems.

1. Introduction

After decades of concerted conservation efforts, populations of green turtles (*Chelonia mydas*) have increased in some areas to the point that they are no longer as endangered as they were even half a century ago (Bourjea et al., 2007; Chaloupka et al., 2008; Mazaris et al., 2017; Putman et al., 2020; Weber et al., 2014). This increase has been attributed to the protection of nesting beaches, reduction in juvenile mortality, reduced fishing bycatch pressure and the cessation of commercial turtle harvesting (Hays, 2004). As a powerful narrative of conservation optimism, the case of the green turtle is a testament to the capacity of marine reptile megafauna to rebound when anthropogenic

pressures are alleviated through conservation action even after populations have been reduced to the brink (Hays, 2004; Chaloupka et al., 2008). How close today's populations are to 'pristine' numbers is a matter of some debate (Bjorndal and Bolten, 2003; Broderick et al., 2006). The green turtle's current success may be due to the reduction of previous impacts but also, at least in part, to a concurrent decline of large marine sharks from the global oceans caused by rampant overharvesting. Sharks are the primary predators of late juvenile and adult green turtles (Heithaus et al., 2008) and it remains unclear if turtle populations, now largely released from predation in many areas (Ferretti et al., 2010), have locally grown beyond historical carrying capacities (Heithaus et al., 2014).

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The green turtle is one of few species that show that with the right set of conservation instruments, recovery is clearly possible. However, conservation successes are not without their attendant dilemmas. Apart from being conservation targets, species are also interacting agents within the ecosystems they inhabit, dynamically modifying their environments and adapting to changing habitat conditions in space and time. When the objects of conservation attention are major ecosystem engineers (as with the Eurasian beaver, *Castor fiber*), or directly compete with human for resources (as with Atlantic grey seal, *Halichoerus grypus*), their numbers can radically alter habitats or be a source of major conflict (Lambert, 2002; Rosell et al., 2005). For these species, success is not merely a numbers game, and requires a much better understanding of how these species interact and modify their environments.

Green turtles are voracious herbivores. Mirroring the increase in their populations, there has been an increase of recorded seagrass overgrazing episodes in turtle feeding grounds around the world, including the Lakshadweep islands, Mayotte island, Bermuda, Akumal in Mexico and Borneo (Ballorain et al., 2010; Christianen et al., 2012, 2014; Fourqurean et al., 2010; Lal et al., 2010; Molina Hernández and van Tussenbroek, 2014). Although these locations vary considerably in environmental context, they follow a remarkably similar pattern of herbivory with increasing green turtle numbers, sometimes leading to meadow collapse (Fourqurean et al., 2019; Christianen et al., 2021). Several factors contribute to these overgrazing events. While green turtles have a varied diet, studies in Lakshadweep showed that they have a clear preference for long-lived seagrasses (Kelkar et al., 2013b). Meadows dominated by these species are preferred feeding grounds (Christianen et al., 2014) where green turtles congregate (Arthur et al., 2013), potentially concentrating their herbivory impact.

For their part, seagrasses are generally well adapted to herbivory. Seagrass species have had a long evolutionary history of grazing (Valentine and Duffy, 2006). A suite of mechanisms including clonal growth, physiological integration among ramets, storage in the rhizomes, protected basal meristems, compensatory growth and high fiber content among others (Marbà et al., 2002, 2006; Valentine and Duffy, 2006; Vergés et al., 2008), make seagrass species able to cope with moderate green turtle herbivory (Aragones et al., 2006). However, these compensatory mechanisms are likely not enough to deal with concentrated feeding aggregations, in which consumption can vastly exceed primary production (Kelkar et al., 2013a; Rodriguez and Heck, 2021). If the pressure of herbivory persists, green turtles can trigger major compositional shifts with short-lived seagrass species substituting the former long-lived dominants, as documented in Lakshadweep and elsewhere (Arthur et al., 2013; López et al., 2019; Molina Hernández and van Tussenbroek, 2014). With above-ground shoots grazed to the base, meadows can still persist as buried rhizomes and roots, with few living shoots. However, as resources deplete, green turtles have been known to modify their foraging behaviour and even dig up remnant rhizomes and roots with their front flippers, leading to habitat collapse (Christianen et al., 2014; Scott et al., 2020). Detailed monitoring studies of seagrass meadows in Bermuda used isotopic analysis to show that the radical decline of meadows was due to sustained turtle overgrazing and not due to decline in water quality (Fourqurean et al., 2019). Habitat collapse caused by herbivore overgrazing is not uncommon. Both terrestrial and marine systems with large concentrations of herbivores are prone to radical transformations due to over-consumption of habitat-forming plants (Bakker et al., 2016). In seagrass meadows, this loss can lead to desertification, with bare sand-dominated areas, that can be colonised by very few other macrophytes. This change could have a strong impact on ecosystem services associated with seagrass meadows, which are among the most important marine habitats in terms of their carbon storage capacities, nutrient filtering, biodiversity, fisheries, and protection from coastal erosion, among others (Fourqurean et al., 2012; Nordlund et al., 2016).

The Lakshadweep archipelago is one of several locations globally with high green turtle foraging aggregations (Arthur et al., 2013;

Christianen et al., 2021). Reports of high turtle abundances go back at least 150 years (an old Kensingtonian, 1868). Surveys for turtles in the 1970s (Bhaskar, 1978) reported green turtles as present, but the unprecedented increase in their numbers occurred in Agatti lagoon only around 15 years ago (Lal et al., 2010). It is difficult to explain why populations grew so rapidly, except that similar increases were recorded around the same time in other parts of the Indian Ocean (Bourjea et al., 2007; Christianen et al., 2014; Lauret-Stepler et al., 2007). An active ban on turtle hunting, conservation efforts in the wider region, and over-fishing of top predators such as sharks may have possibly led to green turtle densities burgeoning in seagrass meadows (Seminoff et al., 2004; Heithaus et al., 2014). Here we document long-term changes in seagrass areal extent and turtle densities across the Lakshadweep archipelago. We report the sequential functional extinction of seagrass meadows across the archipelago and its consequent impacts on two major associated ecosystem services, fish diversity, abundance, and biomass (for artisanal small-scale lagoon fisheries), and carbon stocks in the sediment. We discuss the implications of our results for green turtle conservation, given the vulnerability of their foraging grounds.

