



**MASARYK UNIVERSITY**  
**FACULTY OF SCIENCE**  
**DEPARTMENT OF BOTANY AND ZOOLOGY**

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**HERBIVORY AND ITS EFFECT ON THE  
ECOLOGICAL STABILITY OF CORAL REEFS  
OF LAKSHADWEEP, INDIA**

Ph.D. Dissertation

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Supervisor: doc. RNDr. Michal Horsák Ph.D.

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*“Science is but a perversion of  
itself unless it has as its ultimate  
goal the betterment of humanity.”*

- Nikola Tesla –

*“We need to respect the  
oceans and take care of them  
as if our lives depended on it.  
Because they do.”*

- Sylvia Earle –

*"The person who says it cannot  
be done should not interrupt the  
person doing it."*

- Chinese Proverb –

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## **Statement on the contribution of others**

I declare that this dissertation is my own work and any information from published or unpublished work of others used in this thesis is cited in the text and listed in the list of references.

### **AUTHOR CONTRIBUTIONS TO THE PAPERS PRESENTED IN THE THESIS**

**Paper: Nicole H. Cernohorsky, Timothy R. McClanahan, Idrees Babu, Michal Horsák 2015 Small herbivores suppress algal accumulation on Agatti atoll**

NH Cernohorsky and TR McClanahan conceived the ideas; NH Cernohorsky and I Babu carried out the field work and data collection; majority of the writing was done by NH Cernohorsky who also carrier out the data analysis; M Horsák also carried out parts of the statistical analysis and TR McClanahan also contributed to the writing process; all authors commented on the manuscript.

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## **Prohlášení**

Prohlašuji, že jsem svoji disertační práci vypracovala samostatně s využitím informačních zdrojů, které jsou v práci citovány.

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Jméno Příjmení

## Abstract

Herbivory is an important process in the structuring of algal communities on coral reefs. Benthic algae compete with corals for sunlit space and the outcome of this competition determines which group dominates the reef. On “healthy” coral reefs algae is not very conspicuous and corals dominate the benthic community. However algae is much faster growing than corals and under certain circumstances can outcompete coral and dominate the reef. This thesis focuses on herbivory as an important regulating mechanism of benthic algae both on coral reefs of Lakshadweep as well as on a global scale.

Exclusion cages were used to assess the relative importance of herbivory on coral reefs of Lakshadweep archipelago. Two types of exclusion cages were installed along the backreef habitat of Agatti atoll, Lakshadweep: i) fine-mesh full cages (1 cm x 1 cm mesh openings) which excluded all visible herbivorous fish and sea urchins, ii) coarse-mesh full cages (6 cm x 6 cm mesh openings) excluded only large herbivorous fish with body depth >8 cm body depth. Half cages with tops only, half cages with sides only, and completely open plots were installed to function as controls. A global comparison of herbivore biomass, algal cover, and coral cover was carried out on data from 991 sites.

Algae was observed to rapidly increase in the fine-mesh cages, showing that herbivory rather than nutrients are a limiting factor of algal communities on the reef of Agatti atoll. The removal of large herbivores by the coarse-mesh cages had no effect on the cover, height, and composition on benthic algae, showing that small herbivores can in some cases prevent accumulation of algal biomass. These results are surprising as most previous studies highlight the importance of large herbivores in the removal of algal biomass and regulation of the algal-coral competition. The global comparison of herbivore-algal relationships shows variability among sites with different coral cover, depths, from different habitats, and oceans. The results from Lakshadweep along with results from the global comparison study show that herbivorous fishes and urchins are important for the regulation of algal communities and stress the importance of ecological context when assessing impacts of fishing and management on changes in herbivory, algae, and coral.

## **Abstrakt**

Herbivorie představuje na korálových útesech jeden z nejdůležitějších procesů pro utváření bentických společenstev řas. Bentické řasy soupeří s korály o osvětlený prostor a výsledek těchto konkurenčních vztahů určuje, která z těchto dvou skupin bude na útesu dominantní. Na "zdravých" korálových útesech dominují koráli a i když jsou řasy vždy přítomné, jejich výskyt není ve všech případech zcela zřejmý, nebo se často vyskytuji jen ve velmi nízkých abundancích. Řasy však rostou mnohem rychleji než korály a za určitých podmínek mohou korály rychle přerůst a vytlačit. Tato disertační práce se zabývá úlohou herbivorie na korálových útesech a její relativní důležitostí v regulaci řasových společenstev, jak v lokálním měřítku na Lakadivách, tak i na globální škále.

Klece, které zamezují přístup herbivorů k nárostům bentických řas, byly použity pro posouzení relativní důležitosti herbivorie na korálových útesech na Lakadivském souostroví (Indie). Na zadní mělké část útesu lakadivského atolu Agatti byly instalovány dva typy úplných kleců: i) klece s malými otvory (1 cm x 1 cm), zamezuje vstup všem viditelným herbivorním rybám a ježovkám, a ii) klece s většími otvory (6 cm x 6 cm), zamezuje vstup pouze velkým herbivorným rybám s výškou těla nad 8 cm. Dále byly instalovány i dva typy neúplných kleců, tvořených pouze horní částí nebo pouze boky. Plochy zcela bez kleců byly monitorovány jako kontrola. Globální porovnaní herbivorní biomasy, pokryvnosti řas a pokryvnosti korálů bylo provedeno na existujících datech z 991 lokalit z celého světa.

Řasy rapidně přibývaly pouze v klecích s malými otvory, což ukazuje, že vliv herbivorie byl mnohem důležitějším limitujícím faktorem řasových společenstev na útesech atolu Agatti než živiny. Odstranění vlivu pouze velkých herbivorních ryb pomocí kleců s většími otvory nemělo žádný prokazatelný vliv na pokryvnost, výšku nebo složení bentických řas. To znamená, že malí herbivoři mohou v některých případech účinně zamezit nárůstu řas. Tyto výsledky jsou překvapivé, protože většina předchozích studií zdůrazňuje důležitost velkých herbivorů v regulaci řas a míry konkurence mezi řasami a koraly. Globální porovnaní vztahu mezi herbivory a řasami ukázalo velkou variabilitu v závislosti na pokryvnosti korálů, hloubce, stanovišti a oceánu. Výsledky z Lakadiv i z globálního porovnaní poukazují na to, že herbivorní ryby jsou velmi důležitým faktorem pro regulaci řasových společenstev a zdůrazňují

důležitost ekologického kontextu při hodnocení dopadu rybaření a managementu na změny v herbivorii, společenstev řas i korálů.

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# **CHAPTER 1:**

## **GENERAL INTRODUCTION AND AIMS**

Herbivores, heterotrophs that consume primary producers, play an important role in both terrestrial and aquatic ecosystems (Huntly 1991). Not only do they form important pathways for energy and material flux up the food web, but they can determine things such as population dynamics, community structure, productivity, and spatial heterogeneity of plants and algae (McNaughton 1979, Crawley 1983, Adler et al. 2001). As such they are able to arrest, retard, or even speedup succession. Changes in herbivore communities can cause changes in the dominant growth forms which can lead to substantial shifts in ecosystem structure and functioning. In terrestrial ecosystems such documented changes often represent shifts between herbaceous and woody vegetation (Dublin et al. 1990, Zimov et al. 1995), in marine ecosystems they are often shifts to/from algal dominance (Hughes 1994, Steneck et al. 2002, 2004).

Coral reefs are the most biologically diverse ecosystems in the ocean. On “healthy” reefs the benthos is dominated by reef forming (carbon depositing) organisms, skleractinian corals. However if coral reef degradation occurs the benthic community can become dominated by fleshy algae with only very few corals. Such changes in the dominant benthic taxon/group, often referred to as “phase shifts” or “regime shift”, have occurred many times in the past (Hughes 1994, McClanahan and Muthiga 1998, Ledlie et al. 2007) and are becoming an increasing threat to coral reefs. Such shifts in benthic communities severely alter the whole ecosystem and most ecosystem services are then lost. Thus understanding the coral-algal dynamics has become increasingly important.

Algal dynamics are regulated by two types of mechanisms: bottom-up and top-down (Burkepile and Hay 2006, Smith et al. 2010). Bottom-up control refers to situations where algal/plant communities are governed by recourses that affect primary production. Therefore the bottom-up regulating mechanism on coral reefs include control by nutrient availability and sunlight. Because coral reefs are often oligotrophic ecosystems, algal growth is likely to be limited by the amount of available nutrients (effects nutrient availability is discussed in detail in Chapter 2). However not all coral reefs are nutrient

poor environments (Hatcher 1997, Szmant 1997). The top-down control mechanism is regulation by herbivore pressure. Herbivores control benthic algae by constantly cropping and removing algae, thus preventing the proliferation and expansion of algal communities (Hughes et al. 2007, Mumby and Steneck 2008).

The two most important herbivore groups on coral reefs are fishes (Pisces) and sea urchins (Echinoidea), (Choat 1991). Marine turtles can also potentially be important reef herbivores (Goatley et al. 2012). They however generally are more important for surrounding seagrass beds (Thayer et al. 1984). In the past they were reported to be extremely abundant. Anecdotal evidence from Columbus' voyages to the New World mentions that turtles were so abundant in the Caribbean that they "felt they were going to run aground on them and were as if bathing in them" (Lewis 1940). Marine turtles are the only megaherbivores in the tropical oceans apart from sirenians, and given their extremely high abundances they were likely to be important species not only on seagrass beds, but on coral reefs as well (Jackson 1997, Jackson et al. 2001). However they have been decimated on most reefs worldwide, and although they still play an important ecological role on seagrass beds in some places, their influence on coral reefs is minimal due to their low abundances. Herbivory fish are usually the most abundant and diverse herbivore group and thus often of primary importance. The main herbivorous fish are parrotfish (Scarinae, Labridae), surgeonfish (Acanthuridae), and rabbitfish (Siganidae). They can be broadly divided into four main functional groups based on both morphological features as well as feeding behaviour: grazers, scraper, excavators and browsers (Green et al. 2009). Grazers (which include most rabbitfishes and many species of surgeonfishes) are herbivores that intensely feed on turf algae, often referred to as epileptic algal matrix (EAM, sensu Wilson et al 2003), and due to the anatomy of their mouth, only crop algae and do not usually remove the algae completely from the substrate. Scrapers (mainly parrotfishes) are a group that are able to scrape the algae completely off the substratum using their beak-like mouths which are common to all parrotfishes. Scraper as well as the next group, excavators, also typically feed on turf algae. Excavators are usually large parrotfishes that not only remove the algae completely from the reef substrate, but along with the algae they also remove part of the calcium carbonate reef structure itself, which passes through the fish's digestive system and is excavated in the form of fine sand. These herbivores thus function as important reef bioeroders and producers of sand (Bruggemann et al. 1996, Bellwood et al. 2011).

Some species have been estimated to produce up to one or even five tons of sand per year per individual (Bellwood 1995, Bellwood et al. 2003). The formation of sand is especially important on coral reef atolls, where the islands are made of accumulated sand. Grazers, scrapers and excavators, although very important, have a limited capacity to remove macroalgae and thus also have a limited capacity to return reefs back to coral dominated states after macroalgae has proliferated and become dominant. In this respect, “browsers” are the important group of herbivores. They specialize in removing macroalgae which is generally unpalatable to most other species (Green et al. 2009), and include certain species of surgeonfishes and rabbitfishes. Aside from cropping and removing algae and bioerosion, fish herbivores also indirectly aid in the recruitment of corals. They clear parts of the substrate, by removing algae, and open up new space making it available for the colonization by young coral larvae (Hughes et al. 2007, Mumby 2009). Herbivorous fish thus help lower competition for space between coral and algae not only by keeping algal populations low but also by facilitating coral recruitment.

Sea urchins are less diverse than herbivorous fish and are also much less selective feeders, so they are certainly not ecologically equivalent to herbivorous fish. In some cases though, sea urchins are capable of ecologically replacing herbivorous fish, as urchins also function as both important regulators of algae as well as important bioeroders (Hughes 1994). On reefs that have not been overfished and are still predator rich, sea urchins are often less abundant than herbivorous fish and thus are usually less important in algal control and bioerosion processes. However, on some coral reefs sea urchins have shown to be abundant and important components of the herbivore community despite having abundant and intact fish communities (Johansson et al. 2010). However, more often are high urchin abundances a sign of reef degradation. Sea urchin populations have been shown to rapidly increase in response to reduced predation by triggerfish, which have been overharvested (McClanahan and Muthiga 1988, McClanahan 2000). When herbivore levels are reduced due to factors such as overfishing, algae may be released from top-down control and proliferate, rapidly overgrowing corals. However, sea urchins if abundant enough are capable of taking over the role of herbivorous fish and controlling algae levels, maintaining coral dominated reefs, albeit at lower resilience.

Coral reef herbivores, due to their indirect affects as mediators of competition between corals and algae, thus play an important role in reef health. Under most conditions algae grows much faster than corals, so understanding the forces that regulate algal communities is crucial. There have been numerous studies conducted on this topic, however there is still currently limited understanding of the relative importance of different herbivores and how context specific their ecological functions are.

### Aims and thesis outline

The general aim of this study was to look at herbivory and its ecological importance on shallow coral reefs of Lakshadweep Islands, a largely unfished location. The fact that the local inhabitants largely depend on pelagic fishing, means that reef fish communities are largely intact. This and the location of Lakshadweep, which is an offshore oceanic atoll system, offered a unique opportunity to study herbivore communities and their influence on the coral–algal balance in a coral dominated reef system that has only few human-induced disturbances.

