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An investigation of the relationship between Green Turtle (*Chelonia mydas*) herbivory and Seagrass in the Agatti Lagoon, Lakshadweep

A Dissertation Submitted to
Saurashtra University, Rajkot,
in partial fulfillment of the Masters' Degree in Wildlife Science

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CERTIFICATE

This is to certify that *Ms. Aparna Lal* of the Wildlife Institute of India, Dehradun has carried out original research work titled **'An investigation of the relationship between Green Turtle (*Chelonia mydas*) herbivory and Seagrass in the Agatti Lagoon, Lakshadweep'** towards the partial fulfillment of the M. Sc (Wildlife Science) degree from Saurashtra University, Rajkot, India. The study was conducted under our supervision from November, 2006 to June, 2007. I also certify that this research work has not been submitted for the award of any other degree to any University.

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SUMMARY

Globally, nearshore ecosystems are being increasingly impacted upon by expanding coastal development. The almost complete dependence of marine mega herbivores like Green Turtles (*Chelonia mydas*) on these habitats for food together with their current low population levels in many regions highlights the need to understand this vital relationship. This study was an attempt within this framework. It aimed to quantify the intensity and potential impacts of Green Turtle grazing on the seagrass *Cymodocea rotundata* in the Agatti Lagoon, Lakshadweep. To map the habitat types in the lagoon, points generated from a grid were used, while 23 transects, perpendicular to the shore, formed the basic sampling unit to assess turtle density and map their distribution patterns across the lagoon. The study recorded exceptionally high turtle abundances within the lagoon with their distribution patterns being restricted to certain areas within the seagrass meadow. The magnitude and potential impacts of herbivory were quantified across the established gradient of turtle density in the lagoon. It was found that *C. rotundata* plant parameters like morphology, life history strategies, population dynamics and meadow level characteristics were significantly different in areas with less turtles, indicative of a response to turtle grazing, results supported by experimental evidence. It was found that increased shoot recruitment rather than increased shoot production could be a mechanism whereby seagrass deals with intense herbivory. This study shows that grazing intensity is an important factor potentially regulating the response of seagrasses to grazing.

1. INTRODUCTION

The Green turtle (*Chelonia mydas)* is one of the two marine mega herbivores found in Indian waters and are listed as vulnerable under the IUCN (Seminoff 2004). Green turtles are threatened globally by a multitude of human-induced activities such as over exploitation of eggs and adults from nesting beaches and juveniles and adults from feeding grounds, fatal interactions with fisheries, boat strikes, degradation and loss of feeding and nesting habitats and ingestion of synthetic materials (McCauley and Bjorndal 1999, Seminoff 2004). They are the only marine turtle that is mainly herbivorous, foraging primarily on seagrass and algae (Mortimer 1981). Studies conducted at these critical feeding grounds are necessary to better understand green turtle foraging ecology, their role in the marine ecosystem and assess habitat quality in these coastal foraging areas, a crucial component of conservation management. More importantly, current densities of marine mega herbivores are assumed to be too low to exert a significant influence on seagrass communities, as seagrass morphologies are likely to have been evolved under grazing regimes quite different from those prevailing today. In short, the structure of seagrass beds cannot be understood except in the context of the larger food webs they support. However, studies investigating these aspects of green turtle-seagrass interactions are restricted to the Caribbean (e.g. Bjorndal 1980, Bjorndal 1985, Zieman et al. 1984) and Australia (e.g. Aragones and Marsh 2000).

The present study looks at green turtle distribution patterns in relation to the spatial patterns of seagrass (food) resources in the Agatti lagoon, Lakshadweep. Seagrass meadows were documented to be the best predictor of turtle presence in the study area. The study which also quantified the intensity and potential impacts of green turtle herbivory on seagrass, found a significant effect of turtle grazing on seagrass structural, morphological and life-history parameters.

1.1 A review of literature

1.1.1 A historical perspective on marine ecosystems

The seas, once resplendent with abundant life, where mega fauna often posed serious navigational threats, are today mere memories accounted in past literature. Cumulative effects of pollution, habitat degradation, overuse and abuse have caused the ecological and complete extinction of many marine species (Jackson 1997, Jackson et al. 2001, Pandolfi et al. 2003). For example, in less than 300 years, the Caribbean monk seal (*Monachus tropicalis*), once found from Florida to the West Indies (LeBoef et al. 1986), has been driven to extinction as a result of over hunting (Vermeij 1993). At the ecosystem level, the consequences of such eliminations or severe reductions of consumer diversity are very likely to be mediated via cascading trophic interactions (Duffy 2006). Indeed, comprehensive evidence based on paleoecological, archaeological and historical data suggest that over exploitation, much before any other disturbance, was the primary driver of many unprecedented marine trophic collapses (Jackson et al. 2001). Growing evidence suggests that changes in food web structure as a result of extirpation of mega herbivores has negatively affected the resilience and resistance of nearshore ecosystems (Duffy 2006). The large scale exploitation of long-living and slow reproducing marine vertebrate grazers such as green turtles (*Chelonia mydas)*, manatees *(Trichechus* spp.) and dugongs *(Dugong dugon*) has had a profound ecological impact on the shallow coastal ecosystems which they inhabit (Preen and Marsh 1995). Overfishing of these grazers has been cited as the ultimate cause for the 1980's seagrass die off in the Gulf of Mexico, as a result of its changed ecological state (Jackson et al. 2001). Additionally, this almost complete depletion of vertebrate consumers in marine ecosystems has been held responsible for the increased susceptibility of these nearshore ecosystems to invasions by exotic flora and fauna (Orth et al. 2006). Consequently, mega herbivores have been acknowledged as a functionally distinct link in this food chain (Hughes et al. 2004), a relationship weakened considerably by the over exploitation of these animals (Duffy 2006). Thus, alterations in food web structure as a result of such "ecosystem overfishing" (Dybas 2002) could lead to catastrophic ecosystem collapses.

The expected ecosystem level consequences of such drastic changes in primary consumer diversity are obscured by the complete lack of data on marine mega fauna populations and seagrass ecosystems prior to anthropogenic disturbance. Intense historical exploitation dating back to aboriginal times leaves records on numerical populations of marine mega fauna as well as data on distributions patterns across their former natural range largely anecdotal (Vermeij 1993). Establishment of historically natural and ecologically meaningful baselines for conservation and management is difficult, with each generation of ecologists perceiving 'normal' densities and distribution patterns which are further and further away from the original (Sheppard 1995). This 'shifting baseline syndrome' (Pauly 1995, Dayton et al. 1998) is particularly important when considering that present marine mega fauna populations represent a fraction of their estimated historical density (Jackson 1997). Indeed, the current Caribbean green turtle population is estimated to represent 3-7% of the pre-human green turtle populations (Jackson et al. 2001). For these vulnerable species, such unsuitable reference points could lead to a gross underestimation of the strength and significance of their ecological role, and ultimately erroneous conservation management decisions (Jackson 1997). In fact, a review of fossil history of seagrasses and sirenians in the Caribbean reveals a significant role played by these marine mega herbivores in the development of coastal seagrass ecosystems (Domning 2001). Indeed, it has been suggested that through sustained intense grazing pressure, these animals have exerted important selective pressures on seagrass traits (section 1.1.3). This close evolutionary history between seagrasses and marine mega herbivores (Domning 2001) coupled with the inability of small herbivorous fishes to compensate for their loss (Valentine and Duffy 2005) may potentially result in a significant loss of ecological function in nearshore food webs.

Worldwide, a growing body of evidence strongly suggests that current degradation of nearshore ecosystems is a response to an exponential rise in coastal development (Duarte 2002, Cardoso et al. 2004). This conclusion, coupled with the longevity, slow reproduction, complete dependence of marine mega fauna on these habitats and their current low populations (Preen and Marsh 1995, Moran and Bjorndal 2005) makes elucidation of their evolutionary and ecological relationship imperative to marine ecological research. Moreover, a better understanding and recognition of the importance of these food web linkages to the stability of these nearshore environments is critical to the maintenance of these human dominated ecosystems. Consequently, quantification of mega fauna grazing relationships is crucial, an area of research sadly lacking.

1.1.2 Seagrass ecosystems

Seagrass meadows are regarded as a key coastal ecosystem, responsible for up to 15 % of the total excess carbon produced in the global ocean (Duarte and Chiscano

1999). These highly productive marine angiosperms provide vital foraging, nursery and prey refuge habitats for a myriad of species ranging from invertebrates, commercially important crustaceans and fish species to marine megaherbivores (Thayer et al. 1984). Their structural complexity and dense root-rhizome mat has also been documented to buffer wave action and stem shoreline erosion respectively (Heck et al. 2003). Consequently, the value of these coastal 'engineering species' (Duarte 2000) as "natural capital" has been estimated at US \$19,004ha^{-1} yr^{-1}, placing them among the top three most valuable natural systems in terms of ecosystem functions and services, preceded only by floodplains and estuaries (Costanza et al. 1997).

1.1.3 Seagrass herbivory

This emergent understanding of the importance of seagrass ecosystems in oceanic systems has led to a recent spurt in seagrass research with a subsequent revision of some previously accepted tenets central to seagrass ecology. The paradigm that detritivores are the main beneficiary of the energy stored in seagrasses (Thayer et al. 1984), while direct grazing of seagrasses is minimal (Duarte and Chiscano 1999) is one such example. This theory, based largely on studies using indirect measures of herbivory such as bite marks on leaves (e.g. Zieman et al. 1984) rather than actual estimation of herbivory rates has led to consistent underestimates of the potential direct grazing on seagrasses (Heck and Valentine 2006). In fact, recent quantification of actual herbivory (e.g. Kirsch et al. 2002, Tomas et al. 2005, Prado et al. in press) has helped establish that anywhere between 3% and 100% of net primary production enters the food web through the seagrass grazing conduit (Valentine and Duffy 2005). Thus, the grazing pathway, dominated by large herbivores and characterised by moderate to intensive grazing on living seagrass leaves and rhizomes could be a significant trophic interaction.

The importance of the grazing pathway assumes further significance given that marine megaherbivores in most areas represent only a proportion of past population levels. Seagrass resources continue to be the principal dietary component of both green turtles and dugongs even in areas where both species exist sympatrically (Andrè et al. 2005, Domning 1981), reiterating the importance of these marine angiosperms for species' survival. Thus, the potential strength of this conduit for energy transfer to higher trophic levels is very high, but requires a direct estimation of herbivory rates in areas of high mega herbivore densities in order to better comprehend the significance of grazing in seagrass systems.

Interestingly, the potential strength of grazing as a significant trophic interaction in seagrass meadows is further validated by the morphological traits of seagrasses themselves. Typical seagrass traits like clonal propagation (Valentine and Duffy 2005), substantial energy allocation to underground storage (Duarte and Chiscano 1999) and proliferation of small shoots (Valentine and Duffy 2005) possibly indicating an ability to rapidly regenerate damaged tissues (Valentine and Heck 1999) suggests an analogous growth form to terrestrial grasses (Aragones et al. 2006). This evidence suggests that historical close interactions with grazers have shaped many physical and chemical features of seagrasses as an adaptation to intense levels of sustained herbivory.

1.1.4 Impacts of herbivory on seagrass

The impacts of grazing by large terrestrial herbivores on plant growth form (McNaughton 1984), productivity (Milchunas and Lauenroth 1993), nutrient recycling and availability (McNaughton 1988), reproductive success (Janzen 1969) and plant population dynamics (McNaughton 1984) is well established. In marine systems by contrast, the impacts of grazing are less well-documented, despite evidence that marine mega herbivores have sometimes played an important role in influencing the structure and dynamics of seagrass communities in many areas (Thayer et al. 1984, Aragones 2000, Masini et al. 2001, Andrè et al. 2005). For example, green turtles have been observed to practice 'cultivation grazing', by maintaining select grazing plots in the same area for a considerable length of time (Bjorndal 1985). This strategy presumably allows them to maximise their foraging efficiency and nutritional intake (Whiting and Miller 1998, Taquet et al. 2006). Younger shoots have the highest nutrient value in terms of protein or nitrogen content (Thayer et al. 1984). However, as the leaves grow the C/N ratio rises, thereby reducing its palatability (Valentine and Duffy 2005). Since digestibility of potential foods may affect consumption by turtles (Lopez-Mendilaharsu et al. 2005), regrazing new growth seems to be an ideal foraging strategy. Turtle grazing has also been observed to cause morphological changes in seagrass shoots, with thinner leaves in areas of intense grazing (Zieman et al. 1984). Manatees with their specially adapted down-turned rostrum can dig up entire seagrass beds and cause a lot of physical disturbance (Jackson 1997). Similarly, evidence of intense dugong grazing indicated by the removal of up to 93% of shoots and 75% of rhizomes in an area has been documented (DeIongh et al. 1995, Masini et al. 2001). It has been suggested that dugong grazing works to arrest development of the climax seagrass community, maintaining an early seral stage which favours species preferred by dugongs like *Halodule uninervis* and *Halophila ovalis* (Aragones et al. 2006). However, cessation of ploughing of seagrass beds by dugongs had led to a decline of seagrass in some regions (Jackson et al. 2001), possibly because their ploughing action also buries seeds or grinds the seed coat, thus facilitating germination (Peterken and Conacher 1997).

Apart from grazing by mega-herbivores, the impacts of other herbivores such as sea urchins, gastropods and herbivorous fish on seagrass abundance and productivity should not be underestimated. For instance, the sea urchin *Lytechinus variegates* has significant negative impacts on seagrass biomass at densities of 10-40 individuals m^{-2} (Valentine and Heck 1991), and such continuous grazing could cause permanent denudation of seagrass beds (Heck and Valentine 1995) and create sandy unvegetated patches (Camp et al. 1973). For example, in Florida Bay, Rose et al. (1999) documented that extremely high sea urchin densities (upto 300 individuals m^{-2}) converted lush green *Syringodium filiforme* meadows into a mosaic of heavily and lightly grazed patches, interspersed with unproductive, unvegetated areas. Such overgrazing could increase siltation, which in turn could increase turbidity (Camp et al. 1973) affecting seagrass biomass and productivity.

Several species of herbivorous fishes also consume substantial amounts of seagrass. Kirsch et al. (2002) directly estimated the amount of turtlegrass (*Thalassia testudinum*) tissue lost to grazing parrotfish. To estimate grazing intensity, the areal losses of tissue to these fish were compared to the daily production of tissue. The study found that though parrotfish had a modest impact on seagrass density, they consumed some 80% of aboveground production (Kirsch et al. 2002). The lack of a statistically significant relationship between seagrass density and grazing impact could be due to seagrass compensatory growth (Valentine et al. 1997, Moran and Bjorndal 2005). Using comparable methods, Tomas et al. (2005) estimated that herbivorous fish consumed as much as 70% of seagrass production, therefore proving to be significant seagrass grazers in areas where their populations are high. All these examples suggest that grazing of seagrasses is an important mechanism by which seagrass meadow dynamics are regulated.

The impacts of herbivory on seagrass growth and productivity could be quite variable as there are many factors that could influence the response of seagrasses to grazing. These factors include the dependence of seagrass on seasonal resource fluctuations (Heck and Valentine 1995), grazing intensity (single defoliation events or continuous grazing) (Cebrián et al. 1998), and varying light intensity (Valentine et al. 2000). Nevertheless, while the explicit nature of grazing interactions is yet to be completely understood (Cebrián and Duarte 1998), the surmise that direct grazing of seagrasses is minor should be dealt with cautiously. The examples cited here present an accumulating body of evidence suggesting that seagrass-grazer interactions could possibly regulate seagrass meadows and that seagrass herbivory, though reduced in a historical sense, can potentially represent an important and often underestimated trophic pathway.

1.2 Green turtles and the Agatti lagoon, Lakshadweep

The lagoons of the Lakshadweep atolls support seven seagrass species (50% of India's seagrass species diversity with dense meadows in the islands of Minicoy, Kavaratti and Agatti (Venkataraman and Wafar 2005). The focus of the present study, the Agatti lagoon in the Lakshadweep archipelago, is dominated by *Thallasia hemprichii* and *Cymodocea rotundata* (Jagtap 1998, Jagtap et al. 2003) with *Thalassia* contributing almost 90% of above ground biomass (Jagtap 1991). The island has been identified as an important year-round foraging ground for green turtles (Tripathy et al. 2002). Although globally threatened and regionally important, the green turtle is locally very abundant in the Agatti lagoon (Tripathy et al. 2002). A recent study done by Tripathy et al. (2007) documented intensive use of the Agatti lagoon by a large number of turtles in different life stages, implying that this could be a self sustaining breeding population. Green turtle densities encountered in these lagoons rival some of the highest recorded anywhere globally (Tripathy et al. 2007, Arthur pers comm.). Given these unusually high densities and their possible resident status, the shallow, enclosed Agatti lagoon presented a globally unique opportunity to study the potential impact of high green turtle herbivory on seagrass structure and dynamics, in conditions closer to a pristine past, in terms of 'natural' green turtle densities.

2. OBJECTIVES

This study focussed on the grazing relationship between green turtles and seagrass meadows in the Agatti lagoon, Lakshadweep.

The objectives of this study were

1. To assess the density of green turtles and map their distribution patterns in relation to the spatial distribution of the seagrass meadows in the Agatti lagoon
2. To study the magnitude and impacts of turtle herbivory on seagrass meadows across a gradient of turtle densities and through a simulated turtle herbivory experiment

The major questions asked were-

a. What are the densities of green turtles in the Agatti lagoon, and how are they spatially distributed in relation to food (seagrass) resources?

b. What are the levels of herbivory experienced by seagrass meadows across a gradient of green turtle density?

c. How do differences in green turtle herbivory affect seagrasses, at the level of the shoot, the population and the meadow?

The study was carried out between December 2006 and April 2007.

