Consequences of green turtle herbivory on seagrass meadow dynamics, fish communities and subsistence fishing in the Lakshadweep Islands, India

RSG 41.08.09: Baselines of fish habitat use, recruitment and abundance across differentially grazed seagrass meadows and adjacent non-seagrass habitats of the Lakshadweep islands, India

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by


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**Project Summary**

Green turtles *Chelonia mydas*, although globally endangered, attain exceptionally high densities in the Lakshadweep coral atolls of the Indian Ocean, where they congregate for feeding on seagrasses in shallow lagoons. The herbivorous green turtles are thought to be important ecosystem modifiers of seagrass meadows. Recent studies estimated that the impact of sustained herbivory by green turtles in seagrass meadows in the Agatti lagoon, Lakshadweep Islands was highly significant, and led to declines in abundance, biomass, growth-rates and changes in species composition of seagrasses.

Lagoon fishing in the seagrass meadows is an important activity for the Lakshadweep islanders depend on lagoon fish catch as a means of subsistence. However, lagoon fishers of the Agatti Island have been in conflict with turtles, and perceive that fish catches have declines over the years due to direct and indirect interactions with turtles. Direct interactions involve breakage of nets and gear by swimming turtles, and the driving away of fish schools by approaching turtles. Interestingly, fishers also perceive that the loss in fish catches is due to the turtles overgrazing seagrass, thereby leading to loss of habitat for fish species (indirect interactions). In this study we validate these perceptions by estimating ecological impacts of turtle herbivory on seagrasses, and therefore, to fish communities using seagrass meadows, along a gradient of turtle herbivory involving 3 different lagoons. We use a combination of observational (turtle surveys, seagrass measurements and visual fish transects) and experimental studies (simulated herbivory by clipping, exclosure experiments).
We found that turtles negatively influenced abundance, biomass, juvenile usage and recruitment, species diversity, richness, size-structure and trophic complexity of fish communities using seagrass meadows, through reduction of seagrass canopy height, shoot density (both proxies for seagrass meadow structural complexity) and biomass production through sustained herbivory. We thus found strong empirical support for fishers’ perceptions, and that turtles through their ‘ecosystem engineering’ of seagrass meadows could be important agents of change and conflict. We demonstrate through this study, that for a better understanding and appreciation of conflict, empirical verification of ecological mechanisms elicited from perceptions (lived experience of communities) is an important step. Understanding the long-term impacts of green turtle herbivory on ecosystem services of seagrass meadows and productivity of fisheries can help identify potential solution for coexistence of turtles with fishers in shared spaces.
Introduction

In an increasingly human-dominated world, conflict between humans and wildlife over shared spaces and shared resources, is one of the major challenges to conservation today (Woodroffe et al. 2005; Messmer 2009). Ecological needs of wild species often overlap with human economic activity, and the resulting negative interactions pose problems to both entities. Conflict management and mitigation strategies, often therefore, find themselves in the tough situation of walking the tightrope of reconciling these competing needs (Thirgood et al. 2005; Woodroffe et al. 2005). Any skew in such a balance upsets sharing equations, and erodes public support for conserving wildlife to a large extent, resulting usually in adverse consequences for wild species. In some situations, wildlife conservation and management cannot adequately address human losses incurred on account of ecological needs of wild species, further leading to discontent and loss of goodwill for conservation (McCoy 2003). A complete conceptual understanding of conflict itself becomes necessary therefore to contextualize these losses and changes caused by conflict situations (Manfredo and Dayer 2004, White et al. 2009).

Understanding causes of conflict involves understanding both ecological mechanisms causing conflict and a consideration of the interplay of human perceptions and attitudes about conflict (Dickman 2010). The mechanisms of conflict may themselves be not well-known, owing to the restricted sphere in which ecological investigations mostly take place, that point to the presence and magnitude of conflict, but usually not the underlying processes. Also, human perceptions generating responses that precipitate conflict are often ignored or treated as subjective, intangible and impossible to be measured (Marshall et al.
Human-wildlife conflict is usually direct, with the species involved easily identifiable, and therefore easily targeted and achievable solutions. For instance, a herd of antelope raiding a crop field, or wild carnivores killing livestock, or dolphins negatively affecting tuna catch, are examples of direct conflict where the agents of conflict are identifiable, and the quantification of their impact relatively straightforward. Strategies to mitigate such direct conflict are usually reactive, and involve compensation schemes for economic losses, or in other cases, culling or driving away wild species that cause losses (Treves & Karanth 2003; Sillero-Zubiri et al. 2006).

Green turtles were occasionally killed by angry fishermen in Agatti when numbers were at their peak. Photo: Rohan Arthur.
Often conflict may be driven by highly complex and indirect social and ecological mechanisms, with the real agent of conflict often unidentified, and the historical origins of conflict unknown. However, mechanisms explaining the origins of conflict might be hidden in human perceptions of the lived experience of conflict (Kretser et al. 2009). Thus, a detailed understanding of conflict perceptions can help identify and validate ecological relationships leading to conflict.

The behaviour and ecology of wild species provides us with explanations for the occurrence of these species’ activities conflicting with human production systems. Species with large home ranges, aggressive predators, species occurring in large groups are more likely to cause conflict than those with other traits. Species that are ‘ecosystem engineers’ (Jones 1994) may potentially cause interactions with human activity through indirect mechanisms. Such conflict may be crucial to the conservation of these species that play important functional roles in their ecosystems.