2. Methodology

2.1. Study area

The Lakshadweep archipelago (8°N-12°N and 71°E-74°E) is a chain of low-lying atolls in the northern Indian Ocean (Fig. 1). This archipelago consists of 12 coral atolls, of which 5, Agatti (area = 16.8 km²), Bangaram (area = 15.2 km²), Kavaratti (area = 6.2 km²), Kalpeni (area = 26 km²) and Kadmat (area = 20.9 km²), had extensive seagrass meadows (Fig. 1). Seagrass meadows in the Lakshadweep are restricted to shallow lagoons (henceforth we consider all the area occupied by seagrass in a single lagoon as an individual meadow), and are composed of up to seven seagrass species, typically dominated by the relatively long-lived species, *Thalassia hemprichii* and *Cymodocea rotundata* (Jagtap, 1991, 1998). The lagoons are very similar in their biophysical parameters, depth (2–4 m on average, <5 m), shape, and substrate characteristics (fine sandy bottoms, with scattered coral patches). They are all also subject to similarly low levels of human use and modest fishing pressure (Tamelander et al., 2008). Details of the study area can be found in Arthur et al. (2013).

2.2. Monitoring and sampling strategy

We began monitoring green turtles and seagrass meadows from 2005 at Agatti, in response to a sudden increase in green turtle densities noted in that year (Lal et al., 2010). The clear shallow lagoons made boat-based visual surveys of green turtles and seagrasses relatively simple. From 2010 onwards, we added the lagoons of Kavaratti and Kadmat islands and, from 2013 (Fig. 1), the lagoons of Kalpeni and Bangaram islands to our annual monitoring, when it became clear that turtle densities were increasing at these sites, as turtles shifted their foraging aggregations. Based on our team's observations, we selected the above 5 lagoons for regular monitoring. Two other lagoons (Chetlat and Kiltan) in the archipelago had small seagrass patches, which we did not include in the monitoring due to logistical constraints. All the methods used for the different components of the study were based on observations of animals in their natural habitats, and did not involve animal handling. We procured the necessary research permits from the Department of Science and Technology and the Department of Environment, Forests and Climate Change in Lakshadweep to carry out this research.

2.3. Green turtle aggregation density and seagrass areal extent

We conducted multiple boat-based surveys in each lagoon to directly estimate turtle abundance and seagrass distribution annually from 2005 to 2020, with some missing years (see Fig. 2 for details). We recorded

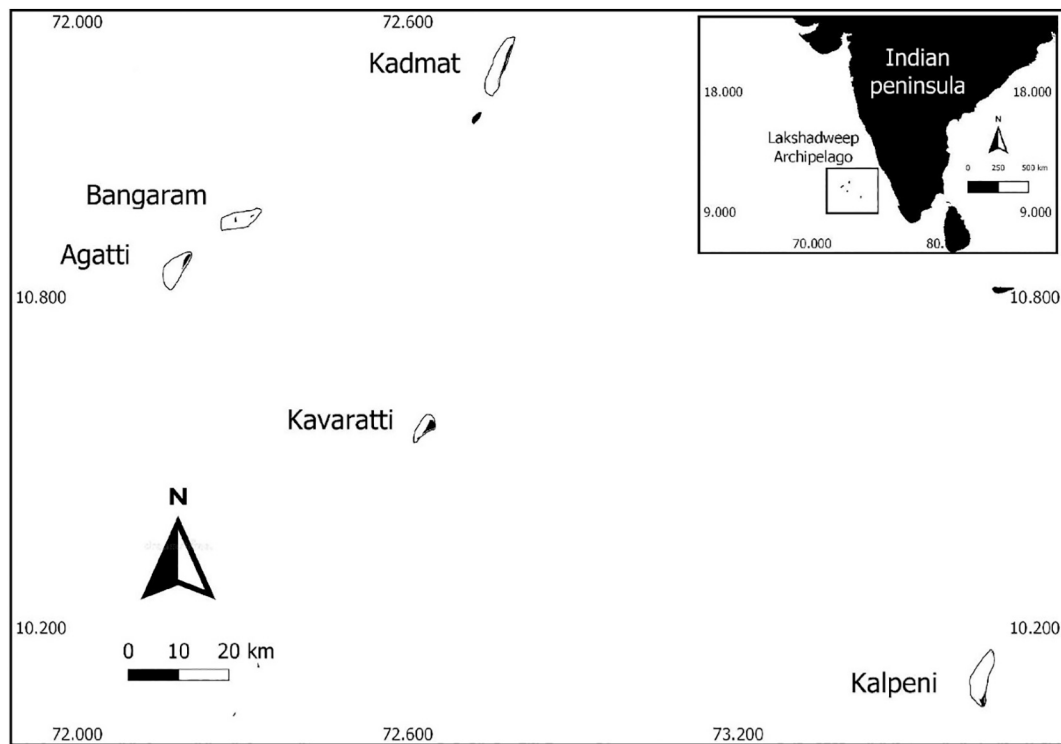


Fig. 1. Study area showing the lagoons where sampling was conducted.