Studying ecological processes on “healthy” close to “pristine” reefs is of prime importance. I will use a quote from Knowlton and Jackson (2008) to explain why this is important: *“Imagine trying to understand the ecology of tropical rainforests by studying environmental changes and interactions among the surviving plants and animals on a vast cattle ranch in the centre of a deforested Amazon, without any basic data on how the forest worked before it was cleared and burned. The soil would be baked dry or eroded away and the amount of rainfall would be greatly decreased. Most of the fantastic biodiversity would be gone. The trees would be replaced by grasses or soybeans, the major grazers would be leaf-cutter ants and cattle, and the major predators would be insects, rodents, and hawks. Ecologists could do experiments on the importance of cattle for the maintenance of plant species diversity, but the results would be meaningless for understanding the rainforest that used to be or how to restore it in the future. Fortunately, ecologists began to carefully describe tropical forests more than a century ago, and vast areas of largely intact forests have persisted until today, so there are meaningful baselines for comparison.”* Unfortunately marine ecology is a very young discipline and underwater observations of coral reefs have begun quite recently

(Mayer 1915, Goreau 1959). Unfortunately, the degradation of oceanic ecosystems has been much more pervasive than on land, and thus many reefs had already been degrading during the first time scientists started studying them. We thus lack proper baseline for pristine coral reefs. Due to the complication of determining what a healthy pristine coral reef looks like, scientists often consider the reef conditions they saw at the beginning of their careers as pristine. Consequently, the idea of what are baseline conditions shifts with each next generation. This phenomenon has been termed the “shifting baseline syndrome”. Although it was first used by a fisheries scientist, Daniel Pauly (1995), to help explain the problem with declining fish stocks due to overfishing, the shifting baseline syndrome applies easily to all ecological disciplines.

What today’s young generation of coral reef scientists usually sees as healthy would be considered degraded by standards of, for example, the 1920’s scientists. Thus gathering data and knowledge about the last few coral dominated predator rich reef ecosystems is of great importance in regards to setting some sort of baseline that will consequently help set better management goals for the rest of the reefs. Studying herbivory in relatively pristine and intact reefs may be crucial for understanding the mechanisms that shape the benthic algal communities and promote coral reef resilience.

We look at herbivory in Lakshadweep in Chapters 2 and 3. Chapter 2 explores the importance of herbivory in preventing shifts towards macroalgae dominance. Chapter 3 studies the relative importance of small versus large herbivores in limiting algal accumulation. Chapter 4 then looks at the overall global picture of herbivory and how it influences macroalgae across oceans and different habitats with different coral cover. During our field research in Lakshadweep we found some new records of butterflyfish species in Lakshadweep, and thus include a short published paper with the findings at the end of the thesis, in the appendices.

# **CHAPTER 2:**

## **VARIATION IN ALGAL SUCCESSION AND GROWTH IN RESPONSE TO THE EXCLUSION OF HERBIVORES**

### **2.1 Introduction**

Tropical coral reefs have many sessile organisms that need sunlight to grow, thus there is high competition for sunlit space between them, especially between coral and algae. Generally coral are the most successful and dominant sessile organism to inhabit the reef. However with increasing natural and anthropogenic stressors to the coral organisms they are losing their superior position in the competition with algae and algae is increasingly taking over the reef benthos. This has often happened after high coral mortalities, such as those induced by coral bleaching or hurricanes (Ostrander et al. 2000, Ledlie et al. 2007). As corals died, new space was opened up on the reef and the fast growing algae quickly proliferated and soon became the dominant life form on some coral reefs. One such extreme coral mortality event took place in 1998 during the warm phase of El Nino Southern Oscillation (ENSO). The warm phase of ENSO is a natural phenomenon that occurs every 2–7 years. During this time the coastal upwelling near Peru and Ecuador disappears and the central and eastern tropical Pacific Ocean experiences warming of sea surface temperatures (SSTs) which can lead to coral bleaching. This in turn induces changes in climate around the globe.

The Indian Ocean sea surface temperatures can be affected by these climate changes as well (Chambers et al. 1999, Yu and Rienecker 1999), and during the 1998 ENSO the SSTs of the Indian Ocean (including Lashadweep) increased for too long, the corals bleached and 50–90% of them died (Wilkinson et al. 1999). In some places like the

Seychelles algae took over the reef and coral never recovered (Ledlie et al. 2007). However, in the Lakshadweep Islands (located just north of Maldives) coral recovered quite rapidly. A study that looked at the recovery of coral reef in Lakshadweep archipelago (Arthur et al. 2006) showed that the recovery was very site specific, but that there was no macroalgal bloom after the mortality.

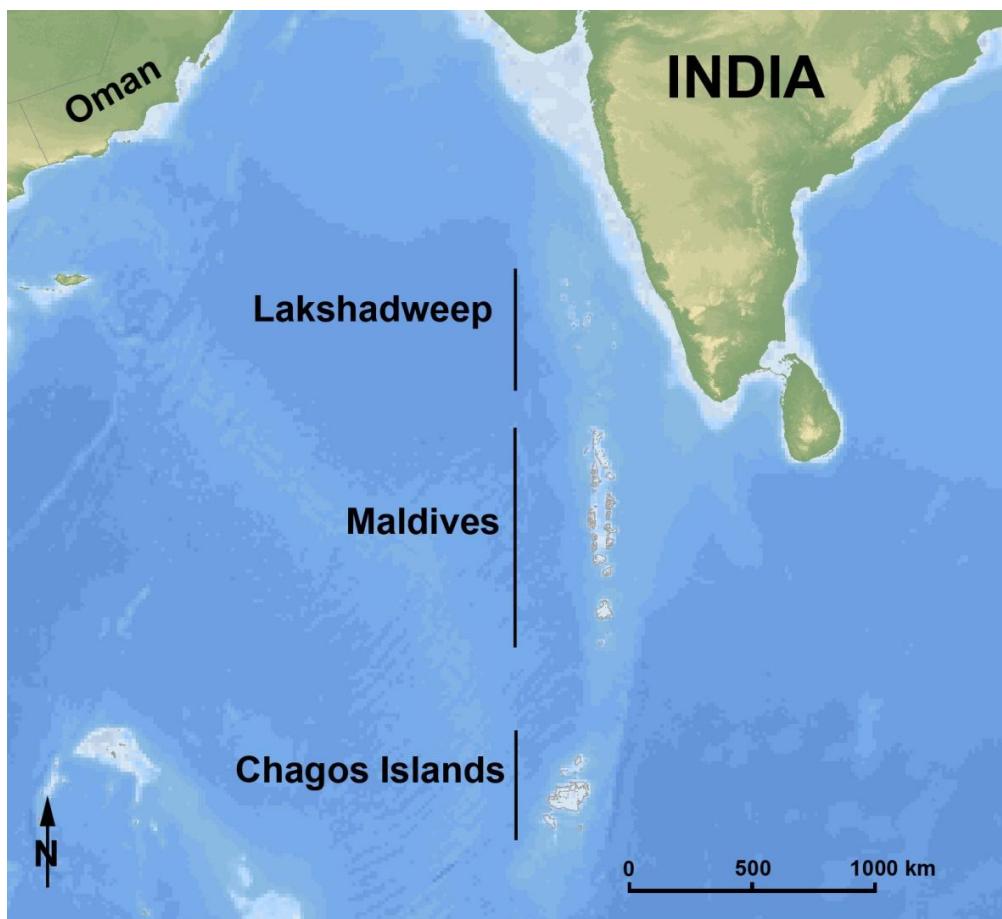
Most coral reefs are oligotrophic, especially those which are oceanic and far away from nutrient flushes from mainland, such as Lakshadweep reefs. Lakshadweep does have a high population and thus relatively high amounts of nutrients are likely to enter the water, however the reefs are separated from the islands by a lagoon. The lagoons contain seagrass beds which are likely to trap the nutrients and prevent them from reaching the reef. Additionally the reefs of Lakshadweep are highly flushed systems and even nutrients that manage to reach the reef are likely to be flushed into the open ocean. There is a possibility that after the coral mortalities of 1998, algae was limited by nutrients and thus did not bloom and dominate the reef. Lakshadweep Islands have a very healthy community of reef fish, because the livelihood of the people is dependent on pelagic fisheries and thus the reef fishes are rarely targeted. Thus, there is also most likely a very strong top-down regulating mechanism of the algae communities by herbivorous reef fish.

Herbivores and nutrients are widely accepted as the two main controlling factors of macroalgal abundance (McClanahan et al. 2003, Hughes et al. 2007). However the topic of whether macroalgae are more “bottom-up” regulated by nutrients or “top-down” regulated by herbivores remains controversial (Littler and Littler 2007). Although there seems to be more evidence supporting the latter (Burkepile and Hay 2006), many studies argue that macroalgae are mainly influenced by nutrients or the combination of poor water quality and low herbivory (Albert et al. 2008, De’ath and Fabricius 2010, Smith et al. 2010). This study uses exclusion cages to look at the relative importance of top-down and bottom-up limitation of algal growth on Agatti Atoll, Lakshadweep, and tries to determine which of these forces were likely to be the main limiting factor for algal growth, after the 1998 coral bleaching event.

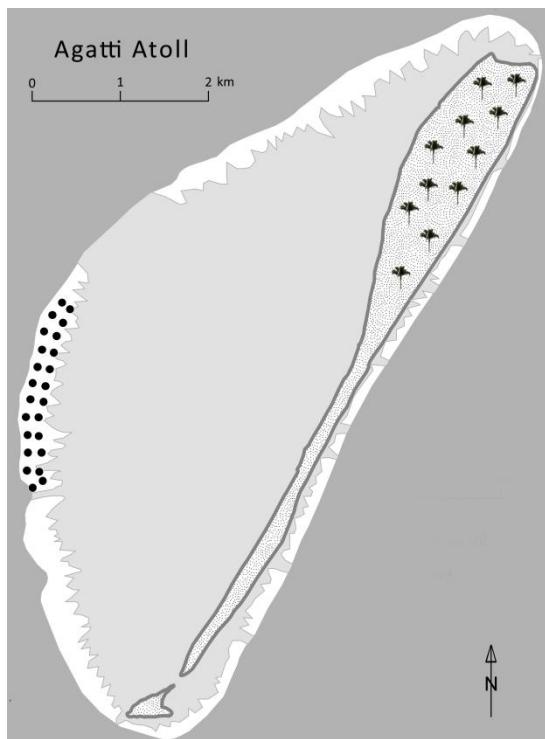
## 2.2 Material and Methods

### Study area

This study was conducted on the back-reef habitat of Agatti Island, Lakshadweep archipelago. Lakshadweep Archipelago is set of oceanic atolls that lie west of India and north of the Maldives in the Laccadive and Arabian Seas. Together with Chagos and Maldives they form a chain of atolls and coral reefs that run north to south along the underwater mountain range called the Chagos–Laccadive plateau (Fig. 2.1 and Fig. 2.2). Lakshadweep islands have a total of 32 km<sup>2</sup> of land made up of 27 islands, from which 11 are inhabited. They have a high population of 64 000 with densities of about 2000 inhabitants per square kilometre. Despite such high human densities on the islands the fishing on coral reefs has been surprisingly low. Reef fishes were historically an important part of the local inhabitants' diet. However in the 1960s the government sought to change the hitherto sustenance artisanal fishing practices and start a commercially viable industry of tuna fisheries. The fisheries department, founded in 1959, then decided to adopt the same fisheries practices already used in the Maldives and the southernmost island of Lakshadweep, Minicoy, which was pole and line fishing (Fig. 2.3) focused purely on catching skipjack tuna (*Katsuwonus pelamis*). Experienced fishers from Minicoy trained the rest of the islanders, and today tuna is the preferred fish for consumption on the island. Some of the tuna is also exported in the form of dried mass (Fig. 2.3). Although this reform was motivated by economical gain it coincidentally (and purely by accident) became an important conservation measure for the coral reefs, which became fished only occasionally during monsoon season, when the seas are too rough for tuna fishing.



**Fig. 2.1.** Map of the Chagos–Laccadive plateau, showing the location of Lakshadweep archipelago.



**Fig. 2.2.** Map of Agatti atoll, its long island (gray area with coconut tree symbols) and surrounding coral reef. Black dots represent studied back-reef sites.



**Fig. 2.3. a)** Pole and line tuna fishing in Lakshadweep; **b)** Processing of caught skipjack tuna; **c)** tuna mass (boiled, smoked, and then dried tuna fish meat), a product for export which is also consumed by the local inhabitants during the monsoon period, when tuna fishing is not possible due to the rough sea conditions. It is during this period that locals will also turn to eating reef fish.

### Experimental design

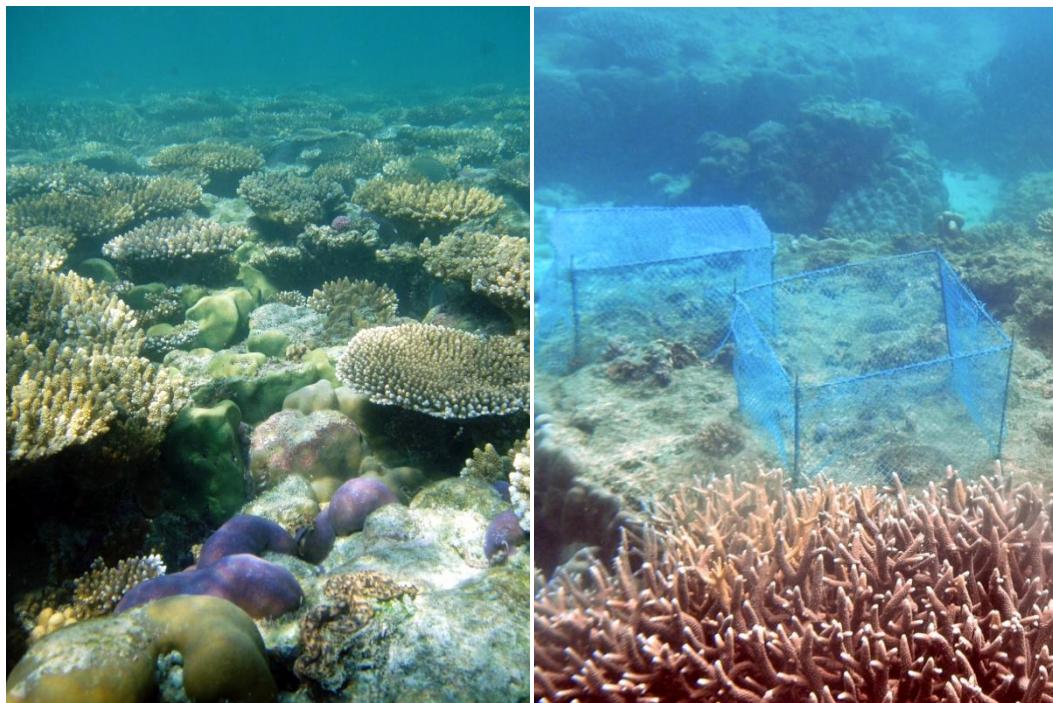
Exclusion cages were used to investigate the ecological impacts of removing fish from the coral dominated back-reefs of Agatti atoll (Fig. 2.2). We used three types of

cages: (i) full cages with small 1 x 1 cm mesh designed to exclude most visible herbivores such as fish and sea urchins, (ii) partial cages with mesh only on the top, constructed to check for the influence of shading, (iii) partial cages with mesh on the sides only to check for the influence of reduced water flow. Lastly, completely open plots were also installed and served as the main controls. Thus a total of four different treatments were used in this sampling design. All cages had dimensions of 40 cm width and length and 20 cm in height and were constructed of a metal frame and a mesh made of fishing net twine (Fig 2.4). They were affixed to the dead coral substratum using stainless steel nails and ties to keep the cages in place and ensure no unwanted incursions of fish.