In the Lakshadweep Islands, exceptionally high densities of endangered green turtles *Chelonia mydas* (Seminoff 2002) were recorded between the years 1995 and 2000 (Tripathy et al. 2002, 2007; personal communication with fishers) from the Agatti lagoon. Lagoon fishing is an important subsistence activity for the islanders who depend on the seagrass meadows and associated habitats for their daily household-scale catch, and for small baitfish used in commercial fisheries of skipjack tuna, the main occupation of island fishers (Hoon 2003; Arthur 2005; Tamelander & Hoon 2008). In 2005, fishers of Agatti strongly perceived turtles in their lagoon as the main cause for declines in lagoon fish catch. Fishers felt that the huge increases in turtle numbers were due to the ban on turtle hunting enforced in the islands (Arthur...
et al. In Prep.). At first glance, this perception of ‘a herbivorous species reducing fish catch’ seems absurd and may lead us to think that turtles are being made a mere scapegoat for declines in fish catch, that may occur due to other reasons (overfishing, oceanographic changes etc.).

Direct interactions with turtles were dominant in fishers’ perceptions and reasoning about declining catch. These included breakage of nets and gear, and turtle presence driving away schooling fishes and bait-fishes in the lagoon. However, interview surveys conducted by NCF in 2005 and 2007 yielded further detailed insights beyond these economic losses attributable to turtles directly. Fisher perceptions that claimed turtles to be causing declines in fish catch were based on ecological knowledge and experience that revealed complex mechanisms fishers described: they explained that turtles had reduced seagrass leading to loss of potential sites for adult and juvenile fishes, and even recruits (Arthur et al. 2010, manuscript in prep.). In a detailed recent study, the negative impacts of turtle herbivory on seagrass growth rates, age-structure, abundance, production, and community composition were estimated (Lal et al. 2010). The need to look at seagrass meadows as not just pastures for green turtles, but as ecosystems supporting a wide range of species themselves, becomes necessary in addressing and understanding this conflict situation (Lal et al. 2010).

This project is a continuation of this previous research. The real reason for conflict was due to the alleged decline of fishes, and not seagrass decline (not of any direct value to fishers). But the effects on fish communities using these seagrass beds were not known. Green turtles are known to be important modifiers of seagrass meadow dynamics, and if their impacts affect fish species inhabiting
seagrasses, conflict will become a serious threat in habitats shared with fishers. In general, little is known as to whether impacts of herbivory by ecosystem modifier megaherbivores cascade down to faunal communities using grazing ecosystems (but see Pringle et al. 2007). Effects on fish and benthic invertebrate communities have been suggested (Bjorndal 1980; Nakaoka 2005); and obvious though these effects seem, little empirical proof of their presence and magnitude exists.


Therefore, in this study, we investigate the effects of herbivory by green turtles (across a density gradient) on seagrass meadows and associated fish fauna. In particular, we 1) tested the magnitude and significance of herbivory in altering seagrass ecosystem dynamics, 2) estimated effects of herbivory-related loss of seagrass structure on fish communities, and 3) validated local fishers’ perceptions suggesting the existence of indirect fisher-turtle conflict in the Lakshadweep Islands.
We conducted field sampling across a turtle density gradient in the Agatti, Kavaratti and Kadmat lagoons and tested with experimental and observational studies the effects of the differential pressure of turtle herbivory in these sites. We conclude by discussing our results in relation to conservation of and conflict between green turtles and fishers using available information on turtle ecology and conservation efforts and the ecology of fisheries in the Lakshadweep islands.

The Lakshadweep islands are a collection of tiny coral atolls. Photo: Nachiket Kelkar.

Methods

Study Area

The Lakshadweep Archipelago in the Arabian Sea, Indian Ocean, forms the smallest Union Territory of India, comprising of 36 tiny islands (11 inhabited) and submerged banks, covering a total area of 32 km². The islands are very low-lying and
occur at the northern end of the Laccadive-Chagos submarine ridge. These islands occur between 8°N to 12°N and 71°E to 74°E, and are of the most densely populated rural regions of India (population density over 2500/km²; Singh et al. 1993). These coral islands are inhabited by Moplahs from the Malabar region (Kozhikode to Mangalore) in Kerala and Karnataka states, India, with the exception of Minicoy Island where the people are Mahl (Maldivian). All people are followers of Islam. Fishing of skipjack tuna (major commercial catch), and coconut production are the main occupations of the islanders. Many islands have shallow lagoons adjacent to the land, with the coral reefs encircling the atolls. Islanders use seagrass meadows, sandy beds and patch reefs in the lagoons for artisanal subsistence fishing and for bait-fishing for catching tuna (Arthur 2005; Tamelander & Hoon 2008). The lagoons are mostly shallow (2-5 m) and dominated by sand, seagrass beds with a few coral patches. They are an important area for subsistence fishers, especially in the monsoon season, when the stormy weather and currents prevent tuna fishing (Shankar et al. 2002). The seagrass meadows are dominated by Cymodocea rotundata and Thallasia hemprichii, but a total of seven seagrass species have been recorded (Jagtap 1991, 1998). This study was conducted in the Agatti, Kavaratti and Kadmat lagoons (Fig.1) that were highly similar in depth profile, sediment influx, fisher densities, and fishing intensity relative to area.
Bait-fishing from the lagoons for sprat and silversides is an important activity as they are used in catching skipjack tuna, the mainstay of commercial fisheries in the islands. Photo: Nachiket Kelkar.

Data collection

The study was conducted from December 2009 to December 2010. Fieldwork was not possible due to the southwestern monsoons that affect the island weather between June and October. We adopted a hierarchical study design (Fig.1) to estimate impacts of turtle grazing on fish communities. In addition, we looked at the relative importance of seagrass meadows for fish species diversity in comparison with other lagoon habitats (sandy bottoms, rubble beds). We also used natural and artificial experiments to verify the ecological processes leading to observed patterns.