3. STUDY AREA

3.1 The Lakshadweep archipelago

The study was carried out on the island of Agatti in the Lakshadweep archipelago. The Lakshadweep group of islands, located in the northern Indian Ocean, comprises 36 coral islands occupying a total land area of approximately 32 km^2, between 8-12° 30′ N and 71-74° E (Fig 1). These islands are at the northern end of the 2500 km Laccadive-Chagos ridge, which is presumed to have resulted from the northward migration of the Indian tectonic plate. Although the total land area covered by the island is quite small, the islands are scattered over a vast stretch of ocean covering about 20,000 km^2 of Indian territorial waters and 40,000 km^2 of the Exclusive Economic Zone. The area covered by the lagoons is 4200 km^2. Of the 36 islands, 10 are inhabited, 14 are uninhabited, three are reefs, five are submerged banks and four are temporary sandbars that remain exposed for at least four months in a year.

3.2 Physical features

Most of the islands are completely enclosed within coral reefs and almost all the atolls have a northeast – southwest orientation with the low lying islands on the east, a broad well-developed reef on the west, and a lagoon in between, connected to the open ocean by one or more channels. The western aspect is of the atoll is less sheltered as this side faces the onslaught of the south-west monsoon. In fact, this shapes the geomorphology of island formation, which is why most islands form on the easternmost aspect of the atoll, as sediments are built up on this aspect. The lagoons are saucer shaped shallow water depressions between the reefs and the islands, varying considerably in depth (3.6-8.0m) and in area (1 km^2-150 km^2). The lagoon bottoms are mostly covered with sand, coral or algal debris.

3.3 Climate

Lying well within the tropics and extending to the equatorial belt, these islands have a typical tropical humid and warm climate, becoming more equatorial in the southern islands of the archipelago. From the point of view of temperature, the climate is equable and air temperatures range from 17°C to 37°C with March, April and May being the hottest months of the year.

The region is strongly influenced by strong wave and current conditions during the southwest monsoonal system. The southwest monsoon period is the chief rainy season which lasts from late May to early October. The atolls have a distinct windward (west) and a leeward (east) aspect in relation to the monsoon.

The average annual rainfall in the region is 1600 mm. The sea surface temperatures range from 28°C to 31°C, while salinity varies from 34-37°/000. A high tidal range is experienced in the region, with spring tides ranging from 0.3m to 3.0m. As a result, wide stretches of the intertidal zone get exposed at low tide.

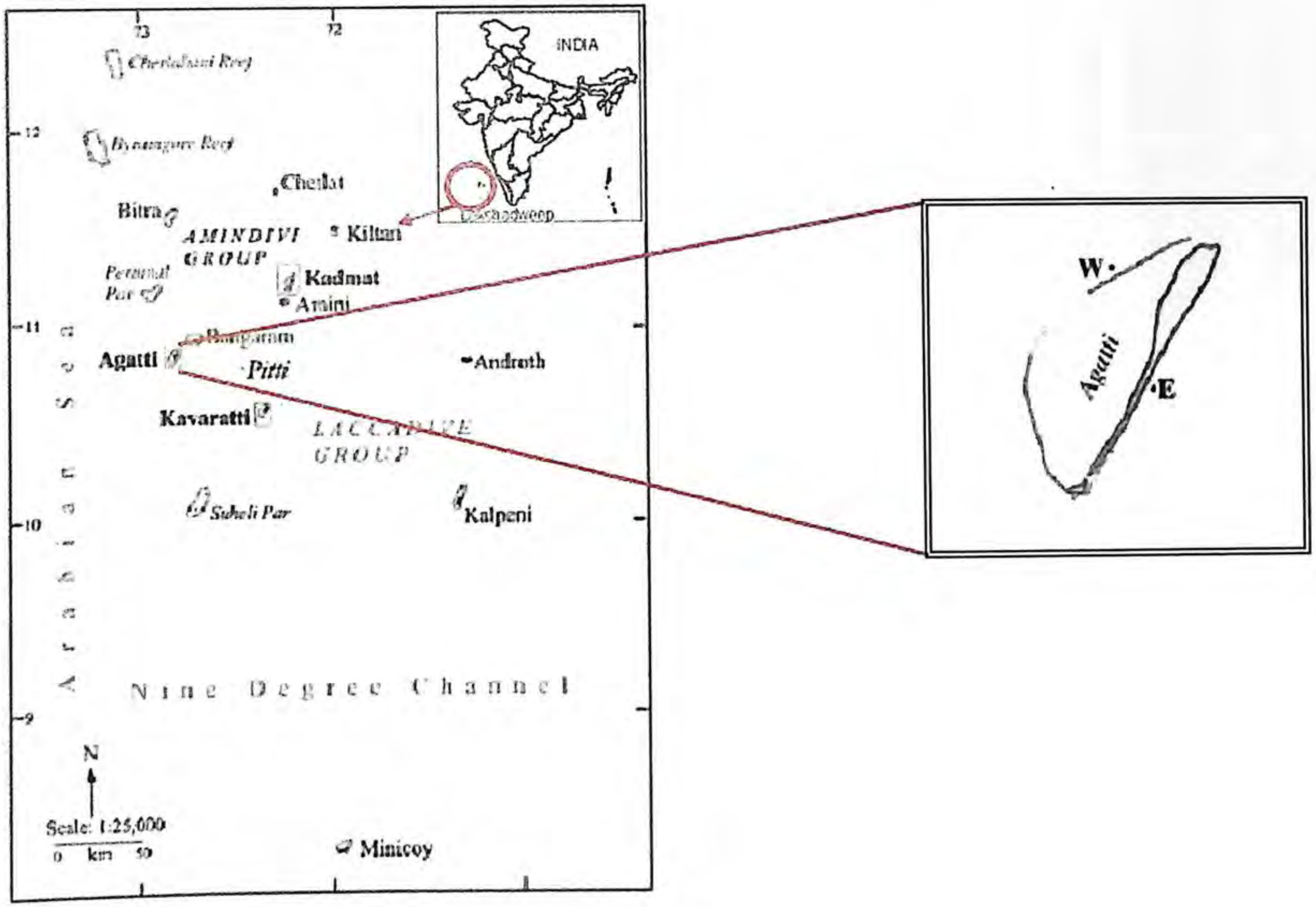


Fig 1. Map showing the islands of the Lakshadweep archipelago and their location in relation to the India subcontinent (inset). The study area, Agatti Island, part of the Laccadive group of islands has been enlarged.

3.4 Vegetation

Given the uniformity of climate, topography and soil on all the islands, the vegetation characterizing all the islands is very similar. The original vegetation was dominated by sand dune species like *Clerodendrum inerme*, *Ipomoea pscaprae, Launaea sarmentosa, spinifex littoreus, Suriana maritime* and littoral shrubs such as *Pemphis acildula* and *Scaevola serica* on the western shore with species like *Cordia subcordata* and *Guettarda speciosa* on the eastern shore. However, very little of the original vegetation remains, with most of the land under coconut plantation (*Cocos nucifera*) together with species like drumstick *(Moringa Oleifera)* and bread fruit *(Artocarpus incise*).

Mangroves are practically absent on all these islands, except for a tiny patch in Minicoy Island consisting of two species, *Ceriops candolleana* and *Bruguiera cylindrica*. The shallow island lagoons support rich seagrass beds with 50% of India's seagrass species diversity (section 1.2)

3.5 Fauna

Given the diverse marine life present in the Lakshadweep Sea, this section is limited to the description of the most common terrestrial animals and some commonly observed marine forms. There are no native mammals on the islands however; cattle, goats, poultry birds and domestic cats are common in the inhabited islands.

Some of the oceanic birds which are commonly seen are sooty tern *(Sterna fuscata),* large crested tern *(Sterna bergiivelox),* brown noddy *(Anous stolidus piletus)* and the bridled tern *(Sterna anethetus)*. Some of the migratory birds are American golden plover *(Pluvialis dominical)* and the whimbrel *(Nuemenius phaeopus)*. The common pond herons *(Ardeola grayii)* and reef herons *(Egretta* spp.*)* are also seen on the islands.

Among reptiles and amphibians the most common include two geckoes (*Hemidactylus* spp.), two agamid lizards *(Calotes versicolar* and *Calotes liocephalus*). Snakes include the common wolf snake (*Lycodon aulicus*), *Lycodon travancoricus* ("Beddomes" wolf snake) and the worm-snake *Typhlops braminus*.. *Duttaphrynus melanostictus* and *Hoplobatrachus tigrinus* are the common frog species found.

The marine reptilian fauna of Lakshadweep is very rich with with four of the seven species of marine turtles being reported from this region. This includes Green turtles *(Chelonia mydas),* Hawksbill *(Eretmochelys imbricata),* Olive Ridley *(Lepidochelys olivacea*) and the leatherback turtle *(Dermochelys coracea)*, this last reportedly very rare in Lakshadweep waters.

3.6 People and Economics

The indigenous population of Lakshadweep is Muslim, belonging to the Shafi School of the Sunni sect. The population of the islands is 60,595 according to the 2001 census (Shukoor et al. 2002). The language spoken on most islands of the Lakshadweep is Jessri, a dialect of Malayalam. In Minicoy, the people speak Mahl, which is very similar to the Maldivian Dhivehi, and shares a common script with it. Fishing is the basic economic activity on these islands, with an estimated 6000 fishermen and about 850 tuna fishing crafts (Venkatraman and Wafar 2005). The fishing season in Lakshadweep extends from October to April. However during the monsoon, (October to April), fishing is carried out in near shore waters, mostly in the lagoons. Gill net, shore seine, anchor net and dragnets are popularly used for lagoon fishing but the largest catch comes from pole and line, which is used for deep sea tuna fishing. The current annual fish landing is estimated at 10,000 tons, consisting mainly of tuna and other commercially viable finfish (Shukoor et al. 2002).

3.7 Agatti

The focus of the present study Agatti Island is one of the ten inhabited islands of the archipelago with and a population of ~ 7000 people (Census of India 2001) (Fig 1). It is the most westernly located island of the group, club shaped, with a broad northern part and narrow southern tip. It is 8 km long and 1 km broad at its widest point and covers an areal extent of 3.84 km^2. The lagoon also encloses the uninhabited island of Kalpitti, which is situated at the southern tip of Agatti and separated from it by a narrow channel connecting the eastern and western lagoon. Thick coconut groves occupy the northern side of the island while scrub jungles dominate the southern side.

As mentioned above, one of the seagrass species dominating the Agatti lagoon is *Cymodocea rotundata*, the species chosen for this study. Given below is a brief introduction to the morphology and phenology of the species.

3.7.1 Cymodocea rotundata

Seagrasses are flowering angiosperms that evolved in the Cretaceous period from terrestrial ancestors. "Seagrasses" is more of a functional group referring to fully submerged angiosperms sharing numerous convergent morphological and physiological characteristics (Larkum and den Hartog 1989). Genetic studies suggest that seagrass diversity potentially represents three separate evolutionary events that physiological characteristics (Larkum and den Hartog 1989). Genetic studies suggest that seagrass diversity potentially represents three separate evolutionary events that resulted in plants that have co-evolved for a completely marine existence (Waycott and Les 1996). *Cymodocea rotundata* is fast proliferating and short lived and is regarded as a "pioneer" species in mixed seagrass communities; as compared to slower growing and long lived "climax" species like *Thallasia* spp. (Brouns 1987). This species is typically a shallow water species, dominating depths ranging from 0.5m to about 35m depth. The genus Cymodoceoideae is monopodial in their branching pattern (Tomlinson 1974) where branching of the rhizome is the main mechanism for vegetative propagation of the plants (Fig 2). These plants are dioecious, with both male and female flowers. Flowering begins with the rise in sea water temperature after the winter, where a minima in growth is seen (Reyes et al. 1995). In April, male and female flowers are easily recognizable, and by the end of the month young fruits can be observed (Reyes et al. 1995). In May, both male and female flowers can still be detected, with pollination reaching an advanced stage in this month. By June, all flowers senescence. The germination of seeds is usually from February to September.

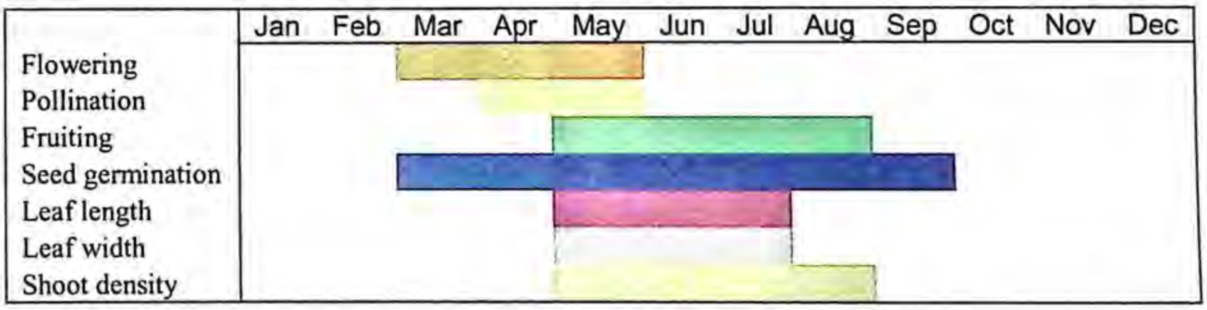


Fig 2. Schematic representation of the morphological and reproductive phenology of *Cymodocea nodosa* a closely related species of *Cymodocea rotundata*. The extent of the highlighted portions represents the period when the event is most intense during the year, while the lightly shaded area corresponds to the sampling period. (Modified from Reyes et al. 1995)

4. METHODS

4.1 Describing spatial patterns of habitat types and green turtles across the lagoon

4.1.1 Distribution of habitat types

4.1.1.1 Sampling design

To assess the spatial distribution of habitats, a grid of a predetermined size was established over the study area. For this study, a 300m x 300m grid was used (Fig 3). The grid was generated using ArcGIS (v.9, 2004, ESRI Inc.) This grid size was chosen as it has been reported to be of a suitable resolution to capture habitat heterogeneity in seagrass meadows (Sheppard et al. 2007) and quantify habitat selection by turtles. Percent cover of habitat types were visually estimated (see below). It was assumed that the spatial distribution of habitats was stable throughout the survey and that observations differed only through measurement error (Reuda 2001).

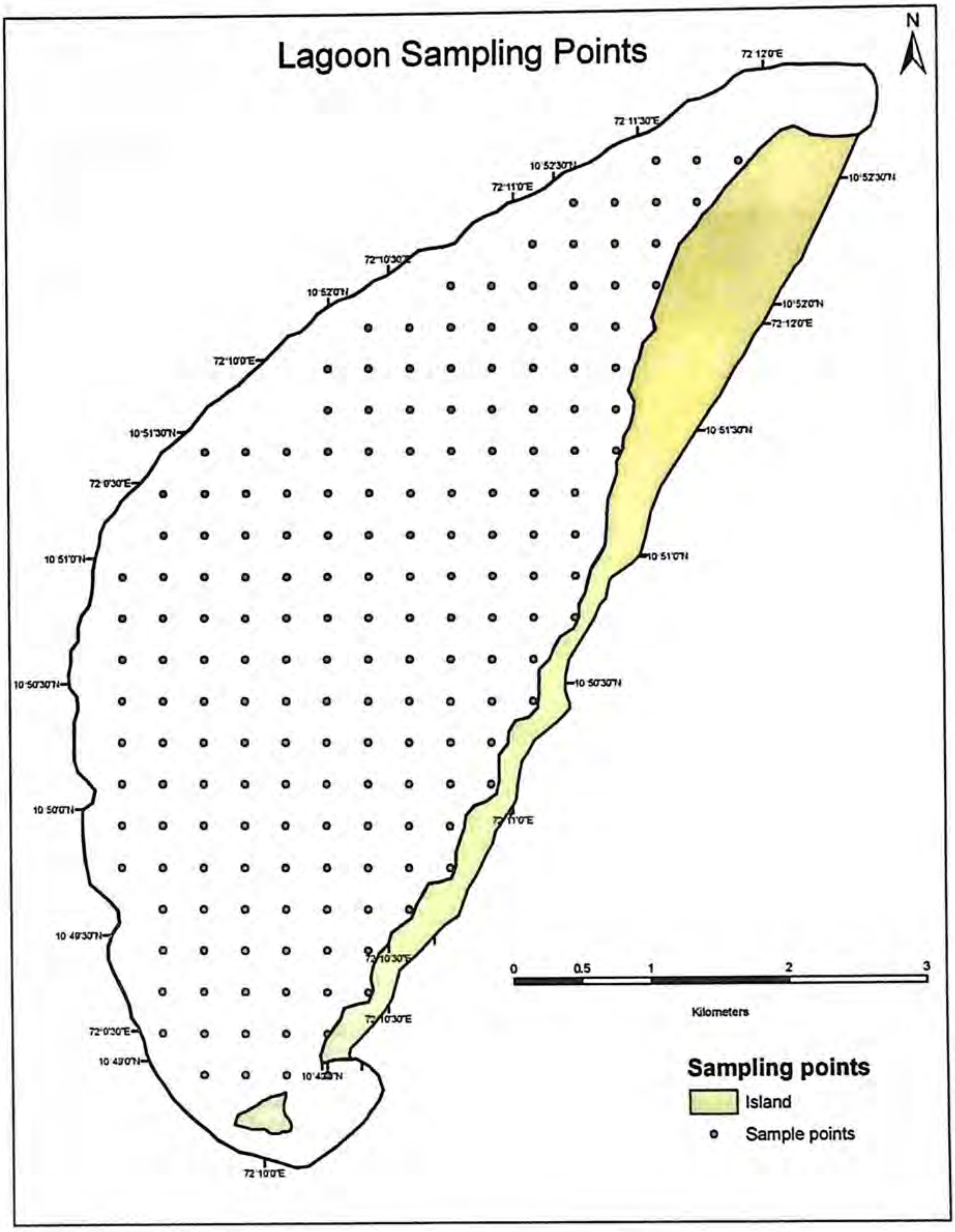


Fig 3. 300m x 300m grid placed on Agatti lagoon, with each point corresponding to a habitat sampling point resulting in 187 lagoon habitat sampling points across a 20 km^{-2} area of lagoon

4.1.1.2 Field methods

Habitat type was quantified at the node of each cell, each point defined by latitudinal and longitudinal co-ordinates (Bulit et al. 2003). Since all the points were subtidal, they were located by boat using a handheld GPS and sampled using a 50 cm x 50cm quadrat with an attached weight and rope allowing it to sink to the substrate. In a 5m radius from the centre of each point, five quadrats were laid at two metre intervals along a 10m rope and percent cover of the benthic community visually estimated (see Dorenborsch et al. 2004). In order to get an estimate of the measurement error associated with this sampling methodology, each point was measured on three separate occasions during the study period. In addition, a standardisation exercise was carried out to determine the error involved in visual estimation. In order to do this, for each quadrat, shoot density was first visually estimated before shoot density was calculated by counting each shoot in the quadrat. This was done across a gradient of shoot density, to determine the reliability of visual estimation at different densities.

