Greener pastures? High-density feeding aggregations of green turtles precipitate species shifts in seagrass meadows

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Summary

1. Historical declines of marine megaherbivores have led to a view of seagrass communities structured largely by abiotic disturbance and plant competition. There is, however, growing recognition of the significance of top-down control through herbivory, on seagrass ecosystem processes, raising the question of how meadows functioned under historically high populations of megaherbivores.

2. We assess the impacts of such intense herbivory on seagrass meadow composition in the Lakshadweep islands (India), where high-density feeding aggregations of green turtles have persisted for over a decade. We use a series of complementary approaches: (i) natural herbivory exclosures (ii) published data on seagrass composition before and after turtles established (at one atoll: Agatti) and (iii) present species composition along a turtle herbivory gradient over multiple atolls.

3. Long-term natural exclosures in Agatti indicated that sustained turtle grazing caused clear shifts in species dominance from the long-lived, higher-successional *Thalassia hemprichii* to the relatively short-lived, pioneering species *Cymodocea rotundata* (dominant in grazed areas). *T. hemprichii* was the dominant species *c.* 20 years ago but is now restricted to areas within exclosures in Agatti, and to the least grazed meadows (<5%) in other atolls.

4. We conducted field experiments to identify possible mechanisms by which herbivory mediated direct or apparent competitive interactions between seagrass species. To verify if grazing reduced growth rates of *T. hemprichii* in comparison with *C. rotundata*, we conducted clipping experiments in 1m^2 plots, simulating turtle herbivory on equal shoot proportions of both species. After 4 months, *T. hemprichii* shoot density showed major declines in clipped vs. control plots, but *C. rotundata* shoot density remained relatively unaffected.

5. To test whether selective grazing on *T. hemprichii* facilitated *C. rotundata,* we established paired seagrass preference experiments. Turtles had clear preferences for *T. hemprichii* (64%), but also grazed on *C. rotundata.*

6. *Synthesis.* Taken together, our results show that high-impact turtle herbivory changes seagrass composition, precipitating dominance shifts in grazed meadows by mediating direct and apparent competition. Given the crucial role of megaherbivores in seagrass meadow functioning, our results suggest that past meadows may have had natural functional limits to megaherbivore densities that they could sustainably support.

Key-words: direct and apparent competition, green turtles, herbivory pressure, historical baselines, megaherbivores, plant–herbivore interactions, seagrass meadows, seagrass species shifts

Introduction

Until very recently, the dominant paradigm in seagrass ecosystems was predicated on the idea that species composition was largely governed by light and nutrient limitation, physical disturbances and interspecific competition, with herbivory playing a relatively minor role (Livingston 1984; Duarte & Cebrián 1996; Cebrián *et al.* 1997; Cebrián 1999; Williams & Heck 2001; Hughes *et al.* 2004; Short & Wyllie-Echeverria 2009). For instance, sediment and nutrient dynamics are

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known to be important drivers in the maintenance of multi-species tropical seagrass meadows (Brouns 1987; Bach *et al.* 1998; Eldridge, Kaldy & Burd 2004; Hughes *et al.* 2004; Boer 2007). Competition and facilitation networks between seagrass species have also been shown to be vital in shaping tropical meadow communities in SE Asia (Marbà & Duarte 1998; Terrados 1999; Duarte *et al.* 2000; Gacia *et al.* 2003). The idea of herbivory as a relatively minor actor in seagrass meadows was probably influenced by the relative absence of megaherbivores from most seagrass meadows across the world today (Cebrián *et al.* 1997; Cebrián 1999), driven down by centuries of human overexploitation (Jackson 1997, 2001; Bjorndal & Jackson 2003). However, herbivore populations that are still relatively intact can have important functional consequences for seagrass meadows (Thayer *et al.* 1984; Preen 1995; Valentine & Heck 1999; Valentine & Duffy 2006; Unsworth *et al.* 2007; Eklof *et al.* 2008; Heck *et al.* 2008; Fourqurean *et al.* 2010; Cook, Vanderklift & Poore 2011; Christianen *et al.* 2012). For instance, herbivory by dugongs and green turtles has been observed to influence seagrass meadow productivity, nutrient cycling and structural complexity (Zieman, Iverson & Ogden 1984; Williams 1988; Aragones 1996; Valentine *et al.* 1997; Moran & Bjorndal 2005, 2007; Aragones *et al.* 2006; Kuiper-Linley, Johnson & Lanyon 2007; Eklof *et al.* 2008). Recent studies conducted by Fourqurean *et al.* (2010) indicate that locally high grazing pressure by green turtles in the 1990s could have precipitated meadow-wide collapse in Bermuda. Importantly, these studies point to recent re-evaluation of the importance of herbivory as a potential structuring process in seagrass meadows.

By contrast, the role of large herbivores in structuring terrestrial systems (grasslands, forests) has always been well established. Interactions between herbivory and interspecies competition have important population and ecosystem-level consequences driving species and community shifts, and being responsible for large-scale movements of animals (McNaughton, Rues & Seagle 1988; Huntly 1991; Anderson & Briske 1995; Briske & Hendrickson 2010). Herbivory can disrupt competitive hierarchies and species dominance patterns either by compromising a species' ability to cope with its competitors or by facilitating growth potentials of usually subdominant species (Holt, Grover & Tilman 1994; Tilman 1997; Moretto & Distel 1997; Hambäck & Beckerman 2003; Maron & Crone 2006). This normally happens in two ways: (i) direct competition, where the activity of the herbivore mediates changes in the inherent competitive abilities of plant species by reducing the growth, production, reproduction and survival of dominant plant species (Huntly 1991; Holt, Grover & Tilman 1994; Denno *et al.* 2000) and (ii) apparent competition, where preferential herbivory on a particular species can depress its growth rate (Lubchenco 1978; Augner, Tuomi & Rousi 1997; Center *et al.* 2005; Briske & Hendrickson 2010); thus, indirectly facilitating the ability of the less preferred species to dominate (Holt, Grover & Tilman 1994; Moretto & Distel 1997; Choler, Michalet & Callaway 2001; Alberti *et al.* 2008). These herbivory-mediated interactions can lead to species shifts and alter successional states

with ecosystem-wide functional consequences (Dethier & Duggins 1984; Anderson & Briske 1995; Denno *et al.* 2000; Ims *et al.* 2007).