Our methodology included the following: 1. Boat-based surveys to estimate density and distribution of green turtles inside the lagoons, 2. Measuring impacts of turtle herbivory on primary production, community composition, growth rate and
structural complexity of seagrass meadows, and 3. Estimating fish abundance, biomass, species richness, diversity in and recruitment / juvenile and adult fish usage of the seagrass meadows, in relation to seagrass meadow structure, and 4. Interview surveys to compare knowledge and perceptions about conflict with turtles, across the three islands. Drawing from previous information available about turtle-fisher conflict from interviews with fishers in Agatti (conducted in 2005), we attempted to characterize perceptions of conflict in the other two islands, differing only with respect to turtle density and grazing impacts. Results obtained from our ecological studies were used to test the validity of the perceptions.

Fig.1. Schematic diagram representing hierarchical design of study and variables recorded across different levels.

Turtle surveys

Boat-based visual surveys of green turtles were carried out in the lagoons of Kadmat, Kavaratti and Agatti. The visibility in the lagoons was usually high (upto 20m) and surveys were conducted only when sighting conditions were excellent. Two observers surveyed a grid with points separated by 300 m x 300 m from each other in the lagoon, tracking with a GPS at a constant boat speed of 8 km. h⁻¹ and
counting turtles in a 10 m belt along transects between these points. Abundance of turtles counted between two points was assigned to the next point on the grid. Grids of Kadmat, Kavaratti and Agatti lagoons had 232, 69 and 173 points respectively. Three replicate surveys each were conducted in the three lagoons to get estimates of turtle densities across seasons. Also, at each grid point, proportions of different benthic cover types were estimated visually with the categories seagrass, sand, rubble, and coral heads. Species of seagrasses were also identified and recorded. Extents of distribution of different benthic habitats were calculated from these points. Turtle distribution was overlaid on seagrass distribution to obtain a measure of spatial correspondence between turtle and seagrass distribution in the three lagoons. Densities of turtles were obtained both per sq.km of lagoon and per sq. km of seagrass meadows. The surveys were conducted in this way so that estimates could be comparable to previous estimates obtained using the same method (Arthur and Madhusudan, unpublished data; Lal et al. 2010).

Lush seagrass meadows at Kadmat exposed at low tide. Photo: Rohan Arthur.
Impacts of green turtle herbivory on seagrass meadow characteristics

The turtle density gradient estimated from the surveys across overlapped the seagrass meadows in the north, central and south areas of all lagoons. Seagrass meadow characteristics and attributes were measured along the turtle density gradient. These included measurement of structural complexity of seagrass meadow, viz. shoot density (shoots/m²) and canopy height (cm). We also noted species composition of meadows, and measured the primary production of seagrasses in terms of cm growth.shoot⁻¹.day⁻¹, as described in Duarte et al. (1994), Short & Duarte (2001) and Prado et al. (2008). Lengths of shoots (n ≥ 50) were measured at this time and these were the initial known lengths. These measured shoots were placed on aluminium pickets and replanted into the sand from the area they were sampled from. For production measurements, seagrass shoots were punched using a hypodermic needle at the sheathing base of the shoots. Neighbouring shoots were also punch-marked. After 3-5 days a sample of these punched shoots was collected and lengths were measured again. The difference in the lengths per shoot was used as a measure of shoot production. Of the sample, lengths of shoots that were grazed by turtles or lost due to death/decay were also recorded. From these production assays we could estimate the proportion of seagrass production (in cm.shoot⁻¹.day⁻¹) consumed through turtle herbivory, based on observed herbivory marks on punched shoots.
Further, in a seagrass meadow area in Kadmat lagoon, where turtles were found absent, we set up experimental ‘clipping plots’ to simulate turtle grazing (e.g. Moran & Bjorndal 2005) by manually clipping seagrass shoots with scissors in a manner similar to how turtles were observed to crop the standing shoots. A total of 5 clipped and 5 control plots was set up in December 2009 and initial shoot density of all species of seagrass was noted. Clipping was continued over a period of 102 days with clipping treatments every fortnight, in order to simulate sustained herbivory by turtles. At the end of 102 days sample of seagrass shoots from the clipped and control plots was harvested and shoot densities measured again. Shoot density was used as an index of seagrass population change (Duarte et al. 1994), in order to test if continued turtle herbivory could lead to a change in shoot abundance. Change in shoot density was compared between clipped and control plots.
We used a natural experiment to estimate the magnitude of recovery of seagrasses by simulating absence of herbivory. Seagrass shoots naturally enclosed (inaccessible to herbivory by turtles) in an array of *Acropora* corals were sampled and their morphometric measurements were made. Canopy height and shoot biomass of these shoots compared with seagrass shoots in adjacent areas that were accessible to turtles.

We also set up exclosures of 1 m² each in seagrass meadows within the lagoons that had turtle herbivory. The exclosures were made of Aluminium wire pieces cut in a U-shape and planted in an enmeshed way with an aim to disallow turtles from grazing the seagrass in that small area. Five such exclosures each, along with 5 corresponding control sites, were set up in turtle-grazed areas of the Kadmat and Agatti lagoons. However, it was impossible to continue this experiment, as the exclosures were lost because of disturbance and burial by sedimentation in lagoons that occurred through the monsoons when sampling and monitoring could not be conducted due to weather conditions.

The Kadmat lagoon, highly similar in biophysical properties and human use patterns to the Agatti lagoon (see Table 1), was used as a control site for surveys of fish abundance in seagrass meadows, as this lagoon differed only in terms of turtle densities and had similar fishing pressure.

**Sampling fish communities in seagrass meadows**

Species richness, diversity, adult and juvenile usage of fish found using seagrass meadows, sand patches, rubble patches, and patch reefs were recorded to assess the relative importance of seagrass meadows for fishes in relation to other highly structured or unstructured habitats.

