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Habitat collapse due to overgrazing threatens turtle conservation in marine protected areas

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Marine protected areas (MPAs) are key tools for combatting the global over-exploitation of endangered species. The prevailing paradigm is that MPAs are beneficial in helping to restore ecosystems to more 'natural' conditions. However, MPAs may have unintended negative effects when increasing densities of protected species exert destructive effects on their habitat. Here, we report on severe seagrass degradation in a decade-old MPA where hyper-abundant green turtles adopted a previously undescribed below-ground foraging strategy. By digging for and consuming rhizomes and roots, turtles create abundant bare gaps, thereby enhancing erosion and reducing seagrass regrowth. A fully parametrized model reveals that the ecosystem is approaching a tipping point, where consumption overwhelms regrowth, which could potentially lead to complete collapse of the seagrass habitat. Seagrass recovery will not ensue unless turtle density is reduced to nearly zero, eliminating the MPA's value as a turtle reserve. Our results reveal an unrecognized, yet imminent threat to MPAs, as sea turtle densities are increasing at major nesting sites and the decline of seagrass habitat forces turtles to concentrate on the remaining meadows inside reserves. This emphasizes the need for policy and management approaches that consider the interactions of protected species with their habitat.

1. Introduction

The establishment of marine protected areas (MPAs) has become the main policy tool for the global protection and recovery of marine habitats and species [1,2], including charismatic species such as sea turtles [3], dolphins and whales [4,5]. By setting up MPAs, protection schemes aim to reduce direct (e.g. fisheries) or indirect (e.g. turtle egg harvesting, fisheries by-catch) forms of human exploitation. As a consequence, MPAs can become 'islands of protection' [2], in which high densities of iconic target species can accumulate, eventually enabling restocking of surrounding areas [6]. It is generally assumed, albeit implicitly, that MPAs will allow sustainable population development of the target organisms as long as protection is successful and that greater animal numbers characterize more 'successful' policies [7]. However, a number of studies highlight that this might not always be true [2,7,8]. Protection [7] of threatened animal species in a number of terrestrial reserves has resulted in accumulation and hyper-abundance of protected species exceeding historic numbers prior to human exploitation, especially inside relatively small reserves [9,10]. The resulting changes in ecological interactions can have severe and undesirable impacts on the (protected) habitat [11]. The indirect effects of increased population density for the habitat on which it relies, found globally in a number of MPAs [12,13], are only rarely considered in conservation policies.

2. Empirical evidence of habitat degradation from marine protected areas

Here, we report on the degradation of seagrass habitat as a consequence of hyper-abundance of an iconic marine species, the green sea turtle *Chelonia mydas*, inside a decade-old Indonesian MPA where turtles are fully protected. Over a 4-year period, we observed an increasing number of turtles (figure 1*a*; $p = 0.01$), especially of the juvenile-size class (see electronic supplementary material, figure S1), up to 20 individuals per hectare observed in 2011 (figure 1*a*). This is the highest density ever reported globally [14–17], even exceeding estimates of population densities prior to human hunting reported for the Caribbean [18]. As green turtles are long-lived and late-reproducing organisms, and hatchlings often do not stay near the nesting grounds where they hatched [19], this sudden increase may be explained by increased immigration rather than by increased reproduction rates. A control-impact study in which three MPAs and three independent control areas throughout the Indo-Pacific were surveyed shows that the turtle densities found inside these MPAs were at least four times the density of the independent control areas (table 1). Combined, these temporal and spatial comparisons point to a dramatic increase in green turtle density in our study MPA.