The five treatments were replicated at each of our 24 sampling sites, resulting in a total of 96 experimental plots. The sites were placed (200 m apart) along a transect that followed the atoll rim, beginning from the main reef channel and ending at the next small channel. Half of these sites (12 sites) were placed on the leeward back-reef (inner back-reef) and the other half on the border of the back-reef and reef flat (outer back-reef), thus covering various back-reef habitats (Fig. 2.2). The distance between the inner and outer back-reef sites was 150 m. Treatment designations of specific cages were randomly determined at each site, but always ensuring that mainly dead coral heads were included in the cages. However, some live coral was always included in the cages. Average depth of the sites at low tide was 1.0–1.5 m.

The experiment was installed for a total of 127 days from December 2009 to April 2010. Cages were visited every 10–14 days to be cleaned of algae and other settling organisms with a plastic brush. During those times algae height was measured and benthic cover data were collected (with one exception towards the end of the experiment as weather conditions worsened) using *in situ* visual coverage estimates. Photographic images of the plots were also taken on each of these visits during the first 3 weeks and then every day after cage removal until plots were completely browsed. Benthic coverage data included coral, other invertebrates, sediment, non-biological (e.g. bare substratum), and algae identified to the lowest possible taxonomic level, but in majority of cases only functional groups were ascribed as detailed identification in the field was not possible. Height measurements of algae were taken separately for each algal group using one measurement for each group, unless height seemed to vary within a group then

3 measurements were taken and an average value was calculated. The following functional groups were used for further analysis of the algal community (Steneck and Dethier 1994, Diaz-Pulido 2008): crustose coralline algae (Corallinales, Rhodophyta, of crustose habit, referred to as CCA), non-calcareous crustose algae (non-coralline algae of crustose habit, e.g. *Ralfsia*), fine low turf (short, around 1mm, and sparsely distributed green/brown filamentous algae and microalgae), turf (higher denser turf made up of a mix of microalgae, filamentous algae, small macroalgae, and sediment), filamentous non-turf algae (long strands of spatially limited microalgae *sensu* Steneck and Dethier (1994) strands of cyanobacteria, and filamentous algae *sensu* Steneck and Dethier (1994) e.g. *Cladophora*), filamentous macroalgae (i.e. genus *Boodlea*) foliose globose (e.g. *Dictyosphaeria* and *Valonia*), foliose corticated (e.g. *Dictyota* and *Lobophora*), corticated macroalgae (upright fleshy algae, such as *Gracilaria* and *Laurencia*), leathery (e.g. *Codium* or *Turbinaria*), calcareous articulated (e.g. *Caulerpa* and *Halimeda*).



**Fig. 2.4. Pictures of the back-reef habitat (left), and a full exclusion cage and partial cage installed on a dead coral head (right).**

## Data analysis

To obtain estimates of algal biomass we calculated algal volume for each cage and each sampling time by multiplying algal cover (in cm<sup>2</sup>) by algal canopy height (in cm) (Steneck and Dethier 1994). Algal volume was standardized to an area of 1 cm<sup>2</sup> of dead coral substrate (i.e. without live coral) to eliminate variability caused by different proportions of live coral in different cages. To verify the accuracy of the benthic coverage data assessed by in-situ estimates, we compared it with the coverage data obtained from the benthic photoquadrats. Image analyses of the benthic photoquadrats were completed using the program PhotoGrid 1.0.

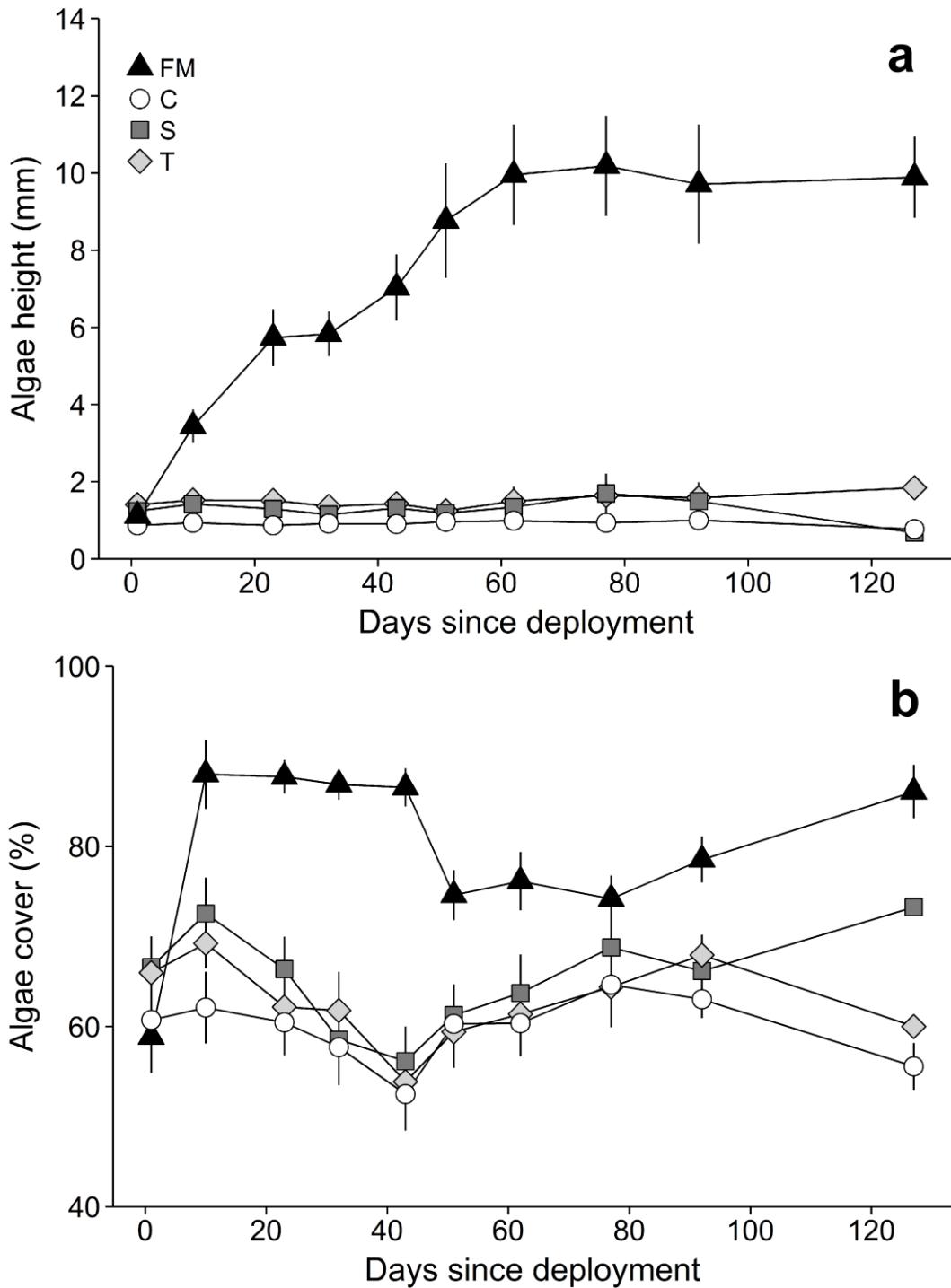
We explored the effect of excluding all herbivores on algae accumulation (i.e. volume) using Linear Mixed-Effects (LME) Models because measurements of the response variable (i.e. algae volume) were not independent (for more details see Data Analysis in Chapter 3). After the 127 days cages were removed from the plots and further observed the plots. In order to assess the influence of reintroducing herbivores to the plots, algal volume data (cover x height) was tested using the Wilcoxon signed rank test.

A multivariate analysis procedure was used to visualise how community structure varied among treatments (on the inner and outer back-reef habitats) over time. For each treatment, habitat, and time a Bray-Curtis similarity index was calculated. Then using a principal coordinates analysis (PCoA), we calculated centroids for each treatment by time combination. These centroids (with their PcoA axes scores) were then ordinated using non-metric multidimensional scaling (NMDS) and plotted in two-dimensional space in order to obtain successional trajectories for each type of treatment. These trajectories show how communities changed in relation to treatments over time. Since the NMDS ordination method preserves the ranked similarities among samples, the closer the samples (centroids in our case) are in the displayed two-dimensional space the more similar they are in composition.

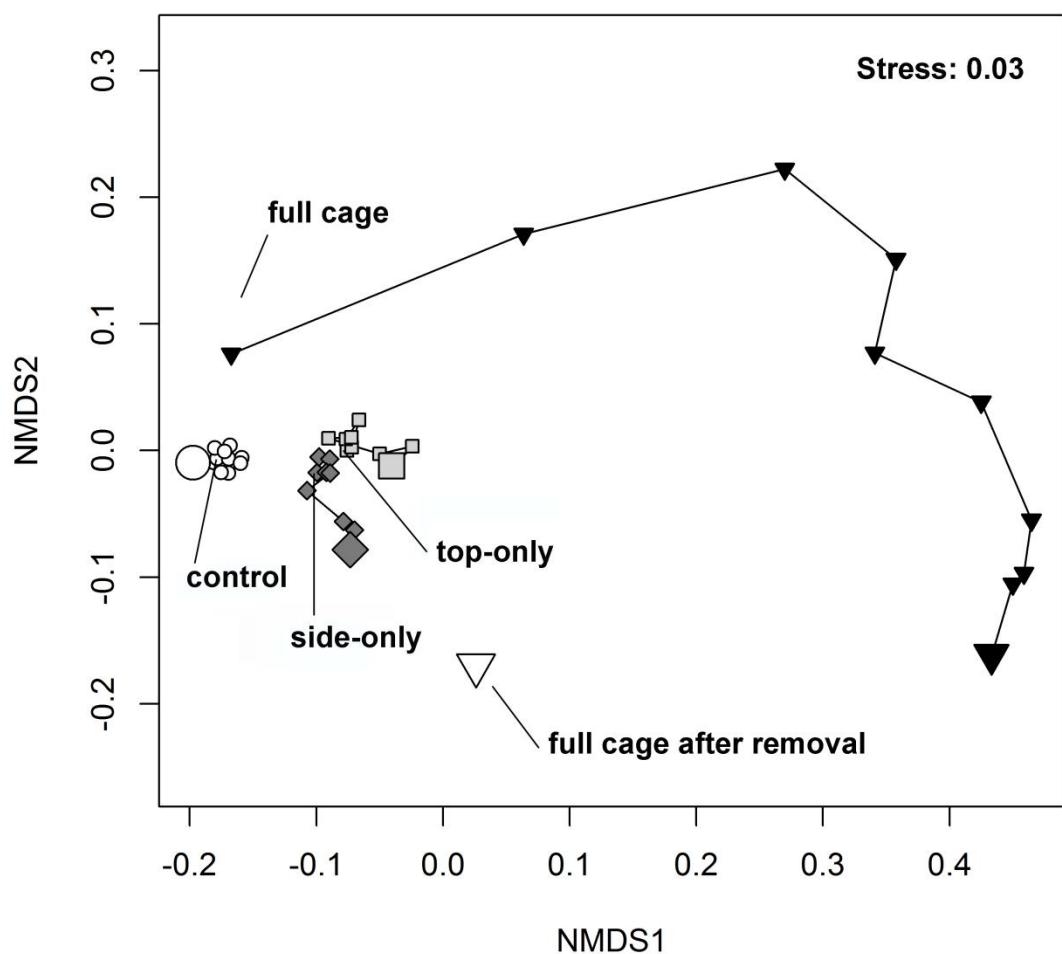
## 2.3 Results

The exclusion of herbivores had immediate effect on the benthic community. Algae cover as well as height increased within the first 10 days after the removal of herbivores (Fig. 2.5). Average height at the end of the experiment was 9.9 mm in the caged plots and 0.8 mm, 1.8 mm, 0.7 mm in the uncaged control, top-only, and side-only plots respectively (Fig. 2.5a). Algal cover reached close to 90% of the available substrate (i.e. hard substrate without live coral) within 10 days of herbivore exclusion but then fluctuated (Fig. 2.5b). Algal cover in the partially caged and uncaged plots remained relatively constant throughout the 127 experimental days. There were no significant differences among plots (treatments) in the coverage of macroalgae, turfs, or corals prior to the exclusion of herbivores (GLM:  $p>0.10$ ). The accumulation of algae (i.e. volume) over time in the caged plot was significant (LME:  $t=9.10$ ,  $p<<0.001$ ). The half cage treatments (top only and side only) had no significant effect on algae and no increase in algae was observed in the open control plots either (LME:  $p>0.177$ ). In the full-cage treatments there were only three cases where live coral cover decreased over the period of the 127 experimental days. Live coral cover remained the same or increased in the rest of the full-caged plots (Fig. A1) as well as in all the partially caged and control plots.