Lagoon habitats were divided into four primary types based on Adams and Ebersole (2002):

- Reef: part of the contiguous reef that encloses the lagoon. These were further classified into live and dead coral.
- Rubble: low relief, calcareous structure composed primarily of shells or dead/dying coral fragments that was not attached to the substrate; rubble habitat occured over extended areas or as isolated fragments within seagrass, sand, or algal plain habitats.
- Seagrass beds: since *Cymodocea rotundata* was the dominant species in the Agatti lagoon, seagrass beds were described as monospecific, or nearly

monospecific, stands of *Cymodocea rotundata,* with varying densities of *Thallasia hemprichii.*

- Sand plains: areas of open sand with no or very little (>10%) cover of plants or coralline material.

Depth as a habitat correlate was also measured at each point. Water depth at each sample point were matched with the tide height at the time the sample was recorded and adjusted to give the water depth at mean sea level (MSL) and high tides.

This point data for habitat as well as bathymetry was used to create GIS surface distribution maps for each habitat type as well as a depth profile for the lagoon (see section 4.5.1).

4.1.2 Turtle distribution in the lagoon

Open width line transects (using a diesel powered fishing boat) formed the basic sampling unit for quantifying distribution patterns and densities of turtles. Perpendicular sighting distance and angle of sighting was visually estimated for each individual sighting. Transect length depended on the distance between the shore and the reef. Since the transects were based on the grid points, they were placed systematically equidistant from each other and perpendicular to the shore. This design resulted in 23 replicate transects (A-W) across the lagoon (Fig 4). To minimize the effect of environmental conditions on the accuracy of the data, surveys were conducted in daylight from 0800hrs to 1400hrs in comparable weather conditions, under clear or partly cloudy skies, where wind speed did not exceed 7km/hr. An effort was made to reduce the effects of tidal variation by sampling only at high tide. Also, boat speed did not exceed 8km/hr. Since it has been noted that daily variation in target organisms can affect such data (Drapeau et al. 1999), repeats were carried out on nonconsecutive days to minimize the effects of daily movement. The surveys were repeated eight times.

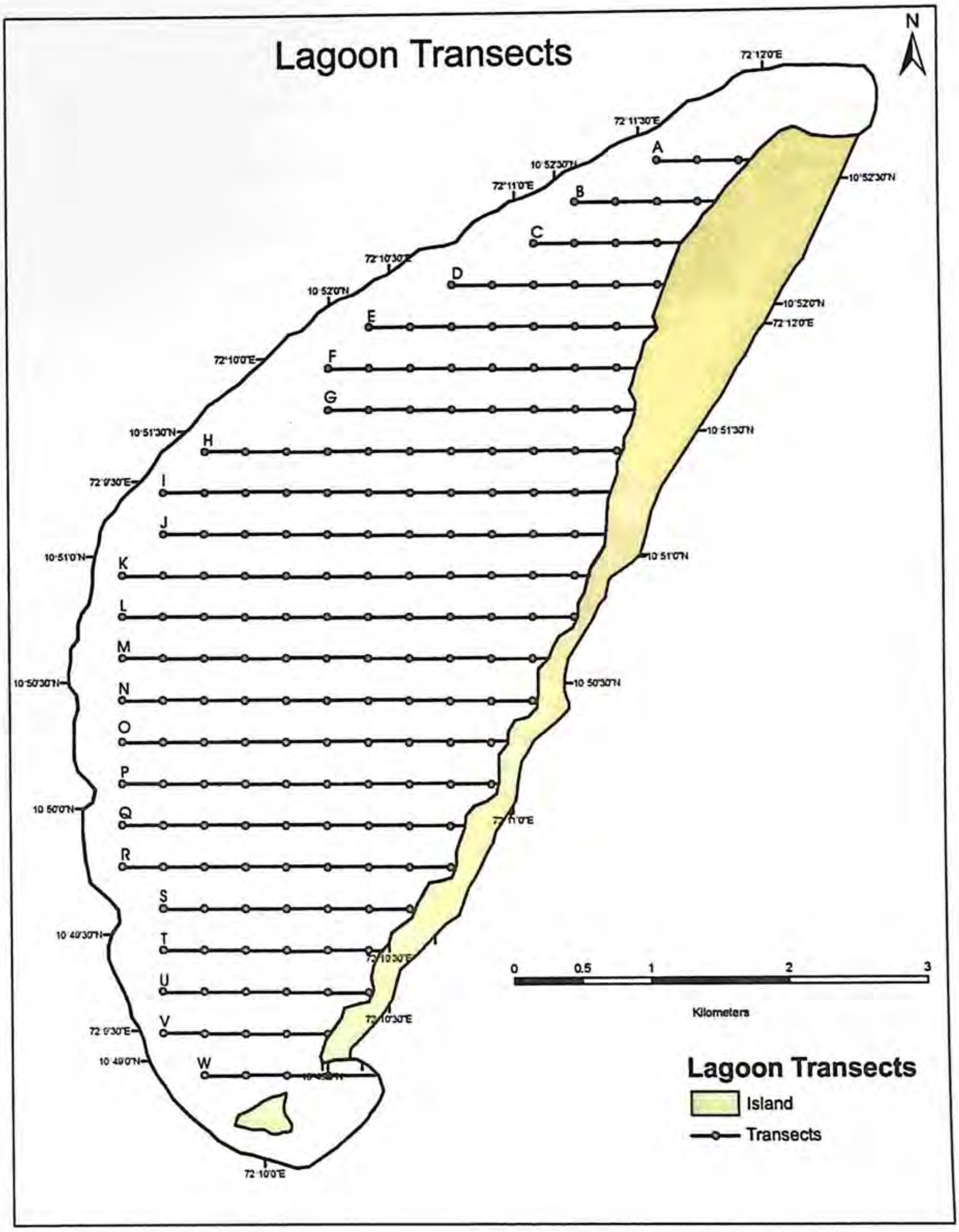


Fig 4. 23 Transects A-W placed systematically 300m apart across the lagoon. Transects were numbered alphabetically from A-W (north to south) and were of varying lengths depending on the distance between the shore and the reef

4.1.2.1 Habitat stratification

Three zones in the seagrass meadow were identified in the western lagoon along a gradient of turtle density, identified from the turtle sampling described in 4.1.2. These strata, representing areas of relatively low, medium and high turtle densities, were used to examine the impacts of turtle density and herbivory on seagrass meadow dynamics. The three zones were defined by mean encounter rates obtained along the transects with high areas characterised by an encounter rate of 16.1 turtles/km, moderate by 11.2 turtles/km and low by 3.7 turtles/km (Fig 5). The northern and southern ends of the lagoon had extensive seagrass meadows that were relatively unaffected by confounding extraneous factors (e.g. effluent discharge from a coir factory), and these were considered to be relatively comparable sites for further work. The site chosen as the moderate turtle density site had other confounding factors such as proximity to a resort which potentially affected seagrass dynamics at this site. Seagrass leaves at this site were heavily colonised by epiphytes possibly because of point sources of nutrient inputs (Van Montfrans et al. 1984). However while the site was used for measurements of seagrass production, it must be recognised that production could be heavily influenced by these factors.

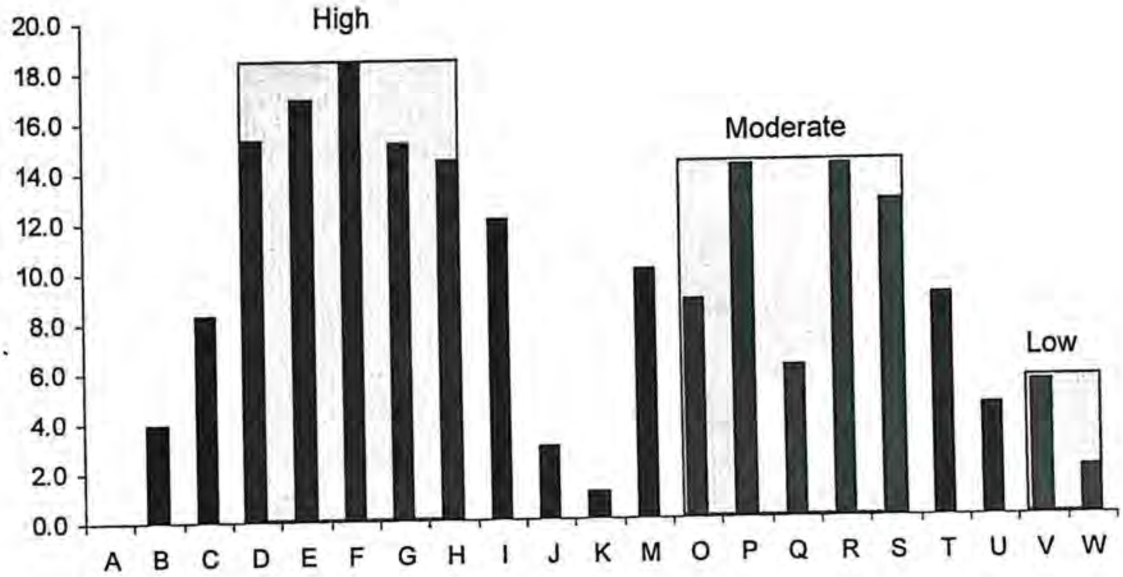


Fig 5. Zones used for stratification of seagrass habitat based on encounter rates for each transect within the seagrass habitat. Zone 1= high turtle abundance (average 16.1 turtles/km). Zone 2= moderate turtle abundance (average 11.2 turtles/km). Zone 3 = low turtle abundance (average 3.7 turtles/km). Encounter rates presented here represent an average across all eight turtle surveys

4.2 Magnitude of turtle herbivory

4.2.1 Sampling design

A feeding assay was carried out to obtain an indirect instantaneous measure of the intensity of green turtle grazing on *C. rotundata* leaves. This tethering experiment (See Mariani and Alcoverro 1999, Kirsch et al. 2002) used *C. rotundata* leaves as it is the dominant species in the Agatti lagoon As far as possible, shoots with undamaged leaves were chosen, without extensive grazing scars (i.e. jagged edges signifying urchin grazing; McClanahan et al.1994, or crescent shaped bite marks signifying fish grazing; Kirsch et al. 2002) or necrosis.

An indirect measure of herbivory, that is, the proportion of grazed leaves at each site (Armitage and Fourqurean 2006), was also estimated by recording grazing signs on each leaf of the shoots collected for quantifying herbivory impacts.

4.2.2 Sample preparation

The shoots used for this experiment were collected from Agatti's eastern lagoon where majority of the leaves were undamaged. After shoot collection, leaf tips were cut to remove previous grazing signs and the number of leaves per shoot, the leaf length (to the nearest mm) and the presence of any lateral bite marks were recorded. To ensure minimum stress to the plants, they were kept submerged in containers of sea water during the handling period.

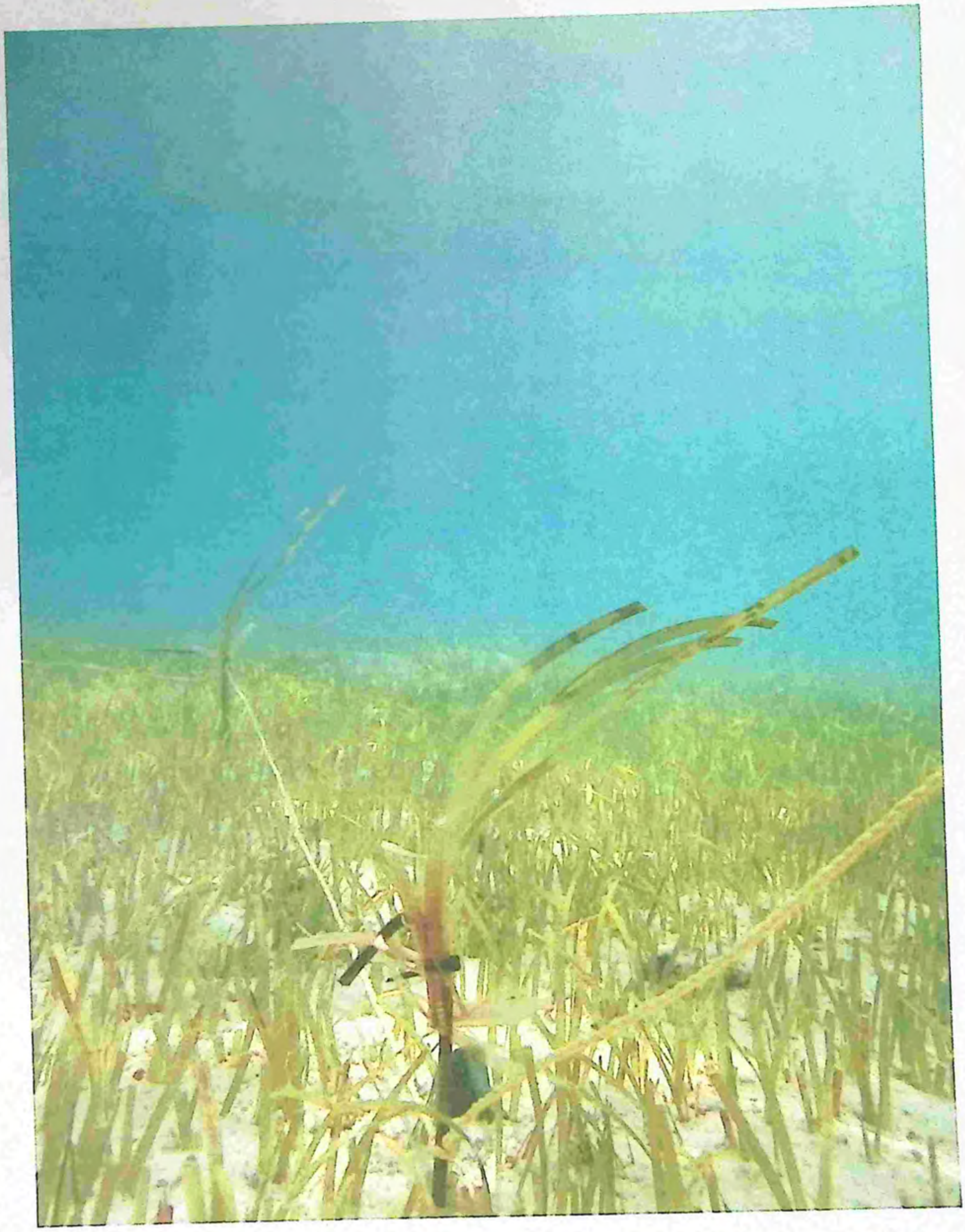
Following this, fifteen tethers per site were prepared. Each tether consisted of two selected seagrass shoots attached by their vertical rhizome to a numbered and labeled metal picket. There were fifteen such pickets per site, attached to each other with a rope and separated from each other by a minimum distance of 0.5m.

4.2.3 Field deployment

Fifteen tethers (replicates) were placed randomly at the low, medium and high turtle density sites (Plate I). The depth at which they were placed ranged from 1.5m to 3m depending on the site. One line of pickets was also placed in the eastern lagoon as a control as the number of turtles in this area is negligible. At each site, the pickets were secured to the bottom, taking care to ensure that the leaves were neither above nor below the average seagrass canopy height. Sites were marked with buoys and landmarks. All shoots were removed two days after the start of the experiment.

After retrieval of the shoots, the final leaf length and the number of leaves per shoot that were missing, broken, intact or grazed were determined. For each shoot, the amount of herbivory (length consumed in one day) was calculated by subtracting the initial leaf length from the final length for each leaf.

Plate 1



Herbivory assay showing one of tethers (two shoots attached to a metal picket by a clamp tie) in the seagrass meadow. Tethers were attached to each other by a rope and there were 15 tethers at each site

4.3 Herbivory impacts on *Cymodocea rotundata*

4.3.1 Seagrass terminology used

The terminology used here mainly follows that of Tomlinson (1974). *Cymodocea rotundata* spreads vegetatively with the help of rhizomes. These may by horizontal (long shoots) or vertical (lateral short shoots). A shoot is defined as a combination of short-shoot and its corresponding leaves, which arise from growing meristems at rhizome apices. A rhizome piece is defined as interval between two successive short-shoots. After senescence, each leaf leaves a scar on the vertical rhizome. The interval between two leaf scars is termed as an internode (Fig 6).