Seagrass meadows have been the green turtle's primary habitat and food source [20] for possibly as long as 50 Myr [21,22]. However, the emerging hyper-abundance of green turtles within our focal MPA severely impacted the seagrass meadow. Beyond removing 100% of the daily seagrass leaf production [17], turtles applied a previously undescribed feeding strategy—to dig for rhizomes and roots with their flippers (figure 2*a*; electronic supplementary material, video S1). This has led to a striking mosaic of unvegetated gaps in the seagrass meadows (figure 2*b*,*c*). The intensity of the digging strategy has increased over time, as shown by the trend in the cover of bare gaps (figure 1*a*; $p = 0.04$). Moreover, in 8 years, there has been a 64% reduction in the average below-ground biomass outside gaps, relative to the below-ground biomass at MPA establishment (figure 1*b*; $p < 0.01$). In addition to creating gaps in the vegetation, digging has led to enhanced erosion, as demonstrated by experimental gap clearings (for experimental set-up, see the electronic supplementary material, figure S2). Erosion of seagrass strips between experimental gaps increased significantly with decreasing strip width (figure 3*a*), and, as a consequence, seagrass regrowth declined with seagrass strip width (figure 3*b*). Hence, there is clear experimental and observational evidence that intense turtle grazing causes severe and ongoing degradation of the seagrass bed.

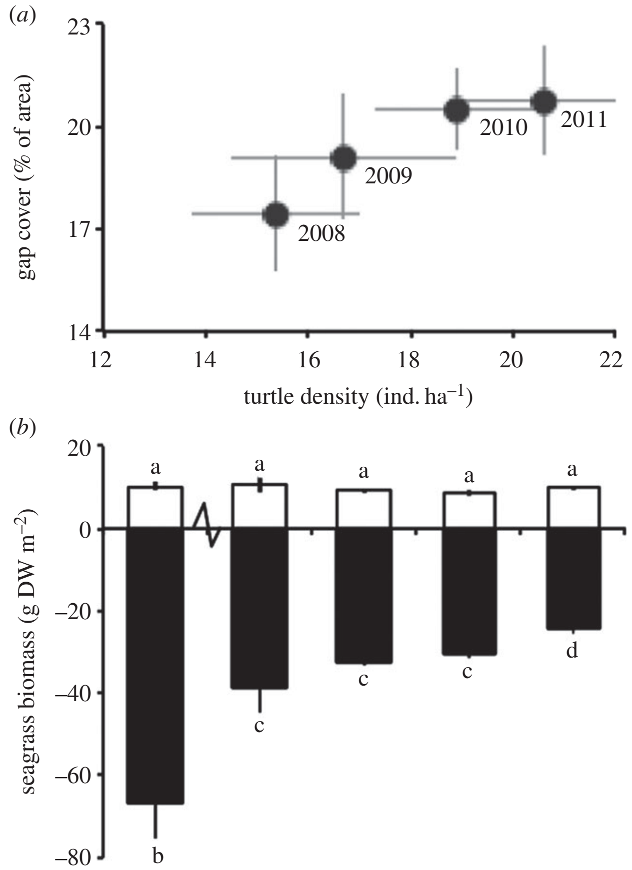

Figure 1. (*a*) Positive relation between green turtle density and the gap coverage in 2008–2011 in seagrass fields around Derawan Island, Indonesia ($p = 0.04$). We counted the highest turtle density ever reported globally, exceeding 20 individuals per hectare in 2011 (± 0.9; 15.4 turtles ha^{-1} in 2008 and 20.6 turtles ha^{-1} in 2011). Turtle density ($p = 0.01$) and seagrass gap cover ($p = 0.04$) increased significantly over time. On average, the gaps covered an area of 19.4% (± 0.8; 17.5% in 2008 and 20.8% in 2011) of the surface area of the seagrass meadow. (*b*) Above-ground (unfilled portion) and below-ground (filled portion) biomass of intensively grazed seagrass (*H. uninervis*) in 2003 (before MPA establishment) and 2008–2011 (after MPA establishment). Over a period of 8 years, below-ground biomass significantly decreased to less than 50% after the establishment of the MPA in 2005, from 67 g DW m^{-2} in 2003 to 24 g DW m^{-2} in 2011 ($p < 0.001$), which suggests a shift from the common leaf-grazing strategy towards the alternative digging strategy. Letters indicate significantly different groups as revealed by *post hoc* tests. Between 2003 and 2011, above-ground biomass remained low but stable ($p > 0.05$), averaging 9.3 g DW m^{-2}.