In terms of community composition low algal turf dominated all the plots at the beginning of the experiment. During the 127 days low algal turf remained the most dominant algae group on the half cage and control plots. Algal communities underwent drastic changes in the caged plots with increases in turf height but also new occurrences of many different macroalgal groups, which rapidly increased in abundance (Fig. A1). There was a lot of variability in algal community changes within caged plots throughout the experiment (Fig. A1). However the variation seemed completely random as no patterns in the developed algal communities were found among sites from similar habitats (i.e. plots from sites A versus plots from sites B, nor sites closer to the channel vs. sites further away from the channel).

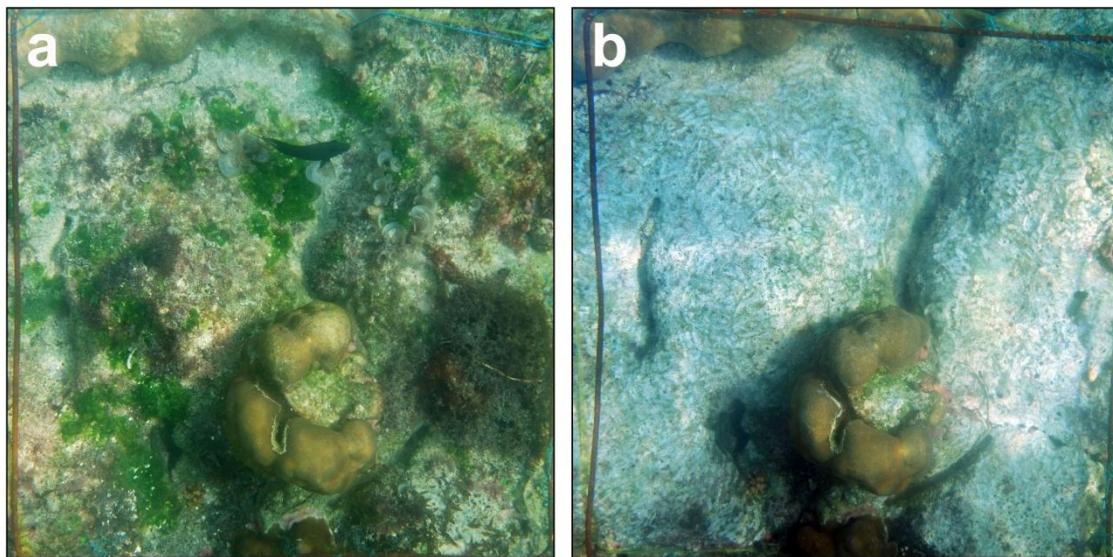


**Fig. 2.5.** Mean algal height (a) and cover (b) in different treatments over time. Error bars represent standard errors. Algal height is calculated as the average height of all the algal groups together. Algal cover is the percent cover on available substrate (i.e. hard substrate without live coral). Black triangles (FM) represent full cage treatments, white dots (C) represent control plots, dark grey squares (S) and light grey diamonds (T) represent side-only and top-only half plots respectively.



**Fig. 2.6.** Successional trajectories of non-coral (non live coral) benthic communities under different treatments (full exclusion cages, controls, side-only and top-only half cages). The ordination plot shows the community similarity of benthic communities, represented by points (centroids, that were calculated from principal coordinates analysis and then ordinated using non-metric multidimensional scaling) and how it changed over time. Labels point at the beginning of the experiment and enlarged points indicate the end of the experimental period. Points that are closer to together are more similar in benthic composition. Stress values under 0.05 indicate that the differences in multivariate community data are very well represented by the distances in two dimensional space (i.e. very good fit). After the removal of cages, the benthic communities of the plots returned to very similar communities as in the beginning, but remained more browsed for a few days. The open triangle represents the full cage plots one day after removal of the cages.

Re-exposing the plots to natural herbivory, by removing the exclusion cages, lead to a significant decrease in algal biomass (Wilcoxon test:  $p<0.001$ ). No caging effects were found after a few days of the removal of the cages (Fig. 2.6). Most cages were browsed completely to bare substratum within 24hours (Fig. 2.7), and typically had even less algae than at the beginning of the experiment and less than the surrounding reef. Only in one plot the removal of macroalgae (i.e. genus *Caulerpa*) by herbivores took seven days to achieve original macroalgal levels.



**Fig. 2.7. Experimental plot after 127 days of herbivore exclusion (a), and 1 day after the removal of the exclusion cage (b).**

## 2.4 Discussion

With global climate change and the increasing associated stresses to corals, coral reefs have been losing their resilience and the threat of becoming low-coral high-algae systems is increasing. Since the 1998 mass bleaching event Lakshadweep coral reefs have been experiencing increased episodes of mass coral bleaching just like many other reefs around the world. Thus it has become increasingly important to understand the role of local stressors that influence the benthic communities. One such stressor is overfishing. Although Lakshadweep has relied on pelagic fishing for over half a decade there has been a lot of pleasure on fisheries development and the utilization of local marine resources, which could potentially result in further undermining of reef health and resilience. While many studies have examined the role of herbivory on coral reef benthic communities, there is still some debate about the relative importance between bottom-up and top-down control. No such studies, examining any of these processes, have ever been conducted in Lakshadweep, despite the importance of understanding local processes for proper reef management in the face of climate change.

After the mass bleaching event and extremely high coral mortalities in 1998, there was not shift towards macroalgal dominance and Lakshadweep reefs managed to recover and have become dominated by corals again (Arthur et al. 2006). Our study indicates that the low occurrence of macroalgae after the coral mortalities was likely due to relatively intact herbivore communities, rather than nutrient limitation despite Lakshadweep being an archipelago of oceanic atolls far way from any major agricultural nutrient inputs.

The results of this study show that experimental exclusion of herbivorous fishes and urchins had a rapid effect on benthic communities. Algae cover and height increased and the community composition changed rapidly as well (Fig. 2.5 and 2.6). Algal cover increased rapidly to more than 80% within the first 10 days (Fig. 2.5), but then fluctuated slightly, likely due to the occurrences of increased wave intensities and/or sedimentation, as after major storms we observed the dislodgement of large chunks of macroalgae stands. Heights of different algae groups also fluctuated as some groups occurred and were later replaced by other types of algae (Fig. A1), however on average the algal height as well as algae volume increased over the whole experimental period.

Benthic communities developed very differently inside the full cages than in the half cages and controls. The benthic communities in the full cages also developed differently across sites (Fig. A1). Most sites developed high stand of various macroalgae, but some became dominated by filamentous algae and cyanobacteria. Despite the fact that in the absence of herbivory algal communities are likely to be influence by recourses and other things such as water motion, light availability etc, no difference in the development algal community structure was found among sites (those closer to the channels and those further away) or habitats (inner and outer back-reef) and the variation in the development of different algal groups thus may be due to purely stochastic processes.

The fact that the developed stands of macroalgae and filamentous algae (in the full exclusion cages) were observed to overgrow corals only in three cases was surprising. Live coral cover in most of our plots was observed to remain the same and even increase in some cases. The mechanisms by which algae have been shown to compete with coral are overgrowth, shading, abrasion, chemical-allelopathy, pre-emption, epithelial sloughing (McCook et al. 2001), and even indirect interactions via microbial activity (Smith et al. 2006). Corals however can also directly and indirectly inhibit algal growth via similar mechanisms, for example by overgrowing, shading, abrasion, but also by stinging etc. (McCook et al. 2001). These interactions between coral and algae often depend on the species or functional groups present. Barott et al. (2012) found that other factors likely influence these interactions as well. They found that on uninhabited islands corals were stronger competitors than the adjacent algae, whereas on inhabited islands algae were winning more of the competitive edge than corals. In our experimental plots corals seemed to be superior competitors against algae, despite Agatti being a densely populated island. However it is possible that our experimental period was not sufficiently long enough to allow for algal overgrowth of corals. Though algae may not always be a superior competitor against corals (McCook 2001), under certain circumstances (especially after large coral mortalities such as those that have occurred due to coral bleaching) algae can gain competitive edge and become the dominant benthic group (Ostrander et al. 2000, Ledlie et al. 2007).

Lakshadweep coral reefs have had healthy reef fish population for many years due to the fisheries practices that target pelagic fish. However, after this study was conducted, fisheries practices have changed and a wider range, and higher amount, of fish are being

now caught, including reef fishes. The fact that coral cover was not reduced by the increased algae stands inside the experimental full cages indicates that coral dominance may be preserved even at low levels of herbivory. However in the event of high coral mortalities, which are an increasing threat due to global climate change, the now fished herbivore communities may no longer be sufficient enough to prevent algal blooms and shifts of reefs towards algal dominance.

The fact that algae cover and height increased in the exclusion cages shows that nutrients were sufficient enough to allow for algae growth and that top-down limitation by herbivores is the main limiting factor for algal communities on Agatti back-reef. Whilst the superiority of top-down limitation over bottom-up control has been observed elsewhere, these results are significant and provide important implications for coral reef management in the Lakshadweep archipelago. It is quite plausible that the recovery of Lakshadweep coral reefs in the past was enabled by the healthy herbivore populations which kept algae low during times of reduced coral cover, and since coral bleaching events are likely to increase in frequency and intensity, focusing on the protection of herbivore fish communities is likely to be crucial to the health and survival of Lakshadweep's coral reefs.

# **CHAPTER 3:**

## **ASSESSING THE IMPORTANCE OF HERBIVORE SIZE: TOP-DOWN ALGAE CONTROL**

*Published in Coral Reefs under the title: Small herbivores suppress algal accumulation on Agatti atoll, Indian Ocean. The final publication is available at Springer via [http://dx.doi.org/\[ DOI 10.1007/s00338-015-1331-x\]](http://dx.doi.org/[DOI 10.1007/s00338-015-1331-x]).*

### **3.1 Introduction**

Coral reefs around the world have been experiencing accelerating degradation (Sheppard 2003, Bellwood et al. 2004, Pandolfi et al. 2005, Graham et al. 2006, Bruno and Selig 2007, Knowlton and Jackson 2008, Veron et al. 2009, Anthony et al. 2011). They are facing various and multiple stresses, both natural (e.g. cyclones and hurricanes, extreme low tides) and anthropogenic (e.g. overfishing, global warming, ocean acidification, and pollution). Coral mortalities are becoming more frequent and are increasingly followed by a shift from coral dominance to algal dominance (Hughes et al. 2007, Graham et al. 2015). These transitions are often referred to as “phase shifts” in coral reef literature (McManus and Polsonberg 2004, Hughes et al. 2007, Cheal et al. 2010). The term „phase shift“, sometimes referred to as „regime shift“, is used to describe a transition of an ecosystem into an alternative stable state (Beisner et al. 2003, Folke et al. 2004). In the course of human history we have witnessed numerous such shifts to alternative stable states in various terrestrial and freshwater ecosystems: e.g. the Sahara desert, once covered in vegetation is now the third largest dessert on Earth (Foley et al. 2003), the Mediterranean maquis and garrigue was earlier covered by evergreen sclerophyllous forests (Archibald 1995), or Siberia where steppe grasslands have shifted to moss dominated tundra (Zimov et al. 1995). Major marine shifts have also been reported, such as shifts from kelp beds to sea urchin barrens or the mentioned shift from coral- to algal-dominance (Steele 1998, Steneck et al. 2002). Whether these shifts on coral reef ecosystems are permanent ecological phase shifts or temporary successional transitions is an area of considerable debate (Beisner et al. 2003, Folke et al. 2004,

Dudgeon et al. 2010, Zychaluk et al. 2012, Mumby et al. 2013). Nevertheless these transitions pose a great threat for coral reef ecosystems, as coral mortalities and increasing overfishing can potentially diminish the ability to reverse these shifts (Bellwood et al. 2006, Hughes et al. 2007, Graham et al. 2013). Consequently, it is increasingly important to understand the factors that influence and control the coral-algae balance.

Herbivores are viewed as key functional components of coral reefs that maintain the coral-dominated state of the ecosystem (Bellwood et al. 2004). They prevent algal proliferation and thus lower the competition between coral and algae (Rasher and Hay 2010). They can also facilitate coral recruitment by providing suitable substrate for the attachment of coral larvae (Hughes et al. 2007, O'Leary et al. 2013). With global warming and the increasing occurrences of disturbances, such as coral bleaching, reefs will be reliant on intact functional herbivore assemblages. The two main herbivorous groups responsible for keeping algae in check and promoting resilience on tropical coral reefs are fish and sea urchins (Bellwood et al. 2004). Within the fish herbivore guild, however, four different functional groups are recognized, based on their feeding morphology, which is inherently connected to foraging activity. These are browsers, excavator, scrapers, and grazers (Green et al. 2009). Sea urchins are usually considered as a separate herbivore group as their foraging behaviour is different from that of most herbivorous fish but can also be classified into similar functional groups (Carreiro-Silva and McClanahan 2012). Nevertheless, their grazing most frequently takes place on open carbonate surfaces and crevices and can be less selective and more intense and localized (Bak 1990, Carreiro-Silva and McClanahan 2001).

Although numerous studies have examined herbivory affects on the coral-algal balance (Hay 1984, McCook 1996, McClanahan 2014), the role that different species or functional groups of herbivores play are only recently being appreciated (Hoey and Bellwood 2009, Hoey et al. 2013, Hamilton et al. 2014, Humphries et al. 2014). Larger herbivores, which have been shown to be extremely important on coral reef ecosystems (Hughes et al. 2007, Hoey and Bellwood 2010), have received lot of attention in the past. The focus on larger fish is likely due to the increasing fishing pressure and the depletion of large fish that has been happening throughout our oceans at alarming rates (Pauly 1995, McClenachan 2009). In fact most of the large organisms have already been

significantly reduced or lost, and we are now facing the effects this has on our oceans today. Larger herbivorous fish have been predicted to be more important than smaller herbivorous fish in terms of removing algae. Although smaller herbivores have been shown to graze larger areas of the reef per unit body mass, most of them only crop the algae and do not remove it completely from the substratum. Larger herbivores graze smaller areas per unit body mass but remove the algae completely along with carbonate substratum, thus providing new open space for coral recruitment (Bonaldo and Bellwood 2008). Apart from this impact, total algal intake has also been shown to correlate positively with the fish body biomass (Bruggemann et al. 1994, Bonaldo and Bellwood 2008, Lokrantz et al. 2008). Therefore, large individuals and species are considered of prime importance in preventing algal dominance (Mumby 2006, Lokrantz et al. 2008, Norström et al. 2009, Edwards et al. 2014, Steneck et al. 2014).