However, unlike terrestrial grasslands, the mechanisms through which megaherbivores influence competitive interactions between seagrass species have received scant attention in seagrass ecosystems. This is due, in part, to the fact that most research on seagrass herbivory has focused on monospecific meadows (Zieman, Iverson & Ogden 1984; Williams 1988; Moran & Bjorndal 2005) or where megaherbivores are absent. While experiments simulating green turtle or dugong herbivory have shown changes in seagrass composition (Aragones & Marsh 2000), direct field-based studies are lacking, mostly because it is difficult to find meadows where extant populations approach historical densities (Jackson 1997; Bjorndal & Jackson 2003; Heck & Valentine 2006). The recent success of conservation actions has seen encouraging local increases in green turtle populations (Broderick *et al.* 2006; Chaloupka *et al.* 2008; Christianen *et al.* 2012). These local, currently high-density populations can offer valuable insights into the mechanisms by which historically high megaherbivore populations could have influenced seagrass ecosystem structure and function through herbivory.

In this article, we examine the influence of a high-density, resident green turtle feeding aggregation on the species composition of seagrass meadows in the Lakshadweep islands, Indian Ocean, where current densities of green turtles at some atolls are among the highest reported globally (Ballorain *et al.* 2010; Fourqurean *et al.* 2010; Lal *et al.* 2010; Christianen *et al.* 2012). To test if green turtle herbivory can cause shifts in meadow species composition, we use three lines of evidence: (i) a natural long-term turtle exclosure at an atoll where turtle densities have been high for the last decade, (ii) a comparison of seagrass species composition before and after turtles increased at this atoll, from published literature and our recent observations and (iii) a spatial comparison of seagrass species composition at meadows along a gradient of turtle density within the archipelago. We use two complementary experiments (clipping experiments and feeding assays) to assess whether herbivory-mediated competition between seagrass species may be driven by direct interference competition and/or apparent competition/facilitation mechanisms.

Materials and methods

STUDY AREA

The Lakshadweep Archipelago (8–12°N and 71–74°E at the northern end of the Laccadive Chagos ridge, Indian Ocean; Fig. 1) is one of few global locations where green turtle populations have shown considerable recovery along with Hawaii, Mayotte Island, Bermuda and Borneo (Balazs & Chaloupka 2004; Taquet *et al.* 2006; Ballorain *et al.* 2010; Fourqurean *et al.* 2010; Christianen *et al.* 2012). At present, turtle densities in the Lakshadweep at *c.* 0.001 turtles per m^2 (1000 turtles per km^2 of seagrass) are considerably higher than past records indicate (Bhaskar 1978) and are similar in density to other locations in the Indian Ocean that have recently documented high
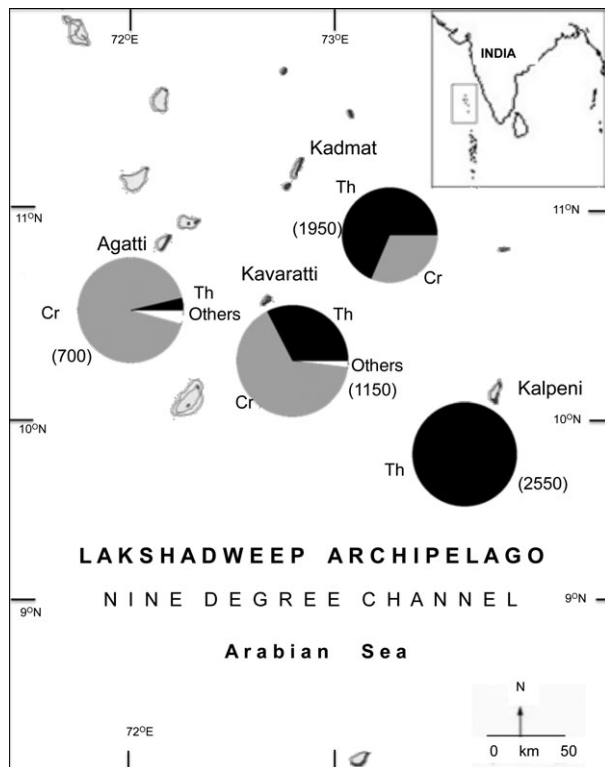
Fig. 1. Pie charts indicate the relative contribution of seagrass species to total shoot density (shoots per m^2) in the Agatti, Kavaratti, Kadmat and Kalpeni lagoons of the Lakshadweep Archipelago, India [dark grey = *Thalassia hemprichii* (Th); grey = *Cymodocea rotundata* (Cr), light grey (others)]. Numbers in parentheses indicate total shoot densities averaged across meadows in each lagoon.

turtle densities. For instance, Ballorain *et al.* (2010) reported 0.0024 turtles per m^2 (2400 turtles per km^2) in Mayotte island, and Christianen *et al.* (2012) estimated 0.0015 turtles per m^2 (1500 km^{-2} of seagrass area) in Indonesia. An effective ban on turtle hunting, conservation efforts in the wider region and overfishing of top predators such as sharks may have possibly led to recent increases in densities of turtle feeding aggregations (interviews with local key informants; Seminoff 2004; Heithaus *et al.* 2008). These trends are supported by similar observations in other regions where effective conservation of green turtles has led to promising recoveries over the last three decades (Seminoff 2004; Broderick *et al.* 2006; Bourjea *et al.* 2007; Chaloupka *et al.* 2008).