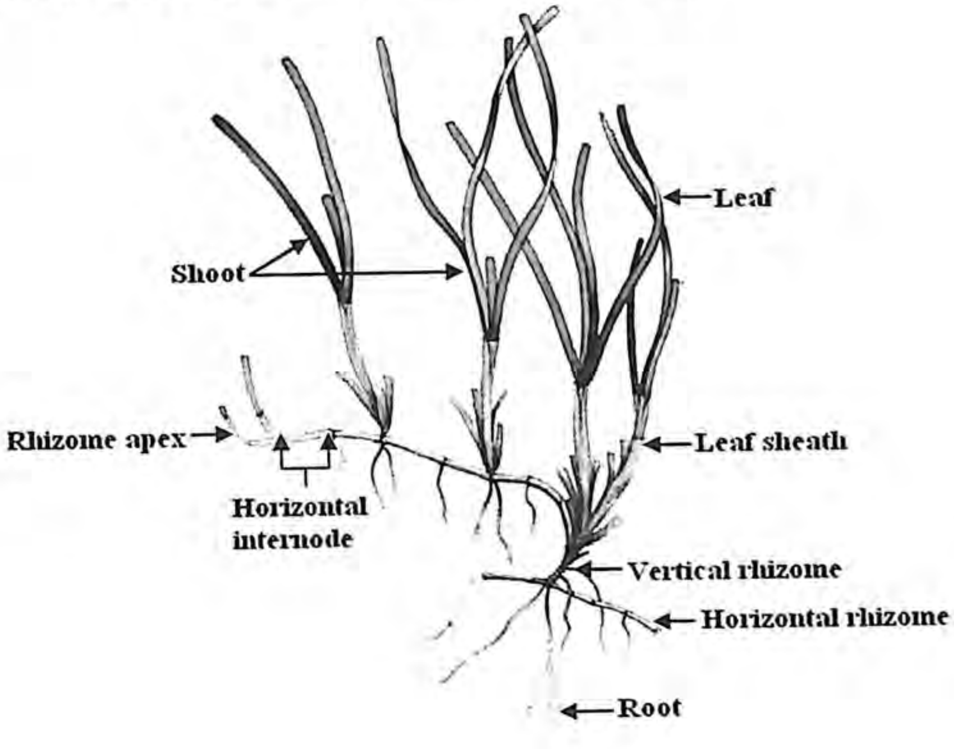


Fig 6. Labelled diagram of a typical *Cymodocea rotundata* shoot cluster

4.3.2 At the shoot level

Grazing impacts on *C. rotundata* shoot structure was examined by randomly collecting 100 shoots from a 1.8 km^2 area within each of the three zones. The number of leaves per shoot, leaf length and width was measured for each leaf on every collected shoot using a vernier calliper (Cebriàn et al. 1996). Leaf length was measured from the leaf blade/sheath junction to the leaf tip and width was measured at the widest part of the leaf (Short and Duarte 2001). In addition, leaf production rates for each site were also estimated. Leaf production rate per shoot was determined by Zieman's leaf marking method (Zieman 1975, Zieman et al. 1984). At each site, 20 randomly selected shoots were punctured with a hypodermic needle at the base of every leaf, just above the shoot sheath. All marked shoots were collected after a period of 10 days. Leaf growth rate per shoot (cm shoot^{-1} day^{-1}) was quantified as the sum of the distances distal to the hole in the marked leaves plus the length of any new unmarked leaves (leaves produced during the 10-day period) divided by the number of days elapsed since marking. These measurements were transformed to dry weight (mg DW shoot^{-1} day^{-1}) using the average leaf growth shoot day (cm shoot^{-1} day^{-1}) and leaf specific weight (mg DW cm^{-1}) calculated from a sample of leaves dried for two days at 50°C (Cebriàn et al. 1998).

Nitrogen content of the leaves was processed using a Kjeltec 2300 Nitrogen Analyser. For nutrient analysis, the new and old leaf growth for each site was analysed separately. Leaves were oven dried for two days at 50°C, weighed, ground and then analysed for % nitrogen.

4.3.3 At the population level

At each site, a minimum of 85 living shoots forming approximately 25 shoot clusters were collected per site. A shoot cluster is defined as a group of shoots attached individually to a common horizontal rhizome axis (Vermaat et al. 1995) (see Fig 6). Clusters were collected by hand to minimise breakage of the connection between shoots and rhizomes. These samples were then sorted and measured. Seagrass shoot demography at each site was characterised by the age distribution, mortality and recruitment rate of shoots, shoot apex density and annual leaf formation rate (number of leaves produced per year; Marba and Walker 1999). Net population growth rates at each site were also estimated.

4.3.3.1 Shoot age distribution

Shoot age was calculated as the product of the total number of leaves produced on the shoot (i.e. number of standing leaves plus number of leaf scars (internodes) on the vertical rhizome) and the leaf Plastrochrone Interval (PI, in days; Duarte et al. 1994).

4.3.3.2 Shoot mortality, recruitment and population growth rate

Exponential shoot mortality rates (M, in units yr^{-1}) were determined using the equation given by Duarte et al. (1994).

$$N_t = N_0 \, e^{-mt}$$

Where N_0 = number of shoots equal to the modal age and N_t = number of shoots older than the modal shoots by time t. Mortality (M) was estimated as the slope of a regression model (Marba et al. 1996). The annual gross shoot recruitment rate (R_{gross} in units yr^{-1}) was calculated using the equation given by Duarte et al. (1994).

$$R_{gross} = \ln \sum N_{t1} - \ln \sum N_{t2}$$

Where N_{t1} is the total number of shoots and N_{t2} is the number of shoots older than a year.

Net shoot population growth rate was estimated as

$$R_{net}= R_{gross}-M$$

To estimate the proportion of horizontal rhizome apices per shoot (apex density), the number of apical shoots in each rhizome piece was determined (Marba and Walker 1999).

4.3.3.3 Annual leaf formation rate

The annual leaf formation rate was calculated from the seasonal variability in vertical shoot growth using 10 to 20 of the oldest living shoots harvested at each site following the methodology described by Duarte et al. (1994). The evident pattern in the sequence of vertical internodal lengths allowed the calculation of the annual leaf formation rate. Therefore, two consecutive maxima were used to define a year and determine leaf formation rates (Fig 7). Because of the close 1:1 relationship between the production of rhizome internodes and leaves for seagrass, the number of vertical internodes produced in one year equals the number of leaves produced that year by a shoot (Duarte et al. 1994). Thus, this method provided an indirect estimate of the annual rate of leaf formation. Leaf Plastrochrone interval was calculated as the inverse of leaf formation rate.

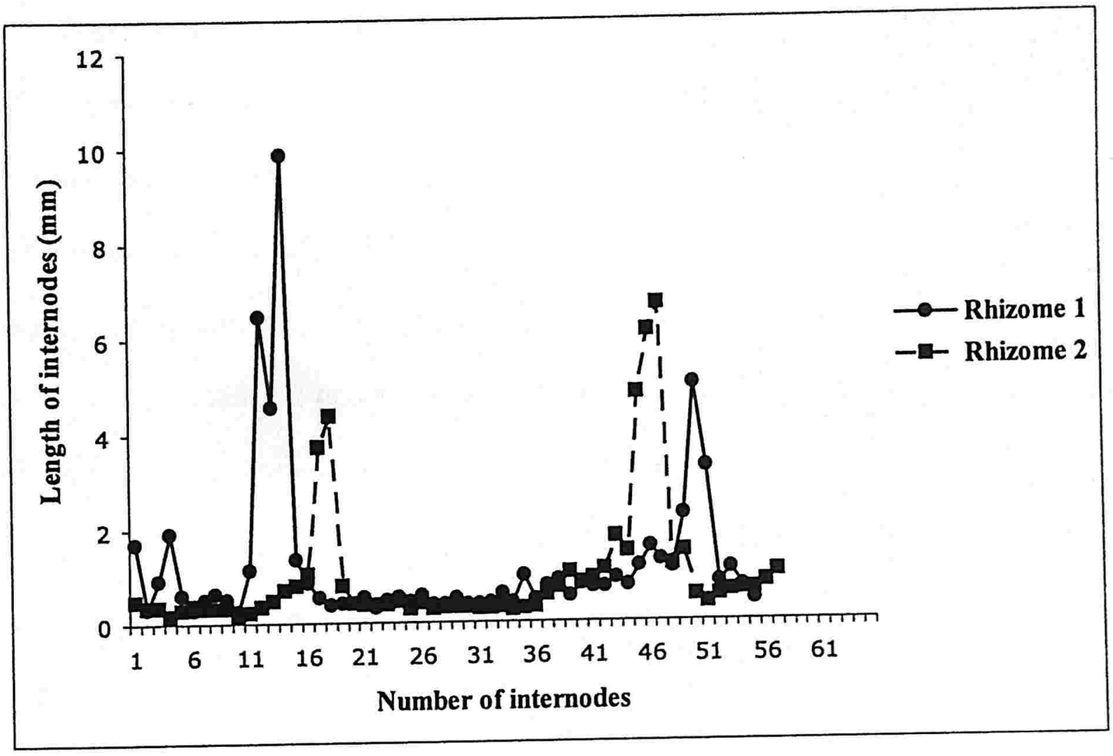


Fig 7. Sequence of vertical internodal lengths for the two oldest *C. rotundata* shoots sampled at high turtle density site. The two maxima correspond to successive monsoons, where *C. rotundata* shows a spurt in vertical growth.

4.3.4 At the meadow level

At the meadow level, seagrass abundance parameters (shoot density and above ground biomass) were assessed at the high, medium and low turtle abundance sites using standard established methods (Valentine et al. 1997). At each site, 20 replicate 50cm x 50cm quadrats were randomly placed and the number of shoots within each quadrat was counted. Shoot density per site was expressed as the average number of shoots m^{-2}. Above ground biomass, comprising of complete shoots, was determined by sun drying and weighing the collected samples. Above ground biomass at each site was determined as the product of shoot density and shoot dry weight (Short and Duarte 2001).

4.4 Experimental grazing

4.4.1 Selection of sampling sites

Simulated grazing experiments (Moran and Bjorndal 2005, Alcoverro and Mariani 2005) were carried out within a primarily monospecific *Cymodocea rotundata* meadow on Agatti's eastern lagoon. This area, with a tidal range of approximately 1.5m, acted as a natural control as no turtles were sighted in this lagoon during the study period. Also, since *Cymodocea* was the dominant species subjected to a gradient of green turtle grazing on the western lagoon, this site was seen as an appropriate experimental control to test the effects of simulated herbivory on seagrass shoot production.

4.4.2 Experimental design

These clipping experiments aimed to examine the response of shoot productivity (mg DW shoot $^{-1}$ day^{-1}) to a mimicked gradient of green turtle herbivory. Nine 1m^{-2} square plots were established in the Cymodocea meadow, with a minimum distance of 50m between plots. Each plot was marked with a buoy attached to a metal pole and flagging tape labels (Plate 2). The treatments were intended to correspond to an herbivory gradient from intact shoots to nearly total removal of the leaf (control, 50% and 80% removal of leaf surface) respectively. Therefore, clipping intensity was defined as the 'the percentage of leaf surface removed per shoot' (Cebrián et al. 1998). Treatments were randomly assigned to the plots, with three replicates for each level of the treatment. The treatment length was applied to all shoots within the 1m^{-2} area of the plot by cutting off the tips of the leaves with a pair of scissors. The experiment lasted one month, with clipping at two week intervals to simulate continual herbivory.

Plate 2

One of the nine $1m^2$ simulated herbivory experimental plots in the eastern lagoon showing the 20cm x 20cm production plots in the centre.

Leaf production was measured by the leaf marking technique (Zieman 1975, Valentine et al. 1997, Alcoverro and Mariani 2005) as described in Section 4.3.2. Almost all shoots within a 20cm x 20cm quadrat placed at the centre of each plot were marked (control and clipped plots). For nutrient analysis, the new and old growth from the marked shoots was analysed separately. % nitrogen was estimated in a Kjeltec 2300 nitrogen analyzer.

4.5 Analysis

4.5.1 Distribution of habitat types

Raster surfaces of bathymetry and each habitat type were generated from the point data using Geographical Information Systems (GIS) techniques. Seagrass meadows in particular, have been found to be successfully mapped using interpolation methods because they form continuous patches with gradual gradients and low canopy height (Sheppard et al. 2007).

In this method, each point in the grid was assigned a single value i.e. percentage cover of a particular habitat type/types. While several interpolation techniques were available, kriging was chosen because recent studies have used this method to map terrestrial grasslands (e.g. Feng et al. 2004) and have found it to be an optimal method for linear unbiased estimation and interpolation.

Ordinary circular kriging produced the best surface and was therefore chosen as the best kriging estimator by ArcGIS (v.9, 2004, ESRI Inc.). Once the seagrass meadow interpolations were generated, the class intervals were specified, which produced a map of varying densities (low to high) of each habitat type corresponding to a gradient of colour from light to dark respectively.

4.5.2 Turtle distribution

To create a raster surface for turtle distribution, each point in the grid was assigned a single value i.e. the number of turtles seen per point. In order to do this, the number of turtles sighted in each 300m transect segment between consecutive points was calculated. Subsequent analysis was the same as above.

To check for differences in detectibility across habitats and differences in Effective Strip Width (ESW), a preliminary analysis of turtle program DISTANCE 5.0 (Buckland et al. 1993, Laake et al. 1993). Since no differences in detectibility across habitat and ESW's were found, encounter rate was used for subsequent analysis. For each transect, encounter rate (number of turtles per km) was used as an index of turtle abundance (e.g. Gomèz de Segura et al. 2006). These encounter rates were calculated separately for the entire lagoon, seagrass areas and other habitat types.

4.5.2 1 Turtle distribution in relation to distribution of seagrass resources

Correlation matrices were made to see associations between the habitat variables and turtle abundances in SPSS (v.14.0) (Norusis 2005). Further correlation analysis was done using Spatial Analysis in Macroecology (SAM) (v. 2.0) (Rangle et al. 2006) to uncover relationships between correlated variables, after correction for spatial autocorrelation.

4.5.3 Magnitude of herbivory

The length of leaves lost to herbivory was averaged for each shoot. This was done for all the shoots at each site. Variation in the rate of herbivory between sites was evaluated using a one-way Analysis of Variance (ANOVA) with site as the fixed factor and the length of leaf consumed as the dependant variable. This was done following the examination of the data testing the validity of the ANOVA model's assumptions by using a Kolmogorov-Smirnov test for normality and Levene's test for homogeneity of variances. If required, data transformations were performed. When significant differences were found, Tukey's Honestly Significant Differences (HSD) test was performed for *a posteriori* comparison among sites (Sokal and Rohlf 1981). All analyses were run in SPSS (v. 14.0).

Since the data on grazing signs on leaves was of a categorical nature, the proportions of leaves with "yes" or "no" were calculated for each site. Chi-square test for multiple proportions was performed to test for differences in grazing intensity across the three sites.

4.5.4 Analyses of plant traits

Differences in shoot structural parameters, growth rates, nutrients, abundance, and biomass between sites were tested using a one-way ANOVA with site as the independent factor and the measured variables as dependant factors. This was done following the examination of the data testing the validity of the ANOVA model's assumptions. If significant differences were detected, *a posteriori* comparisons were conducted using the Tukey's test (Sokal and Rohlf 1981).

4.5.5 Experimental grazing

The variability in the rate of leaf production (g DW shoot $^{-1}$ day^{-1}) per shoot among treatments and the control was analysed using a one- way ANOVA after testing the validity of the model assumptions with the data. If significant differences were detected, Tukey's HSD was carried out to test for differences between treatments (Sokal and Rohlf 1981).

5. RESULTS

5.1 Spatial distribution of habitat types and turtles across the lagoon

5.1.1 Distribution of habitat types

Kriging interpolations of point grid data created continuous surfaces of the different habitat types from raw quadrat data. Majority of the lagoon was dominated by sand (71.97%), followed by seagrass (9.99%), reef (2.69% live coral and 6.0.5% dead coral) and rubble (7.7%) (Fig 8a, b, c, d, e, f). The middle of the lagoon was purely a sand bed, with increasing amounts of rubble towards the reef edge and towards the lagoon entrance. Live coral was found mainly on the northern side of the lagoon, with a majority of dead coral on the southern side. Rubble was concentrated towards the southern side and the lagoon entrance. Spatial interpolation of percent seagrass cover, which provides a detailed description of spatial patterns of seagrass beds, reveals clear differences in shoot density across the lagoon. Seagrass meadows covered approximately (10%) of the lagoon, with *C. rotundata* monospecifically dominating most areas. High density *C. rotundata* patches were concentrated towards the southern end of the lagoon, with low density patches towards the lagoon entrance and medium (50-60%) cover towards the northern end of the study area. *T. hemprichii* accounted for less than 5% of cover in the lagoon, increasing marginally towards the southern subtidal end of the lagoon. *Syringodium isoetifolium* was seen only once during the sampling period. All these species were of small morphology with a canopy height of >10cm. The seagrass distribution patterns documented here exhibited consistent patterns in relation to bathymetry.

Standardisation of visual estimates to estimate the error associated with visual estimates of shoot density produced a strong relationship, suggesting that that visual estimates can reliably be used to describe spatial patterns in seagrass shoot density (R^2=0.866, F= 432.05, df =1, p< 0.001) (Fig 9).