However, the commonly-used phrase “large herbivores” can be interpreted in different ways. For example, studies using exclusion cages have defined large herbivores as those unable to pass through a certain mesh size.

Although many herbivore studies refer to large herbivores as fish unable to pass through a 5–6 cm mesh (Bellwood et al. 2006, Hoey and Bellwood 2010, McCauley et al. 2010), there are also studies that refer to “large herbivores” as fish unable to pass through much larger as well as much smaller mesh sizes, e.g. 1x1 cm, 10x10 cm, or even fail to specify the mesh size (Hughes et al. 2007, Jayewardene 2009, Mörk et al. 2009, Burkepile and Hay 2011). Such variable definitions can lead to ambiguity and result in different macroalgal responses and associated management recommendations. Especially where small mesh sizes were used (such as 1x1 or 2x2 cm mesh) the term “large herbivore” may be very misleading. These cages exclude not only “large” herbivores but also all size classes of herbivorous fish and sea urchins and allow only tiny fishes and mesoherbivores (such as crustaceans) to enter the cages. In this study we assessed the relative importance of large herbivores and define them as those unable to pass through 6 cm mesh. We compared algal accumulation rates in various cages and mesh sizes on coral reefs of an oceanic atoll of the Lakshadweep Islands, a largely unfished location. The location and reliance of the human population on tuna fishing provided an opportunity to eliminate possible interactive effects between water quality, fishing, and body size that might otherwise confound studies in reefs that are more eutrophicated and

influenced by fishing. This is the first study, to our knowledge, to examine the herbivorous fish and sea urchin communities in the relatively isolated Lakshadweep atolls and the first to use herbivore exclusion cages on atolls of the Indian Ocean.

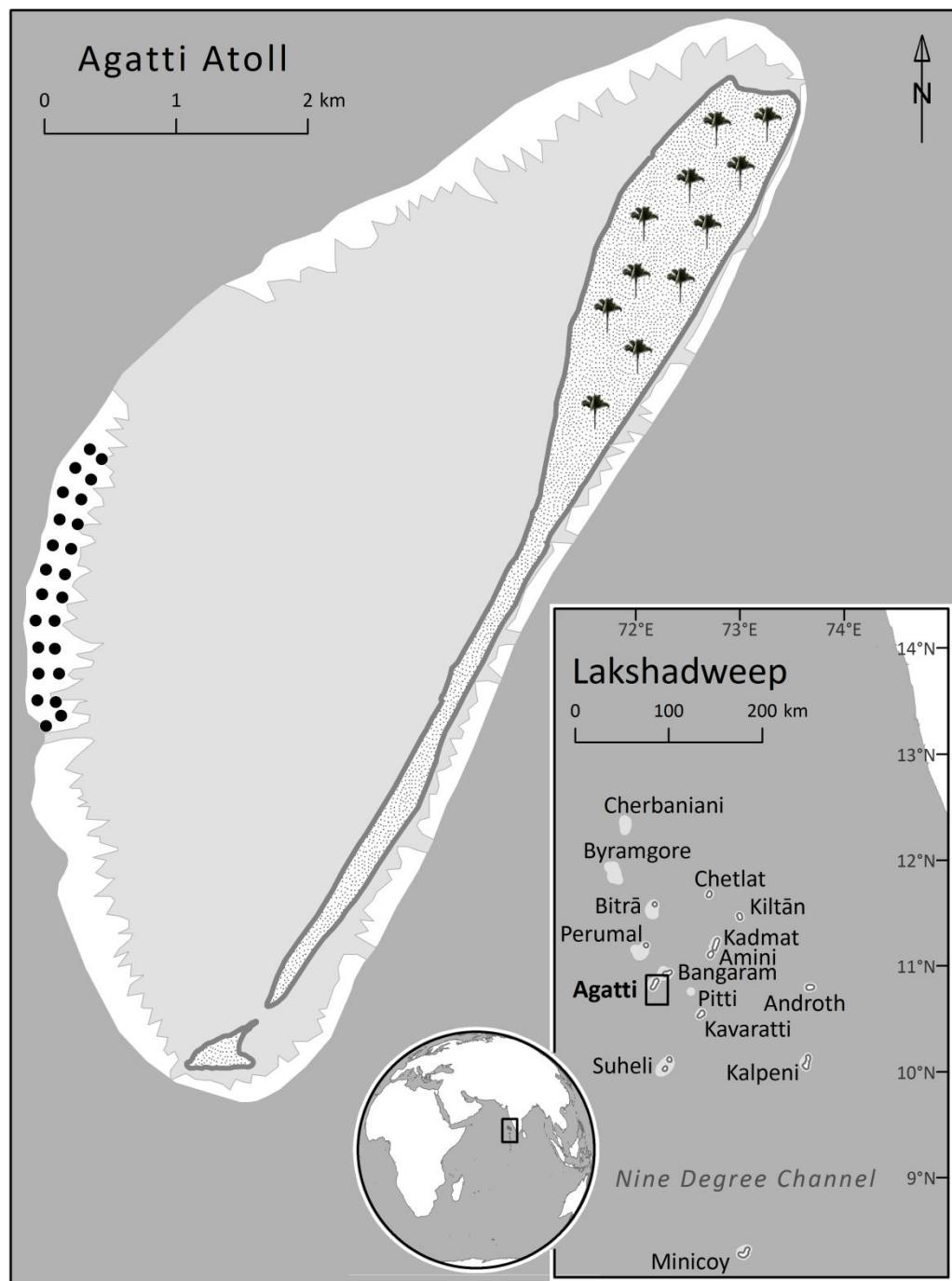
## 3.2 Material and Methods

### Study area

Agatti atoll and its back-reef on the southwest side (Fig. 3.1) was chosen for this study, due to the following characteristics: relatively large lagoon separating the reef from the populated island, high coral coverage, macroalgae being uncommon, and unfished reef fish populations because most all fishermen from this island solely target pelagic fish, with few exceptions during the rough south-west monsoon. Agatti atoll is part of Lakshadweep archipelago, situated off the west coast of India located between 8–12°N and 71–74°E. Lakshadweep forms the northernmost part of the Chagos–Maldives–Laccadive plateau (Fig. 2.1). It has a total of 32 km<sup>2</sup> of land made up of 27 islands, from which 11 are inhabited by a total of 64,000 people - the average density being ~2,000 per km<sup>2</sup>. Despite the high density of people on the island their main sources of income are artisanal tuna fisheries and dried coconut production and no one was ever observed fishing on the coral reefs during our survey. This cultural habit of targeting skipjack tuna using the traditional pole and line fishing is common for these offshore islands and has left the reef and reef associated species largely unutilized.

In 1998, the reefs experienced extensive coral bleaching. There are few reliable estimates of benthic reef communities for Lakshadweep reefs prior to 1998., but Arthur et al. (2006) states that before the major bleaching event in 1998 benthic composition was similar to Maldivian and Chagos reefs, with estimates of 60–90 % coral cover, which are consistent with large scale compilations of coral cover in this region (Ateweberhan et al. 2011). The recovery after the bleaching event was very site specific (Arthur et al. 2006), however in many places the recovery was rapid. The back-reef of

Agatti had an average of ~40–60% coral cover during the study period and reached 80% coral cover in some areas (Cernohorsky NH, personal observation; Fig. 3.2)



**Fig. 3.1.** Map showing the location of Lakshadweep islands, Agatti atoll. The 24 sites (black dots) are situated in 12 pairs on the back-reef of the atoll starting from the main channel and distributed south along the atoll rim.



**Fig. 3.2. Photograph of part of the back-reef habitat with the highest coral cover.**

### Experimental design

Using exclusion cages we investigated the ecological impacts of removing fish, especially large fish, from the coral dominated back-reefs of Agatti atoll (Fig. 3.3). We used two types of exclusion cages that differed in mesh size: (i) full cages with small 1 x 1 cm mesh (referred to as FM or fine-mesh cages) designed to exclude most visible herbivores such as fish and sea urchins, (ii) full cages with large 6 x 6 cm mesh (referred to as CM or coarse-mesh cages) designed to exclude only large fish (i.e. > 8 cm body depth) – those from size classes that were demonstrated to be highly important in macroalgae control (Bellwood et al. 2006, Fox and Bellwood 2008, Steneck et al. 2014).

Body depth is likely to be a better estimate of a fish's ability to pass through a mesh than body length, as found in studies of fish that escape traps (Robichaud et al. 2000, Gomes et al. 2014). Consequently, we estimated body depth (using body proportion data, i.e. body depth/total length available at <http://www.fishbase.org>) of each fish found at

our study site based on its total length and species and assessed its likelihood of entering the cages. Coincidentally, all fish larger than 8 cm body depth had total lengths greater than 22.5 cm and vice versa (Table B1). We present this information here only for comparative purposes as most exclusion cage studies only report the lengths of fish unable to enter cages (Bellwood et al. 2006, Jayewardene 2009, McCauley et al. 2010), however body length is not likely a good estimate of a fishes ability to enter an exclusion cage. This information combined with observations on fish entering the cages resulted in a list of species and size classes using the large-mesh cages, and also confirmed that small fish were neither aggregating inside nor avoiding cages.

Apart from these two types of full cages, two other partial cages were employed: (i) cages with tops only (referred to as T) constructed to check for the influence of shading, and (ii) cages with sides only (referred to as S) to check for the influence of reduced water flow. Partial cages were only made of the 1 x 1 cm mesh as the wider spacing of the 6 x 6 cm mesh was expected to have little to no influence on algal community development, light, and water flow. Numerous studies using similar exclusion cages found no significant effects of the caging structure on the benthic community other than the exclusion of herbivores (Russ 1987, Hixon and Brostoff 1996, McCauley et al. 2010). Lastly, completely open plots were also installed and served as the main controls (referred to as C). Thus a total of five different treatments were used in this sampling design. All exclusion cages had dimensions of 40 cm width and length and 20 cm in height and were constructed of a metal frame and a mesh made of fishing net twine. They were affixed to the dead coral substratum using stainless steel nails and ties to keep the cages in place and ensure no unwanted incursions of fish.

The five treatments were replicated at each of our 24 sampling sites, resulting in a total of 120 experimental plots. Because foraging activity is known to vary among different parts of the reef (Robertson et al. 1979, Hoey and Bellwood 2008), we placed the sites (200 m apart) along a transect that followed the atoll rim, beginning from the main reef channel and ending at the next small channel. Half of these sites (12 sites) were placed on the leeward back-reef (inner back-reef) and the other half on the border of the back-reef and reef flat (outer back-reef), thus covering various back-reef habitats (Fig. 3.1). The distance between the inner and outer back-reef sites was 150 m. Treatment designations of specific cages were randomly determined at each site, but

always ensuring that mainly dead coral heads were included in the cages. Average depth of the sites at low tide was 1.0–1.5 m.

The experiment was installed for a total of 127 days from December 2009 to April 2010. Cages were visited every 10–14 days to be cleaned of algae and other settling organisms with a plastic brush. During those times algae height was measured and benthic cover data were collected (with one exception towards the end of the experiment



**Fig. 3.3. Photograph of the four different cages installed.**

as weather conditions worsened) using in situ visual coverage estimates. Photographic images of the plots were also taken on each of these visits during the first 3 weeks and then every day after cage removal until plots were completely browsed. Benthic coverage data included coral, browsed substratum, other invertebrates, non-biological

substratum, and algae identified to the lowest possible taxonomic level, but in majority of cases only functional groups were ascribed as detailed identification in the field was not possible. Height measurements of algae were taken separately for each algal group using one measurement for each group, unless height seemed to vary within a group then 3 measurements were taken and an average value was calculated. Algae was then pooled into the following groups for further analysis: Macroalgae (upright fleshy and calcareous algae, such as *Gracilaria*, *Caulerpa*, and *Halimeda*, but also foliose algae such as *Dyctyota* and *Padina*), Fine low turf (short, around 1mm, and sparsely distributed green/brown filamentous algae and microalgae), turf (higher denser turf made up of a mix of microalgae, filamentous algae, small macroalgae, and sediment), filamentous non-turf algae (filamentous algae *sensu* Steneck and Dethier (1994), and long strands of cyanobacteria often growing out from holes in the reef), crustose coralline algae (Corallinales, Rhodophyta, of crustose habit, referred to as CCA), non-calcareous crustose algae (non-coralline algae of crustose habit, e.g. *Ralfsia*).

### **Herbivores and herbivory**

For each of the 24 sites, sea urchin and herbivorous fish were censused using belt transects and visual counts. For the fish census, a 50 m transect rope was laid parallel to the reef crest at each site with cages situated in the middle part of each transect. After 5 minutes, allowing the fish to acclimate, timed swims (15 – 20 minutes) were conducted along the transect, counting all herbivorous fish 5 m on either side, thus covering an area of 500 m<sup>2</sup>. Four to five fish counts were conducted at each site during various times of the day (0900 hrs – 1700 hrs) evenly distributed between low and high tides. Water clarity exceeded 10 m during each of the sampling times. Censuses were done by a single person, Cernohorsky NH, who recorded the species, number of individuals, and estimated their total length. Size classes were recorded in increments of 1 cm up to 5 cm TL, 5 cm between 5 and 40 cm TL, and of 10 cm above 40 cm TL. Small juvenile parrotfish species were difficult to reliably identify to the species level in the field and were therefore grouped into the category *Scarus* spp. *Ctenochaetus* species were grouped into a *Ctenochaetus* spp. category due to difficulties in making reliable in-situ identification.