Seagrass meadows in the Lakshadweep are restricted to shallow atoll lagoons and are composed of up to seven seagrass species, typically dominated by *Thalassia hemprichii* and *Cymodocea rotundata* (Jagtap 1991, 1998). The study was conducted across four coral atolls in the archipelago where resident green turtle populations have been recorded: Agatti, Kavaratti, Kadmat and Kalpeni (Fig. 1). The atolls are north-south oriented, and their lagoons are very similar in their biophysical parameters, depth (2–4 m on average), shape and substrate characteristics (fine sandy bottoms, with scattered coral patches). They are all also subject to similarly low levels of human use and fishing pressure (Tamelander & Hoon 2008). Of these, Agatti has had high densities of resident feeding aggregations of turtles that have persisted for about the last 15 years (Table 1). Resident turtle densities are much lower at other atolls, and aggregations have established more recently, creating a

natural gradient in turtle densities across the four islands (Table 1). The study was conducted over 2 years between 2010 and 2011. Relevant literature over the last three decades was also reviewed to compile information on turtle densities and seagrass characteristics (species composition and shoot densities) across meadows in these four lagoons.

CHANGES IN SEAGRASS SPECIES COMPOSITION AND TURTLE DENSITIES

To identify temporal changes, we compiled secondary data on seagrass composition and species occurrence in Agatti island before and after green turtle populations became resident at this atoll (*c.* 1998) from available literature between 1991 and 2011 (Jagtap 1991, 1998; Jagtap & Inamdar 1991; Rodrigues, Caeiro & Raikar 1997; ICMAM PD 2001; Nobi *et al.* 2011). Additionally, species composition and shoot densities in Agatti, Kavaratti and Kadmat were tracked between 2007 and 2011 (Lal *et al.* 2010; this study), after resident turtle numbers increased in Agatti island. We compared proportional abundance of seagrass species (rather than actual shoot densities) across islands to clearly document relative dominance patterns.

We also compiled information on historical turtle occurrences across the archipelago from available literature (Bhaskar 1978; Tripathy, Shanker & Choudhury 2006). Additionally, for the studied lagoons, we conducted multiple boat-based surveys in each lagoon to directly estimate turtle abundance and distribution during 2009, 2010 and 2011 (for Kavaratti, Kadmat and Kalpeni), and from 2007 to 2008 until the present day for Agatti (see Table 1). In these surveys, observers counted turtles within a 10 × 300 m belt transect between grid points (between 70 and 232 points depending on the size of the lagoons), on both (non-overlapping) sides of the boat, for each point on a 300 × 300 m grid. All surveys were conducted during the pre-monsoon season (Feb–Mar 2009–2011) when similar turtle densities were noted in individual atolls across years. The counts made by each observer at grid points were summed to obtain total counts per point. The number of turtles counted along each transect was assigned to the subsequent grid point. We sampled turtle abundance 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). Changes in turtle numbers with tidal variation were also relatively uniform across all lagoons, with most turtles staying within lagoons throughout the sampling season. Densities of turtles (km^{-2}) for meadows and for lagoons remained similar between different survey years during the study period.

Spatial changes: We selected eight meadows distributed across the four sampled islands (Agatti, Kavaratti, Kadmat and Kalpeni), representing a gradient of turtle densities. At each meadow, we measured shoot density for each seagrass species (shoots per m^2), estimated in 10–15 randomly distributed quadrats within each seagrass meadow. For each meadow, we also measured instantaneous turtle herbivory rates (cm eaten per shoot per day) using 50 random shoots of *T. hemprichii* and *C. rotundata* (the two dominant species, accounting for a proportion of *c.* 99% in natural abundance in the meadows). For each shoot, we initially measured the length of each leaf, the number of leaves per shoot and scarred the sheath base with a needle. The shoots were marked with pegs and rope to relocate them. After 3–5 days, the shoots were collected to estimate herbivory rates. We measured shoot elongation (the distance the scar had travelled from the sheath base) and total leaf length for every leaf in the shoot.

Table 1. Temporal changes in turtle density (km^{-2}) in the Agatti, Kadmat, Kavaratti and Kalpeni lagoons (Lakshadweep Archipelago, India, Indian Ocean)

Island	Year when significant increases in turtle numbers recorded	Estimated current densities of turtles (2011) [Mean(range)]	Estimated past range of turtle density (range from year of increase to 2010)	Remarks on temporal changes
Agatti	1997–1998	6.3 (1–11.5)	8–30	Bhaskar (1978) reported very few turtles in Agatti. Numbers were negligible until the late 1990s, but a sudden increase possible around 1998*, Arthur and Madhusudan (unpublished data from 2005), recorded densities of *c*. 30 turtles per km^2 in Agatti. Densities were high (10–12 km^{-2}) until 2007 (Tripathy, Shanker & Choudhury 2006; Lal *et al.* 2010); but considerable recent declines have been recorded (this study, 2010–2011)
Kavaratti	2008–2009	14.4 (12.8–15.7)	10–13	Increases in turtle numbers recorded first in 2008–2009*·†, recent surveys indicate exceptional increases (this study)
Kadmat	2011	11.67 (3–20)	0–3	Exceptional increase in 2011 (this study); very few turtles seen inside the lagoon until this increase†
Kalpeni	No increases recorded, very few turtles have been seen	1.4 (0–2.2)	0–2	Very few turtles recorded in 2011 (this study)

*From interview surveys with fishers conducted by authors.
†Personal communication with Jafer Hisham.