3. Modelling the balance between grazing and recovery

We investigated the implications of the interaction between increasing turtle densities, below-ground foraging and subsequent erosion for the future persistence of the seagrass bed, and hence for the functioning of the MPA. To this end, we compared two fully parametrized mathematical models using our experiments and observations (for full details and parameters, see the electronic supplementary material, text S2 and table S2). The models represent the balance between grazing and regrowth of seagrass in the MPA, either excluding (model 1) or including (model 2) below-ground grazing. The models follow the general differential equation: $dB/dt = G(B) - F(B - B_b)H$, where $G(B)$ and $F(B - B_b)$ describe logistic

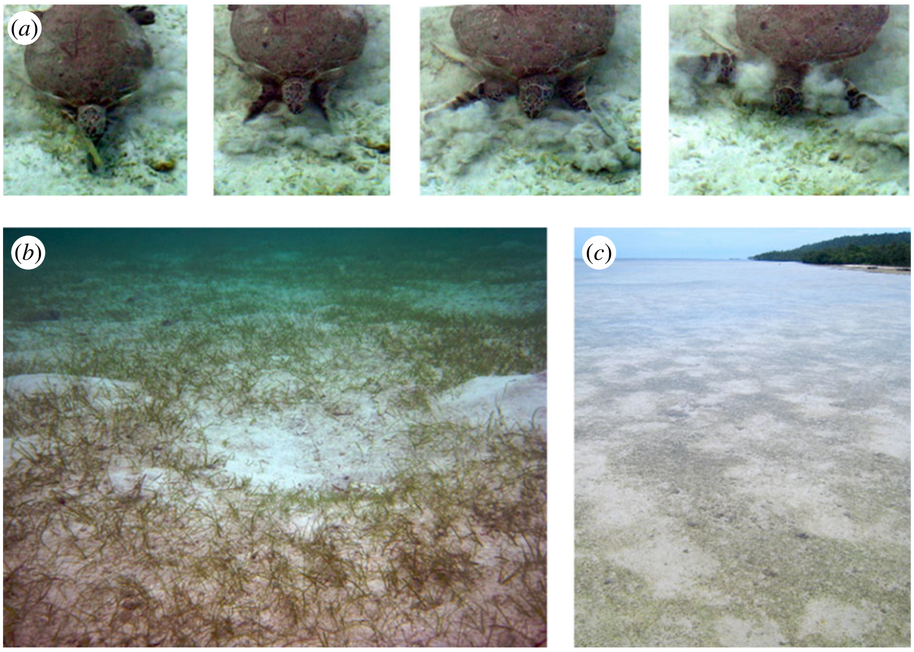

Figure 2. (*a*) Stills from a video (see electronic supplementary material) of a green turtle (*C. mydas*) showing the newly described foraging strategy 'digging', in which the turtle excavates sediment with its front flippers to access below-ground parts of seagrass (*H. uninervis*). (*b*) A typical grazing gap consisting of bare sand enclosed by two sediment bulges created by the flippers. From this gap, 96% of above-ground and 88% of below-ground biomass is removed on average. (*c*) Striking mosaic of gaps in the seagrass meadow generated by green turtles that use the alternative foraging strategy, where spots in the mosaic represent the unvegetated gaps resulting from green turtle digging. Photos by M.J.A.C. and L.P.M.L. (Online version in colour.)