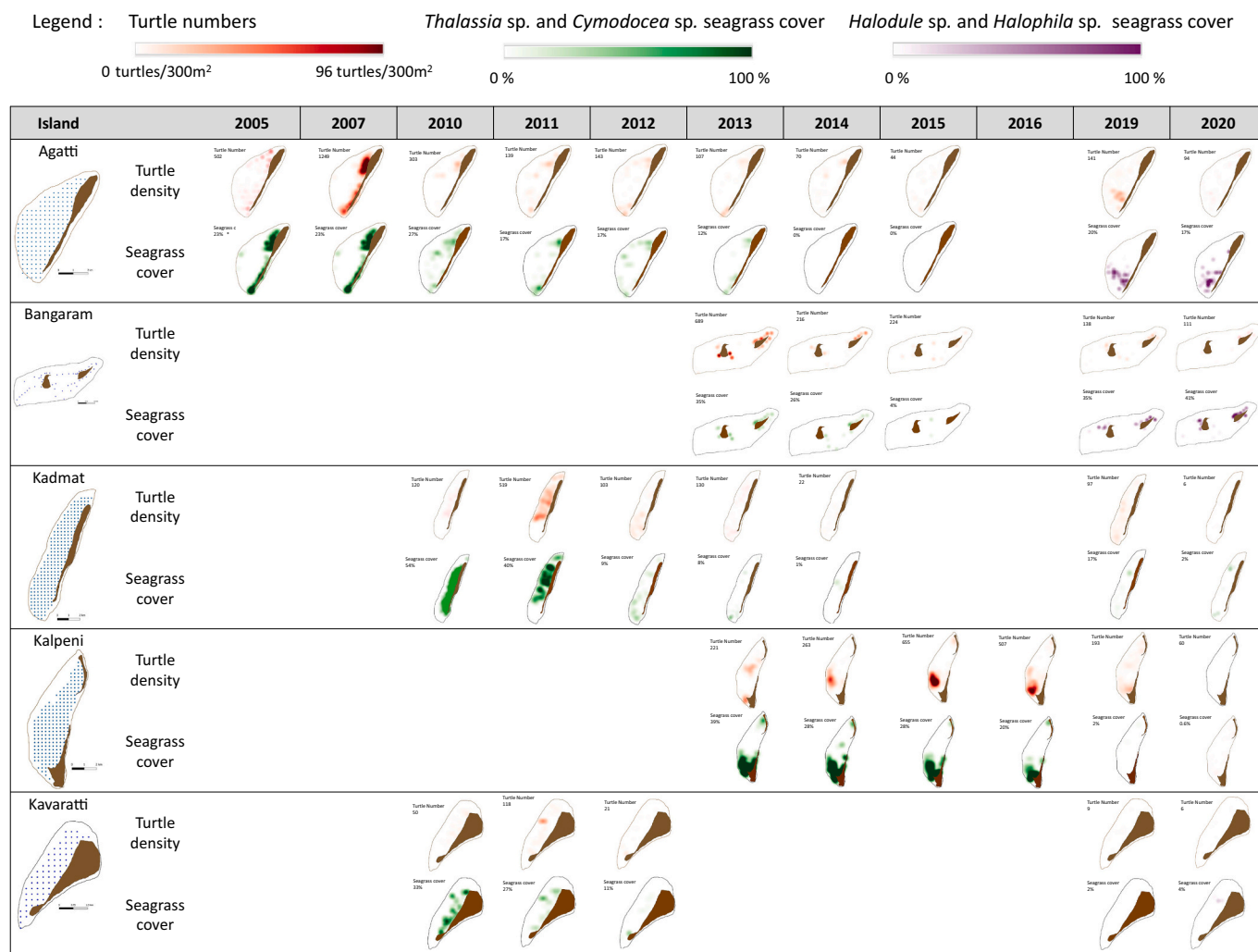
green turtle counts and seagrass areal extent along transects laid between points on a 300 m × 300 m grid covering the entire lagoon. The total number of grids varied from 70 to 232 points depending on the size of the lagoon (Table 1). Along transects, we counted turtles within a 20 m × 300 m belt (10 m on either side of the boat), moving slowly (~8 km/h) between grid points. All turtles encountered were classified into 5 different size classes based on carapace size viz., 0–30 cm, 30–60, 60–90, 90–120 and > 120 cm. Turtle diets show ontogenic shifts. Diet of turtles with carapace size >60 cm is shown to be dominated by seagrass (Burgett et al., 2018). We conducted all surveys during the pre-monsoon season (Jan–Apr), and the same grid points were tracked each year. Changes in turtle numbers with tidal variation, seasons, and survey dates were also relatively uniform across all lagoons, with most turtles staying within lagoons throughout the sampling season (Kelkar et al., 2013a). We did this in order to minimise any errors arising from turtle movement between islands, thus assuming temporally closed population within each sampling period. We summed the counts made by each observer, on the right and left side of the boat, at each transect to obtain total counts per transect (number of turtles observed in 0.6 ha), which were indexed with respect to the subsequent grid point. We sampled turtle abundance only when sighting conditions were excellent (high water clarity, horizontal visibility 20–25 m). The shallow depth made it easy to scan the water for turtles from small boats and this method provided a highly efficient survey technique that yielded reliable snapshot estimates of turtle densities (see Lal et al., 2010 for details). Transects covered almost the entire lagoon area, except for the slightly deeper lagoon of Bangaram, where we limited our sampling to the seagrass-dominated areas of the lagoon. The area directly sampled in our transects represented ~6% of the total lagoon area. At each grid point, we visually estimated the meadow area (%) and species composition within a 5 m radius, using a snorkel and mask to ensure the highest possible accuracy. We used the area covered by seagrasses estimated at each grid and averaged it across all grid points to estimate the seagrass areal extent of the lagoon. In addition, we transformed the seagrass areal extent at each lagoon to biomass for the two principal seagrass habitats. To do that, we first estimated shoot density in 40 cm² quadrats placed in

the two principal seagrass habitats (*Thalassia hemprichii* + *Cymodocea rotundata* and *Halodule uninervis* + *Halophila* spp. Complex) ($n = 7$ in each habitat). To convert shoot density into biomass per quadrat we used the average shoot weight from our own studies for *Thalassia-Cymodocea* dominated meadows (Kelkar et al., 2013a), and from the literature for the *Halodule-Halophila* meadows (Vonk et al., 2008). This information (biomass per quadrat) was used together with the habitat-specific areal extent obtained at the grid-point/transect level to obtain seagrass biomass estimates for each lagoon (in tonnes).

2.4. Estimating the effect of green turtles on fish community composition

We compared fish community composition in meadows before and after peak turtle densities were observed at that meadow. The ‘before overgrazing’ treatment included the meadows in Kadmat and Kalpeni (in 2010) before green turtles arrived (see Fig. 2) while the ‘after overgrazing’ treatment included the meadow in Agatti (2010, 2011–12 and 2013), Kadmat (2011, 2012–13), Kavaratti (2012–13), and Bangaram (2012–13) after green turtles had grazed (Fig. 2). Within each lagoon, we sampled at three locations, in the north, central, and southern parts. Within each location, we recorded fish species in 50 m × 5 m underwater transects randomly located ($n = 10$, range: 5–12 transects per location and at each time step; total $n = 120$). In the ‘after overgrazing’ treatments, transects were established in areas where seagrass meadows were once abundant (based on our long-term monitoring), even if they now consisted of only few shoots. Team members with long-term experience in fish identification conducted transects. We identified all fish to the species level and visually assigned them to size classes (<5 cm, 5–10 cm, 11–20 cm, 21–30 cm, 31–40 cm, >40 cm) after calibrating visual estimates with actual fish sizes, using scaled photographs. We calculated fish biomasses using standard volumetric conversions: $W = a \times L^b$, where W is weight, L is estimated length (midpoint of size-class) and a and b are species-specific constants obtained from FishBase (Froese and Pauly, 2000).

In order to calculate total fish biomass, we pooled the biomass estimates of all fish species within each transect and then compared



*Although Agatti lagoon was sampled first time in 2005, the standardise sampling regime has started from 2007. Thus, we are excluding observations from 2005 in this table

Fig. 2. Changes in turtle densities and seagrass areal extent in 5 lagoons between 2005 and 2020.

transect-wise biomass data from the time periods ‘before overgrazing’ and ‘after overgrazing’. We then compared biomass data of different fish species with respect to their fishery value, to evaluate change in ecosystem services of seagrass meadows to island fisheries. For fishery status, we classified all species into 3 groups, based on the observed fishing preferences of island fishers, and selling prices (in INR per kg; see Arthur et al., 2013). The three groups were high-value (regularly fished and preferred species selling at high prices, e.g. emperors, rabbitfish, goatfish, mojarras, jacks), medium-value (fished regularly but not highly valued e.g. surgeonfish, large wrasses, breams), and low-value (species not fished or having almost no value in the fishery e.g. pipefish, wrasses, gobies) (Annexure1). We used box plots to compare fish biomass across these groups with respect to the ‘before overgrazing’ and ‘after overgrazing’ periods.