Total shoot elongation was obtained as the sum of the distance between the scar and the base for all leaves divided by the time elapsed. We calculated leaf defoliation (shoot herbivory, cm per shoot per day) by adding shoot elongation to initial length and subtracting the total from the final length (based on Prado *et al.* 2007). We preferred this method to leaf tethering, as we were interested in estimating direct *in situ* herbivory rates. Only leaves that had clear turtle crop marks were attributed to herbivory, which may represent a conservative underestimation. We refer to defoliation rate as herbivory rate, with the realistic assumption that they are very similar; given the unmistakable cropping mode that green turtles employ when feeding on seagrass shoots (Bjorndal 1985; personal observations). Other herbivores also leave distinctive feeding signs on the seagrass leaves; fish herbivores feed on individual blades, leaving behind clean crescent-shaped bites while urchin herbivory leaves serrated crop marks on individual leaf blades (Thayer *et al.* 1984; Kirsch, Valentine & Heck 2002). In contrast, turtles cropped seagrass shoots very close to the base and left ragged tear marks on the eaten leafs and shoots. Our observations of the few rare instances of fish grazing never found marks remotely similar to those made by turtles. Based on these signs, we attributed herbivory to each herbivore in our measurements. We did not record any herbivory by sea urchins and amphipods, and the extent of fish herbivory was extremely low (<1%), allowing us to safely attribute the bulk of herbivory to green turtle grazing.

ASSESSING SEAGRASS SPECIES SHIFTS: NATURAL EXCLOSURES

We compared grazed areas with adjacent, naturally occurring patches of seagrass protected by dead branching corals (*Acropora* sp.), which have been used effectively to test the impacts of herbivory in other systems (Bennett, Vergés & Bellwood 2010). The coral branches served as an effective long-term refuge for seagrass from green turtle herbivory. To reduce the potential influence of confounding factors related to the presence of coral structures (e.g. through fertilization by fish or modification by currents) on seagrass biomass, we selected the 'ungrazed plots' to be very close to 'grazed plots' and thus be subjected to the same levels of potential nutrient enrichment or exposure to currents. We compared the proportional abundance of *T. hemprichii* and *C. rotundata* (measured in 40 × 40 cm quadrats) inside and outside these exclosure plots (six plots each). We believe that this natural system, with minor potential confounding factors, can adequately replace an ideal, controlled before–after experiment or an artificial exclosure (which were logistically impossible to maintain over several years).

CLIPPING EXPERIMENTS

We set up experimental 'clipping plots' of 1 m^2 (10 clipped and 10 unclipped controls) to simulate turtle grazing in a meadow in Kadmat where turtles were absent (e.g. Moran & Bjorndal 2005, 2007). Plots were set up in 2010 and 2011 (10 plots each year, five control and five clipped) in areas where *T. hemprichii* and *C. rotundata* co-dominated the meadow. We measured the initial shoot density in each plot and then manually clipped all seagrass shoots to canopy height of 2–3 cm within the clipped treatment to simulate non-preferential turtle cropping of standing shoots. We clipped the plots for a period of 100 days, before the monsoon began, with clipping treatments every 14 days (number of clippings at each plot = 8) to simulate grazing that mimicked daily rates of green turtle herbivory (*c*. 0.5 cm per shoot per day) observed in high turtle density areas. Each clipping resulted in an offtake of approximately 10 cm per shoot per 14 days. In our field observations, turtles cropped seagrass closely at the base of the shoot with each bite and moved from patch to patch grazing the meadow down, which was reflected in the mode of our clipping. Turtle herbivory was also concentrated in small plots over time-periods comparable to which the clipping experiments were run. After 100 days, we re-measured shoot densities of clipped and control plots. Shoot density was always measured at the centre of the plot in a subsample (20 × 20 cm quadrat) to avoid the effect of clonal

integration in clipped shoots near the edge of the quadrat (Vergés *et al.* 2007). We estimated net population growth rates (μ per day) of *T. hemprichii* and *C. rotundata* during the experiment as, μ $(\text{day}^{-1}) = \ln (N_t/N_0)/t$ where N_t and N_0 were shoot densities of each species at the end and beginning of the experiment, respectively, and *t* the duration of the experiment (in days).

TESTING TURTLE FEEDING PREFERENCES

In order to test whether selective feeding by turtles could lead to apparent competition effects, we conducted an *in situ* field feeding preference assay (e.g. Mariani & Alcoverro 1999), where turtles were offered paired shoots of *T. hemprichii* and *C. rotundata*. These shoots were tethered to pegs with cable ties and each peg contained a replicate pair of each species (total of 25 pairs). Each pair was prepared to have a similar amount of leaf length (cm) for both species (*c.* one shoot of *T. hemprichii* and three shoots of *C. rotundata*). Paired replicates were set sufficiently apart from each other (*c.* 5 m) to ensure independence of trials. The experiment was set up in a zone of moderate turtle densities in Kadmat island, at a depth of 2.5 m, in sandy patches at least 10 m away from the neighbouring seagrass meadows. To standardize replicates, we cut-off any already existing herbivory marks from the leaf apices. We also used seven paired replicates as controls protecting them from herbivores with a herbivore enclosure in order to confirm that all shoot losses in the assay were due to herbivory and not physical removal by ocean currents or tidal action. The controls confirmed that no shoots were lost due to currents or wave action, and that all losses could be attributed to turtle herbivory during the 7 days of the experiment (paired *t*-test before–after in controls for both *T. hemprichii* and *C. rotundata*). The experiment was monitored daily, and shoots in replicate pairs showing the first signs of turtle herbivory were removed from the assay. We measured shoot lengths grazed (cm), and results were tabulated for both *T. hemprichii* and *C. rotundata* for each paired replicate. The experiment was continued until about 70% of the treatment shoots were eaten. The experiment was stopped after 7 days when all remaining replicate pairs were collected.

DATA ANALYSIS

We used regression analyses to estimate effect sizes for the relationship between turtle density and instantaneous herbivory rates. We calculated an index of 'cumulative turtle impact' on seagrasses through herbivory estimated as the mean current turtle density × number of years since arrival of turtles in that lagoon (Table 1). This index was used as an explanatory variable in another set of linear regression models to estimate the effect of turtle grazing on seagrass shoot densities along the gradient of turtle densities. We used the natural logarithm of the 'cumulative turtle impact index' as the covariate in these models, which helped in model fitting. We used a two-way ANOVA to test the response of *T. hemprichii* and *C. rotundata* population growth rates between clipping and control experiments, with 'clipping' and 'year' as fixed factors and a clipping*year interaction term. One-way ANOVA was used also to test the effect of herbivory (control) vs. exclosure (treatment) effects on percentage of *T. hemprichii* out of total shoot density (arcsine-transformed values) within and outside the natural green turtle exclosure. We used a paired *t*-test to assess if one species was consistently consumed more than the other. All analyses were conducted in R 2.13.1 (R Development Core Team, 2011).