Table 1. A regional survey comparing green turtle density, gap observations and fishermen's perceptions of the trend in turtle and seagrass change inside and outside of MPAs of the Indo-Pacific suggests a higher turtle density on seagrass meadows inside the MPAs compared with control areas ($p = 0.024$, t-test one-tailed, equal variances not assumed, Levene's 0.043). I, Indonesia; M, Malaysia.

	turtle density ind. ha^{-1} $\pm$ s.e.	trend turtles	trend seagrass	gaps obs.	location	latitude	longitude
in MPA	21 ± 1.6	↑	↓	Y	Derawan (I)	2°17′11.31″ N	118°14′50.98″ E
	20 ± 1.8	↑	↓	Y	Balikukup (I)	1°32.12.54″ N	118°36.11.42″ E
	18 ± 1.4	n.a.	n.a.	Y	Sipadan (M)	4°06′39.78″ N	118°37′50.72″ E
out MPA	12 ± 1.7	n.a.	n.a.	N	Pandanan (M)	4°34′31.38″ N	118°55′03.71″ E
	1 ± 0.3	↓	=	N	Batanta (I)	0°48′17.88″ S	130°420′4.05″ E
	0 ± 0.2	↓	=	N	Barang Lompo (I)	5°00′48.72″ S	119°19′34.44″ E

growth of seagrass (see electronic supplementary material, text S2), and a linear feeding rate per herbivore as a function of seagrass biomass B and an ungrazable below-ground reserve B_b (figure 4*a*,*c*), respectively. We consider an ungrazable, below-ground reserve in model 1 only, having $B_b = 0$ in model 2, as grazing also affects below-ground biomass in this model. Model 2 introduces a reduction of seagrass growth at low biomass in function $G(B)$ (see electronic supplementary material, figure S4). Here, reduced seagrass cover causes gap formation, generating patches in various stages of recovery. We integrate the regrowth over these stages and multiply the resulting production with a subsequent erosion term to yield the degree to which gap formation is limiting (but not eliminating) seagrass regrowth. In both models, we assume that the turtle population dynamics is disconnected from that of the seagrass owing to the concentration effect of the MPA, which is supported by our observations (table 1). By comparing these two models, we assessed the potential effects of below-ground foraging on the future development of the seagrass bed.

4. Habitat collapse under currently increasing grazer densities

Our model analyses reveal that below-ground grazing significantly decreases the resilience of seagrass ecosystems to increasing turtle density. With only above-ground grazing (model 1), the interaction between turtles and seagrass is stable, as seagrass collapse is prevented by continued regeneration from its below-ground biomass (roots and rhizomes), counteracting above-ground losses owing to consumption (figure 4*c*). This result is in close agreement with empirical evidence found in the literature [23]. However, when below-ground grazing and subsequent erosion are also included (model 2), the dynamics change fundamentally. At low seagrass biomass, the 'digging' strategy triggers erosion and depresses seagrass regrowth, which then cannot compensate for turtle consumption (figure 4*d*). As a consequence, a threshold occurs at high turtle densities, beyond which vegetation collapses to an erosion-driven regime