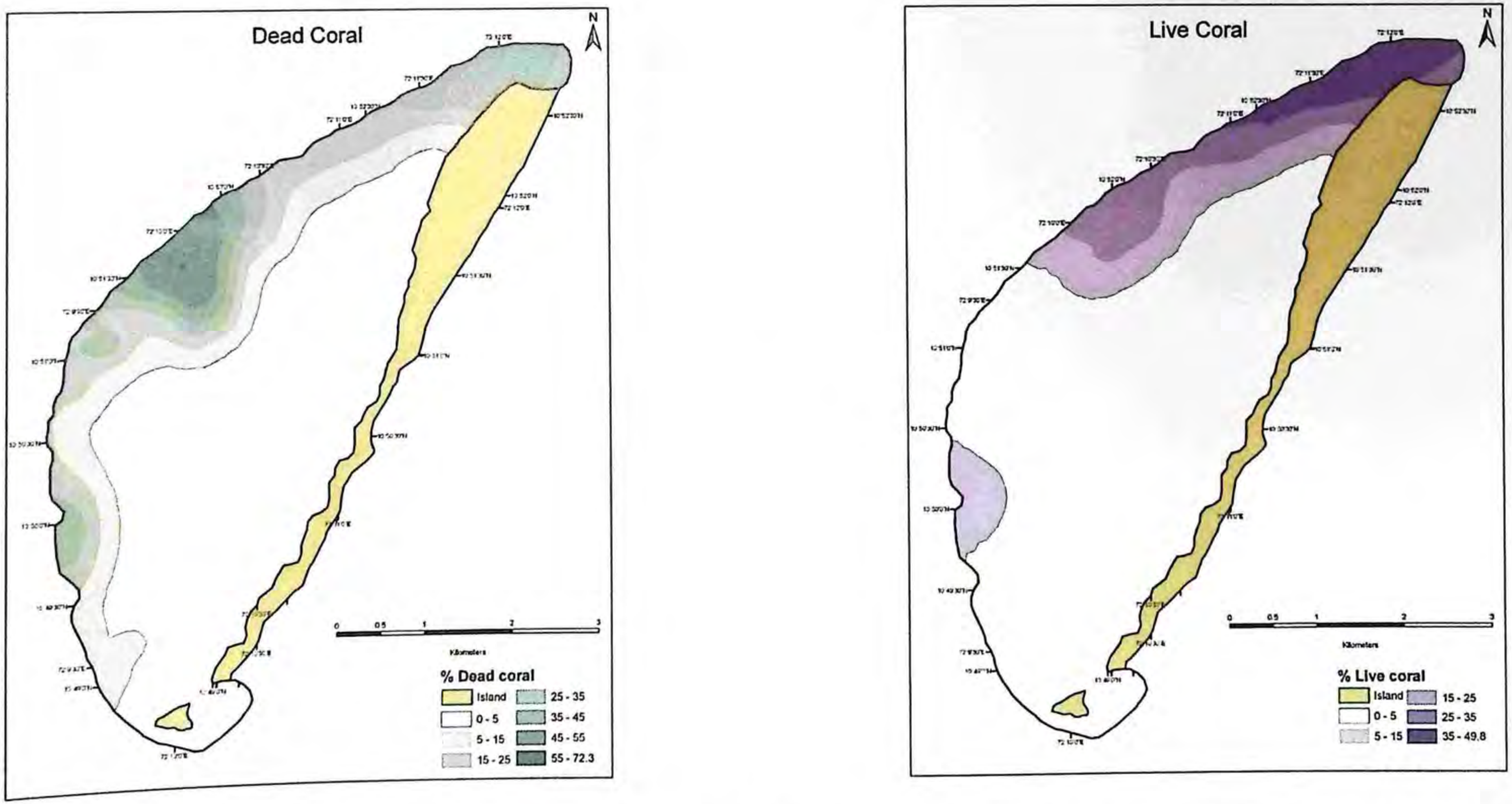


Fig 8. Kriging interpolation map of the mean percent coverage of each habitat type within the lagoon. Maps were generated from 187 sampled points (a) Dead coral (b) Live coral

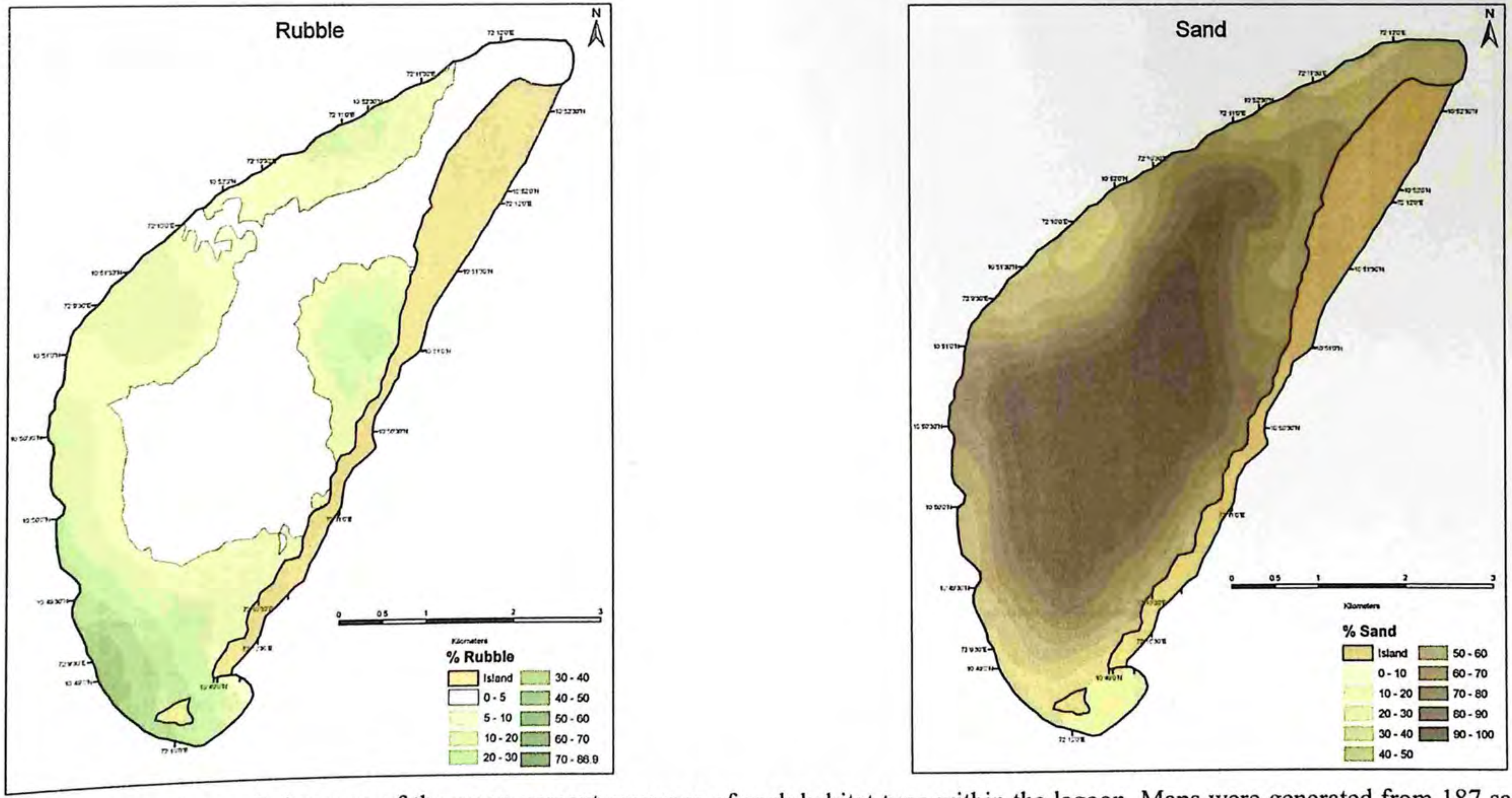


Fig 8. Kriging interpolation map of the mean percent coverage of each habitat type within the lagoon. Maps were generated from 187 sampled points (c) Rubble (d) Sand

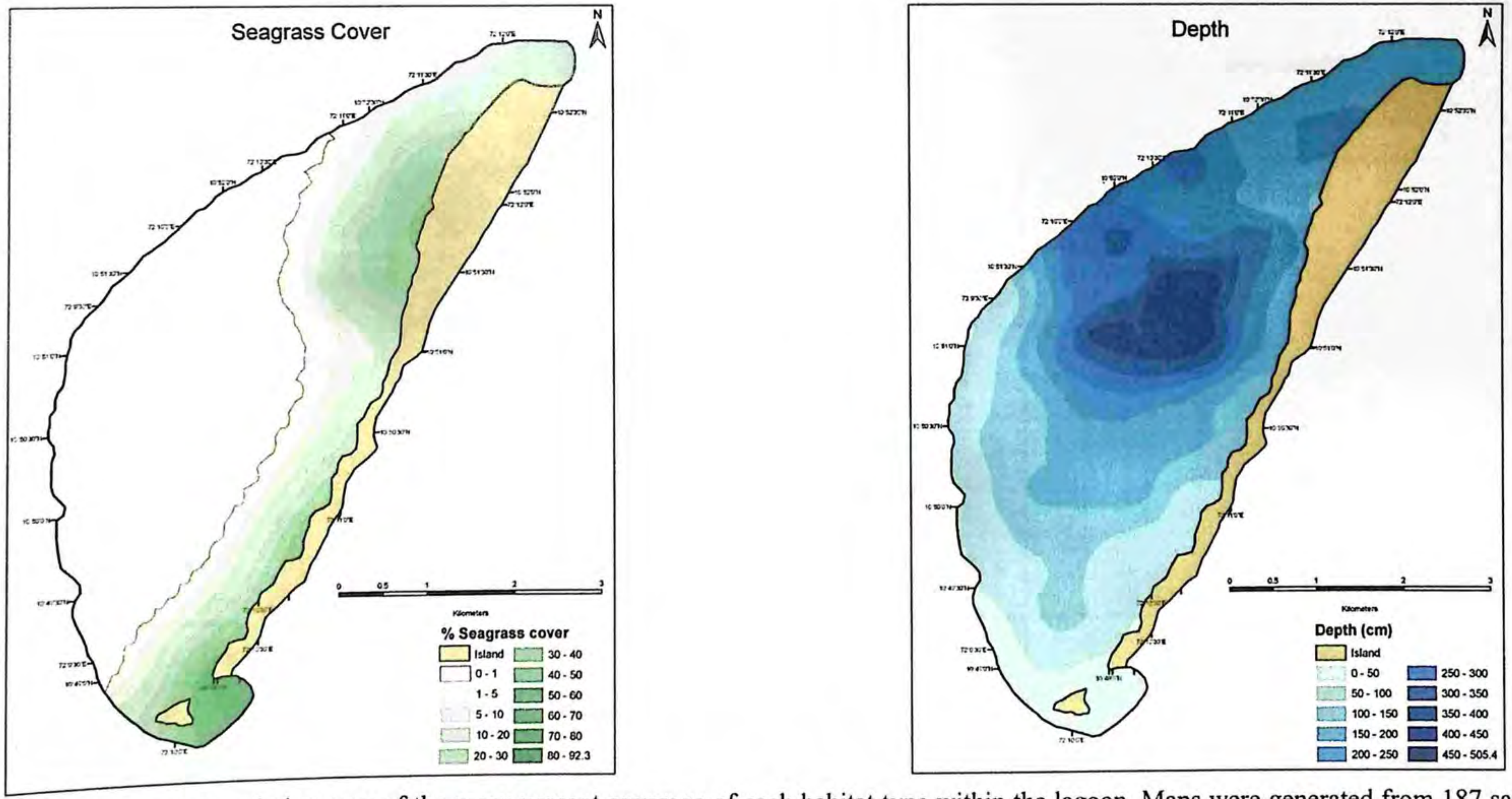


Fig 8. Kriging interpolation map of the mean percent coverage of each habitat type within the lagoon. Maps were generated from 187 sampled points (e) Seagrass (f) Depth

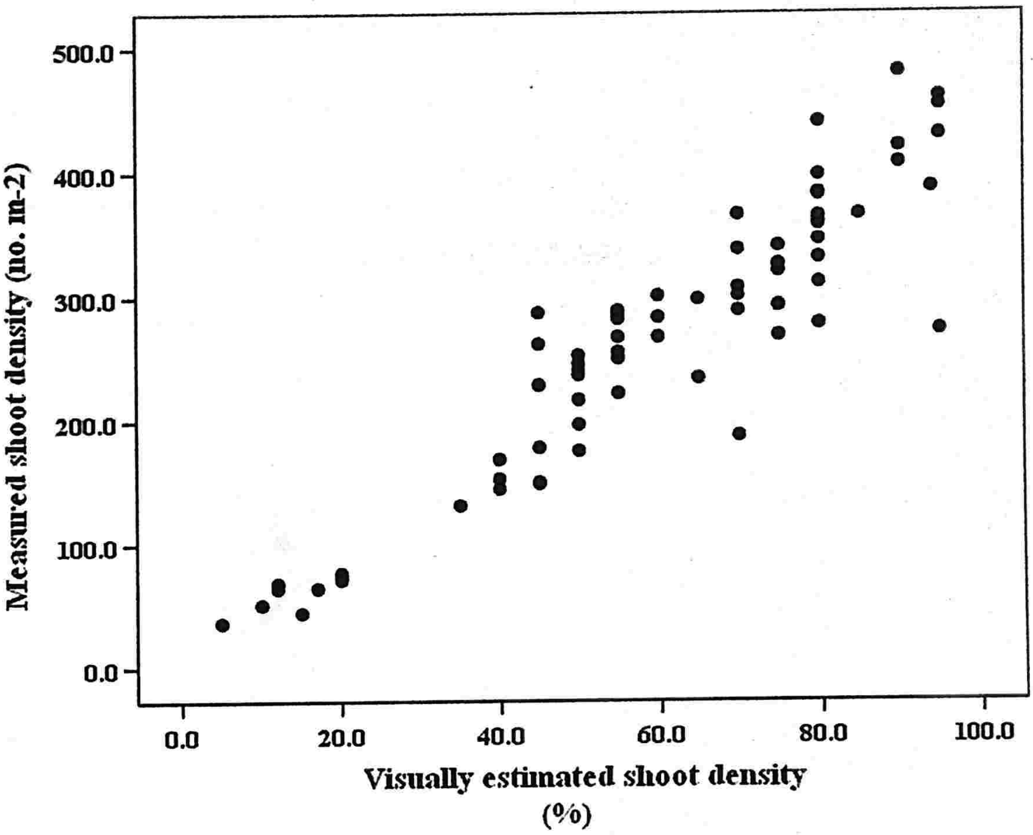


Fig 9. Linear regression of visual estimated values of shoot density against quantified values of shoot density across varying shoot densities

5.1.2 Turtles distribution in the lagoon

In this study, it was found that turtles exhibited a highly clumped distribution at the seagrass meadow level. Turtles tended to cluster in the northern part of the lagoon, decreasing towards the centre of the lagoon, with an additional moderately high density patch towards the south (resort). Turtle density dropped again sharply towards the southernmost corner of the lagoon, south of the channel that separates the main island of Agatti from the tiny island of Kalpitti (Fig 10). This distinct gradient of turtle distribution and density from north to south was maintained throughout the study period (Dec-April) (Fig 11). The mean encounter rate (number of turtles per km) per transect corroborated this finding with an average of 16.1 turtles/km at the end, 11.2 turtles/km in the moderately high density site and 3.7 turtles/km in areas of low turtle densities at the southern tip.

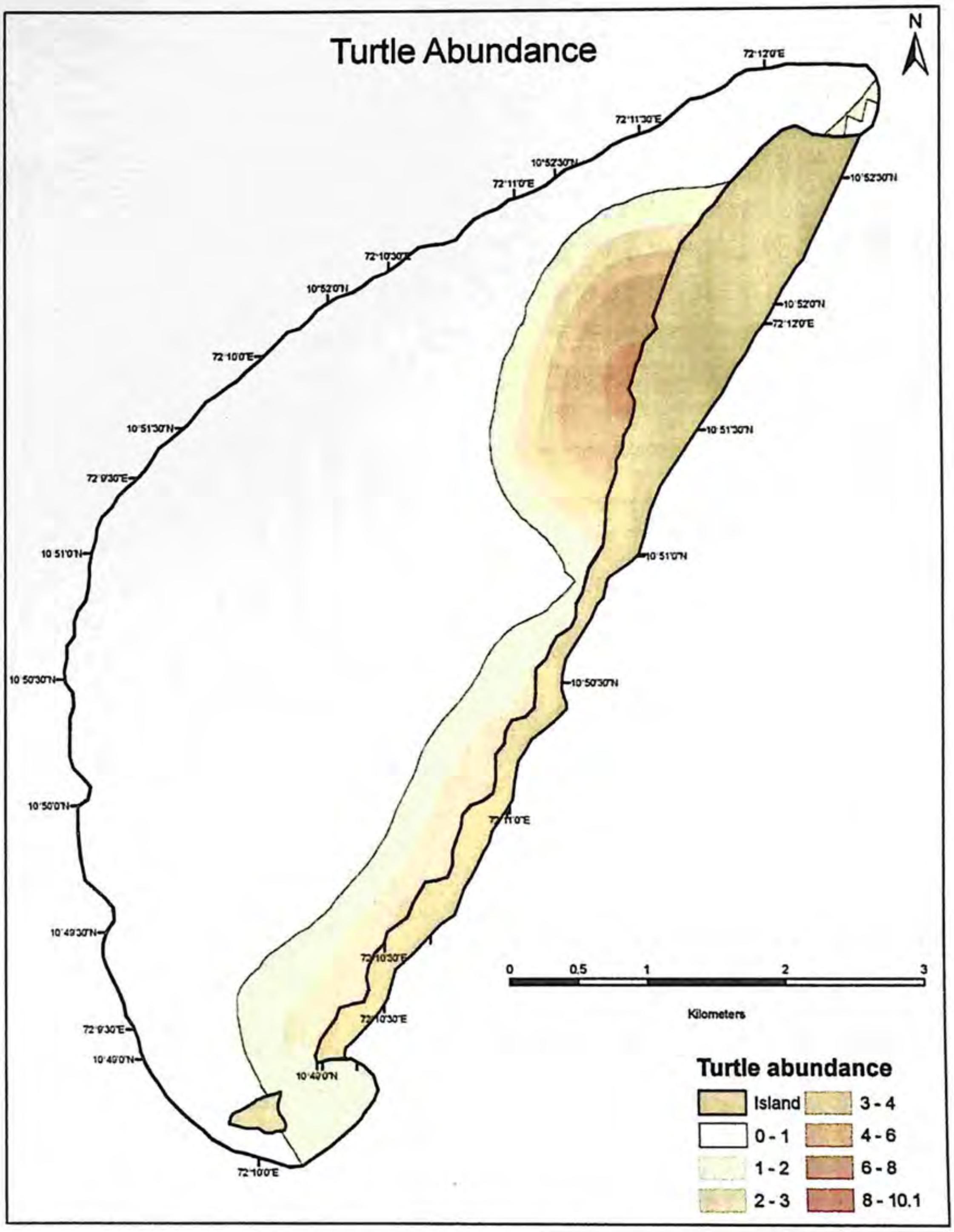


Fig 10. Kriging interpolation map of the average turtle abundance per point one each of the 23 transects (A-W)