Results

TRENDS IN GREEN TURTLE DENSITIES

Although green turtles have sporadically used beaches of the Lakshadweep Archipelago to nest in the past, turtle densities have been typically low, at least from the 1970s, when the first systematic turtle studies were conducted in these islands, until the late 1990s (Table 1). The late 1990s saw substantial increases in green turtle numbers, with population densities concentrated in Agatti, followed by Kavaratti, and later Kadmat and Kalpeni (Table 1). Our recent surveys (2010–2011) indicate that Kadmat and Kalpeni currently have low turtle densities, whereas Kavaratti and Agatti have high turtle densities. At Agatti, these populations have been resident at least since about 1998. Green turtle densities have increased more recently in other lagoons: Kavaratti, about 2006 (interview surveys with fishermen, and R. Arthur pers. comm.), and in Kadmat (2011–2012).

TEMPORAL CHANGES IN SEAGRASS COMMUNITY COMPOSITION (AGATTI ATOLL)

The reduction in *T. hemprichii* has been accompanied by an increase in *C. rotundata* that is now the dominant seagrass in the meadows (Fig. 1). Agatti lagoon, with high turtle densities since 1998, has shown important transitions in seagrass meadow composition over the last 20 years, with *T. hemprichii* declining consistently over this period (Fig. 2).

HERBIVORY RATES AND SEAGRASS SPECIES COMPOSITION ALONG A TURTLE DENSITY GRADIENT

Turtle density (per km² of lagoon) was strongly correlated with herbivory rates (Fig. 3) indicating that turtle aggregations
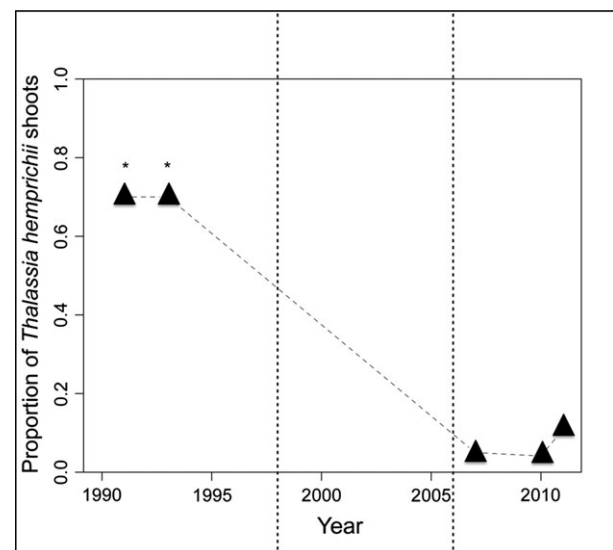
Fig. 2. Temporal changes in the proportion of *Thalassia hemprichii* shoot density in seagrass meadows of the Agatti lagoon. Dotted lines indicate period of highest turtle numbers (1998–2006). Asterisks (*) indicate data from published literature (pt. 1 from Jagtap 1991, 1998; pt. 2 from Rodrigues, Caeiro & Raikar 1997). Refer to Table 1 for associated changes in turtle densities.

are responsible for higher rates of herbivory. Seagrass meadows ($n = 2$) in Agatti had the highest average values of cumulative turtle impact (*c.* turtle density of 1800 turtles per km^2 seagrass per year for 12 years) with present herbivory rates of *c.* 450 cm seagrass eaten per m^2 per day (1.1 cm per shoot per day). More interestingly, we observed a negative exponential decline in shoot density with increasing cumulative green turtle herbivory along the meadows studied (Table 2). This negative trend was largely driven by the decrease in *T. hemprichii* shoot density although *C. rotundata* under high turtle densities also occurred at low shoot densities (Table 2, Fig. 4). The annual decline of *T. hemprichii* and *C. rotundata* (from 2010 to 2011) was estimated at 17% (SE 17.97) and 10% (SE 5.26), respectively, from shoot density data. More strikingly, meadows where turtles were absent or at low densities, *T. hemprichii* was monodominant, and only at meadows with moderate or high cumulative turtle herbivory was *C. rotundata* a significant compositional element (Fig. 4), accounting for between 50% and 100% of total seagrass shoot density.
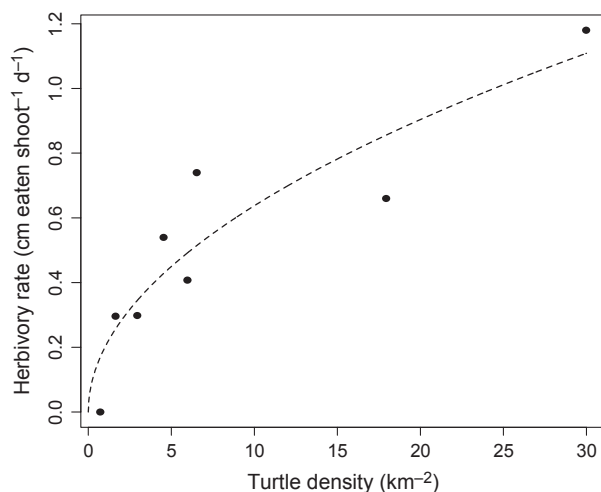

Fig. 3. Relationship between turtle densities and herbivory rates in Agatti, Kadmat and Kavaratti lagoons. The dotted line indicates the fitted equation (herbivory rate = A*turtle density^B; $R^2 = 0.89$, $P = 0.003$, parameter estimates $A = 0.199$, $B = 0.504$).