For estimating fish species abundance in seagrass meadows, strip transects of 50 m x 5 m were carried out by snorkelling in seagrass meadows in each of the 9 zones mentioned above. The number of transects sampled in each zone was based on area under seagrass meadows in that zone. Transects were laid parallel to the shore and the observer noted size-classes, abundance, and species of each fish individual observed to be actively using the seagrass meadow. Presence of recruits and juveniles of different species, if any, was also noted. Abundance of different
size-classes was used to calculate biomass of each species based on known length-weight relationship for the species, obtained from field guides and the website FishBase (Lieske & Myers 2001; Froese & Pauly 2010). Along each transect, seagrass canopy height, seagrass species, and presence of algal cover (if any) was also measured. We compared fish adult abundance, biomass, juvenile usage, recruitment, size-structure, trophic complexity, species richness and species diversity across the gradient of turtle herbivory, within each atoll and across atolls.

*Juveniles of many important foodfishes (goatfishes, parrotfishes, rabbitfishes seen here) use the seagrass meadows for feeding and shelter. Photo: Nachiket Kelkar.*

**Turtle-fisher conflict: perceptions and attitudes of fishers across islands**

Detailed semi-structured interviews were conducted with lagoon fishers in Kadmat island to record attributes of lagoon fishing (habitats and preferred locations for lagoon fishing, trends in fish catch, difficulties in fishing if any) and understand perceptions and attitudes towards conflict with turtles (if perceived) (see Appendix
Interviews were conducted in Malayalam, with the help of a translator. From open-ended answers to some questions about fisheries and about conflict, a simple textual analysis was conducted to extract dominant themes mentioned by the fishermen. These categories, based on their presence or absence in respondents’ answers, were assigned a ‘1’ or ‘0’ value for analysis. Responses from Kadmat were compared with interviews conducted with fishers in Agatti (in 2005, by Rohan Arthur and M.D. Madhusudan) when conflict was at its peak. This was done to test if responses and perceptions differed, when conflict existed (as in Agatti in 2005), and when it was imminent (as of now, in Kadmat).

Interviews over tea with fishers in Kadmat. Photo: Nachiket Kelkar.

Interviews were started also in Kavaratti and Agatti in 2010, but decent sample sizes have not yet been obtained, and they are currently ongoing. With these interviews, an updated comparison could emerge. In addition, we tried to estimate lagoon fish catch per fisherman and areas mostly preferred by fishers for fishing in
the lagoon. These areas were mapped out from interviews as well as with the help of lagoon fishers who were provided datasheets to record their own fish catch for a period of 15 days. In these datasheets, fishers recorded information about weather, time of day, fishing effort, habitat(s) where they fished, fish species caught, and their lengths and abundances. The areas mapped and the points at which fishing was carried out were entered in a GIS. These variables were compared across Agatti and Kadmat islands. Lagoon fish catch estimates for Agatti were obtained from Tamelander & Hoon (2008).

Data analysis

Turtle surveys

Turtle densities were estimated for the lagoon based on point counts that were summed up and divided by area. Turtle densities were calculated for different zones within the lagoon to identify the gradient to estimate effects of increasing turtle herbivory on seagrass meadows and fish communities.

Impacts of green turtle herbivory on seagrass meadow characteristics

We compared seagrass meadow characteristics (canopy height, seagrass production consumed by turtles) for different zones along the density gradient for the three lagoons using box-whiskers plots and bar plots. Measurements on shoot density and production could not be made in Kavaratti lagoon as diving facilities were unavailable through the study period. Growth rates under simulated turtle grazing were calculated for Thallasia hemprichii and Cymodocea rotundata in the experimental clipping plots based on changes in shoot density and production. A t-test for statistical significance was used for differences growth rates in clipped vs.
control plots. ANOVA was used to test for significance of differences in structure and production of seagrass shoots within and outside exclosures.

**Fish communities in seagrass meadows**

We compared fish abundance, biomass, species richness and diversity, juvenile usage, recruitment and trophic complexity at transect-level in seagrass meadows across the 9 zones along the turtle density gradient. Linear regression was used to test if fish variables (recruit biomass, food fish biomass) were affected by meadow structure (canopy height).

![Species richness graph](image)

*Fig. 2. The importance of seagrass meadows for juvenile settlement and as nursery habitats. The clear bars represent species richness of juvenile fishes (higher in seagrass meadows compared to adult usage of the seagrasses) and black bars represent adult fish species.*

**Turtle-fisher conflict: perceptions and attitudes of fishers across islands**

Responses from Kadmat and Kavaratti (n=36) were compared with previous interviews from Agatti (in 2005, n=60) and proportions of different responses were contrasted. In particular, we compared 1) whether perceptions about conflict with turtles were positive (perceived conflict), neutral, or negative (including attitudes to
turtle conservation), 2) proposed solutions to turtle conflict mitigation (radical/neutral/mild), and 3) details of first-order conflict (if any), and recognition of second-order conflict. Mapped areas and locations preferentially and regularly used by fishers were compared with turtle distribution maps to obtain a relative measure of spatial overlap between turtles and fishers in Kadmat. All analyses were conducted in the software R 2.10.1 (R Development Core Team 2010).