2.5. Effects of green turtles on buried organic carbon

To determine the impacts of green turtle grazing on sediment stocks of organic carbon, we compared sediment organic carbon stocks (C_{Org}) from two meadows already overgrazed by green turtles (Kadmat and Kavaratti, referred to as ‘after overgrazing’) with a meadow where green turtle feeding aggregations had not yet arrived (Kalpeni, referred to as ‘before overgrazing’). We sampled in March–April 2016 when the seagrass meadow in Kalpeni was almost un-grazed and large-scale compositional shifts had not yet occurred (see results, Fig. 2). We

collected 3 sediment cores per meadow (5 cm diameter and up to 43 cm long). In overgrazed locations, the cores were located in denuded areas which once had thick seagrass cover, while in the lightly grazed location, the cores were taken in un-grazed areas (with no turtle herbivory marks on shoots).

In the laboratory, we sliced the cores at 1 cm intervals and measured sediment bulk density and the content of organic matter as loss on ignition (LOI) at 550 °C for 4 h. We analysed organic carbon (C_{Org}) content in pooled sediment organic matter using an elemental analyser FlashEA1112 (ThermoFinnigan) at the University of La Coruña (Service of Scientific Support (SAI)). We estimated sediment C_{Org} density (in mg/cm³) in each slice by multiplying sediment bulk density, the content of organic matter and C_{Org} content in organic matter (46.30% for Kalpeni, 41.33% for Kavaratti and 39.17% for Kadmat). For each core, we calculated sediment C_{Org} stocks (in Mg C/ha) as the sum of sediment C_{Org} densities within the upper 19 g/cm of accumulated sediments (i.e. the maximum accumulated mass of the shortest core; corresponding to the top 22 cm and 15 cm sediment layer at vegetated and overgrazed atolls, respectively) divided by 10. Data from the two overgrazed meadows (‘after overgrazing’ treatment) were pooled together to compare with the un-grazed location (‘before overgrazing’).

2.6. Estimating the effect of green turtles on seagrass recovery potential

The reduction in seagrass areal extent in the Lakshadweep was

Table 1
Changing turtle densities and seagrass areal extent in 5 lagoons of the Lakshadweep archipelago between 2005 and 2020.

Time of observation	Island	Lagoon area sampled (ha)	Year	Seagrass extent (ha)	Turtle density/ha
First year of sampling	Agatti ^a	1599	2007	367.77	11.14
	Kavaratti	408	2010	134.64	1.2
	Kadmat	1343	2010	725.22	0.76
	Bangaram	441	2013	154.35	23.34
	Kalpeni	2086	2013	813.54	1.75
Peak turtle densities	Agatti	1599	2007	367.77	11.14
	Kavaratti	408	2011	112.34	2.83
	Kadmat	1343	2011	526.78	3.71
	Bangaram	441	2013	154.35	23.34
	Kalpeni	2086	2015	588.87	5.20
Least seagrass areal extent	Agatti	1599	2014	0	0.67
	Kavaratti	408	2019	11.82	0.21
	Kadmat	1343	2014	17.36	0.15
	Bangaram	441	2015	18	2.98
	Kalpeni	2086	2020	13.20	0.63
Latest observations	Agatti	1599	2020	286.52	0.90
	Kavaratti	408	2020	18	0.17
	Kadmat	1343	2020	35.81	0.04
	Bangaram	441	2020	171	2.98
	Kalpeni	2086	2020	13.20	0.63

^a Although Agatti lagoon was sampled first in 2005, systematic sampling started from 2007. Thus, we are excluding observations from Agatti in 2005 from this table.

already established to be caused by green turtles (Kelkar et al., 2013b). However, in order to confirm that the recovery was also protracted due to persistent grazing by remnant turtles, we established turtle herbivory exclosures in Kalpeni lagoon in 2019 after green turtle numbers and seagrass cover had reduced considerably. We installed two 2 m × 2 m exclosures in remnant, very shallow patches of meadows which still had few seagrass shoots left. The sides of the exclosures were made of metal wire with a mesh size of 10 cm. We left the tops of the exclosures open to prevent shading. The height of the exclosures ensured that no turtles could enter even during high tide, although other herbivores like rabbitfish or herbivorous sea urchins could enter. However, the abundances of these herbivores were very low in all meadows. We cleaned the mesh once in two weeks to prevent the lateral growth of algae. Only one exclosure survived the southwest monsoon, which we continued to monitor further. We measured seagrass density at the start of the experiment inside the cage and in some patches of seagrasses outside the cage, 10 and 16 months later (inside and outside). To avoid any potential cage artefacts, we took all measurements in the centre of the exclosure, avoiding the edges. In the second exclosure, no additional measurements were made, but some recovery was already observed before this exclosure was lost. There was no replication of the cages but we present the important observations in the Results section.

3. Results

3.1. Changes in turtle densities and seagrass composition through time (Fig. 2)

Over the 15 years of our observations, green turtle densities shifted constantly across the archipelago, persisting at one foraging ground for a few years before pulsing at another, after resources had been depleted at the first foraging ground. Seventy-five percent of green turtles observed had a carapace size greater than 60 cm and hence seagrass was their predominant diet. Agatti was the first atoll to see large aggregations. In our earliest surveys (in 2005), we counted nearly 4.55 turtles/ha in the lagoon, which nearly tripled to 11.13 turtles/ha in 2007 (Fig. 2, Table 1). Seagrass meadows shrank considerably after this peak, and in the subsequent years, turtle numbers declined to nearly 0.67 turtles/ha by 2014. This pulsed pattern of seagrass persistence and sudden decline

was remarkably similar at every lagoon we tracked, although the number of years high turtle densities persisted at each foraging meadow varied with the extent of each meadow (Fig. 2). The trend we documented in Agatti repeated in Kavaratti (where turtle densities peaked in 2010), Kadmat (where turtle densities peaked in 2011), Bangaram (where turtle densities peaked in 2013), and once again in Kalpeni (where turtle densities peaked in 2015, Fig. 2, Table 1). In 2019 and 2020 we did not encounter concentrated foraging aggregations of turtles in any meadow, although turtles now persisted at low densities ranging between 0.17 and 2.98 turtles/ha in all meadows across the archipelago (Fig. 2, Table 1). From our own observations and anecdotal information from islanders, we are confident that we sampled most atolls before turtle numbers peaked, or in the year that they peaked. Bangaram was the only exception and it is possible that the lagoon may have had a high density of turtles prior to our first sampling in 2013. It is an uninhabited atoll, which we were unable to regularly monitor. Although we did not systematically sample other lagoons between 2005 and 2010, our own observations along with anecdotal information across the archipelago confirmed that high-density aggregations of green turtles were limited to Agatti over this initial period.