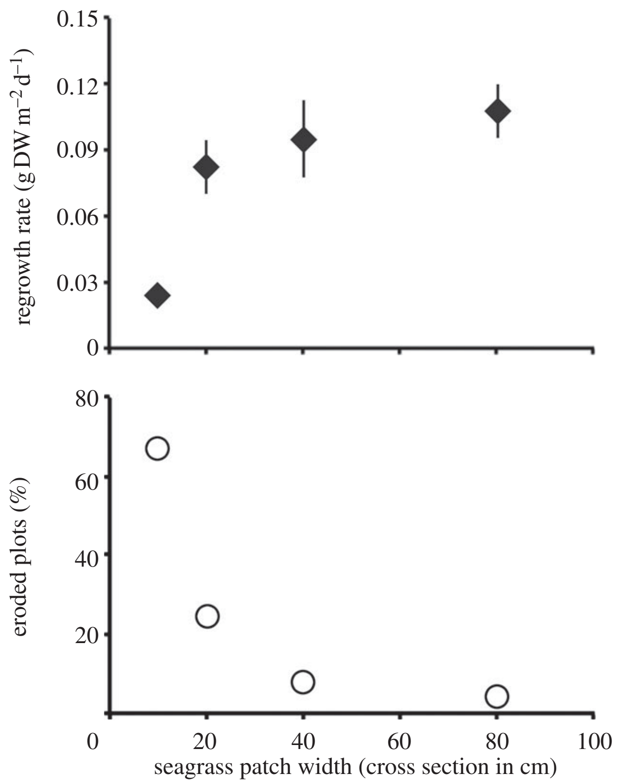

Figure 3. Effect of increasing gap distance as a proxy for increasing grazing pressure by digging on (*a*) seagrass regrowth rates and (*b*) erosion of seagrass plots in a field experiment (84 days). (*a*) Seagrass regrowth rates show a stronger decline with decreasing seagrass strip width. Regrowth of 10 cm strips was significantly lower ($p < 0.01$) than that of strips of 20, 40 and 80 cm width, for all plant parts. (*b*) The proportion of seagrass strips that had been eroded at the end of the experiment.

without seagrass (figure 4*d*). Moreover, despite conservative parametrization of the erosion function in the model, our model analysis prediction highlights that turtle numbers have to be decreased to nearly zero for seagrass to recover, rendering the MPA ineffective as a tool for the protection of green turtles.

5. Discussion

Our results have important implications for marine conservation policies. Marine protection schemes that do not fully consider the effects of increased densities of target species on habitat integrity may well overestimate the long-term effectiveness of the reserve in providing a sustainable habitat and food source for the target species. Using a combination of experimental and modelling approaches, our study provides a clear example of the unintended consequences of MPAs, strengthening earlier concerns regarding the functioning of MPAs [8]. Increasing abundance of green turtles, observed in a number of seagrass beds worldwide [13,16], has resulted in overconsumption of seagrass meadows in our study area. If this increase in densities continues, our model analysis predicts severe degradation and points to the principal danger of collapse of the seagrass habitat within 5–10 years. Our results undermine current policies for the protection of green turtles; ultimately, MPA policies may suffer from their own success, especially when protection leads to hyperconcentrations of turtles or other target species.

6. Hyperconcentration of grazers in marine protected areas

An important attribute of MPAs is the ability to act as a source of juvenile or adult individuals that spill over to the surrounding areas or migrate to alternative feeding grounds [24], especially when local population numbers approach the carrying capacity of the habitat. Our results, however, show that despite deterioration of the food supply, turtles continue to concentrate in the protected area, rather than using it as a stronghold for expansion into neighbouring areas. Although green turtles used to be very abundant before human hunting began (up to 300 times more abundant in the Caribbean [18]), the recently reported consumption rates at our study site are more than twice the historic levels (100% versus 45%). The observed hyper-abundance of turtles in this study is likely to be the result of three interacting processes. First, a chronic decline of seagrass habitat has occurred in non-reserve areas around this MPA, probably because of high sedimentation rates, turbidity, eutrophication and mechanical disturbance [25]. The decline in seagrass habitat is a global phenomenon [26] and can be expected to cause increased turtle abundance in remaining habitats. Second, large sharks, predators of green turtles, have dramatically declined worldwide [27], which could facilitate turtle population increase. Third, turtle foraging is highly sensitive to predation risk [27]. If the fishing intensity outside reserve boundaries is high, which is the case for this reserve (by humans; M.J.A.C. 2010, personal observation), turtles do not leave the shelter offered by the reserves. These processes combined probably explain the sustained hyper-abundance of turtles and the observed below-ground feeding strategy, which has not been reported outside of reserves. MPA-based population enhancement is further strengthened by the natural history (migration and reproduction rates) of green turtles as small MPAs often include not only nesting beaches but also seagrass-covered shallow areas in front of nesting beaches that are used by turtles during the largest part of their lives.