Table 1. Similarities in biophysical and anthropogenic characteristics of the Agatti and Kadmat lagoons. High similarity in these factors validates comparison of turtle herbivory effects on seagrass meadows and fish communities across these two lagoons.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Agatti</th>
<th>Kadmat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lagoon area</td>
<td>16.8 km²</td>
<td>20.9 km²</td>
</tr>
<tr>
<td>Orientation</td>
<td>North-South (western aspect of island)</td>
<td>North-South (western aspect of island)</td>
</tr>
<tr>
<td>Tidal influence</td>
<td>Entrance points 3, at north, central and south locations</td>
<td>Entrance points 3, at north, central and south locations</td>
</tr>
<tr>
<td>Mean depth at high tide</td>
<td>2.5 m</td>
<td>2.2 m</td>
</tr>
<tr>
<td>Seagrass cover</td>
<td>7.02 km²</td>
<td>7.76 km²</td>
</tr>
<tr>
<td>Fisher density (fishers/km² of lagoon per day)</td>
<td>3.75 (SD 0.95)</td>
<td>3.89 (SD 1.42)</td>
</tr>
<tr>
<td>Population (2009)</td>
<td>8,145</td>
<td>6,440</td>
</tr>
</tbody>
</table>

Results

Turtle density gradients within and across islands

Turtle densities were the highest in Agatti between 2005 and 2007 (22-26 turtles per sq.km), but turtle numbers in our surveys showed an overall decline since then. In 2010-11 we estimated highest densities in the Kavaratti lagoon, followed by Agatti where the numbers seem to have correspondingly declined, and Kadmat had
the lowest densities (Table 2). Within these lagoons, it was found that turtle numbers were usually highest in the region closer to the inlets made on reefs for boats to move in and out of the lagoon, and highly overlapped with seagrass distribution. Turtles maintained a consistent density gradient in all lagoons (Table 2).

Table 2. Turtle densities across three lagoons in the Lakshadweep Islands.

<table>
<thead>
<tr>
<th>Island-lagoon</th>
<th>Overall turtle density (turtles/sq.km of lagoon area)</th>
<th>Turtle density per sq.km of seagrass meadow</th>
<th>Region of high density</th>
<th>Region of moderate density</th>
<th>Region of low density</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agatti</td>
<td>7.80 (SD 2.13)</td>
<td>27 (SD 7.39)</td>
<td>north⁴</td>
<td>south⁴</td>
<td>central²</td>
</tr>
<tr>
<td>Kavaratti</td>
<td>12.8 (SD 6.72)</td>
<td>38.41 (SD 20.15)</td>
<td>central</td>
<td>north</td>
<td>south</td>
</tr>
<tr>
<td>Kadmat</td>
<td>3.21 (SD 0.34)</td>
<td>7.14 (SD 0.73)</td>
<td>central⁵</td>
<td>north⁵</td>
<td>south¹</td>
</tr>
</tbody>
</table>

N.B.: ¹, ², ³, ⁴, ⁵, ⁶ represent points along turtle density gradient (low-1 to 6-high). The corresponding production measurements (see fig.3) could not be made for Kavaratti lagoon. The turtle density gradient mentioned in the text ahead refers to comparisons of seagrass and fish characteristics only between Agatti and Kadmat.

Magnitude of sea turtle herbivory and impacts on seagrass meadows

Six species of seagrasses were recorded across the three lagoons in our surveys. These were *Cymodocea rotundata*, *Thalassia hemprichii*, *Syringodium isoetifolium*, *Halophila ovalis*, *Halodule uninervis*, and *C. serrulata* in the respective order of abundance, from common to rare. Meadows in Agatti and Kavaratti were dominated by *C. rotundata* and *S. isoetifolium* whereas in Kadmat *T. hemprichii* and *C. rotundata* were the dominant species. Across the lagoons, in regions of high or moderate densities, turtles accounted for almost 30-70 % of the primary production of seagrasses (Fig.2). Turtle density was recorded as zero in the seagrass meadows of the southern region of the Kadmat lagoon, which was used as a control site for experimental clipping of seagrasses. Growth rates of *T. hemprichii* after the clipping treatment were negative whereas growth-rates of *C. rotundata* showed small positive values, very close to zero (Fig. 4). Thus, a population-level change in the
seagrass species composition of the meadow was noted following continued clipping (herbivory). Canopy height of seagrasses showed a negative relationship with turtle densities (Fig. 3, 5) and proportion of production of seagrasses consumed by turtles (Fig. 6), resulting in loss of structural complexity of the seagrass meadows. Highest shoot density, canopy height, and production were recorded in Kadmat lagoon, and these values were lower in Kavaratti and Agatti. Inside exclosures seagrass canopy height was about 4 times more than that outside exclosures (Fig. 7).
Fig. 3. Overlap of turtle distribution and seagrass meadows in Agatti Island. The high turtle density area (zone A) lies in the northern region of the lagoon and the low density area (zone B) in the south-central region.
Fig. 4. Population change in seagrass species (*Thalassia* – negative growth rates), and *Cymodocea* (weakly positive growth rates) in simulated turtle herbivory (clipped plots), as against uniformly positive growth rates of both species in control plots.

Fig. 5. Seagrass shoot density in Agatti (highly grazed) and Kadmat (low-grazed) lagoons.
Fig. 6. Effects of proportion of production consumed by green turtles on seagrass structure (canopy height).

Proportion of seagrass biomass consumed by green turtles (cm/shoot/day)
Fig. 7. Seagrass shoots in exclosures have significantly higher canopy height than open shoots accessible to turtles. ANOVA results for exclosure experiment in Agatti lagoon are provided.
Fig. 8. Number of species with juveniles and recruits using seagrass meadows in Agatti, Kavaratti and Kadmat, along the gradient of turtle density.

Fig. 9. Biomass of seagrass fish species in Agatti (red), Kavaratti (black) and Kadmat (green) in relation to seagrass meadow structure (canopy height).
Fig. 10. A) Effects of reduced canopy height on recruitment of fishes, and B) Biomass of preferred food fish species (*Parupeneus barberinus* and *Lethrinus harak*) declines with reduction in canopy height. The X-axes are inverted.