The shifting patterns of green turtle densities were reflected in the seagrass meadows they foraged on. Within a year or two of high-density aggregations, the extent of meadows shrank dramatically in each atoll under sustained and cumulative herbivory (Fig. 2). Together with the loss of areal extent, the cover of seagrass had reduced until no above-ground biomass was left standing (Fig. 3). The number of years to complete above-ground depletion varied with the size of the meadow—relatively small meadows like Bangaram and Kavaratti reached close to zero within 2–3 years of intense herbivory, while larger meadows like Kadmat, Kalpeni and Agatti persisted for 6–9 years. (Fig. 2, Fig. 3). As turtle densities shifted between lagoons, they radically altered lagoon seascapes in their wake. Prior to the arrival of foraging aggregations, the lagoons were all largely dominated by *T. hemprichii* and *C. rotundata* (Fig. 3). Within a few years of intense turtle grazing, they transformed to bare sand. By 2019, virtually every large meadow in Lakshadweep had only bare sand left. Five years after turtle numbers declined in Agatti and Bangaram, seagrass meadows showed a small recovery. Much of this recovery was characterised by early colonisers like *H. uninervis* and species in the *Halophila* complex (Fig. 3).

3.2. Changes in fish species diversity, abundance, and biomass

Fish species richness, biomass, and abundance all showed dramatic reductions in the meadows after green turtles arrived (Fig. 4). On average, before overgrazing, seagrass meadows had 5.71 (SE 0.42) species of fish, which reduced to 2.11 (SE 0.11) species after overgrazing and the consequent loss of seagrass (Fig. 4a). The average fish abundance per transect reduced 13 times, from 76.53 (SE 14.41) to 5.83 (SE 0.73) after turtle overgrazing (Fig. 4c). Similarly, average fish biomass reduced from 551.78 (SE 55.73) g per transect before peak turtle densities to a mere 44.30 (SE 14.43) g per transect after peak turtle densities in the meadow (Fig. 4b). Among the fish species inhabiting the meadows, species of high and moderate commercial value for fisheries became almost absent from the lagoon in the years following peak turtle densities (Fig. 4). Fish species of low commercial value also showed substantial reduction (Fig. 4).

3.3. Effects of turtles on buried organic carbon

Green turtle grazing resulted in about 40% losses to buried organic carbon, indicated by the difference in sediment carbon stocks between overgrazed and vegetated meadows. The meadow that experienced only mild turtle grazing (Kalpeni, before overgrazing), had around 45.6 (SE 2.1) MgC/ha of buried organic carbon compared to the over-grazed meadows (Kadmat and Kavaratti, after overgrazing) which had a buried organic carbon of 26.5 (SE 0.8) MgC/ha.

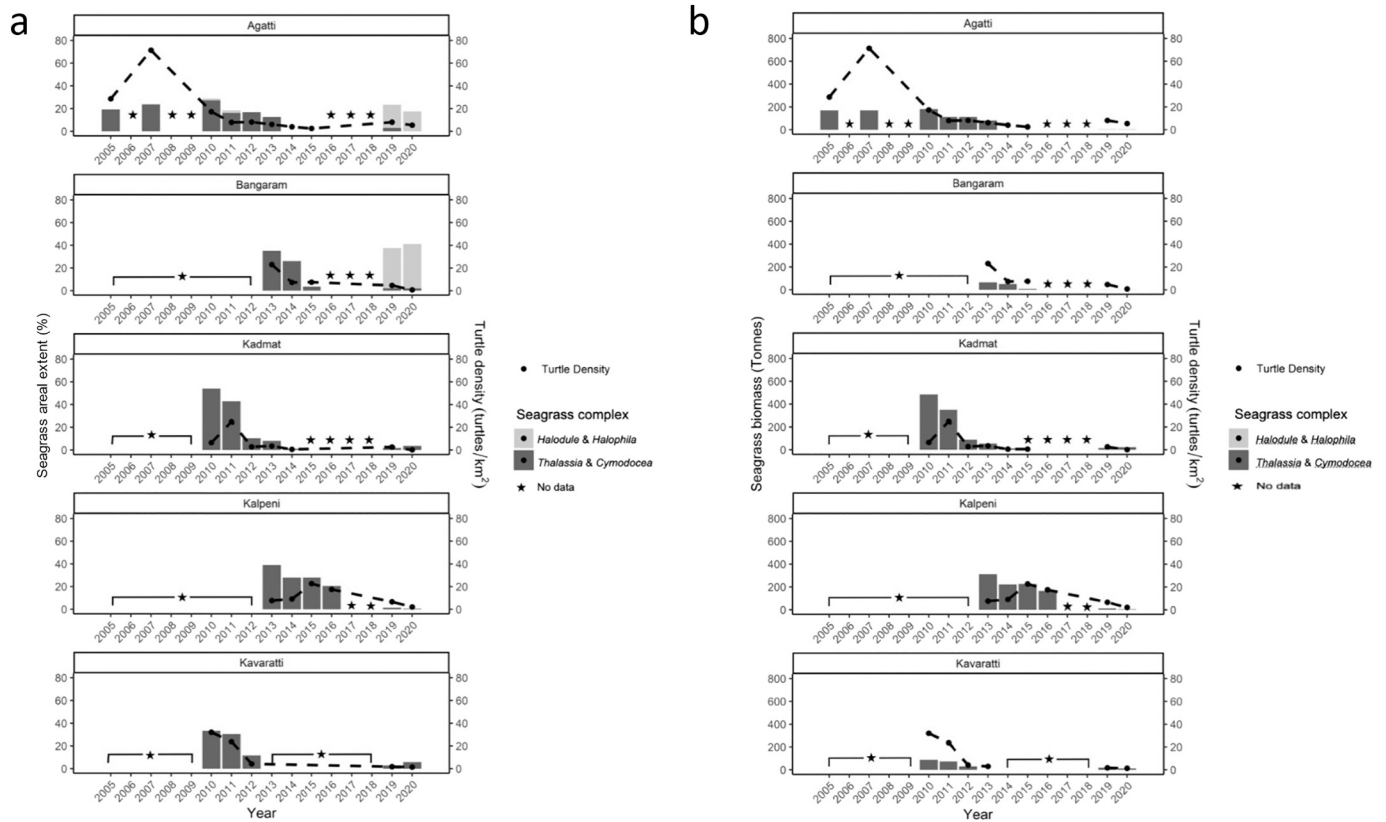


Fig. 3. a) Changes in seagrass areal extent in 5 lagoons between 2005 and 2020, b) Changes in seagrass biomass in 5 lagoons between 2005 and 2020.