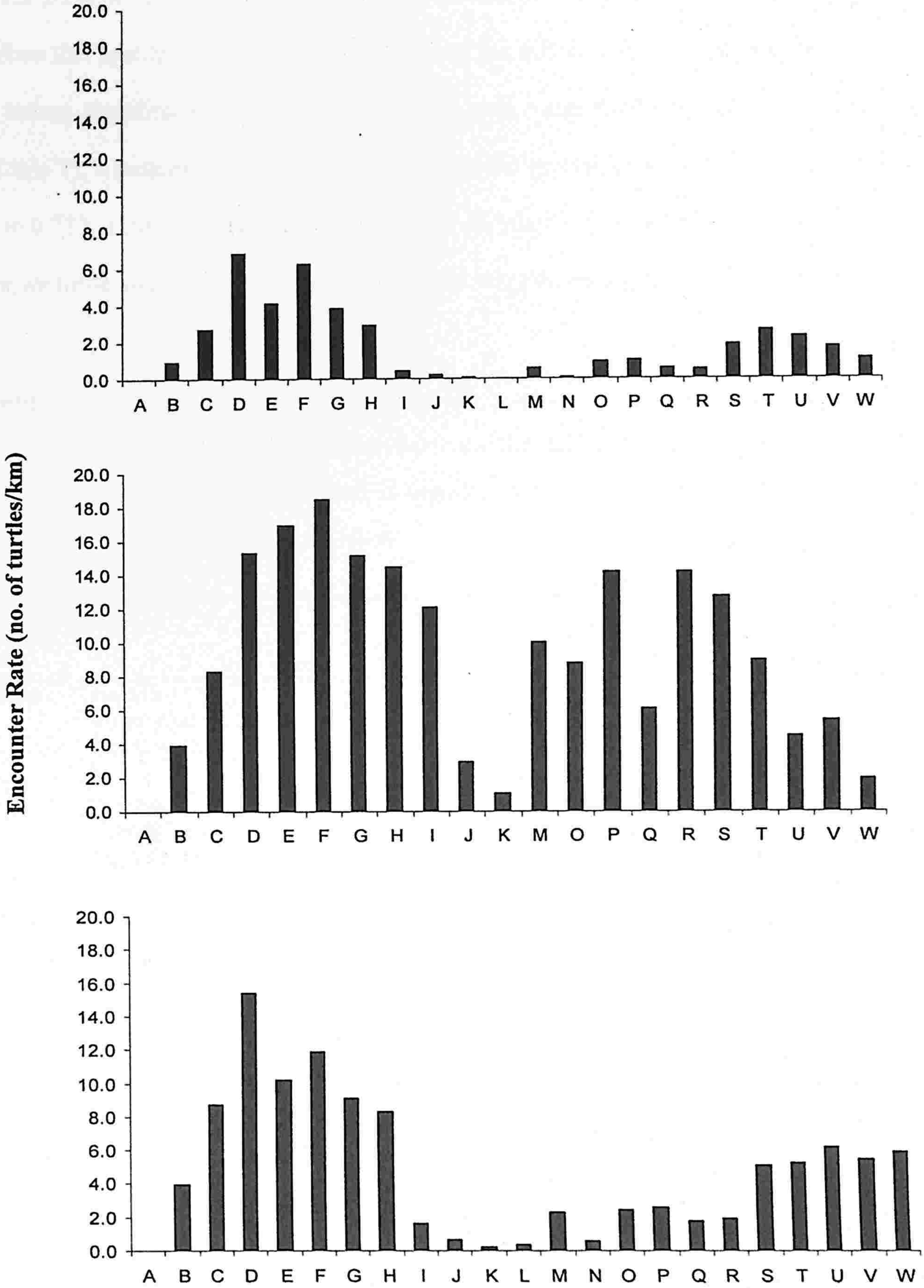


Fig 11. Mean turtle encounter rate (number of turtles/km) per transect (A-W) for a) the entire lagoon b) for seagrass areas c) other habitat types

5.1.2.1 Turtle distribution in relation to distribution of seagrass resources

When this spatial pattern was correlated with the different habitat types in the lagoon, a strong significant relationship (p<0.001) with seagrass distribution was recorded (Table 1), a pattern maintained irrespective of the spatial location of points (Pearson's r = 0.737, (Dutilleul corrected degrees of freedom) df = 44.671, p<.001). Fig 12 shows turtle spatial distribution in relation to seagrass resources in the Agatti lagoon.

Table 1. Correlation matrix describing the relationship between different habitat types and the correlation between the different habitat types and turtle abundance. *Correlation is significant at the 0.05 level. **Correlation is significant at the 0.01 level.

		depth	live	dead	sand	seagrass	rubble	mean turtle abundance
depth	Pearson Correlation	1	.062	.096	.175(*)	-.177(*)	-.230(**)	-.125
	Sig. (2-tailed)		.403	.195	.017	.016	.002	.090
	N	186	185	185	185	185	184	186
live	Pearson Correlation	.062	1	.566(**)	-.453(**)	-.133	.002	-.137
	Sig. (2-tailed)	.403		.000	.000	.071	.974	.063
	N	185	185	185	185	185	184	185
dead	Pearson Correlation	.096	.566(**)	1	-.528(**)	-.174(*)	.047	-.179(*)
	Sig. (2-tailed)	.195	.000		.000	.018	.525	.015
	N	185	185	185	185	185	184	185
sand	Pearson Correlation	.175(*)	-.453(**)	-.528(**)	1	-.523(**)	-.455(**)	-.353(**)
	Sig. (2-tailed)	.017	.000	.000		.000	.000	.000
	N	185	185	185	185	185	184	185
seagrass	Pearson Correlation	-.177(*)	-.133	-.174(*)	-.523(**)	1	-.136	.737(**)
	Sig. (2-tailed)	.016	.071	.018	.000		.067	.000
	N	185	185	185	185	185	184	185
rubble	Pearson Correlation	-.230(**)	.002	.047	-.455(**)	-.136	1	-.117
	Sig. (2-tailed)	.002	.974	.525	.000	.067		.113
	N	184	184	184	184	184	184	184
mean	Pearson Correlation	-.125	-.137	-.179(*)	-.353(**)	.737(**)	-.117	1
	Sig. (2-tailed)	.090	.063	.015	.000	.000	.113	
	N	186	185	185	185	185	184	186

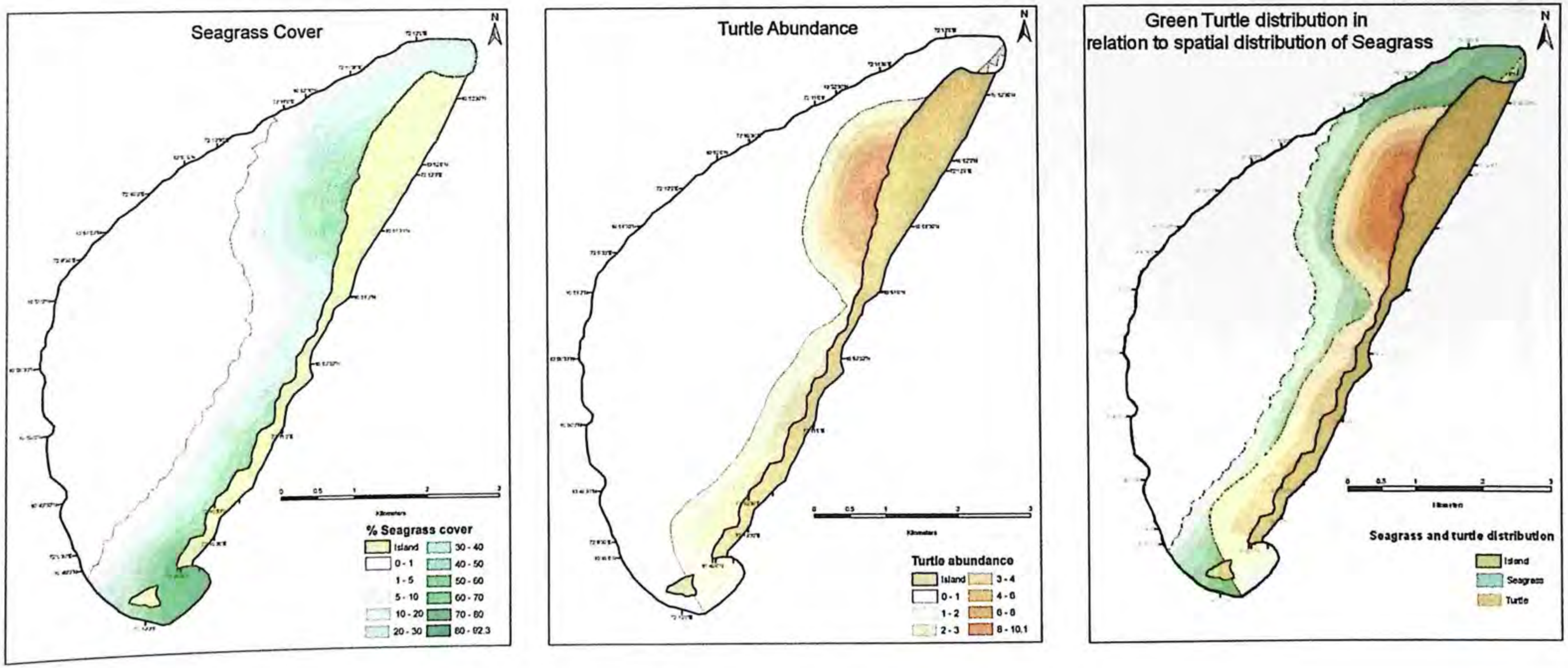


Fig 12. Turtle spatial distribution in relation to distribution of seagrass resources

5.2 Magnitude of turtle herbivory

Most of the plants collected from the meadows showed clear signs of herbivory. The shape of the observed bite marks were neither suggestive of sea urchin or fish grazing (McClanahan et al. 1994, Kirsch et al. 2002). Moreover, the low density of sea urchins and fish in the seagrass meadow coupled with the closely cropped nature of the leaves with entire leaves missing were clearly indicative of green turtle grazing (Bjorndal 1980) as opposed to neat fish bite marks (Fig 13) confirmed that the high rate of herbivory recorded in areas of high turtle density was due to turtles alone. In most cases, it was possible to clearly distinguish between turtle herbivory and herbivory by other forms including fish. For these reasons, it was assumed that the analysed shoots, unless stated otherwise were eaten by turtles. The calculated rate of herbivory (centimetres of leaf consumed per day) was found to vary significantly among the sampled sites (F =23.06, df =2, $p<0.05$). Post-hoc comparisons revealed that though the rate of herbivory in the control and low turtle abundance areas were not statistically different from each other, herbivory rate at all the other sites were significantly different from each other (of high turtle density was significantly different from all the other sites (Table 2 and Fig 13). The proportion of grazing signs on leaves collected from each site were significantly different ($\chi^2 = 21.29$, df =2, $p<0.001$). The proportion of leaves with grazing signs at the low turtle abundance site (0.5) was significantly lower than the proportion of grazed leaves at the both the moderate (0.64) ($\chi^2 = 9.37$, df =2, $p<0.01$) and high turtle density site (0.70) ($\chi^2 = 20.35$, df =2, $p<0.001$).

Table 2. Estimated herbivory rates (±1SE) at each of the four sites (control, low, moderate, high) (n = 15/site). The rate of herbivory is an instantaneous comparison of herbivory between the different sites

Site	**Rate of herbivory (cm/day)(±1 SE)**
Control	0.32 ± 0.25
Low herbivory	1.41 ± 0.88
Moderate herbivory	6.28 ± 1.78
High herbivory	16.8 ± 2.47

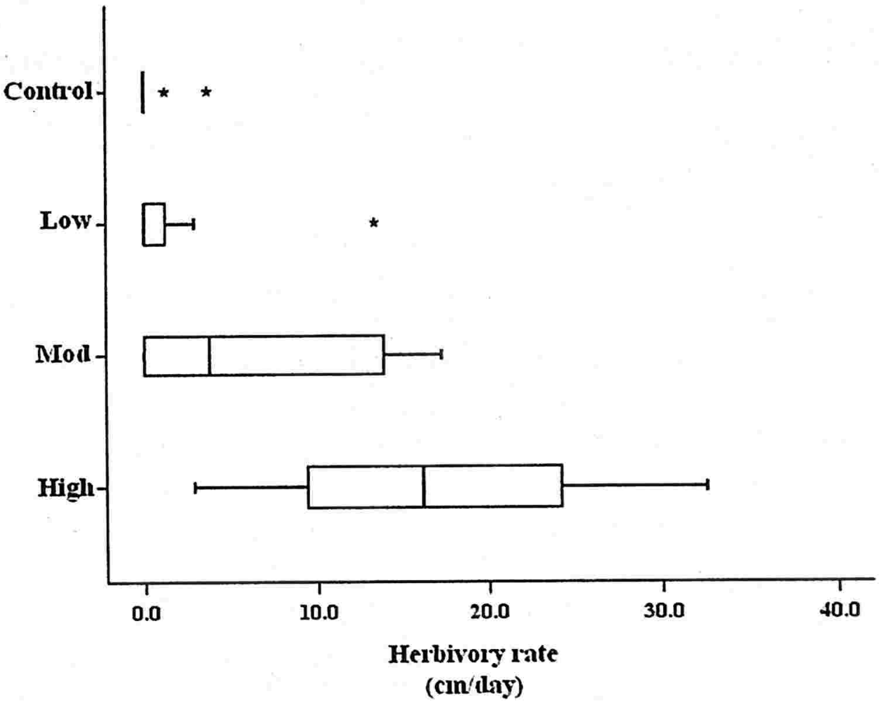


Fig 13. Herbivory rate (cm of leaves consumed per day), compared between control, low, medium and high turtle density sites (N=15). Boxes encompass 25% and 75% quartiles, and the central line represents the median, and bars include 95% of the values. Stars indicate observations outside the 95% limits. ANOVA gave a p< 0.01. Turtle abundance (low, moderate, high) at each site is given in Fig 5

5.3 Herbivory impacts on *Cymodocea rotundata*

5.3.1 At the shoot level

At the level of the individual shoot, turtle herbivory pressure appeared to produce a marked effect on seagrass morphology and structure. While the number of leaves per shoot did not vary significantly across the gradient of herbivory (F=2.19, df =2,

$p>0.05$), leaf width ($F= 13.22$, $df=2$, $p< 0.01$) and leaf area ($F= 18.35$, $df=2$, $p< 0.01$) differed significantly among the three sites, being highest in the low herbivory site and lowest in the high herbivory site. Mean values for each parameter are given in Table 3. Leaf production rates also showed the same general tendency with much higher rates of leaf production in areas of low turtle abundance (Table 3).

Nutrient content of new leaf growth was also different between sites with the lowest percentage of leaf nitrogen in areas with the lowest density of turtles and highest where turtle densities were the highest (% N= 2.54 at the high site, %N=2.19 at the moderate turtle density site and %N= 2.24 at the low turtle abundance site).

In the simulated herbivory experiment, the leaf production (g DW shoot $^{-1}$ day^{-1}) varied significantly ($F=10.49$, $df=2$, $p<0.01$) among clipping treatments (Tukey's multiple comparison, low > mod $\leq$ high, $p< 0.05$). This trend was analogous to that found in the western lagoon (Table 3), except that the moderate (50% clipping) treatment showed a stimulation in leaf production contrary to that reported from the western lagoon for the same site (Table 3).

Table 3. Shoot characteristics at each site (n = 90 for number of leaves per shoot, n = 200 for leaf width and leaf area and n ranges from 15-26 for leaf production per shoot as this was based on marked shoots. Turtle abundance (low, moderate, high) at each site is given in Fig 5.

Turtle abundance	**Number of leaves per shoot**	**Leaf width (± se) (mm)**	**Leaf area per shoot (± se) (cm-2)**	**Leaf production per shoot (± se) (mg DW/shoot /day)**
Low	2.38 ± 0.05	3.40 ± 0.03	1.51 ± 0.05	1.19 ± 0.06
Moderate	2.53 ± 0.05	3.47 ± 0.05	1.25 ± 0.04	0.85 ± 0.06
High	2.47 ± 0.05	3.12 ± 0.04	1.18 ± 0.04	0.93 ± 0.07

5.3.2 At the population level

5.3.2.1 Shoot age distribution

Living shoot age structure at each site was characterised by a high abundance of young shoots followed by an exponential decline in the number of shoots as shoot age (PI) increased (Fig 14). The age distributions showed that the site with high turtle densities had a high abundance of shoots younger than a year old, while the low density site had a high number of shoots more than 1.5 yrs old. The median age of living shoots (yr) varied more than three fold from 1.78 in the low site to 0.58 in the high site (Table 4). The maximum age of shoots (yr) were less variable ranging from 4.13 in the site with low turtle numbers to 2.76 in areas with a high number of turtles (Table 4). Thus, the age structure in general shows a decreasing trend, with older shoots in areas with less turtles and considerably younger shoots in areas with high turtle densities.