7. Global recovery of turtle population sizes

Although in many parts of the world green turtles remain highly threatened, recent efforts to protect major nesting beaches, tightened hunting restrictions and additional conservation measures have been very successful in many areas [12], including MPAs [28]. As a result, green turtle populations of major nesting beaches around the world have been increasing at 4–14% per year over the past two to three decades [12]. Moreover, seagrass fields have been declining worldwide at a fast rate as a result of anthropogenic forcing [26], both inside and outside MPAs. Both changes in concert will lead to a strong and rapid decrease in the per capita availability of suitable foraging area. The effects of hyperdensities of green turtles have already resulted in substantial alterations in ecosystem functioning in a number of regions including the Bahamas [13], Lakshadweep Archipelago, India [16] and Azumal, Mexico [29]. Although the above-mentioned locations are unique in their high turtle densities to date, the combination of our results and the finding that turtles aggregate inside MPAs worldwide [30] reveal the unrecognized, yet imminent threat of habitat degradation that many MPAs globally may be facing.

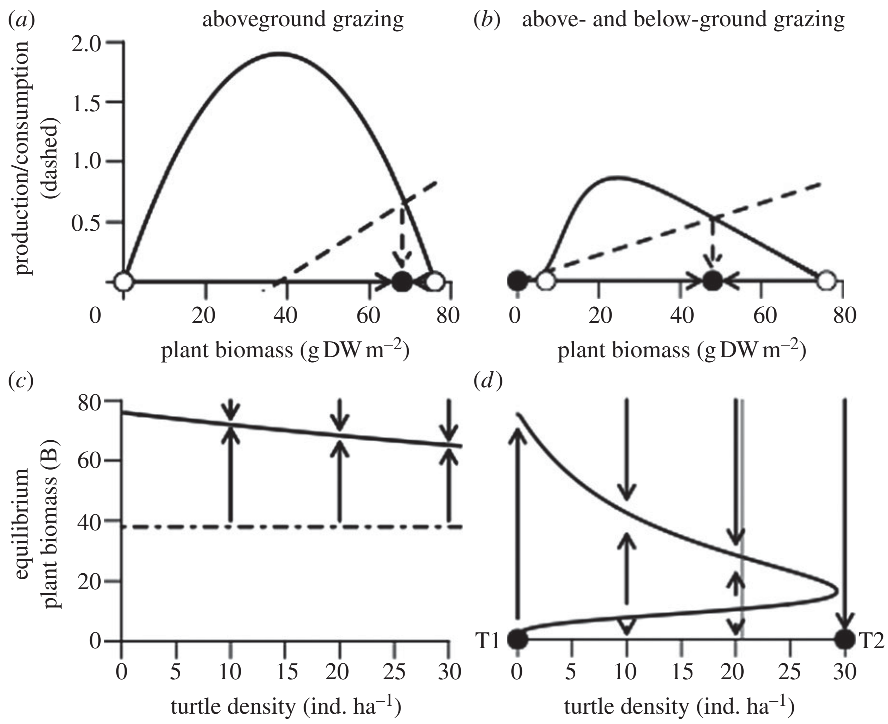

Figure 4. Graphical comparison of two fully parametrized models describing the balance between green turtle grazing and seagrass regrowth, and its implications for the response of seagrass to increased turtle density and grazing strategy. (*a*,*c*) Model 1 describes classical above-ground grazing with an ungrazable below-ground reserve, revealing a very stable interaction between turtles and seagrass. When seagrass biomass is below the stable equilibrium biomass (closed black circle), seagrass regrowth (*a*; solid line) always exceeds turtle grazing (*a*; dashed line), and as a consequence there is a gradual decrease in seagrass biomass with increased turtle density until all above-ground biomass has disappeared (*c*) and only the ungrazable reserve remains (*c*; dashed line). As a result of the remaining below-ground reserve, seagrass biomass can easily recover with a small decrease in turtle density. (*b*,*d*) The second model includes below-ground grazing ('digging') and the effects of reduced cover in gaps and subsequent erosion on seagrass regrowth. Here, increased erosion at low seagrass density (figure 3) depresses the potential regrowth of seagrass biomass (*b*; solid line), and hence at low seagrass biomass, consumption (*b*; dashed line) can overwhelm seagrass regrowth, left of the unstable equilibrium (*b*; open circle). As a consequence, the relation between equilibrium seagrass biomass and turtle grazing becomes folded (*d*), and beyond a threshold grazing intensity, T2, no seagrass can persist and collapse is inevitable. The grey line depicts the current turtle density. The turtle biomass needs to be reduced to levels close to zero (T1) for the seagrass to recover.