Table 2. Estimates of regression models between total seagrass; *Thalassia hemprichii* and *Cymodocea rotundata* shoot density (m^{-2}) and cumulative turtle impact across the four lagoons studied

Response (Shoot density in per m^2)	Parameter estimates			
	A (SE)	B (SE)	R^2	P-value
Total seagrass	−14.48 (3.25)	91.51 (8.76)	0.74	<0.0001*
Thalassia hemprichii	−12.73 (3.004)	61.67 (9.553)	0.51	<0.0001*
Cymodocea rotundata	−1.746 (3.41)	29.84 (10.83)	0.03	0.014*

The models have the form shoot density = A × log (cumulative turtle impact) + B, where A and B are model parameters. * significant at a = 0.05.

SEAGRASS SPECIES SHIFTS: NATURAL EXCLOSURES IN AGATTI

Natural long-term herbivory exclosures within the Agatti lagoon, which had the highest cumulative turtle herbivory over the last decade, suggested a significant shift in species dominance as a result of turtle herbivory. *Thalassia hemprichii* was the dominant seagrass species interspersed within the *Acropora* branches (Fig. 5) that rendered small patches of seagrass inaccessible to green turtles (ungrazed plots). Outside these areas, in grazed plots subject to turtle herbivory, the meadow had abundant signs of turtle cropping, and *T. hemprichii* abundance significantly declined (ANOVA: $F = 13.34$, $P < 0.001$), becoming virtually absent (Fig. 5).

CLIPPING EXPERIMENTS

After 100 days of repeated simulated non-preferential herbivory in experimental plots with both species co-dominant, shoot densities of *T. hemprichii* showed significant reductions, at a rate of $\mu = -0.005$ shoots per day, compared with control plots, with no change (Table 3 and Fig. 6). The net population growth rates observed during the clipping experiment indicated that if similar experimental herbivory intensity would have persisted, *T. hemprichii* shoot density could reduce to 10% of its initial density within 1.3 years. In contrast, repeated clipping did not appear to influence the shoot densities of *C. rotundata,* and there were no major differences between clipped and control plots (Table 3 and Fig. 6). This pattern was consistent in both years of clipping.

TESTING TURTLE FEEDING PREFERENCES

Green turtles consumed both species of seagrasses offered to them in the paired feeding preference experiment. Turtles demonstrated a clear and unambiguous preference for *T. hemprichii* over *C. rotundata* (Paired *t*-test: $t = 2.49$, $P = 0.02$, significant at $\alpha = 0.05$; Fig. 7), suggesting that differential, selective grazing could mediate apparent competition between the species.

Discussion

At high green turtle densities, our results indicate that herbivory in seagrass ecosystems can be the principal driver of meadow species composition, modifying both direct competition and facilitation. Our results re-emphasize the growing recognition that, when herbivores are abundant, top-down control may be an important structuring agent in seagrass ecosystems. We used multiple lines of evidence to reconstruct the long-term impacts of grazing on meadow composition in the Lakshadweep archipelago, and these indicated a remarkably predictable pattern of species shifts with meadows being progressively grazed to lower successional stages. Our comparison of seagrass species composition in naturally occurring adjacent grazed and ungrazed small areas within a meadow (although not an ideal before–after exclosure experiment) additionally supported the influence of green turtle grazing on
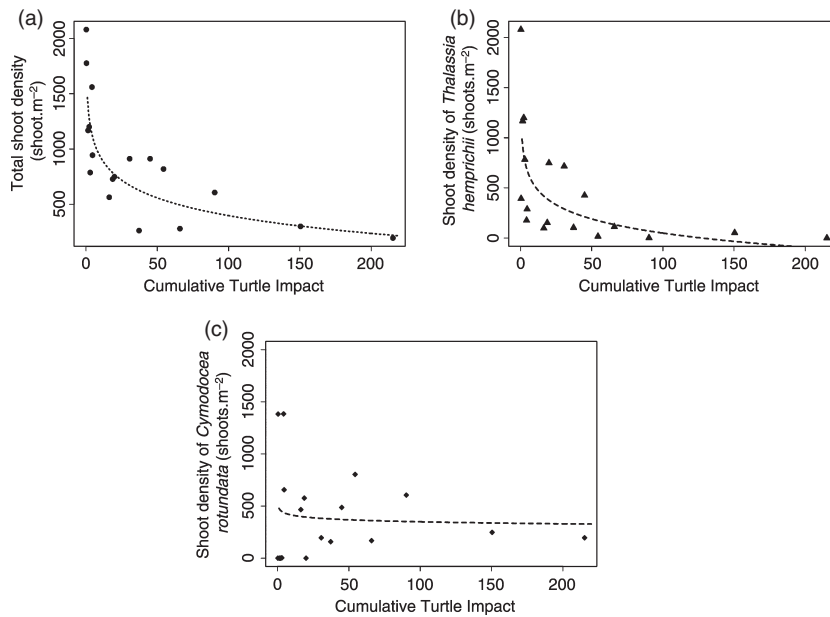
Fig. 4. Relationships between sustained turtle herbivory (cumulative turtle impact) and total shoot density (a) shoot density of *Thalassia hemprichii* (b) and *Cymodocea rotundata* (c). The lines represent the fitted equations summarized in Table 2.
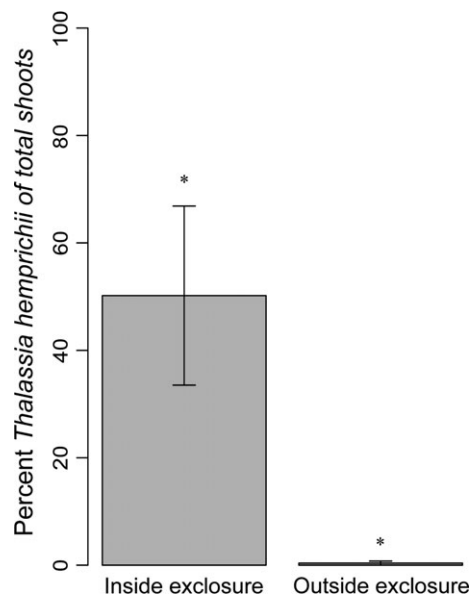