Sea urchin numbers were assessed using the same belt transect method. However, searches for urchins were done on a much smaller area (20 m x 6 m transect) and the observer meandered along the rope, crisscrossing the transect looking under coral heads and into all crevices. The method is time consuming and the mobility of sea urchins rather limited; consequently, the sea urchin count was carried out only once per each site and only during the day. In each census the species and number of individuals were recorded. Species of the genus *Echinostrephus* were grouped into the category *Echinostrephus* spp. because their identification characters cannot be seen in the field.

## Data analysis

To obtain estimates of algal biomass we calculated algal volume for each cage and each sampling time by multiplying algal cover (in cm<sup>2</sup>) by algal canopy height (in cm) (Steneck and Dethier 1994). Algal volume was standardized to an area of 1 cm<sup>2</sup> of dead coral substrate (i.e. without live coral) to eliminate variability caused by different proportions of live coral in different cages. To verify the accuracy of the benthic coverage data assessed by in-situ estimates, we compared it with the coverage data obtained from the benthic photoquadrats. Image analyses of the benthic photoquadrats were completed using the program PhotoGrid 1.0.

Fish biomass estimates were calculated by converting total lengths (TL) of fish into biomass based on length-weight relations published in literature or available online (Kulbicki et al. 2005, <http://www.fishbase.org>). For the few species lacking specific allometric constants for the conversion, parameters from a closely related and similarly shaped species were used. Parrotfish species < 3 cm of TL were excluded from the analyses, due to the fact that they were not likely to have undergone ontogenetic changes from carnivores to herbivores (Bellwood 1988). The fish counts took place during the last month of the experiment when *Ctenochaetus* recruits were present on the reef in large numbers. These new small recruits were also excluded from the analyses, due to their short-term episodic occurrence. As the relationships between individual species and ecosystem processes are still poorly understood, fish were analyzed as functional groups: grazers/detritivores, scrapers, excavators, and browsers (Steneck 2001, Bellwood et al. 2004, Green et al. 2009). Sea urchins were analyzed as a separate functional group

within the herbivore guild, as their functional role in the ecosystem is abundance dependent (Carpenter 1981, McClanahan and Shafir 1990).

Differences in algal cover and height among treatments at the end of the experimental period were statistically tested. The data showed non-normal distribution and heteroscedasticity. We thus used Welch's analysis of variance (ANOVA) followed by Games-Howell post-hoc test, as these methods do not assume homogeneity of variance (Brown and Forsythe 1974, Games and Howell 1976).

We explored the effect of excluding all herbivores or only large herbivores on algae accumulation using Linear Mixed-Effects (LME) Models because measurements of the response variable (i.e. algae volume) were not independent. The algae volume data were transformed by a decimal logarithm to meet the normal distribution assumptions. In this study we used a split-plot design with five types of cages (i.e. treatments) spatially clustered and with multiple observations for each cage. We used two levels of groupings (location and cage) to assess two possibly different random effects. The significance of the effect of the treatment (five types of cages), time (sampling occasions), and reef position (inner and outer back-reef) on algae volume were tested using the *F* test with a critical significance level established as 0.05. As no significant effect was found for the position (LME:  $F_{1,22} = 1.0$ ,  $p = 0.44$ ), the final model included only the treatment and time as fixed effects. This final model was also corrected for the heteroscedasticity by using the variance function (varIdent) with time as a covariate. Several cages were lost during the experiment, and the losses increased after the ninth sampling interval (after the 93<sup>rd</sup> day), which resulted in an unbalanced number of observations among treatments. Therefore we limited data for the LME modeling to the first nine sampling occasions, which were based on 88 samples from 110 cages of which most (70%) were sampled during the whole period. All graphs and statistical analyses were done using R software (v. 3.1.3, R Core Team 2015).



**Fig. 3.4. Photograph of common herbivorous fishes on the coral reef of Agatti atoll**

### **3.3 Results**

#### **Herbivore abundance and biomass**

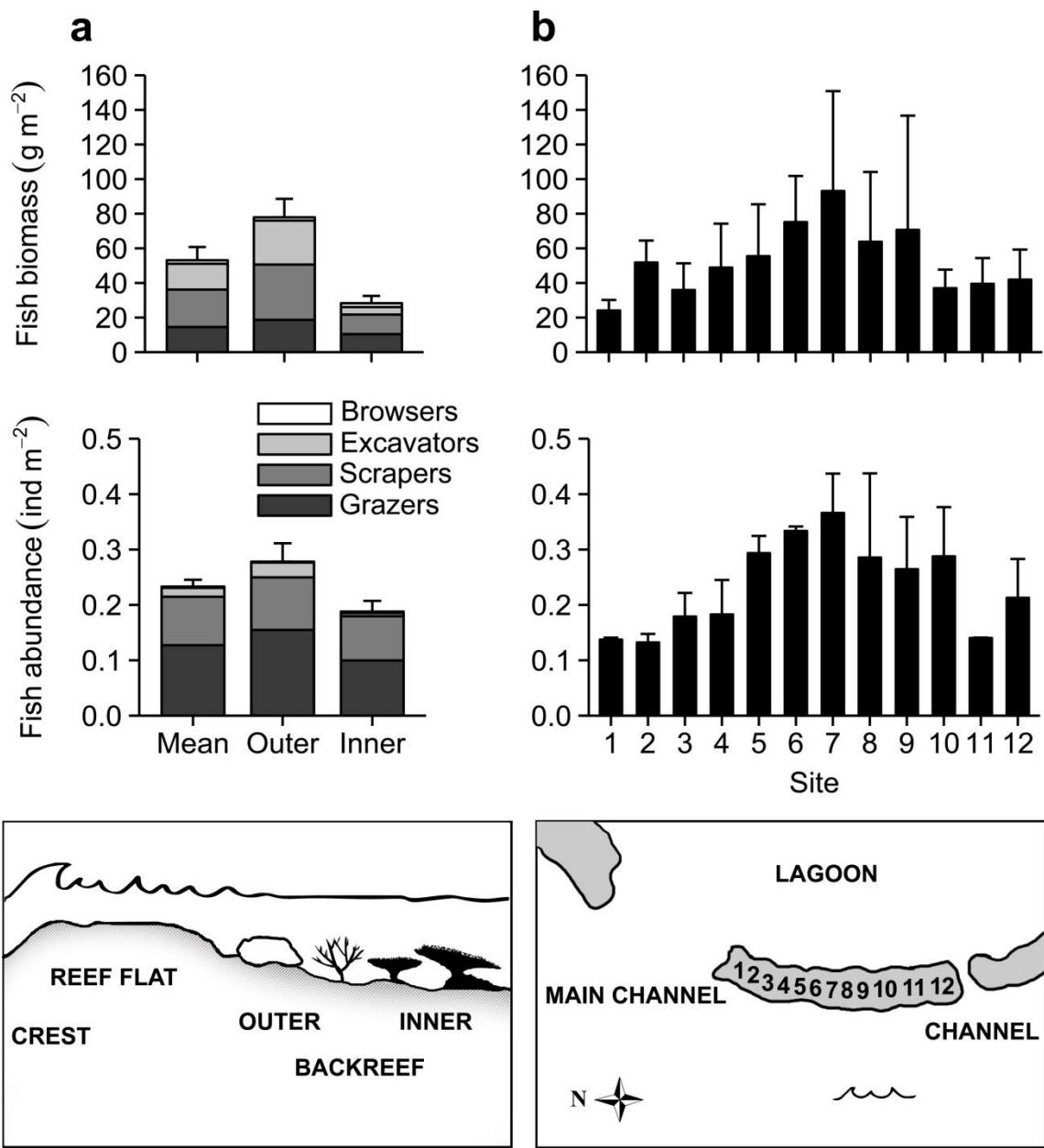
A total of 38538 herbivorous fish comprising 24 species in 3 families were counted (Fig. 3.4) and revealed an average herbivorous fish density of 0.23 individual m<sup>-2</sup> ( $\pm 0.01$ ) or 53.11 g m<sup>-2</sup> ( $\pm 7.66$ ). Grazers comprised 27%, scrapers 41%, excavators 28%, and browsers 4% of the total fish biomass (Fig. 3.5a). The herbivorous fish community numbers were strongly dominated by *Acanthurus triostegus* (0.057 ind. m<sup>-2</sup>) and juvenile parrotfish species (0.057 ind. m<sup>-2</sup>). In terms of biomass, the dominant species were: *Chlorurus enneacanthus* (14.07 g m<sup>-2</sup>), *Scarus rubroviolaceus* (12.72 g m<sup>-2</sup>), *Acanthurus lineatus* (7.09 g m<sup>-2</sup>), *Scarus prasiognathus* (5.32 g m<sup>-2</sup>), and *Acanthurus gahhm* (2.64 g m<sup>-2</sup>). Fish abundances as well as biomass were higher at the outer than inner back-reef sites (Fig. 3.5a) and this gradient is shown by the good fit of a

polynomial equation to the rim “transect” ranging along the atoll from sites 1 to 12 for abundance ( $F_{2,9}=9.69$ ,  $p=0.006$ ) and biomass ( $F_{2,9}=6.63$ ,  $p=0.017$ ) (Fig. 2b).

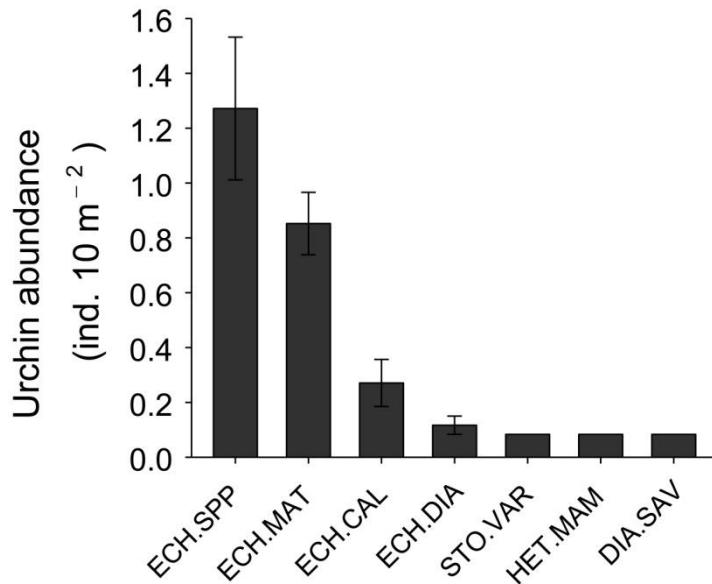
The total number of sea urchins counted was 604 individuals comprising 7 species in 3 families and revealed an average sea urchin density of 0.23 individuals per m<sup>2</sup>. The two small-bodied urchins, *Echinostrephus* spp. and *Echinometra mathaei*, were the most abundant species accounting for 58% and 37% of all counted sea urchins respectively (Fig. 3.6).

### Caging effects

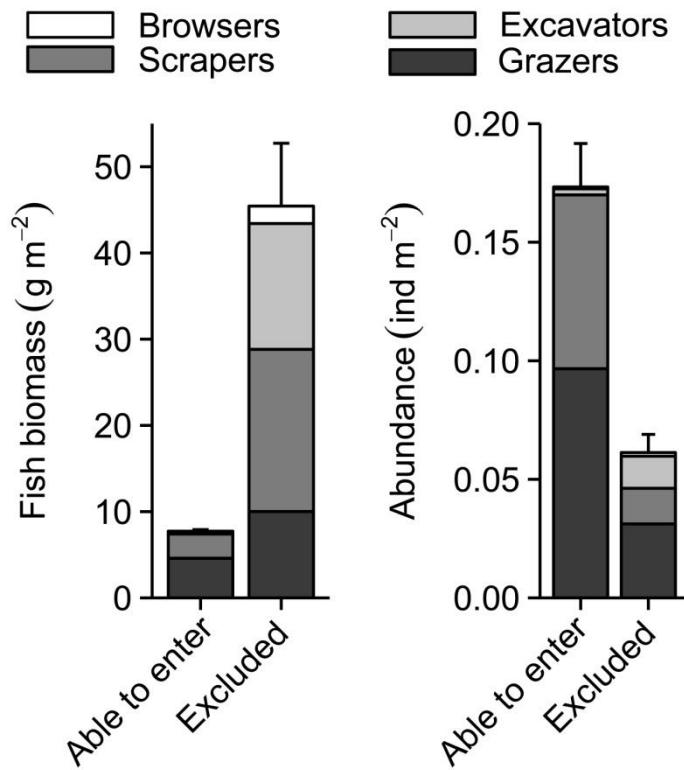
The fine-mesh full (FM) cages were assumed to effectively exclude all herbivorous fish and urchins greater than ~1 cm body depth/diameter. Based on body depth-length relationships and the size of the mesh, the coarse-mesh full (CM) cages were assumed to effectively exclude only fish with body depth greater than approximately 8 cm (which coincidentally corresponded to total body lengths greater than approximately 22.5 cm) and comprised most of the browsers, majority of excavators, some scrapers, and only few grazers (Fig. 3.7 and Table B1). Fewer fish were capable of entering or observed entering the coarse-mesh full cage and were represented mainly by grazers and small, often juvenile, scrapers (Fig. 3.7). Twelve fish species were potentially able to enter the cages and eight species per site was the average (Table 3.1). Although fish capable of entering the cages were present in much higher numbers than those excluded from the cages (0.17 ind. m<sup>-2</sup>, 0.06 ind. m<sup>-2</sup>, respectively), their total biomass was much lower (7.7 g m<sup>-2</sup> versus 45.44 g m<sup>-2</sup>, respectively). Echinoidea were also capable of entering the CM exclusion cage, but were present on the reef in low numbers (Fig. 3.6). Further, the dominant species were *Echinostrephus* spp. and *Echinometra mathaei*, species mostly restricted to their burrows.



**Fig. 3.5. Mean values of fish biomass and abundance in different reef habitats: a) at outer and inner back-reef sites and the mean across all sites, showing different proportions of each functional group, error bars represent standard errors of the mean (SE) of total herbivore biomass; b) polynomial distribution of fish abundance and biomass from the main channel (site 1) along the atoll rim to the small channel (site 12), error bars represent maximum/minimum (as within sites only two replications were available).**



**Fig. 3.6.** Sea urchin species found on the back-reef and their mean background population densities. Error bars represent standard errors of the mean, ECH.SPP = *Echinostrephus* spp., ECH.MAT = *Echinometra mathaei*, ECH.CAL = *Echinothrix calamaris*, ECH.DIA = *Echinothrix diadema*, STO.VAR = *Stomopneustes variolaris*, HET.MAM = *Heterocentrotus mammillatus*, DIA.SAV = *Diadema savignyi*.