3.4. Turtle exclusion and seagrass recovery (Fig. 5)

Only one herbivore exclusion persisted for an entire year. However, within less than a year of being protected from green turtle herbivory, the single exclusion plot that survived the monsoon showed a seagrass cover of nearly 100% (Fig. 5). At the start of the experiment, shoot density was around 162 (SE 55) shoots/m² inside the cages and 91 (SE 48) shoots/m² outside. After 16 months, densities inside the cage showed a 13-fold increase to around 2125 (SE 84) shoots/m² compared to a 4-fold increase of around 379 (SE 128) shoots/m² outside. No signs of herbivory by fish or urchins were observed inside the plot. The other plot survived merely 3 months, but even after this short interval, seagrass cover had already begun to recover although we were unable to measure it (personal observations).

4. Discussion

The recovery and restoration of endangered populations in the wild is predicated on the ability of extant habitats to sustain them. Green turtles, like many other species of conservation interest, are strong interactors or ‘ecosystem modifiers’ in the systems they inhabit, capable of radically transforming them and potentially even driving them to functional extinction. With seagrass ecosystems no longer able to support turtle grazing at the same intensity, and with protracted rates of habitat recovery, reconciling population recovery with habitat conservation is a new challenge across seascapes where turtle populations are rebounding.

4.1. Green turtle population dynamics in the Lakshadweep archipelago

Global efforts to bring the green turtle back from the brink have been remarkably successful (Chaloupka et al., 2008; Mazaris et al., 2017). Within Indian waters, green turtles have the highest level of protection

under the Indian Wildlife (Protection) Act, 1972, which has been strictly enforced in Lakshadweep. Green turtles do not nest in large numbers within Lakshadweep and without dedicated tracking studies or genetic analyses, we cannot determine from which nesting grounds these populations arose. The main determinant of feeding ground composition is the size of the rookery and how close it is to the feeding site (Bass and Witzell, 2000). The closest nesting sites are likely along the Indian west coast, where green turtles nest sporadically, but tagged individuals we have observed in Lakshadweep indicate that at least a fraction of the population came from Sri Lanka (personal observations). Sri Lanka has had a long history of green turtle conservation including protection of nesting beaches, hatchery programs, tagging, and bycatch reduction initiatives, and it is possible that it is at least one source population for Lakshadweep’s foraging aggregations (Scott et al., 2012). However, as genetic studies elsewhere have shown, it is likely that feeding aggregations may have individuals that originate from multiple nesting colonies (Dethmers et al., 2006; Dutton et al., 2019; Lahanas et al., 1998; Luke et al., 2004), aggregating there following oceanographic currents or by actively moving between feeding grounds (Lahanas et al., 1998; Nishizawa et al., 2013).

4.2. Sequential seagrass functional extinction

Green turtles have clearly had a far-reaching impact on meadows across the Lakshadweep. Before the arrival of dense feeding aggregations of turtles, seagrass meadows in Lakshadweep formed extensive multi-specific stands dominated by *T. hemprichii* and *C. rotundata* in many shallow lagoons across the archipelago (Jagtap, 1998; Kelkar et al., 2013b). Within 15 years, they have radically transformed every large meadow, and 3 of 5 lagoons today are dominated by bare sand where once highly structured seagrass ecosystems stood. The number of years turtles fed in the same meadow was clearly dependent on the initial extent of the meadow: Agatti and Kalpeni, with extensive