Fig. 5. Percentage of *Thalassia hemprichii* shoots in the seagrass meadow in the absence (inside exclosure) and exposed (outside exclosure) to herbivory in natural long-term herbivory exclosures (see text) within the Agatti lagoon. Values represent the average ± standard deviation, and asterisks indicate significant differences.

reducing the dominance of *T. hemprichii*. Clipping experiments and preference assays suggest that turtle herbivory can perhaps mediate direct and apparent competitive pathways between these species and is principally responsible for these compositional shifts, with a short-lived, early successional species (*Cymodocea rotundata*) replacing a longer-lived later-successional dominant (*Thalassia hemprichii*).

Characteristic herbivore-induced shifts from long- to short-lived species are well documented in a range of terrestrial ecosystems (Milchunas, Sala & Lauenroth 1988; Anderson &

Briske 1995; Augner, Tuomi & Rousi 1997; Augustine & McNaughton 1998; Ritchie & Olff 1999; Briske & Hendrickson 2010). It is also well recognized that selective herbivory can cause compositional shifts without requiring a modification of direct competitive abilities, allowing less competitive but less preferred species to dominate over selectively grazed competitively superior species (Bengtsson, Fagerstrom & Rydin 1994; Hambäck & Beckerman 2003; Alberti *et al.* 2008). Observational and experimental studies have documented similar compositional shifts in seagrass systems associated with intense grazing by marine herbivores like dugongs and turtles (Aragones & Marsh 2000; Peterson *et al.* 2002; Armitage & Fourqurean 2006; Ballorain *et al.* 2010; Fourqurean *et al.* 2010). Our observations from the Lakshadweep meadows validate this trend at ecologically relevant scales, and the field experiments help identify the mechanisms through which these compositional shifts may take place, indicating that green turtles modify both direct and indirect competitive interactions between seagrass species.

The high-intensity green turtle herbivory we recorded in the Lakshadweep meadows resulted in a major decline in the dominance of *T. hemprichii* over four decades in the Lakshadweep archipelago (Qasim & Bhattathiri 1971; (Kavaratti lagoon); Jagtap 1991, 1998). In meadows where herbivores are absent, the ecomorphological traits of *T. hemprichii* (longer petioles, thicker and wider leaf blades/ rhizomes, protected shoot bases; low antiherbivory chemical defenses (Bjorndal 1985, 1997; Duffy & Hay 1994; Terrados 1999; Duarte *et al.* 2000; Vergés *et al.* 2007) make this species competitively superior to the more pioneering *C. rotundata*. However, in the presence of herbivores, *T. hemprichii* may be less able to sustain herbivory pressure due to its slow growth rate and slower recovery potential (Zieman, Iverson & Ogden 1984; Duarte 1991; Marbà & Duarte 1998). In addition, grazing pressure may potentially change sediment

Table 3. Simulated non-preferential herbivory on a seagrass meadow codominated by *Thalassia hemprichii* and *Cymodocea rotundata*

Species	Parameter	Year	Clipped	Control	ANOVA: *F*-statistic	*P*-value (α = 0.05)
Thalassia hemprichii	Net population growth rate (shoots per day) (±SE)	2010 2011	−0.0051 ± 0.003 −0.0053 ± 0.001	0.0012 ± 0.002 0.00016 ± 0.002	Clipping: 7.18 Year[NS] Clip*Year[NS]	0.015*
Cymodocea rotundata	Net population growth rate (shoots per day) (±SE)	2010 2011	0.0021 ± 0.0007 −0.00018 ± 0.0009	0.0059 ± 0.0009 −0.00064 ± 0.001	Clipping 3.42 Year 22.99 Clip*Year 5.51	0.08° 0.0002*** 0.0321*

NS, not significant.
Net population growth rate (day^{-1} ± Standard Error) of both species in clipped and control treatments are provided. The results of the analysis of variance (for effects of clipping, effect of year and clipping-year interaction) are provided. (***Significant at α < 0.0001, **significant at α < 0.001, *significant at α < 0.05, °significant at α < 0.1, [NS]Not significant).
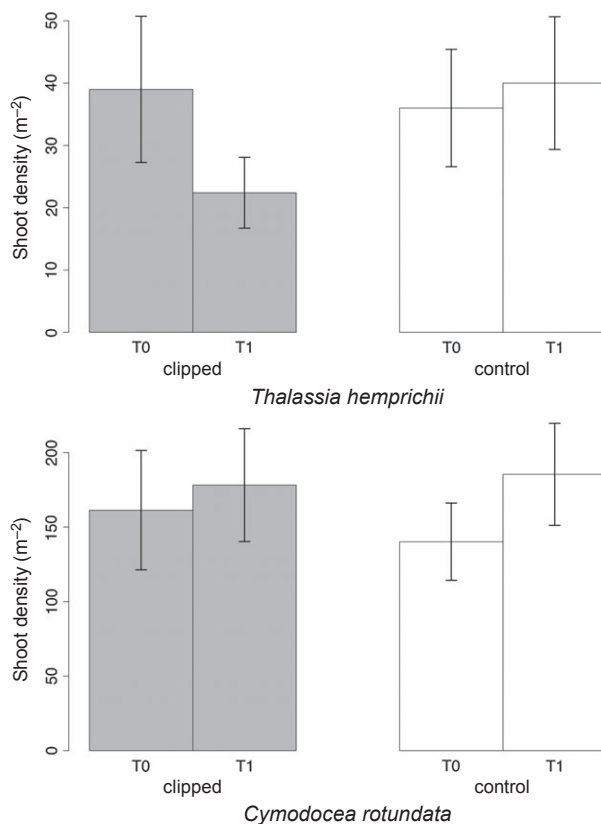

Fig. 6. Shoot densities of *Thalassia hemprichii* and *Cymodocea rotundata* from start time (T0) to end time (T1) of the clipping experiments (combined over years 1 and 2). Values represent the average ± standard deviation. See Table 3 for significance values.