**Fig. 3.7.** Mean abundance and biomass of fish excluded from the coarse-mesh cages (=excluded) and those potentially able to graze in coarse-mesh cages (=able to enter); showing different proportions of each functional group. Error bars are one standard error of the mean.

**Table 3.1. All censused herbivorous fishes present in the location, plus abundance and biomass values of those capable of entering (based on body depth) into the coarse-mesh cages and those excluded by the coarse-mesh cages (6 x 6 cm).**

All herbivore fish species		Fish able to enter coarse-mesh cages		Fish excluded by coarse-mesh cages	
Species	Functional group	ind. 500 m <sup>-2</sup>	g 500 m <sup>-2</sup>	ind. 500m <sup>-2</sup>	g 500 m <sup>-2</sup>
<i>Acanthurus gahhm</i>	Grazer	1.06	89.06	2.48	1189.97
<i>Acanthurus leucosternon</i>	Grazer	6.28	119.24	—	—
<i>Acanthurus lineatus</i>	Grazer	2.73	11.05	11.62	3418.65
<i>Acanthurus nigricauda</i>	Grazer	0.45	12.91	0.97	179.67
<i>Acanthurus tennentii</i>	Grazer	—	—	0.06	18.41
<i>Acanthurus triostegus</i>	Grazer	28.49	1084.75	—	—
<i>Chlorurus enneacanthus</i>	Excavator	—	—	6.70	6979.26
<i>Chlorurus sordidus</i>	Excavator	1.29	153.39	—	—
<i>Chlorurus</i> <i>strongylocephalus</i>	Excavator	—	—	0.04	295.43
<i>Ctenochaetus</i> spp.	Grazer	8.56	953.01	—	—
<i>Hipposcarus harid</i>	Scraper	—	—	0.49	415.74
<i>Naso brachycentron</i>	Browser	—	—	0.08	304.19
<i>Naso elegans</i>	Browser	0.16	4.42	0.39	227.75
<i>Naso</i> spp.	Browser	0.10	0.56	—	—
<i>Naso unicornis</i>	Browser	0.12	0.85	0.27	453.70
<i>Naso vlamingii</i>	Browser	0.01	0.10	—	—
<i>Scarus frenatus</i>	Scraper	0.11	7.49	0.12	35.32
<i>Scarus ghobban</i>	Scraper	—	—	0.04	80.83
<i>Scarus prasiognathus</i>	Scraper	—	—	2.77	2630.25
<i>Scarus quoyi</i>	Scraper	—	—	0.02	3.47
<i>Scarus rubroviolaceus</i>	Scraper	—	—	4.06	6202.38
<i>Scarus scaber</i>	Scraper	7.76	364.50	—	—
<i>Scarus</i> spp.	Scraper	28.37	1019.20	—	—
<i>Siganus lineatus</i>	Grazer	0.19	1.67	0.14	57.87
<i>Zebrasoma desjardinii</i>	Grazer	0.02	3.30	0.24	115.95
<i>Zebrasoma scopas</i>	Grazer	0.35	6.82	—	—

### **Algal accumulation**

There were no significant differences among plots (treatments) in the coverage of macroalgae, turfs, or corals prior to the exclusion of herbivores (GLM:  $p>0.10$ ). Algal turfs dominated the Agatti back-reef algal communities and covered about 50–70% of the dead coral substratum. Macroalgae cover was low across the back-reef habitat, usually  $< 5\%$ . At the end of the experiment coarse-mesh cages and controls were still dominated by very low turf but the fine-mesh cages were dominated by macroalgae (Table 3.2).

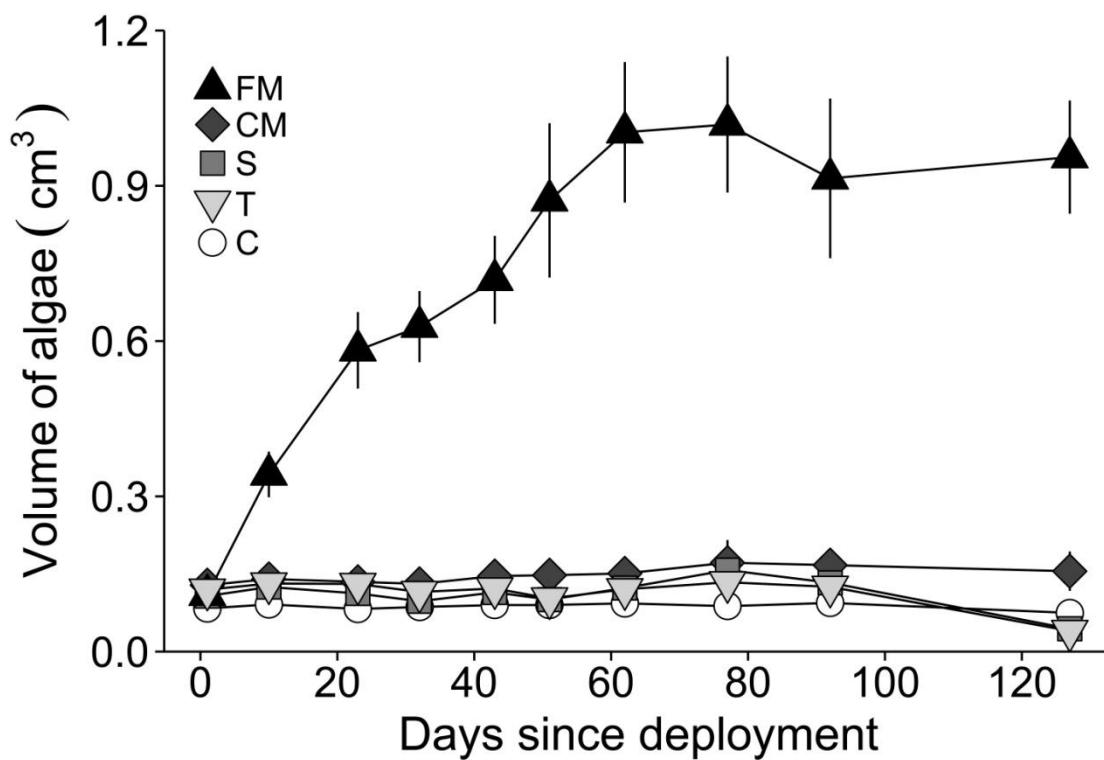
We found significant effects of treatments (LME:  $F_{4,82}=54.4$ ,  $p<0.001$ ), sampling time (LME:  $F_{1,772} = 58.1$ ,  $p < 0.001$ ) and their interaction (LME:  $F_{4,772}=33.0$ ,  $p<0.001$ ) on algal accumulation. Although recorded volumes of algae were significantly higher for all types of cages when compared with the control (highest positive effect was found for FM cages (LME:  $t=5.11$ ,  $p<<0.001$ ), smaller for CM cages (LME:  $t = 3.51$ ,  $p<0.001$ ) and least for the top- and side-half cages (LME:  $t=2.67$  and  $2.03$ ,  $p=0.009$  and  $0.046$ , respectively), this was not the case when analyzing algal increase/decrease over time. The exclusion of all herbivores by the FM cages had rapid effects on the benthos communities and after the 127 days there was a significant increase in algae (Fig. 3.8). The increase of algae volume in the FM cages during the experiment significantly differed against the control (LME:  $t=9.10$ ,  $p<<0.001$ ). However, where only large herbivores were removed (CM cages) no differences in the increase of algae were observed when compared to controls (LME:  $p=0.829$ ). In the half cages (top only or side only) and control plots no significant increase in algae was observed either (LME:  $p>0.177$ ). With exception of the FM cages, the amount of algae found in all these plots remained relatively constant throughout the experiment (Fig. 3.8).

**Table 3.2. Comparison of mean ( $\pm$ SE) percent cover and height (mm) of different benthic groups in coarse-mesh cages (CM), fine-mesh cages (FM), and control plots (C) at the end of the experimental period (127 days). Welch's ANOVA test followed by Games-Howell post hoc test (GH test) was used to test the differences in cover and height; \* $P<0.05$ ; \*\* $P<0.01$ ; \*\*\* $P<0.001$ . CM= 6 x 6 cm, FM = 1 x 1 cm mesh openings.**

Benthos groups	Coarse-mesh cages		Fine-mesh cages		Control		Welch (cover / height)			GH test (cover / height)		
	Cover	Height	Cover	Height	Cover	Height	Statistic	p	CM	FM	FM	
									vs. C	vs. C	vs. CM	
Macroalgae	4.3 ( $\pm$ 2.0)	9.1 ( $\pm$ 2.6)	24.4 ( $\pm$ 3.8)	19.1 ( $\pm$ 2.3)	3.1 ( $\pm$ 2.1)	3.9 ( $\pm$ 1.1)	$F_{2,22}=17.5$ / $F_{2,22}=19.4$	***/***	—	***/***	***/**	
Fine low turf	38.1 ( $\pm$ 5.5)	1.29 ( $\pm$ 0.1)	4.7 ( $\pm$ 2.5)	2.1 ( $\pm$ 0.4)	36.5 ( $\pm$ 2.8)	0.9 ( $\pm$ 0.1)	$F_{2,27}=37.6$ / $F_{2,24}=1.0$	*** / 0.36	—	** / —	*** / —	
Turf	8.0 ( $\pm$ 4.2)	3.4 ( $\pm$ 0.7)	29.8 ( $\pm$ 3.6)	5.8 ( $\pm$ 0.7)	2.5 ( $\pm$ 1.3)	3.0 ( $\pm$ 0.9)	$F_{2,21}=23.8$ / $F_{2,23}=18.9$	***/***	—	***/***	***/*	
Filamentous non-turf algae	0.2 ( $\pm$ 0.1)	18 ( $\pm$ 11.14)	4.9 ( $\pm$ 2.6)	13.2 ( $\pm$ 2.4)	2.5 ( $\pm$ 1.3)	35 ( $\pm$ 17.6)	$F_{2,26}=1.5$ / $F_{2,29}=0.6$	0.23 / 0.56	—	—	—	
Crustose coralline algae	4.2 ( $\pm$ 0.9)	—	2.9 ( $\pm$ 0.9)	—	7.2 ( $\pm$ 1.1)	—	$F_{2,30}=4.4$ / —	* / —	—	* / —	—	
Non-calcareous encrusting algae	0.3 ( $\pm$ 0.1)	—	2.0 ( $\pm$ 0.8)	—	0.5 ( $\pm$ 0.1)	—	$F_{2,25}=2.0$ / —	0.15 / —	—	—	—	
Browsed coral substrate	26.6 ( $\pm$ 4.0)	—	0.7 ( $\pm$ 0.6)	—	34 ( $\pm$ 2.6)	—	$F_{2,22}=89.8$ / —	*** / —	—	*** / —	*** / —	
Other invertebrates	0.3 ( $\pm$ 0.3)	—	1.9 ( $\pm$ 0.6)	—	0.1 ( $\pm$ 0.05)	—	$F_{2,19}=4.1$ / —	* / —	—	* / —	—	
Non-biological	6.4 ( $\pm$ 1.7)	—	12.9 ( $\pm$ 1.9)	—	4.4 ( $\pm$ 1.2)	—	$F_{2,27}=6.8$ / —	** / —	—	** / —	* / —	
Hard coral	12.4 ( $\pm$ 2.1)	—	15.9 ( $\pm$ 2.5)	—	12.9 ( $\pm$ 1.6)	—	$F_{2,27}=0.6$ / —	0.54 / —	—	—	—	

### 3.4 Discussion

Our study is one of the few studies to experimentally examine the influences of different sized herbivorous fish using exclusion cages with two mesh sizes (Jayewardene 2009, Steneck et al. 2014) and the only one to do so in the back-reef habitat of an oceanic atoll in the Indian Ocean. We installed fine-mesh full cages (excluding all visible herbivorous fish and urchins) and coarse-mesh full cages (excluding large fish) at each of the 24 sites studied and monitored algal accumulation for 127 days. In contrast to most previous studies, which have shown that large herbivorous fish are likely the most important group of herbivores in preventing algal blooms (Bruggemann et al. 1996, Bonaldo and Bellwood 2008, Hoey and Bellwood 2010, McCauley et al. 2010, Steneck et al. 2014), we found no effect of removing large herbivores on the algal accumulation.



**Fig. 3.8. Algal accumulation over 127 days at 24 back-reef sites of Agatti atoll for each treatment type (FM=fine-mesh cages, CM=coarse-mesh cages, S = partial cages with sides only, T = partial cages with tops only, C = controls). Algal abundance expressed as mean volume ( $\pm$ SE) for a standardized area of  $1 \text{ cm}^2$  of dead coral substratum.**

In these coarse-mesh full cages and the side and top controls, the benthos did not undergo significant changes indicating that small herbivores were sufficient to prevent algal accumulation at our study sites.

The ability of small fishes to prevent the accumulation of algal biomass was unexpected, and highlights the importance of considering the local ecological context of a reef in influencing algal responses. In this study it seems that small herbivorous fishes were present in sufficient numbers to maintain a low algal state. Other influential factors could include storms and saltation by sediment, but given the clear conditions and the ability to maintain these cages intact for most of the study, these factors seem less likely to have influenced the outcome.

Low nutrients could have also explained the absence of algal accumulation in the coarse-mesh cages. Yet, the fact that algal volume significantly increased in our fine-mesh cages supports the assumption that nutrients and sediments were not the main causes of the zero algal increase in the coarse-mesh cages (McClanahan et al. 2003). Sea urchins were likely to have little impact as well, as they were present on the reef in very low densities (Fig. 3.6) and were not observed to aggregate inside nor near the cages. Further, in wave swept and predator-abundant environments the dominant urchins, *Echinometra mathaei* and *Echinostrephus* spp., are often restricted to their burrow and feed on algae that drift and settle into their burrows (Campbell et al. 1973, McClanahan and Kurtis 1991, Vanderklift et al. 2009). Patterns of low urchin numbers and their restriction to burrows and wave swept environments are expected for high fish biomass reefs of this region (McClanahan et al. 1994, 2011).