8. Optimal design of effective reserves

Our findings point out that conservation policies should match efforts of protecting endangered turtles with equal efforts of protecting their foraging habitats, both inside and outside the protected areas. Offering sufficient alternative foraging opportunities to the turtles may prevent concentration and hyper-abundance of turtles inside MPAs. Only then are MPAs more likely to act as a source of turtles that spill to surrounding foraging areas, instead of being mere sinks. To accomplish this, management measures could minimize seagrass habitat loss in the locality of the reserve, for instance through improved river catchment management [31] to reduce run-off and erosion in the coastal area. Alternatively, turtle hyper-abundance can be countered by integrating MPAs into networks of reserves. These networks can prevent overexploitation and habitat collapse by stimulating migration to other areas, thereby compensating for limited resource availability at the local scale, as was found in terrestrial systems [32]. Moreover, the protection of natural predators in larger protected areas may prevent hyper-abundance and disperse turtles over larger areas. Most importantly, however, our study emphasizes that the conservation of marine endangered species requires not only their direct protection, but also in-depth scientific understanding of the interactions and feedbacks with their supporting habitat and the food web that it harbours, both locally and regionally.

9. Material and methods

(a) Site description

Experiments and monitoring were carried out at a shallow, subtidal mono-specific (*Halodule uninervis*) seagrass meadow along Derawan Island, 16 km from the coast of East Kalimantan, in Indonesia, Indo-Pacific ocean (2°17′19″ N, 118°14′53″ E; for a map and further discription, see [17]). Green turtle nesting beaches were actively protected around Derawan from 2002 onward, and the Derawan archipelago that includes Derawan Island was given MPA status in 2005, covering a surface area of 1.2 million hectares.

(b) Green turtle density

The green turtle density on seagrass meadows was followed over a 4-year period (2008–2011; $n = 65$; figure 1*a*). Turtles were counted during visual surveys from a boat along random line transects, within 10 m of each side of the front of the boat [16] at a maximum speed of 7 km h^{-1}. Transect lengths were determined using GPS (6–22 transects yr^{-1} between August and November). The detectability was high as the water was clear and shallow (less than 3 m), and turtles were counted only on days with calm weather conditions. Turtles were observed to forage almost exclusively on seagrass biomass [25] and grazed year round at our field site at constant densities, as shown by extra monthly assessments of densities throughout 2009.

(c) Size–frequency distribution

Green turtles were captured on the seagrass meadow using the rodeo method [29] in December 2009 ($n = 116$) and December 2011 ($n = 141$). Once captured, turtles were tagged with a unique numbered Inconel tag to prevent double sampling. The carapace length was measured along the midline from the junction of the skin and carapace at the neck to the posterior margin of the carapace [33] (for size–frequency distribution, see the electronic supplementary material, figure S1)

(d) Gap cover and gap initiating mechanism

Gap cover in the seagrass meadow was determined in fixed transects of 50×10 m ($n = 3$) by measuring length and width of gaps using 5 cm size classes from a minimum gap size of 20 cm. The gap cover was measured for 4 consequtive years (2008–2011) between August and November (figure 1*a*), and extra monthly assessment of gap cover between August and November of 2009 did not show any change of gap cover. To measure grazing rate, gap initiation was followed daily, and gap edges were marked using small sticks to be able to identify old gaps and measure new grazing at edges of existing gaps. Turtles alone were responsible for the observed gaps as no gaps were initiated in seagrass meadows under turtle exclosures (5 cm mesh, 2 m^2) that were surveyed for three months ($n = 20$).