*Effects of seagrass loss on fish species variables, mediated by turtle herbivory*

In contrast with other lagoon habitats, seagrasses had a higher species richness of juvenile fishes than adults (Fig.1). Other habitats had a higher ratio of adults to juveniles. A total of around 80 fish species were found to use seagrass meadows either as juvenile habitat or feeding grounds. These species mainly included wrasses, emperors, goatfishes, parrotfishes, surgeonfishes, and some species of blennies, gobies, juvenile jacks and barracuda (Appendix 1). Fish abundance, biomass, species richness, species diversity, trophic diversity, size-structure, adult and juvenile usage and number of fish species recruiting in seagrass
meadows increased with increasing canopy height (Fig. 8), consistently along the gradient of turtle densities, correlated positively with removal of seagrass production by turtles (Fig. 3, 9, 10). Important trophic guilds (e.g. piscivores, seagrass-specialist herbivores: Siganids and Scarids) were found absent from seagrass meadows in lagoons with progressively higher turtle herbivory (Fig. 11). On the other hand, open-habitat species using sandy beds (e.g. Gerreids, pipefishes) were more common in highly grazed areas. Other factors that seemed to influence fish species presence and abundance were algae and differential sediment arrival in different zones of the lagoons.

Fig. 11. Increase in trophic guild diversity of fishes, with decline in turtle density and grazing pressure along the gradient, from Agatti to Kadmat.
Perceptions and data: the conformity and non-conformity

Agatti fishermen had held turtles strongly responsible for declines in fish catch (61%), but this perception was mentioned by much fewer respondents in Kadmat (13%) (Fig. 12). In Agatti, a larger number of fishers mentioned the presence of second-order conflicts (indirect effects of turtle herbivory), along with first order conflicts, of which the latter dominated the responses of people in Kadmat (Fig. 13). Measures suggested by respondents to solve the problem were mostly drastic or radical in Agatti (‘kill turtles’, ‘lift the ban on turtle hunting’: 22%), but most respondents in Kadmat said that there was no solution possible (59%). In Kadmat, respondents mostly said that the seagrass meadows caused difficulty in catching fish because of low visibility, and because fish could hide in the grass on detecting nets. In Agatti, perception of second-order conflict was positively related to age and experience of fishermen in seeing turtles (Multinomial logistic regression: Adjusted McFadden’s R-squared = 0.74, Slope =0.38, p <0.01). Few data from Kavaratti are available, but the responses appear rather similar to Agatti fishers already.

Fig. 12. Fishers from Agatti, in 2005, predominantly laid the blame for declining fish catch on turtles. In Kadmat, today, when turtle numbers are still low, other factors were pointed out as the main causes.
Fig. 13. Fishers from Kadmat cited mostly first-order conflicts with turtles, whereas fishers from Agatti reported considerably higher second-order conflict.

Agatti fishers had a higher frequency of gear damage as compared to Kadmat, whereas availability of seagrass food fishes and CPUE values were four-fold higher in Kadmat, reflecting the differences in intensity of conflict with turtles (Table 3).

Table 3. Differences in direct and indirect effects of turtles on fishers in Agatti and Kadmat, reflected in frequency of gear loss, fish biomass caught per unit effort and market rates of common food fishes.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Agatti</th>
<th>Kadmat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Frequency of Gear Damage/fisher/yr</td>
<td>2.03</td>
<td>1.88</td>
</tr>
<tr>
<td>Fish Biomass (kg/250 sq.m)</td>
<td>0.05656 (SE 0.013)</td>
<td>2.6136 (SE 0.912)</td>
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<tr>
<td>Avg. biomass (kg/sq.m)</td>
<td>0.00022624</td>
<td>0.0104544</td>
</tr>
<tr>
<td>CPUE (kg/fisher.day)</td>
<td>1.66 (SE 0.07)</td>
<td>6.27 (SE 3.79)</td>
</tr>
<tr>
<td>Market Rates (INR)</td>
<td>85.38 (SD 19.83)</td>
<td>55 (SD 15)</td>
</tr>
</tbody>
</table>
Discussion

Our results show that green turtles exert a considerable influence on the ecosystem dynamics of seagrass meadows and have significant effects on fishes that use seagrass meadows for shelter, recruitment, juvenile usage and as feeding grounds. Ecosystem engineers such as green turtles in high densities can have negative effects on seagrass meadow abundance and distribution at least in the short term. The role of large herbivores in maintaining ecosystem dynamics of grazing ecosystems is fairly well studied in both aquatic and terrestrial landscapes (Cebrian & Lartigue 2004; Pringle et al. 2007; Thayer et al. 2007), but the emphasis has been on how these herbivores impact plant communities. It is rather poorly known as to whether these modifications to plant communities in turn affect faunal elements using grazing ecosystems, by their dependence on plant structure, or specific associations with plant species (e.g. insects, ground-dwelling arthropods) due to morphological, physiological and environmental constraints.