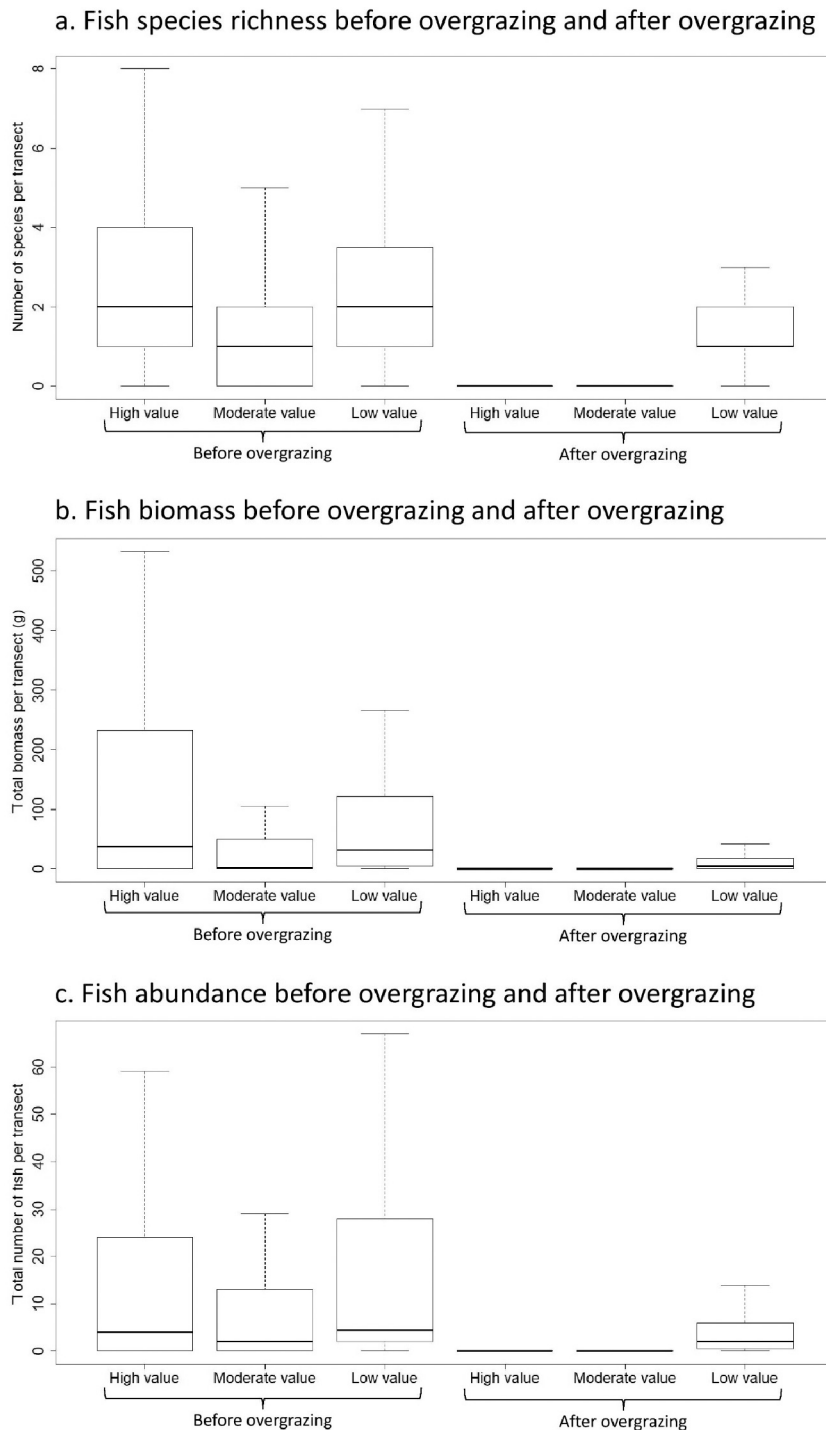


Fig. 4. Changes in fish community composition before turtle overgrazing and after turtle overgrazing.

meadows supported feeding aggregations for several years longer than Kavaratti and Bangaram, where meadows were relatively small. The case of Kadmat seems to be an exception as the seagrass meadow was very large, yet was depleted in fewer years than expected. Most seagrasses have a raft of mechanisms to deal with herbivory (Heck and Valentine, 2006), but the concentrated impact of foraging aggregations likely overwhelmed all compensatory mechanisms of maintaining productivity (Vergés et al., 2008; Kelkar et al., 2013a; Fourqurean et al., 2010; Rodriguez and Heck, 2020). Seagrasses, where present (Agatti and Bangaram), are limited to small, fast-growing species (*Halodule* sp. and *Halophila* sp.) that represent a functionally different ecosystem from the

meadows of the past with respect to habitat structure, fish diversity and carbon sequestration. With the shift in seagrass composition, meadows are able to support a highly reduced and less diverse fish community. Fish of high commercial value are almost absent, affecting local artisanal fisheries (Arthur et al., 2013). The loss of above-ground biomass has also resulted in a loss of buried organic carbon, suggesting that overgrazed meadows have not merely lost their sequestration ability, but are now losing their historic stores of carbon, that have been created and buried over decades. The shift to fast-growing species with shallow root structures may also mean lower sediment binding abilities, resulting in reduced beach stability (Nordlund et al., 2016; Scott et al., 2020). Such

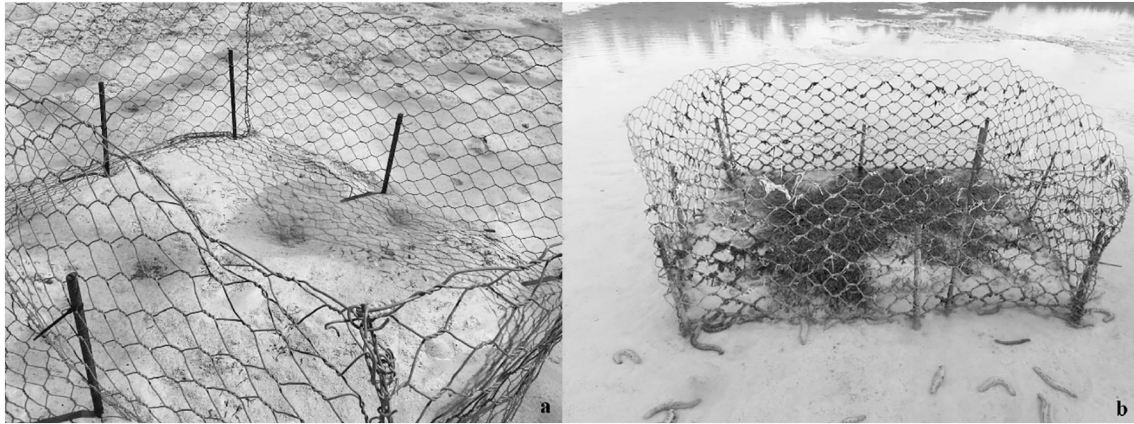


Fig. 5. a) Sparse seagrass cover at the start of the enclosure, b) Dense seagrass cover after 10 months.

losses of ecosystem services are not unique to the Lakshadweep and are likely characteristic of green turtle aggregations globally (Christianen et al., 2021).

4.3. Behavioural mechanisms that contribute to functional extinction

Several factors have caused green turtles to become devastating interactors in seagrass meadows. They appear to be social feeders, returning to the same seagrass meadow year on year in large aggregations when resources are abundant (Molina Hernández and van Tussenbroek, 2014; Christianen et al., 2021). Although without tracking studies we cannot claim this for certain, our work suggests that turtles show decadal fidelity to foraging sites and may potentially even trade the possibility of better foraging grounds for the certainty of a familiar location, as is true of other long migratory species (Shimada et al., 2020). The shallow lagoons are also predator-free zones for adult turtles, which they may be unwilling to abandon. In addition, green turtles have slower metabolic rates than mammalian herbivores or birds, which allows them to spend long periods without feeding (Hays et al., 2002; Franz et al., 2011), allowing them to persist in resource poor areas. Turtle diets show ontogenetic shifts with larger individuals (carapace size > 60 cm) predominantly being seagrass feeders (Burgett et al., 2018). The majority of the turtles we tracked in Lakshadweep had carapace sizes >60 cm (75% of individuals), suggesting that the population fed largely on seagrass species. Turtles have clear diet preferences and prefer *T. hemprichii* (Kelkar et al., 2013a), but they are also remarkably flexible both in their diet as well as in their feeding behaviour (Amorocho and Reina, 2007; Burgett et al., 2018; Christianen et al., 2014; Santos et al., 2011). This may explain why green turtles in Lakshadweep continued to stay in lagoons long after seagrasses were depleted before shifting to another island within the archipelago. Turtles, at least in Lakshadweep, appear to shift between foraging grounds *en masse*, concentrating their impact on one meadow at a time. The sequential shift in densities from Agatti to Bangaram to Kavaratti, to Kadmat and finally to Kalpeni, indicates a population persisting for as long as possible at a location before moving to another feeding ground. It was only in 2019, when seagrass meadows across the archipelago were in retreat, that this *en masse* movement could no longer be sustained. What remains now are diffused, low-density turtle populations distributed across all lagoons (Table 1). It is likely that a greater proportion of the past turtle meta-population no longer returns to Lakshadweep and has dispersed to new feeding grounds elsewhere in the Indian Ocean.