5.3.2.2 Shoot mortality, recruitment and population growth rate

Shoot recruitment rates also revealed important differences between sites. Recruitment rates varied more than six times between sampling sites. Shoots where turtle densities were the highest seemed to recruit the fastest (1.24 shoots yr^{-1}) and areas with low turtle numbers showed the slowest recruitment rate (0.2 shoots yr^{-1}) (Table 4). The high density of horizontal apices, the parts of the clone where new shoots are produced, in areas of high turtle numbers with 59.55 apices m^{-2} as compared to 13.85 apices m^{-2} in areas of low turtle density corroborated this finding. Shoot mortality rates however, showed an opposite trend and the estimates for the high turtle density site was almost twice the estimates recorded for the low density site. The shoot mortality rate ranged from 0.94 shoots yr^{-1} in high turtle areas to 0.44 shoots yr^{-1} in low turtle areas (Table 4). The net population growth rate also differed between sites. Population growth rates indicated that in areas of high turtle densities the shoot population was growing positively, in areas of moderate densities the population was in a steady state, while in areas with low turtle numbers there was a net loss of shoots annually.

5.3.2.3 Annual leaf formation rate

Average leaf life span, although statistically indistinguishable, also varied between sites, (Table 5). However, leaves at the high and moderate density sites had a shorter life span (27.54 and 27.95 days respectively) than leaves at the low turtle density site (30 days). The time elapsed between the formation of two consecutive leaves (leaf PI) ranged from 11.61 d in the high turtle density site to 13.61 d in the low turtle density site. These results, show a higher leaf turnover in areas of high turtle numbers.

The seasonal cycles shown by the sampled vertical rhizomes (Fig 6) revealed distinct differences in the annual number of leaves produced per shoot across the sites examined (Table 5). The number of leaves produced in a year by a single shoot varied from 26.81 at the low site to 31.42 leaves shoot^{-1} year^{-1} at the high herbivory site (Table 5).

Flowering scars were found only on the vertical rhizomes collected from the eastern lagoon and the area of low turtle density (Fig 15). Flowering intensity at these sites was 0.0001 flowers PI $^{-1}$ at the low site and 0.002 flowers PI $^{-1}$ on the eastern lagoon.

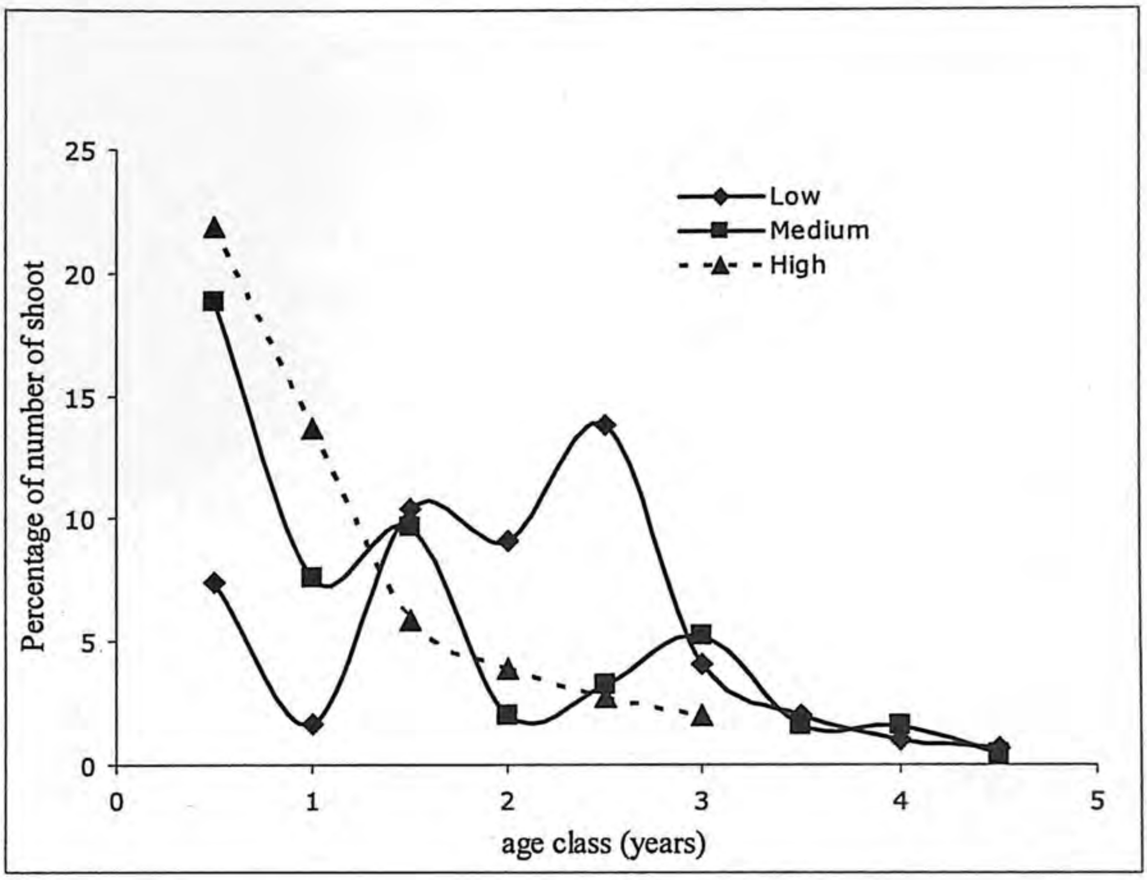


Fig 14. Age distribution of living shoots at high turtle density (*n=128*) moderate turtle density (*n*= 125) low turtle density (*n*= *149)*. Turtle abundance (low, moderate, high) at each site is given in Fig 5

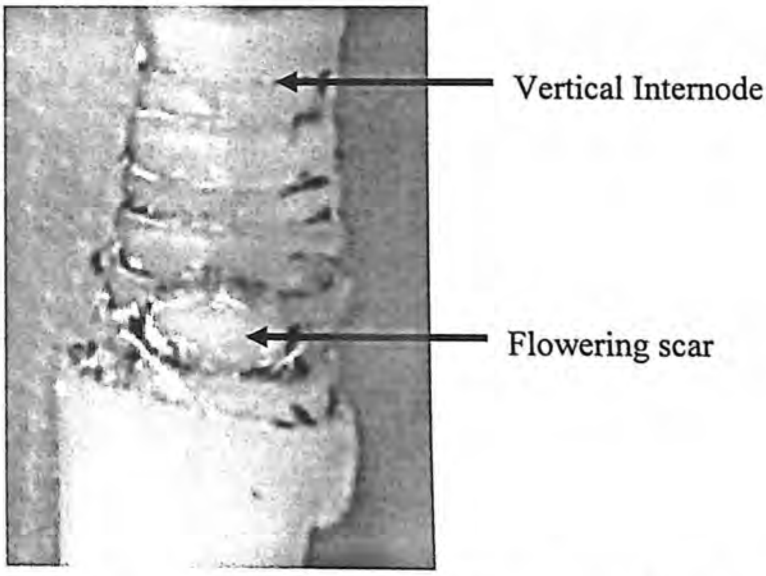


Fig 15. Flowering scars found on the vertical rhizomes collected from the control site on the eastern lagoon.

Table 4. Variables used to characterise shoot demography at each of the three sites (low, moderate, high). N= 15 to 20 vertical rhizomes from each site. Turtle abundance (low, moderate, high) at each site is given in Fig 5.

Turtle abundance	Median shoot age (yr)	Max shoot age (yr)	Shoot mortality rate (yr-1)	Shoot recruitment rate (yr-1)	Net population growth rate (yr-1)	Flowering intensity (flowers yr-1)
Low	1.789	4.13	0.436 ± 0.21	0.200	-0.236	0.000
Moderate	0.952	4.10	0.734 ± 0.13	0.751	0.017	0.000
High	0.588	2.76	0.944 ± 0.22	1.241	0.297	0.004

Table 5. Average number of leaves produced annually, time interval between production of two successive leaves (PI) and leaf life span (days) at each site. Turtle abundance (low, moderate, high) at each site is given in Fig 5.

Turtle abundance	Number of leaves yr-1	Leaf PI (days)	Leaf life span (days)
Low	26.81 ± 1.01	13.61 ± 0.03	30.24 ± 1.32
Moderate	27.30 ± 0.83	13.36 ± 0.03	27.95 ± 0.96
High	31.42 ± 2.10	11.61 ± 0.09	27.54 ± 0.97

5.3.3 At the meadow level

Herbivory impacts were also detected at the meadow level seagrass abundance parameters like shoot density and above ground biomass showed a clear decreasing trend from areas of low turtle densities to high turtle density areas. There was a difference of several orders of magnitude in shoot density and above ground biomass between sites. Shoot density ranged from 1281 shoots m^{-2} to 963 shoots m^{-2} in low and high turtle density areas respectively and above ground biomass varied from 55.68 g DW cm^{-2} to 28.81 g DW cm^{-2} in low turtle areas and high turtle areas respectively. These differences were significant at the 0.05 level for shoot density (F=8.751, df =2, p<0.01) as well as above ground biomass (F =46.05, df =2, p<0.01).

The site with high turtle abundance was distinctly different from the other sites in terms of shoot density and above ground biomass (Tukey's multiple comparisons, low ≥ moderate > high, $p < 0.05$) (Fig16a and b respectively).

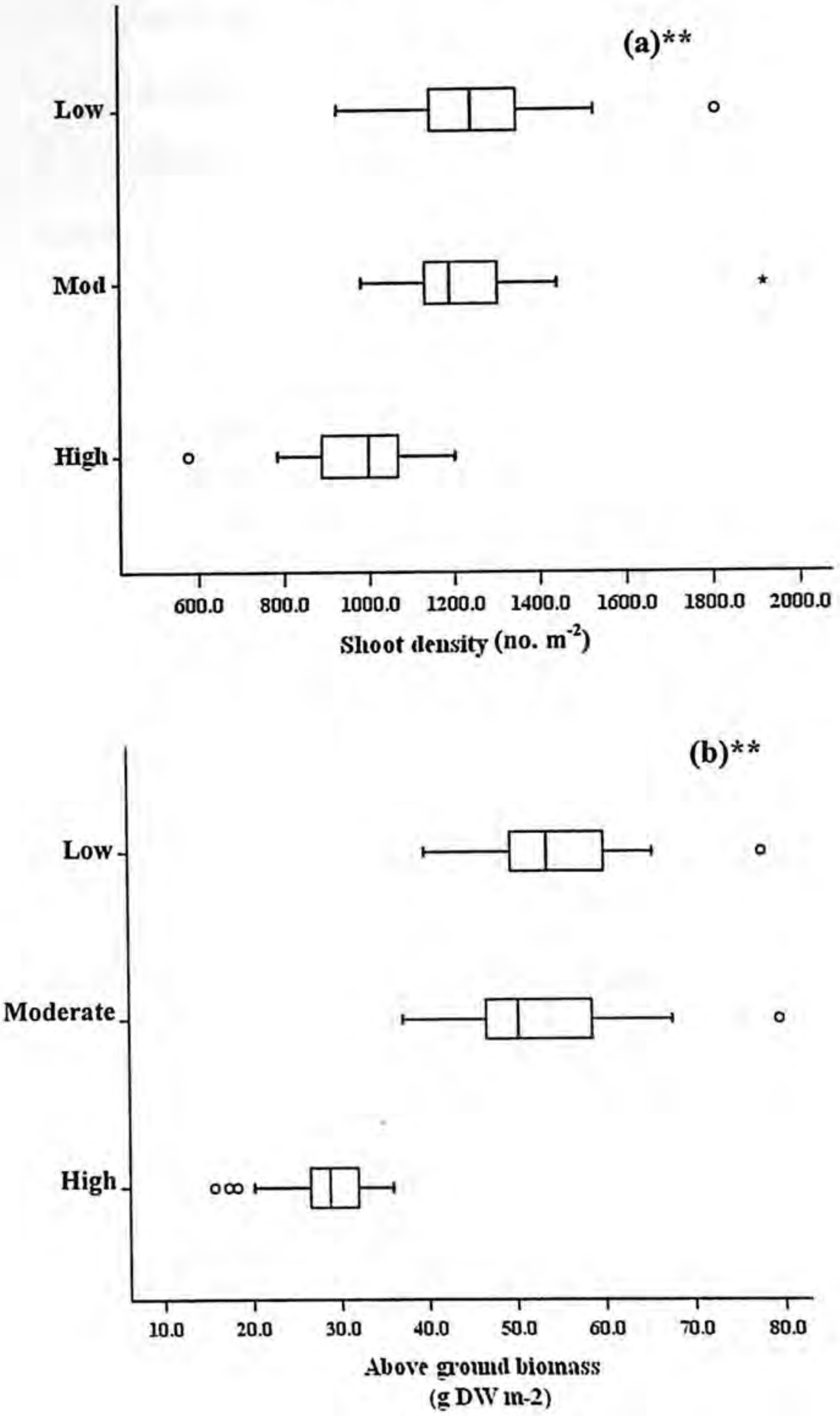


Fig 16. Boxplots showing the distribution of a) shoot density (number of shoots m^{-2}) and b) above ground biomass (g DW m^{-2}) for *Cymodocea rotundata* at low, moderate and high turtle abundances. ** indicates a $p < 0.01$. Turtle abundance (low, moderate, high) at each site is given in Fig 5

6. DISCUSSION

6.1 Green turtle distribution and habitat relationships

Knowledge of the spatial distribution of green turtles is central to understanding their profound influence on the dynamics of nearshore marine ecosystems. In this study, it was found that turtles exhibited a highly clumped distribution. Turtles tended to cluster in the northern part of the lagoon, decreasing towards the centre of the lagoon, with an additional moderately high density patch towards the south (resort). Turtle density dropped again sharply towards the southernmost corner of the lagoon, south of the channel that separates the main island of Agatti from the tiny island of Kalpitti. This distinct gradient of turtle distribution and density from north to south remained throughout the study period (Dec-April). A correlation of turtle abundances with the different habitat types in the lagoon, when corrected for spatial autocorrelation, revealed a strong significant relationship only with seagrass habitats. This finding is further strengthened by a significantly greater proportion of turtle sightings in seagrass beds (~86%) as compared to sightings in other habitat types (~14%). The results of the present study are supported by studies elsewhere documenting concentration of green turtles in seagrass meadows (e.g. Hasbŭn et al. 2000, Andrè et al. 2005) as well as their apparently high affinity for specific areas within a seagrass meadow (e.g. Whiting and Miller 1998, Taquet et al. 2006). Moreover, a recent satellite telemetry study looking at the foraging movements of green turtles in the Atlantic has reported a concentration of home ranges around the specific distribution of food resources (Makowski et al. 2006). In a similar study documenting the spatial distribution of grazing dugongs in Australia, Sheppard et al. (2006) found that they rarely ventured >20km from the coast, and attributed this pattern to the availability of suitable seagrass beds. Thus, coastal seagrass habitats appear to be of prime importance for these large grazing marine herbivores.

There are three major theories postulated as explanations for large herbivore aggregation. The first is the predation risk hypothesis, whereby predation risk is reduced either by enhanced chances of predator detection or simple dilution (Jarman 1974). Tiger sharks have been documented as the primary predator of green turtles with tiger shark movement patterns in Australia restricted to shallow seagrass habitats where prey availability (green turtles and dugongs) was high (Heithaus et al. 2002). In this study, no adult sharks were observed in the lagoon during the study period, suggesting that the presence of predators may not be the primary factor governing green turtle distribution in the lagoon.

Secondly, the 'forage-maturation hypothesis' (McNaughton 1984,1986) proposes that herbivore aggregation may be adaptive because vegetation is maintained more readily at low biomass (supposed grazing lawns) by such high density aggregations. In other words, since digestibility of forage is often inversely related to plant age, maintaining vegetation at an immature growth stage may prove to be nutritionally more valuable to the herbivores (more nitrogen, less fibre). Grazing herbivores characteristically adjust their densities and vegetation consumption patterns according to the productivity potential of their food sources, aggregating where the potential is high and dispersing from areas where that potential is low (McNaughton 1984). Indeed, 'cultivation grazing'(Bjorndal 1985) practiced by green turtles, whereby they show a preference for select grazing plots in foraging areas seems to offer support for this hypothesis. Additionally, in mixed seagrass species communities, it is nutritionally superior pioneer species that have been documented to dominate existing dugong feeding trails (Preen 1995, DeIongh et al. 1995). Sheppard et al. (2006) suggest that grazing dugongs track the nutritional content changes in their principal forage plants, moving to a new seagrass patch when the costs of foraging in a particular area eclipse the benefits. Thus, it seems that this latter hypothesis could be a possible explanation for the documented spatial distribution patterns in the present study.

The last hypothesis proposes that herbivore aggregations are a result of intrinsic spatial variations in the nutritional quality or productivity of vegetation (Sinclair 1977, McNaughton 1988). Such spatial variation could be the result of many physical and chemical factors. Assuming that herbivores are distributed in an ideal-free manner (Fretwell and Lucas 1970), such spatial discrepancies could result in a clumped distribution of herbivores. For example, movements of Florida manatees appear to be influenced by fluctuations in the palatability of their food, with individuals exhibiting high site fidelity to areas of core habitat (Weigle et al. 2001, Deutsch et al. 2003). However, whether this is due to intrinsic properties of the vegetation or due to facilitation by the animals themselves is not clear. For example, in this study nutrient analysis of the youngest leaves at each of the three sites with varying turtle densities showed higher leaf nitrogen content in areas where turtle densities were maximum. Consequently, both declining forage quality with plant maturation and spatial variation in average forage quality could potentially be responsible for the observed spatial patterns. It is quite possible that these factors may be acting together in some way, making it difficult to discriminate between them, except with careful experimentation. Nevertheless, the study presents an important synoptic snapshot of turtle distribution in their foraging areas. It has clearly shown that even in areas of such high density, they were not uniformly distributed. Since green turtles are important seagrass community grazers throughout the tropics and subtopics (Thayer et al. 1984), documenting their distribution patterns in relation to seagrass resources represents a first step towards understanding their role in this vital ecosystem.