The role of green turtles and dugongs as important megaherbivores of seagrasses has been very well understood, and a lot of work has been dedicated to the subject of herbivory on seagrasses (e.g. Valentine and Heck 1999; Alcoverro and Mariani 2002; Heck and Valentine 2006; Valentine and Duffy 2006). The key role of large herbivores in meadow maintenance and modification might have important effects for faunal communities using seagrass meadows (Nakaoka 2005; Duffy et al. 2003). Nakaoka et al. (2002) showed that sustained grazing by dugongs could lead to change in benthic fauna in seagrass meadows. However, for turtles, to the best of our knowledge, our study is the first that provides empirical evidence of turtle herbivory reducing fish abundance and modifying fish communities to a significant
extent. This process would seem obvious on reviewing the numerous studies on ecological requirements of fishes and their dependence on seagrass meadow structural complexity, productivity and biomass (e.g. Bostrom and Bonsdorff 2000; Heck et al. 2003; Pihl et al. 2006; Nakamura et al. 2007; Hori et al. 2009; Attrill et al. 2009) at various stages of their life-cycle. However, these studies have not been linked with the detailed understanding of turtle-seagrass relationships (Ogden et al. 1980, 1983; Bjorndal 1980; Moran & Bjorndal 2005, 2007), perhaps because such a situation may be rare, and thus less likely to compel an investigation of the seemingly obvious process. It is well known from most tropical areas that seagrasses provide the important ecosystem service of juvenile nursery habitats to coral reef fish communities (Nagelkerken et al. 2001; Dorenbosch et al. 2005; Gillanders 2006) and even to other faunal assemblages in shallow near-shore substrates (Dahlgren et al. 2006). This is also an important ecosystem service on which fishers rely for subsistence fishing activities. The modification of seagrass meadows by turtles significantly alters the benefits of this service for fishes and fishers both, leading to conflict.
What makes this story furthermore interesting and challenging as a conservation issue, is the conflict situation in the Lakshadweep islands. If green turtles can modify the availability of this service even to the extents we estimate, negative perceptions and attitudes towards their conservation, in the minds of local fishers may not seem too extreme a reaction. Our results also suggest that such modifier species, in particular situations, may cause trouble for their own conservation due to their natural impacts on systems they share with human economic and subsistence needs (Lal et al. 2010). It stresses on the need to question if species abundance may be the only benchmark for assessing conservation success for endangered species. In the case of species that are ecosystem modifiers, due consideration to their impacts on other species and local livelihoods is necessary.

From a conflict management perspective, the more important point, however, is the necessity to assess and verify the veracity of people’s perceptions. Perceptions of local stakeholders may often be easily dismissed by conflict managers as intangible beliefs without any reasonable basis. However, we prove that
perceptions themselves may be based on valid ecological mechanisms that have been understood through years of lived experience of resource users. These mechanisms can be deconstructed to validate the presence of causal relationships, only if human perceptions of conflict are well-documented and analyzed.

Having said that, it is important to remember that turtles are not the sole cause for loss of seagrass habitat. Seagrass meadows have been threatened by a number of other large-scale factors across the globe (Duarte 2002). Coastal and lagoon dredging, changes in sedimentation regimes, organic pollution, algal blooms caused by eutrophication, and dumping of wastes in lagoons are serious threats that need to be addressed immediately. In the Lakshadweep Islands, although the magnitude of these threats is low, they are still a serious concern for safeguarding near-shore ecosystems, and in particular seagrass meadows in the lagoons. Conscious policy decisions are needed to protect seagrass meadows from these threats, and directed action by government departments may help in controlling their negative impacts to some extent (Duarte 2002). The turtle conflict, on the other hand, is a far more difficult situation to manage because of the multitude of causal linkages and ‘conservation vs. resource use’ paradoxes that carpet its paths.

It is crucial thus, to further ask what may have caused such high turtle abundances in the first place. Fishers of Lakshadweep have historically used turtle meat, eggs and oil for lubricating boats, and have thus been turtle hunters till the ban was actively enforced. They unanimously believe, today, that the ban on hunting of the ‘endangered’ turtles has led to such increases. In fact, a global recovery of the endangered green turtles has been recently recorded (Bourjea et al. 2007; Chaloupka et al. 2008). Culling has been supported by fishers as the best solution,
However; in practice controlled culling may be rather difficult given the poor monitoring and implementation of such management measures. Also, fishers mainly use sardine oil for boat lubrication, and culling may only encourage wanton killing of turtle populations. Apart from the ban, other causes for high abundances may seem equally, if not more, plausible. Hawkes et al. (2009) note that turtle abundances at feeding grounds peak after ENSO sea-surface temperature rise events, owing to increased seagrass production. Claims from Agatti claimed that turtle numbers increased between the years 1995 and 2000, and this could be connected (but in the absence of any data) to the El-Nino Southern Oscillation (ENSO) mass bleaching event of 1998. Sea surface temperature rise is thought to trigger seagrass growth, and it has been speculated that turtles may aggregate in higher numbers in hitherto less exploited meadows. Further, successful ongoing conservation and research programs on green turtles on the western coast of Sri Lanka have found that many satellite-tagged green turtles travel to islands of the Lakshadweep archipelago (Peter Richardson, personal communication). It is likely that conservation success in Sri Lanka might have actually led to higher densities from feeding aggregations in the Lakshadweep lagoons. Also, sustained removal of top predators of turtles (e.g. tiger sharks) across their range may lead to increased survival and abundance of green turtles (Heithaus et al. 2007, 2008).

Finally, through this example and its rather far-flung, yet possible external links, we suggest that human-wildlife conflict, at small scales, is often not a static and persistent event, but is highly dynamic in space and time. Our data on change in turtle abundance across islands, and particularly, the increase of turtles in Kavaratti lagoon corresponding with decline of turtles in Agatti lagoon, may suggest turtle
movement between islands. This may be due to rotational grazing by turtles for optimal exploitation of seagrass resources over large temporal scales (e.g. Preen 1995; Aragones et al. 2006) that causes them to migrate from one patch to another after having reduced the seagrass resources in the former patch, to be revisited in the rotations. At high densities, turtles may thus carry conflict with them as they exploit other seagrass meadows in shallow lagoons of the Lakshadweep islands. These hypotheses will eventually have to be tested using studies involving satellite telemetry on turtles, and potentially the use of stable isotope techniques and genetics to show actual evidence of turtle movements across these lagoons. At large temporal scales, the rotational grazing by green turtles might even be causing changes in the long-term persistence, population dynamics and distribution of seagrass meadows.

Conflict with fishers may itself depend on spatiotemporal factors that influence turtle movements. Thus, knowledge and perception of conflict, or rather, an appreciation of the mechanisms that result in losses to fishers, can also help in the evolution of ecological knowledge in local communities based on their lived experience of new events such as increased turtle densities. The complexities of turtle-fisher conflict in the Lakshadweep islands, would serve to emphasize on a critical look at current marine conservation paradigms on the one hand, and perceptions, experience and fallacies of resource users and managers that find themselves trapped in conflict situations, on the other.