4.4. Recovery potential of meadows

After high density feeding aggregations, in a decade on average, meadows are showing recovery (Fig. 2, Fig. 3). The few green turtles

that continue to persist (Fig. 2) may likely exert sufficient herbivory to maintain meadows across the archipelago in a state of arrested recovery. Our observations in the enclosure in Kalpeni (Fig. 5) are also highly instructive, despite the lack of replication. They show that the herbivory impact of even the few remaining green turtles can be exceptionally high. Remnant shoots were limited to extremely shallow areas, where turtles find it more difficult to graze. In fact, during our 2019 and 2020 surveys we observed several green turtles stranded on the shore during low tides, attempting to access these remnant patches (personal observations). The recovery documented at Agatti, Bangaram, and Kavaratti is dominated by short-lived early successional species such as *H. ovalis* and *H. uninervis*, while *C. rotundata* and *T. hemprichii* are still largely absent. This new community forms meadows that are functionally quite different from the dense, high-canopy meadows of the past (Kelkar et al., 2013a). While *T. hemprichii* and *C. rotundata* are not yet locally extinct and can still be found as stray shoots in some lagoons, the meadows they once formed are functionally extinct, with their attendant fish diversity considerably reduced (this study, Arthur et al., 2013). The possibility that these meadows recover from seeds and rhizomes transported from other atolls in the archipelago can take several years, given the relatively large distances and isolation between meadows. An interesting mechanism of meadow recovery observed in the Caribbean shows how free-living coralline algae can limit grazing and facilitate seagrass regrowth in areas overgrazed by seagrass (Leemans et al., 2020). Without these natural mechanisms of recovery, proactive management of degraded meadows may be required to promote the recovery of these meadows including protecting remnant shoots in herbivore enclosures to maintain the species in the meadow until turtle densities are low enough to permit recovery. In addition, if long-lived species have been lost from some islands, active transplantation of small areas may be necessary to assist in the re-colonisation process. However, this may only be successful when green turtle densities are low enough to allow the colonisation of the seagrass species that green turtles prefer.

4.5. Caveats and unknowns

There are still several unknowns in our understanding of the coupled dynamics of green turtles and seagrasses in Lakshadweep. For one, there appears to be a small window of opportunity for seagrass recovery. The short-lived species we observed in 2020 starting to colonise the lagoons may herald a potential path of succession towards a fuller recovery if the herbivory stays low. This recovery is predicated on having remnant populations of long-lived species present in the lagoons. Our study also makes the simplifying implicit assumption that the green turtle population in Lakshadweep is a closed system. This may not be true and we need a better understanding of turtle population dynamics, genetics, and movement to know if the turtles are actually leaving the system to find

new feeding grounds, or if turtles are dying due to resource depletion. In addition, our study did not evaluate herbivory pressure by other seagrass herbivores like rabbitfish (Siganidae) and herbivorous sea urchins like *Tripneustes gratilla*. Where abundant, these species can be devastating and cause massive overgrazing events as well (Alcoverro and Mariani, 2002). However, in Lakshadweep, although present, the numbers of these herbivores were always low in the meadow, and their contribution to herbivory is likely to be marginal compared to green turtles. Indeed, as meadows became overgrazed, the abundances of rabbitfish declined dramatically (pers. obs), suggesting that other herbivores were also strongly affected by green turtle grazing. Although we documented some seagrass recovery, we need a much better understanding of how fast this recovery will translate to a recovery of fish abundance and diversity, and carbon sequestration and burial. There is also a possibility that such events are cyclic in nature and constitute a part of the interactions between turtles and seagrasses. The lack of memory about such events in islanders can be due the larger temporal scales at which such events occur. Filling these gaps is crucial to predict the long-term impact of green turtles on seagrass ecosystems.

4.6. Green turtles or seagrasses? a conservation dilemma

As our study shows, to sustain conservation gains, managing success once it has been achieved is perhaps as important as achieving success in the first place. These gains ought to be thought of as two phases of an evolving conservation strategy, each with its own priorities and approaches. Since its beginnings in the early 1970s, turtle conservation worldwide has focused on protecting nesting beaches, raising hatcheries, promoting the use of bycatch reduction devices in fisheries, and rallying citizens and governments around the need to protect turtles with stringent laws and monitoring programs (Godley et al., 2020). As a strategy for a group of species that were in serious decline, it has been a model of how conservation action should proceed. While the threats to turtle species have far from retreated, the recovery of green turtle numbers in many parts of the tropics from Bermuda and Mexico to Australia, Borneo and Mayotte, shows that these efforts are working, at least in some pockets (Christianen et al., 2021). Yet, at these locations, the dilemmas of success require another set of instruments to manage, as turtle populations press up against the capacities of seagrass ecosystems to sustain them. As we have suggested, an expanded toolbox will need to consider habitat management options such as setting up seagrass refugia or seed bank protection sites, or restoration programs to promote recovery once green turtles have left. It may even need to consider population management measures to ensure that turtle numbers do not overshoot ecosystem capacities. In addition, it may require preparing local communities to deal with the livelihood consequences (e.g. for subsistence fisheries) that could result when seagrass habitats they depend on are modified by turtle overgrazing.

It is additionally important to recognise the role that overfishing of sharks has potentially had on green sea turtle populations and the subsequent decline in seagrass meadows (Heithaus et al., 2007, 2008). In this regard, regulating shark fisheries could be an important component of conserving seagrass ecosystems as green turtle numbers increase. Whether the current situation more closely resembles how seagrass meadows functioned in the age of mega-herbivores, or merely reflects an artificial inflation of turtle numbers due to the absence of predatory controls, is still an open question. What is clear however, is that while plenty of conservation thinking has focused on the restoration phase of reversing endangerment and rewilding ecosystems, we need a much more nuanced understanding of how ecosystems respond to these measures, once success is achieved. This will ensure that conservation successes are not short-lived or pyrrhic victories.

CRedit authorship contribution statement

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analysis, Investigation, Methodology, Project administration, Validation, Visualization, Writing – original draft, Writing – review & editing. **Al-Badush Gafoor:** Data curation, Formal analysis, Investigation, Project administration, Validation, Visualization, Writing – original draft, Writing – review & editing. **Elrika DSouza:** Data curation, Investigation, Project administration, Validation, Visualization, Writing – original draft, Writing – review & editing. **Nachiket Kelkar:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Validation, Visualization, Writing – original draft, Writing – review & editing. **Rucha Karkarey:** Data curation, Investigation, Project administration, Validation, Visualization, Writing – review & editing. **Núria Marbà:** Formal analysis, Methodology, Resources, Supervision, Validation, Writing – review & editing. **Rohan Arthur:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Teresa Alcoverro:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

Declaration of competing interest

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

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