6.2 Distribution patterns of habitat

6.2.1 Seagrass spatial distribution patterns

Spatial interpolation of percent seagrass cover, which provides a detailed description of spatial patterns of seagrass beds, reveals clear differences in shoot density across the lagoon, a pattern documented for other seagrasses like *Posidonia oceanica* using comparable methods (Balestri et al. 2003). More importantly, a similar approach was used to characterize the value of seagrass habitats for dugongs in Australia (Sheppard et al. 2007).

The primarily subtidal distribution of *C. rotundata* found in the present study is consistent with its position as a relatively shallow water species (Duarte 1991, Reyes et al. 1995) with an average depth of 2.5 m. Jagtap (1998) has reported a maximum depth of 3m for seagrasses in the Lakshadweep, with a maximum above ground biomass occurring at a depth of 2m. Interestingly, *Thalassia hemprichii*, reported to be a deep water species (Duarte 1991) was also documented at depths >2m in the Lakshadweep, as compared to the relatively shallow water distribution of *Cymodocea* in the lagoon (0-1.7m) (Jagtap 1998). In this study, these species-depth zonations seem to be reversed with *Thallasia* demonstrating a restricted distribution, found densely only in depths ranging from 0.5m -1.5m. Nevertheless, *Cymodocea* and *Thallasia* occurred in the depth ranges reported for both species (Coles et al. 1987).

The presence of a high density of green turtles in the lagoon (section 4.2) might influence the observed distribution pattern. Indeed, marine mega herbivores have been documented to alter seagrass distribution patterns either by directly grazing on seagrass leaves or by physical disturbance of the habitat (Thayer et al. 1984). For example, grazing dugongs are capable of removing up to 91% of seagrass biomass, leading to a change in meadow structure (Sheppard et al. 2006) and community composition (DeIongh et al. 1995). It has been documented that in areas of intense grazing by dugongs, slow growing species like *Zostera capricorni* may be competitively excluded by faster growing pioneer species like *H. uninervis* (Preen 1995). It has been suggested that *Cymodocea* could potentially support high grazing pressure with a significant amount of primary production entering the grazing pathway as compared to slower growing species like *Thallasia*. In the light of the green turtle distribution patterns documented in this study, it was observed that *Thallasia* was found to occupy majority of the bed only in areas with very low turtle abundance. This restricted distribution of *Thallasia* is contrary to that reported by Jagtap in 1991 and 1998 in which he has repeatedly stressed the dominance of *Thallasia hemprichii* in the Agatti lagoon. This evidence, together with the possible increase in turtle numbers in the lagoon over the last ten years (a conjecture based on information from the locals) supports the assumption that intense green turtle herbivory could change seagrass community composition to favour fast growing species. Thus, it is possible that *C. rotundata* could potentially have taken over from *T. hemprichii* as a direct result of increased herbivory, an interesting hypothesis to be tested through future research.

It must also be recognised that a host of physical factors such as light (Dennison 1987), water temperature (Bulthuis 1987) nutrient availability (Short 1987), sediment type (Livingston et. al.1998), hydrodynamic forces (Hemminga et al. 1999), turbidity (Short 1987), and physical perturbations (Erftemeijer et al. 1994) may regulate seagrass distribution patterns. Variations in the above factors may change the relative strengths of the mechanisms regulating seagrass distribution in different regions, factors which were not accounted for in the study. Nevertheless, despite these limitations, this study provides important quantitative baseline data on the distribution of seagrass beds in the lagoon, at least for this particular period of the year, against which future changes can be detected. Moreover, this approach, based on intensive sampling has proved to provide biologically realistic and accurate representations of pelagic seagrass systems from quadrat data (e.g. Balestri et al. 2003, Barbera et al. 2005). Regarding green turtles, documenting the spatial distribution of seagrass beds is especially important as they are almost exclusively seagrass feeders, and their survival depends on the stability of these food resources.

6.3 Herbivory impacts on *Cymodocea rotundata*

6.3.1 Magnitude of turtle herbivory

Feeding assays are a simple, powerful technique that has been successfully used to quantify herbivory in marine environments. They have been utilised to determine grazing intensity on seagrass (Tomas et al. 2005) and mangrove leaves (Micheli 1993), to test for food preferences among seagrass grazers (Valentine et al. 1997) and to study how macroalgae distribution on coral reefs is controlled by herbivores (Hay 1981). The results shown here demonstrate that there is a distinct spatial pattern in turtle grazing intensity on *C. rotundata* corresponding to the established gradient of turtle density across the lagoon. Additionally, the length of leaf eaten which is an indication of above ground biomass consumed by turtles shows significant differences in the rate of herbivory across sites. An analogous trend was detected using indirect estimates of gazing intensity from bite marks on leaves, indicating that both these estimates of grazing were closely related to actual grazing intensity (Alcoverro and Mariani 2004). Also, since the average number of bites on tethered leaves was lower than observed on leaves harvested for biomass estimates, it is likely that these estimates of grazing intensity are not over-estimated (Kirsch et al. 2002). However, it must be highlighted that in this study the herbivory estimates were used merely as an instantaneous index of grazing intensity, and not as a measure of absolute offtake from the meadow. Nevertheless, the consistency among sites in the patterns of herbivore grazing scars on leaves of different ages and the congruence between the number of turtle bite marks and the abundance of turtles among sites confirms a gradient of herbivory across the lagoon. The data presented here is based on a very short sampling period, and is potentially subject to a few limitations. On the one hand, defoliation could be overestimated since lateral fish bites often leave behind a very fragile blade, which is prone to breakage due to wave action (Kirsch et al. 2002). On the other hand, repeated attacks to the same leaf may mask the marks of previous attacks, causing underestimation of defoliation rates (see Tomas et al. 2005). However, fish densities on the western lagoon (where the herbivory assay was conducted) were very low. Additionally, since green turtles close-cropped seagrass blades very near the base of the stem, seagrass defoliation and seagrass consumed by turtles were probably very similar and therefore turtles were responsible for most of the herbivory seen in the assay. Our results indicate that in all probability fish-related herbivory may not be as important in this lagoon as turtle herbivory. In general, this study suggests that herbivores play a very important role in seagrass meadow dynamics, which is in agreement with recent reviews on global seagrass ecosystems (Valentine et al. 1997, Kirsch et al. 2002, Alcoverro & Mariani 2004).

6.3.2 Impacts of herbivory on *Cymodocea rotundata*

The results strongly suggest that green turtle herbivory has a considerable impact on *C. rotundata* shoots, population structure, and meadow dynamics. In particular, seagrass shoot morphology, abundance and demography seem to respond to varying turtle densities.

6.3.2.1 Shoot level impacts

Previous studies conducted at the shoot level have shown that the repeated removal of seagrass by grazers can lead to temporal decreases in morphological parameters such as leaf width, and leaf density (number of leaves per shoot) and leaf area (e.g. Greenway 1976, Zieman et al. 1984, McGlathery 1995, Armitage and Fourqurean 2006). In this study, similar patterns in shoot characteristics were observed with areas of high turtle densities having significantly lower values for leaf width and leaf area than areas of low turtle densities.

A reduction in leaf width for leaves of mature shoots can indicate plant stress (Zieman 1975), a finding corroborated by McMillan and Phillips (1979), who documented a reduction in leaf width with increasing duration of exposure to air on low tides symptomatic of a stress effect on leaf width. Similar reductions in leaf width and leaf density have been observed in areas of intense grazing by green turtles in the Caribbean (Zieman et al. 1984). These patterns have also been documented in a 16 month simulated turtle herbivory experiment, where clipped plots had significantly lower leaf width, length, and leaf density as compared to the controls (Moran and

Bjorndal 2005). Thus, the results obtained here seem to be in accordance with other similar observational and experimental studies demonstrating reduced seagrass structural complexity in high turtle density areas.

The extent to which the grazing response of plants can stimulate above ground productivity, either through compensatory growth in which net primary production (NPP) remains unchanged, or over-compensatory growth (increased NPP) varies among systems (Belsky et al. 1993, Milchunas and Lauenroth 1993). For example, McNaughton (1979) reported a stimulation of above ground productivity in response to ungulate grazing in the Serengeti. Similarly, for seagrass systems, Moran and Bjorndal (2005) found that *T. testudinum* exhibited compensatory growth in response to clipping, thereby maintaining productivity levels relative to the background controls. This was contradictory to that reported by Zieman et al. (1984) where a decrease in aboveground productivity of *T. testudinum* grazed intensively by sea urchins and green turtles was found. These latter results are substantiated by this study, where a considerable reduction of above ground productivity, was documented in high turtle density areas as compared to areas with low turtle numbers. These observational results were further validated by the parallel clipping experiment, where above ground production was depressed at an 80% removal of leaf surface (mimicking intense grazing). The present study also found higher leaf nitrogen content in areas with high turtle abundances as compared to lower leaf nitrogen content in areas with low turtle abundances. Higher leaf nitrogen content in areas grazed by marine mega fauna has been documented both observationally (Zieman et al. 1984) and experimentally (Moran and Bjorndal 2005). Thus, it is difficult to discount the possibility that grazing intensity could lead to the observed patterns at the

The results also suggest that the direction of future research in elucidating the impacts of turtle herbivory on nitrogen content of seagrass leaves might prove fruitful.

6.3.2.2 Population level impacts

The age structure of a population simultaneously reflects the outcome of past temporal variation in recruitment and mortality as well as provides an indication of its future dynamics. For example, Rose et al (1999) has shown that intense sea urchin grazing can have significant impacts on seagrass shoot demography and disrupt the age structure of the population. However, it must be recognised that this method assumes a stable age distribution (Duarte et al. 1994), which in reality is not constant in either space or time (Jensen et al. 1996). Therefore, while this method does not provide a definitive estimate of shoot age structure or demography, it is a simple and comprehensive method for historical reconstruction of seagrass population dynamics. Moreover, compared to direct labour intensive methods like quadrat census (Short and Duarte 2001), where individuals are tagged and monitored over time, reconstructive techniques are relatively cheap and easy to employ. Therefore, these methods are a powerful tool for elucidating the population dynamics of seagrass species (Gallegos et al. 1993, Duarte et al. 1994).

The present study revealed large-scale patterns in *C. rotundata* shoot demography coherent with varying turtle densities. The age frequency distributions showed a significant drop in the maximum and median shoot age from areas of low turtle densities to areas of high turtle densities. Moreover, the greatest proportion of growing tips, in accordance with the highest net population growth rates was recorded in the high turtle density site. Thus, intense turtle grazing seems to result in younger in the high turtle density site. Thus, intense turtle grazing seems to result in younger and faster growing shoots, indicative of a colonizing population. In fact the strong regenerative potential of fast growing pioneer species like *Halodule ovalis* has been cited as the primary cause for it being preferred by dugongs in both tropical and temperate regions (Preen 1995, Yamamuro and Chirapart 2005).

Discrete areas of high and low mortality and recruitment were observed in the study area, again consistent with varying turtle abundances. In areas of high turtle abundance, higher recruitment and mortality was observed while low mortality and recruitment was observed in areas of low turtle abundance. Thus, the greatest risk of mortality occurred in areas where gross recruitment was highest. Consequently, net population growth was positive in areas of high turtle abundances, while in areas with low mortality and low recruitment i.e. areas with low turtle abundances, there was an annual net loss of shoots. Such patterns have also been documented for perennial and annual terrestrial plants (Noble and Dirzo 1997) and have been attributed to intraspecific competition. Thus, it would seem that turtles, through their foraging strategy, maintain the meadow in a steady state and possibly even an early successional state. Also, it has been reported that one of the apparent mechanisms by which seagrass deals with sustained herbivory is to increase the recruitment of new shoots rather than increasing the production of existing shoots (Valentine et al. 1997), a finding substantiated by this study.

The number of leaves produced per year was also higher in areas of high turtle densities. However, it was within the range recorded for *C. rotundata* (Vermaat et al. 1995). While it is possible that this sampling period occurred during summer sexual

1999) (Fig 2), the low rate of sexual reproduction documented here contradicts this assumption making these results more attributable to grazing pressure. Indeed, Durako (1994) noted that a pattern of decreasing time interval between the production of new leaves, concurrent with increasing level of disturbance. This may be coherent with the compensatory leaf production recorded for *C. rotundata* seagrass species subjected to intense herbivory pressure.

6.3.2.3 Meadow level impacts

This study also revealed a significant reduction in shoot density in the areas with high turtle abundance that together with lower shoot biomass (see previous section) resulted in a reduced above ground biomass when compared with the uncropped areas. Evaluating the impacts of turtle grazing at a slightly larger scale reveals a substantial amount of evidence documenting the effects on seagrass meadow characteristics like shoot density (Valentine et al. 1997) and above ground biomass (McGlathery 1985, Valentine et al. 2000). For example, significant negative impacts of green turtle and sea urchin grazing on shoot density and above ground biomass have been repeatedly observed in manipulative experiments and through field observed herbivory gradients (Valentine et al. 2000, Alcoverro and Mariani 2002). However, an increase in shoot density has also been shown in areas of intense sea urchin grazing, allowing the persistence of seagrass in these areas despite heavy grazing pressure (Valentine et al. 1997). The lack of a significant relationship between above ground seagrass biomass and grazing impact could be due to seagrass compensatory growth (Moran and Bjorndal 2005). Since seagrass can respond to herbivory by increasing shoot density or by increasing individual shoot growth or biomass, simply measuring above ground sea grass biomass as a response variable may not be appropriate (Valentine et al. 2000) as it might lead to a significant underestimation of the power of this interaction (e.g. Sand-Jensen et al. 1994). In this study, shoot biomass, shoot growth and shoot density present lower values in areas with high turtle abundances when compared with areas that present low turtle abundance. However, the persistence of the Agatti meadows in areas where the herbivory pressure is very high will finally depend on the ability of those meadows to maintain a good balance between shoot mortality and shoot recruitment, aspects discussed in the previous section. Also, although speculative, the possibility that sustained turtle herbivory could change the species composition of the seagrass meadow towards a species tolerant of relatively high herbivory (e.g. *Cymodocea*) underscores the potential strength of this trophic relationship.

7. GREEN TURTLES AND THE AGATTI LAGOON- A SUMMARY OF THE FINDINGS

1. In summary, this study clearly shows that the green turtle population is exceptionally high in the Agatti lagoon, that seagrass resources are a habitat hotspot and turtle herbivory has potentially very significant consequences for seagrass plant architecture, life history strategies, population dynamics and meadow structure.
2. The seagrass meadow within the study area was dominated by *Cymodocea rotundata*, with varying shoot densities across the lagoon.
3. Green turtles were found to be primarily within the seagrass beds with a distinct gradient of abundance across the lagoon from north to south.
4. The magnitude of herbivory across the lagoon was also found to be consistent with this established gradient of turtle abundances, suggesting a preference for certain areas within the seagrass meadow.
5. A closer analysis of *Cymodocea* population and individual shoot traits revealed significant trends in plant characteristics indicative of a response to turtle herbivory pressure. At the population level, significantly higher levels of shoot recruitment and positive population growth rates in areas of intense herbivory as compared to lower recruitment and growth rates in areas of low turtle abundance demonstrate that the increased recruitment of shoots could be a potential mechanism allowing the persistence of seagrass meadows subjected to intense grazing pressure.
6. Intense herbivory could also lead to potential changes in the reproductive strategies of seagrass in the lagoon, as a drastic reduction in the frequency of sexual reproduction was documented in areas of high turtle abundance.

7. At the individual shoot level, it seemed that turtle foraging behaviour resulted in localised areas of younger seagrass shoots of *C. rotundata*, which possibly provided a higher nutritional quality of resources. This concentrated feeding, however also resulted in a decrease in plant morphological characteristics as compared to areas where turtle numbers were low. Thus, the patterns of magnitude and impacts of herbivory on seagrass traits observed and quantified here are substantiated by the established gradient of turtle density across the lagoon, an inference further strengthened by the evidence from the experimental clipping. Thus, the hypothesis that grazing intensity is an important regulatory factor governing seagrass response to herbivory (Aragones and Marsh 2000, Valentine and Duffy 2005) is validated by this study.

8. CONSERVATION IMPLICATIONS

With respect to conservation management implications, this study points at distributing conservation effort and resources to protect these vital seagrass habitats and the megaherbivores they support. These habitats are easily accessed and impacted upon by increasing anthropogenic activities in the lagoon. Moreover, mere legal protection of these herbivores alone does not diminish their vulnerability in the study area and given their significance in seagrass systems, active steps are required to monitor this population and prevent detrimental factors that could potentially contribute to their decline. Regionally, the Indian Ocean appears to be an exceptional site for green turtles as previous studies done in the Lakshadweep Archipelago (e.g. Tripathy et al. 2007) have documented the use of Agatti as an important foraging ground and nesting beach for green turtles. The implications of this are important as Mayotte Island in the South West Indian Ocean is the only other island known so far in the Indian Ocean where green turtle breeding and foraging takes place in the same area (Taquet et al. 2006). Assuming that the health off seagrass meadows in the Agatti lagoon are equally important for the reef fish populations as foraging and nursery grounds, understanding green turtle herbivory on seagrass in the context of reef fish also needs to be studied.

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