Studies on recovery of seagrass meadows are necessary to unravel the after-effects of sustained turtle herbivory for over a decade, and Agatti seems to provide a new opportunity at investigating new hypotheses about ecosystem re-establishment.
following decline of green turtles. If turtles would carry conflict with them as they
move from lagoon to lagoon, mowing down the meadows before going away, they
would provide just the incentive for knowing them better. In conclusion,
conservation of green turtles in shared spaces with human users could greatly
benefit from understanding these large-scale, landscape-level and historical changes
in detail. With such an understanding, turtles may not be perceived a catastrophe or
calamity but more so as an irregular yet explicable weather phenomenon, that gets
bad in some years someplace, better in others.

Conclusions

1. Green turtles attained exceptionally high densities, congregating in the
   shallow lagoons of the Lakshadweep Islands that owing to seagrass meadows
   act as important feeding grounds.
2. Sustained herbivory by green turtles reduced seagrass growth rates, possibly
   modified meadow species composition, and led to declines in primary
   production, shoot density and canopy height of seagrasses. This loss in
   structure and production, negatively affected fish communities using
   seagrass meadows for shelter/food.
3. Green turtles have a very significant role to play in modifying and controlling
   seagrass meadow distribution and abundance in the lagoons of the
   Lakshadweep islands. They may consume up to 70% of seagrass production.
   Continued herbivory by green turtles may not only affect seagrass meadows
   negatively, but have cascading effects on faunal communities in seagrass
meadows, and most importantly, fish communities. They thus act as major ecosystem modifiers of seagrass meadows.

4. As these fish resources are of high importance to lagoon-based artisanal and subsistence fishing in the islands, conservation of green turtles has translated into challenges for their conservation, via conflict with fishers through direct and indirect mechanisms.

5. In the understanding of conflict, people’s perceptions, although often treated as ‘subjective’ or intangible, can lead to the identification of complex ecological mechanisms that can be tested with ecological studies. The role of perceptions in understanding that conflict may not always be as straightforward and measurable an interaction as is often assumed in contemporary systems of conflict mitigation and management. It becomes necessary to acknowledge the role of lived experience of local stakeholders in management of conflict interactions.

6. Turtles follow rotational grazing patterns and thus severely deplete seagrass meadows, before moving on to other areas. This may imply that conflict caused by turtles, may itself be temporally dynamic and may lead to potential problems both for turtle conservation, and fisher folk livelihoods, when densities are exceptionally high. Conservation of endangered species such as green turtles, therefore, needs to be more flexible in its objectives, and sensitive to economic losses incurred by human stakeholders in situations such as in the Lakshadweep Islands.

7. As the mechanisms, so the solutions to mitigating conflict situations may be highly complex, with many historical and even current unknowns. Solutions
may seem simple (such as the active control of increasing turtle abundance, reducing access of turtles to seagrasses, or increasing extent of seagrass meadows), yet these aims in reality may be highly complex to achieve. Turtle movements and rotational grazing over time, aggregations in very high densities at feeding grounds, migration from nearby protected seascapes (e.g. Sri Lanka), and the thinning of predatory control over turtle survival (e.g. declines of large sharks); are a few cases in point that serve to amply illustrate the vast scope and magnitude of conflict, and the surprisingly small, or rather, infinitesimal solution space that exists for conservation and management of endangered species in the face of real-world uncertainties.

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**Turtle conservation in the Lakshadweep Islands: an overview**

1. Turtle Action Group (TAG)-India conducted awareness programs for turtle conservation between 2006 and 2008. These programs were conducted by Mr. Jafer Hisham and his team, with a grant from Seacology, supervised by Dr. Karthik Shanker.

2. Targeted killing is not prevalent anymore, except some cases of clandestine persecution in Agatti some years back, when the conflict was at its peak.

3. Our project involved detailed formal and informal discussions with fisher families and fisher groups. Believing that giving fishers a clear idea about the importance of turtle conservation and the reasons for the ban, we are conducting informal sessions for educating fishers, interview respondents and key informants about the role of turtles in modifying the landscape, tolerance towards the situation, and ecological details. Our first step in involving local stakeholders is to create awareness by sharing results with local communities. We have also planned discussions with Panchayat members of islands where turtle numbers have increased recently.
References


Additional References


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Appendices

Appendix 1. Fish species recorded from seagrass meadows, with notes on their observed use of the seagrass habitat.

**Key:** Columns: Species; Trophic guild; Usage = Primary use of seagrass meadow by the species, ABD = Abundance categories: 1-Rare, 2-Occasional, 3-Uncommon, 4-Common; T = recorded in transects (1), not recorded in transects but observed (0); Kd, Kv, Agt = Kadmat, Kavaratti and Agatti respectively; Rc = recruitment observed (1), not observed (0); Juvenile usage observed (1), not observed (0); Ad = Adult use observed (1), not observed (0).

<table>
<thead>
<tr>
<th>Family</th>
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<th>Trophic guild</th>
<th>Usage</th>
<th>ABD</th>
<th>T</th>
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<th>Kv</th>
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<td>Bothus sp.</td>
<td>Macroinvertivore</td>
<td>feeding</td>
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<tr>
<td>Balistidae</td>
<td>Balistoides viridescens</td>
<td>Omnivore</td>
<td>feeding, resting</td>
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<tr>
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<td>Sufflamen chrysopterus</td>
<td>Omnivore</td>
<td>resting</td>
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<td>Rhinecanthus aculeatus</td>
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<td>resting</td>
<td>3</td>
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<td>Canthigaster solandri</td>
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