Fig. 7. Turtle herbivory rates (cm per day) on *Thalassia hemprichii* and *Cymodocea rotundata* in preference assay conducted in Lakshadweep Archipelago (India, Indian Ocean). Values represent the average ± standard deviation, and asterisks indicate significant differences.

dynamics, which could also differentially influence the species' ability to cope with multiple stressors (Cebrián 1999; Gacia *et al.* 2003; Bowles & Bell 2004; Eldridge, Kaldy & Burd 2004; Rasheed 2004; Boer 2007). In the long term, any initial competitive advantage of *T. hemprichii* over *C. rotundata* may not be enough to compensate for biomass loss from cumulative herbivory (Bastow Wilson 1988).

The preference of green turtles for *T. hemprichii* over *C. rotundata* contrasts with previous observations where
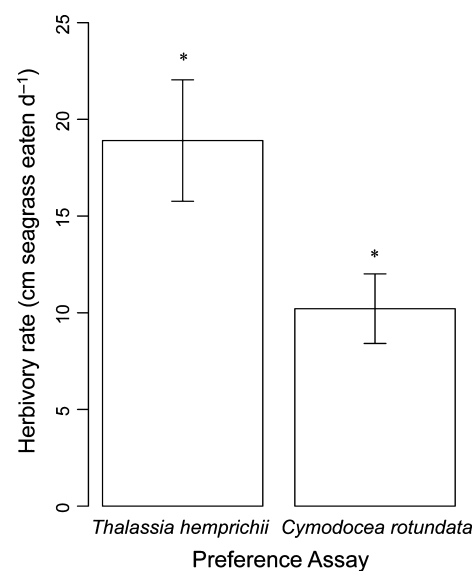
turtles preferred faster-growing species (Zieman, Iverson & Ogden 1984; Aragones 1996; Aragones *et al.* 2006). This preference could be due to significant nitrogen stock retention or lower antiherbivory defences in *T. hemprichii* as has been reported in similar systems (Terrados 1999; Stapel *et al.* 2001; Valentine *et al.* 2004; Moran & Bjorndal 2007; Ballorain *et al.* 2010). However, green turtles are also known to be fairly plastic in their dietary preferences (Mortimer 1981; Bjorndal 1985; Hays *et al.* 2002; Burkholder *et al.* 2011) and may be able to switch diets to less favored species after cropping out *T. hemprichii*. Following the loss of *T. hemprichii* from heavily grazed meadows, we observed substantial declines in shoot densities in monospecific meadows of *C. rotundata*, leading to further successional downgrading to species such as *Syringodium* spp. and *Halophila* spp. This suggests that meadow shoot density, while perhaps able to offset short-term turtle herbivory, can dramatically decline

beyond a threshold cumulative impact (*c.* 1500 turtles per km^2 seagrass per year) sustained over 6–7 years (as observed in Agatti). Beyond this threshold, turtles may be forced to move in search of more distant foraging grounds in other lagoons, a trend our most recent observations appear to confirm. Whether these movements correspond to a long-term rotational grazing system as has been reported for dugongs (e.g. Preen 1995; Aragones & Marsh 2000), needs to be monitored.

Herbivory-induced modifications of species successional patterns could directly affect meadow structural complexity, with multiple functional consequences for seagrass ecosystems (Eklof *et al.* 2008; Fourqurean *et al.* 2010). This can, in turn, lead to a decline in nutrient retention (Valentine *et al.* 2004) and cause potential modifications to fish abundance in the meadows. Mature seagrass meadows with longer-lived species perform important feeding and nursery roles for fish communities within the larger seascape (Nagelkerken *et al.* 2002; Dorenbosch *et al.* 2004; Unsworth *et al.* 2007). In the Lakshadweep islands, seagrass fisheries are an important means of subsistence to local fisher communities (Tamelander & Hoon 2008; Unsworth & Cullen 2010). Following sustained turtle herbivory, we have documented an escalating long-term conflict between fishers and green turtles in the islands (Lal *et al.* 2010), as ecosystem-wide effects of turtle herbivory are becoming increasingly apparent to local fishers. Such conflict poses serious challenges for local green turtle conservation given the flow-on impacts of green turtle grazing.

The resident high population densities of green turtles in the Lakshadweep islands provide a unique opportunity to examine top-down control on the functioning of seagrass meadows (Duffy 2002) under the influence of high megaherbivore densities, comparable to putative historical estimates (Jackson 1997, 2001). The now-common ecological narrative of shifted baselines due to human exploitation, assumes explicitly or implicitly, that so-called 'pristine' ecosystems with their full complement of unexploited species, functioned 'better' in the historical past than the increasingly depauperate systems of the present (Bjorndal & Jackson 2003). This admittedly normative assumption is seldom easy to test in the field, because extant conditions rarely allow us to reconstruct ecosystems with high megafaunal abundances. Our study suggests that seagrass meadows, with high densities of megaherbivores would be dominated by early successional seagrass species with long-lived species restricted to areas these herbivores could not access. Whether meadows in these islands can sustain heightened levels of herbivory is still an open question. In more natural past systems, megaherbivores were likely to also be strongly controlled by top predators such as tiger sharks, which may have dampened the effect of herbivory on seagrass meadows, both through direct control and behaviourally mediated indirect interactions (Heithaus *et al.* 2008). Without these controls in extant systems, locally high green turtle populations can have disproportionate impacts on the ecological functioning of seagrass meadows. Understanding these impacts may help us critically re-evaluate the ecological services that we could realistically expect from 'healthy' seagrass meadows both in the past and the present day.

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