(e) Long-term seagrass biomass

To assess long-term impacts of intense turtle grazing on standing biomass, seagrass biomass data were collected for 5 years (2003 and 2008–2011) between August and November ($n = 128$). Seagrass biomass samples were taken using corers (diameter 23 cm) outside gaps, within 100 m of transects where gaps were monitored. Seagrasses were cleaned from epiphytes and divided into above-ground and below-ground parts, and dry weights were determined after drying for 48 h at 60°C (figure 1*b*).

(f) Field experiment: analysis erosion mechanism

Experimental gap clearings were used to test whether increased digging of turtles could hinder seagrass recovery and regrowth by initiating focal points for erosion of apical rhizomes. We measured the seagrass regrowth and erosion probability of seagrass strips between gaps under increasing 'digging' intensities, and hence decreasing gap distance. To this end, we created artificial gaps that border seagrass strips of four different widths ($n = 5$; for experimental scheme, see the electronic supplementary material, figure S2). Each experimental unit consisted of a strip of seagrass (length 50 cm, width 10, 20, 40 or 80 cm) bordered by two gaps of bare sand (50×50 cm; for experimental set-up, see the electronic supplementary material, figure S2). To exclude green turtle grazing, experimental units were located within a large cage ($l \times w \times h$: $15 \times 10 \times 3.5$ m), made of fishing net (2.5 cm mesh), on a subtidal seagrass meadow. As a measure for regrowth, after 84 days, we harvested seagrass that had expanded clonally into a 30×30 cm area adjacent to the strip–gap border (see electronic supplementary material, figure S2) that was selected to exclude possible edge effects. Erosion of the seagrass strips was estimated as the percentage of area loss using a measurement frame that was placed on top of the strip, and a reference picture of the strip at the start of the experiment.

(g) Control-impact survey: green turtle densities and gap cover within and outside of marine reserves

To measure whether the protection by MPA affects green turtle densities, we performed a regional survey of turtle density between three MPAs and three independent control areas using line transects. Sites were selected based on historical evidence of green turtle presence, and comparable subtidal reef-top seagrass meadows that were spread throughout the Indo-Pacific within 1400 km. In addition, we used a historical survey of islanders' knowledge by interviewing a minimum of 10 persons older than 50 years per location. First, we asked them to identify the green turtle image from a collection of images of different species of sea turtles, and likewise to identify seagrass from pictures of different macroalgae and seagrasses. Next, we asked them to estimate the change in green turtle and seagrass density during recent decades, and asked whether green turtles were currently harvested. From these results, we extracted information on turtle harvesting and average perception of change of turtle and seagrass density. Furthermore, we estimated gap cover at all sites following the methods described above. Typical turtle gaps (figure 2) were observed in foraging grounds inside MPAs but not outside of reserves.

(h) Statistical analysis

One-way ANOVAs were used to analyse changes in turtle density and biomass between years and to analyse the effects of increasing grazing intensity (decreasing seagrass strip width) on seagrass biomass regrowth and erosion probability (figure 3). We evaluated the differences in seagrass biomass between years and the differences in regrowth and erosion between seagrass widths using pairwise *t*-tests with a Hochberg adjustment to control for false discovery rates with unequal sample sizes. Data were log-transformed when necessary to meet assumptions of the tests. We used linear regression to test the relation between gap cover and turtle density. Differences with $p < 0.05$ were considered significant. R (v. 2.11.1, January 2012) was used for all analyses.

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Data accessibility. Full description, parameters and derivations of the model, and supplementary figures and movies, are available in the electronic supplementary material. The data are deposited in DRYAD at http://doi.org/10.5061/dryad.jh58p.

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