Some caution should be applied when inferring the importance of small herbivorous fishes as the current study was spatially and temporally limited. Certainly, longer and larger spatial scale studies and improved measures of potentially important grazing factors (numbers, biomass, feeding rates and types) would better determine the exact effects of large-herbivore exclusion. According to the space availability model (Williams et al. 2001), if more space is available for the growth of algae, then the grazing capacity of herbivores may eventually become overwhelmed and algae will be released from top-down control. Thus, the location of this study is consequential, as the back-reefs of Lakshadweep have relatively high coral coverage. However, shortly after the major bleaching event in 1998, when most of Lakshadweep corals bleached and died, space for

algal growth was high. Nevertheless, no macroalgae blooms were reported despite this rapid increase of available space (Arthur et al. 2006), which suggests considerable capacity for herbivores to compensate for the increased algal production.

In spite of the fact that fish able to enter the coarse-mesh cages were present in high abundances, their biomass was low and yet algae cover stayed relatively constant throughout the experiment. Although this is unexpected, many studies show that some reefs have low macroalgae cover despite low herbivore biomass (see Chapter 4). The highest abundance of fish was repeatedly registered at sites A (sites closer to the reef crest). This perhaps may be due to the higher productivity of algae, owing to the better light supply at the reef crest, but simultaneously it being too shallow and turbid for the healthy growth of coral, resulting in lower coverage of coral and higher coverage of EAM. Sea urchins were also more common at sites A. Another important factor that would explain higher fish and urchin densities at these sites may be the risk of predation, which is lower in shallow waters. This could also explain the lower abundance of fish near lagoonal entrances which connect the inner protected back-reef with the outer (predator rich) reef slope and open ocean.

A further unexpected result was the lack of differences among-habitats in the accumulation of algae within the coarse-mesh cages despite large differences in fish biomass and abundance (Fig. 3.7). The impact of various levels of herbivory were likely to have been offset by other factors, such as depth, coral cover, or wave and current intensity, which also differed among the different habitats. Furthermore, they differed such that where herbivore levels were low, depth, and either coral cover or water motion, were greater, and vice versa – thus likely compensating for the expected effects on algae (Table 3.3). Other studies show that spatial dynamics of herbivorous fish can cluster within reef habitats (Fox and Bellwood 2014) with herbivore intensity varying among locations at distances < 100 m apart (Cvitanovic and Bellwood 2009, Hoey and Bellwood 2010, Bonaldo and Bellwood 2011). The degree to which herbivore clustering is stable or a transient behaviour will influence estimates of herbivory and thresholds for preventing macroalgal dominance.

We found no build up of algae even though the biomass of herbivorous fishes was relatively low in the coarse-mesh cages ( $7.7 \text{ g m}^{-2}$ ). This suggests some need to reassess the roles of different functional groups. For example, among the four main herbivore

functional groups, browsers are considered the main group responsible for removing macroalgae (Green et al. 2009). Yet, due to their large body depths, only the very smallest browsers were capable of entering the coarse-mesh cages, leaving grazers and scrapers as the main groups responsible for cropping algae inside the coarse-mesh cages. We therefore conclude, that browsers, particularly large-bodied ones, played little role in the suppression of macroalgae and this observation may apply to reefs more broadly.

**Table 3.3. Factors (and their potential influence) possibly offsetting the impact of variable herbivory levels at different habitats by influencing algal growth/accumulation; + = positive influence, – = negative influence on algae. Coral cover represents live coral cover.**

Habitat	Depth	Coral Cover	Water Motion	Herbivory
Outer Reef	Shallow	+	Low	+
			High	–
			High	–
vs.				
Inner Reef	Deep	–	High	–
			Low	+
			Low	+
Near channel	Deep	–	Low	+
			High	–
			Low	+
vs.				
Far from Channel	Shallow	+	High	–
			Low	+
			High	–

Recent studies reveal that some herbivore species from non-browser functional groups also consume macroalgae despite some taxa being unpalatable to many herbivores (Ledlie et al. 2007). In the Seychelles, for example, *S. rubroviolaceus* and *A. triostegus* have been observed to forage on macroalgae (Ledlie et al. 2007), in Fiji *Ch. sordidus* was observed to be responsible for the removal of red macroalgae (Rasher et al. 2013), and in the Line Islands some species of grazers and scrapers were found to predominantly graze on non-turf algae (Hamilton et al. 2014). There is also some evidence that suggests that feeding habits of some parrotfishes (Nash et al. 2012), surgeonfishes and rabbitfishes (Chong-Seng et al. 2014) can change in response to changing reef ecology. Consequently, we suggest that other non-browser species may have been responsible for removing macroalgae from our experimental coarse-mesh

cages. However, macroalgae was scarce at the back-reef study sites relative to the epilithic algal matrix (EAM; Wilson et al. 2003), which is preferred by most herbivores. The EAM consists of algal turfs, microalgae, macroalgal germlings, detritus, sediment, and other small organisms, which may mean that herbivores that feed on EAM will tend to graze unselectively. Consequently, they are likely to consume or damage macroalgae germlings in the process, which will prevent germlings from growing into mature thalli (Lewis 1986). The failure of macroalgae to increase in our coarse-mesh cages is likely caused by an abundance of EAM-feeding herbivores in Agatti back reef (Fig. 3.7). Since the species responsible for controlling algae were not monitored in the experimental plots, the various species-specific roles remain uncertain.

Reefs with low human impacts, such as Agatti, may simply have more potential functional redundancy and more dietary overlap than presumed from species-specific diet studies (Johansson et al. 2013). Many recent studies have suggested limited dietary overlap and functional redundancy among herbivores, but these studies have focused mostly on browsers in the presence of macroalgae (Bellwood et al. 2003, 2006, Cvitanovic and Bellwood 2009, Hoey and Bellwood 2009, Brandl and Bellwood 2014). Many macroalgae taxa are, however, generally scarce on coral-dominated reefs (where EAM and coralline algae dominate), and higher abundance of macroalgae is more typical of later successional stages often associated with regime shifts (Hay et al. 1983, Hay 1984, Lewis and Wainwright 1985, Wismer et al. 2009). On coral dominated reefs, some herbivore resistant macroalgae taxa, such as *Amphiroa* and *Turbinaria*, will develop adult thalli even when the EAM is intensely grazed, but most other macroalgal taxa will rarely develop into adult macroalgal stands. In such cases, where macroalgae is scarce, only a limited number of species from the overall herbivore community will actually feed on or make macroalgae an important part of their diet (Johansson et al. 2013).

Low macroalgal diversity on coral dominated reefs could force species to adapt to feeding on the more abundant EAM and hide the full herbivore functional specialization. In contrast, herbivores on reefs with high and diverse macroalgal cover may utilize their diet specialization potential, which would create an impression of limited functional redundancy. Distinguishing and understanding these types of adaptations and complex interactions between the state of the algae and feeding behavior and diet specialization is difficult. Nevertheless, assuming more adaptation potential than found in time and space-

limited studies is expected to reconcile the many contradictory studies (Robertson and Gaines 1986, Hamilton et al. 2014).

Although many recent studies promote species specific protection instead of overall biodiversity conservation, we argue that, although the protection of the few highly specialized macroalgae consumers is no doubt important, especially as they are usually large fishes and are thus more susceptible to overfishing, biodiversity too needs to be sustained in order to ensure maximum resilience of coral reefs, which are under threat of phase shifts due to stresses and the rapidly changing environmental factors. Although the biodiversity – stability relationship is still a subject of constant debate, it does seem that on longer, geological, time scales ecological stability of coral reefs is indeed related to biodiversity (Newell 1971, Buddemeier and Hopley 1988, Jackson 1992, Kiessling 2005). Unfortunately, anthropogenic effects are incomparable to most “natural” stress factors coral reefs have experienced in the past. Humans are affecting marine ecosystems on many scales in various ways and with immense intensity, and thus in the face of increasing environmental perturbations reefs may no longer have enough resilience to deal with all the stresses and thus more often become dominated by algae especially after such huge and repeated disruptions such coral bleaching events.

In this study there must have been considerable functional redundancy between the large and small herbivores, since the removal of large herbivores did not result in algal accumulation as may have been expected. Large herbivores, however, play other ecological roles, such as bioerosion (Bruggemann et al. 1996, Bellwood et al. 2011), which is especially common on atolls and low-lying islands, such as Lakshadweep. Small herbivores are unlikely to be able to equal or compensate for the role of large herbivores in bioerosion. Nevertheless, we show that smaller herbivores play an important role in reef ecosystems, especially because they are much less susceptible to fishing. Consequently, we suggest they provide an important component of functional redundancy when disturbances, such as coral bleaching events or selective fishing pressure, are common. Furthermore, this study stresses the importance of ecological context and herbivore plasticity when assessing potential impacts of fishing and management on changes in herbivory, algae, and coral.

# **CHAPTER 4:**

## **GLOBAL ALGAE-CORAL-HERBIVORE**

## **LITERATURE COMPILATION AND**

## **COMPARISONS**

*The contents of this chapter are to be submitted for publication  
(planned submission September 2015)*

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## **CHAPTER 5:**

### **CONCLUSIONS AND IMPLICATIONS**

With increasing coastal development, population growth, and global climate change (especially increased sea surface temperatures, ocean acidification, and changes in storm intensities and frequencies) it is important maintain, and in some cases increase, the capacity of coral reefs to cope with these threats. Thus it is important to understand factors that influence coral reef resilience and the regulating mechanisms of algal communities, since corals are often replaced by benthic algae on degraded reefs.

This thesis explores the relative importance of herbivory as one of the regulating mechanisms of benthic algae communities on the coral reefs of Lakshadweep archipelago and on reefs across the globe. During the last few decades many studies have tried to assess the relative importance of top-down and bottom-up regulation of algal communities (Hughes 1994, Lapointe 1997, 1999, Mora 2008, Mörk et al. 2009, Sjöö et al. 2011), and the results in this thesis are in accordance with most studies that have found herbivory (i.e. top-down mechanism) to be of superior importance in regulating algal communities on coral reefs. The removal of herbivorous fish and urchins on Lakshadweep coral reefs, resulted in an increase in algal cover and height (Chapter 2). The experimental plots (caged parts of naturally occurring reef substrate) were covered by very low turf (~1 mm high) prior to the experiment. After only a few days of full herbivore exclusion, algae not only increased in volume but also changed in species composition, with less turf and a lot of macroalgae (which was nearly absent at the beginning of the experiment). These changes happened across all sites with no relation to depth or the proximity of channels. After the reintroduction of herbivores, the algae were again browsed to very low turf and bare substrate. The fact that algae grew inside the caged plots shows that nutrients were not a limiting factor, and herbivory was the main regulating factor of algal abundance and composition. However the fact that algae did

not overgrow live coral inside these plots shows that algae are not necessarily competitively superior to coral. The removal of only large herbivores using coarse-mesh exclusion cages, surprisingly, did not result in any significant change in algal abundance or composition, indicating that the abundance and composition of small herbivorous fishes was sufficient to maintain low algal abundance (i.e. height and cover).

The fact that algae did not overgrow live coral in the fine-mesh exclusion cages (those excluding all visible herbivores) and the removal of large herbivores had no effect on algae during the 127 day experimental period, suggest that the impacts of overfishing of reef herbivores on coral reef health in Lakshadweep may not be immediately visible. However as coral reefs are facing increasing global and local stress, mortalities are likely to increase, and after such mortality events algal regulation by herbivores will be especially important. If herbivores are not present in sufficient numbers and diversity during such times, the reef ecosystem will most likely undergo a shift towards an alternative algal dominated state, and the human population will no longer be able to benefit from ecological goods and services of the coral reef ecosystem. The results of this thesis suggest that if Lakshadweep's herbivorous reef fishes are overharvested, there may be no warning sign (i.e. no gradual change) prior to a sudden shift. Specifically there is likely to be no increase in algae or overgrowth of coral by algae despite depleted herbivore communities, at least not until coral cover is significantly reduced in Lakshadweep. Unfortunately once a shift from coral to algal dominance is established it may be difficult to return the system back to coral dominance, due to a hysteresis effect (Nyström et al. 2008) and various feedback mechanisms; e.g. algal inhibition of coral recruitment (Szmant 2002, Kuffner et al. 2006).

From the global comparison presented in this thesis it is clear that other factors are likely to be important in governing macroalgal abundance besides herbivory and that a more regional and holistic approach may be appropriate when assessing the impacts of management and fishing on in the algal-coral dominance relationships. Nevertheless the results in this thesis show that in Lakshadweep herbivory is truly a very important regulating factor. After the 1998 bleaching event and massive coral mortalities in Lakshadweep reefs managed to recover, likely due to intact herbivore populations. However as fisheries practices have been changing and fishing of reef fishes has been increasing in Lakshadweep the resilience is likely (silently) decreasing, and whether or

not the reefs will manage to recover after another such bleaching event is now less certain.

Until species specific feeding behaviours and ecological roles of herbivores are understood on Lakshadweep reefs it is advisable to protect all herbivores from fishing pressure. Although the protection of key herbivores is extremely important for maintaining coral dominated reefs, depleting other reef fishes may indirectly affect the coral-algal balance as well. For example McClanahan (McClanahan and Shafir 1990) found that the depletion of triggerfish, the main predator of sea urchins, resulted in high abundances of sea urchins, which ended up overgrazing the reef, causing extensive bioerosion and decrease in coral cover. Thus due to changing fisheries practices and population growth on Lakshadweep islands these relationships need to be investigated, because understanding the ecological roles of reef fishes will be crucial for proper fisheries and coral reef management, especially as overharvesting of reef fishes have been shown to have drastic effects on the functioning of coral reefs elsewhere.

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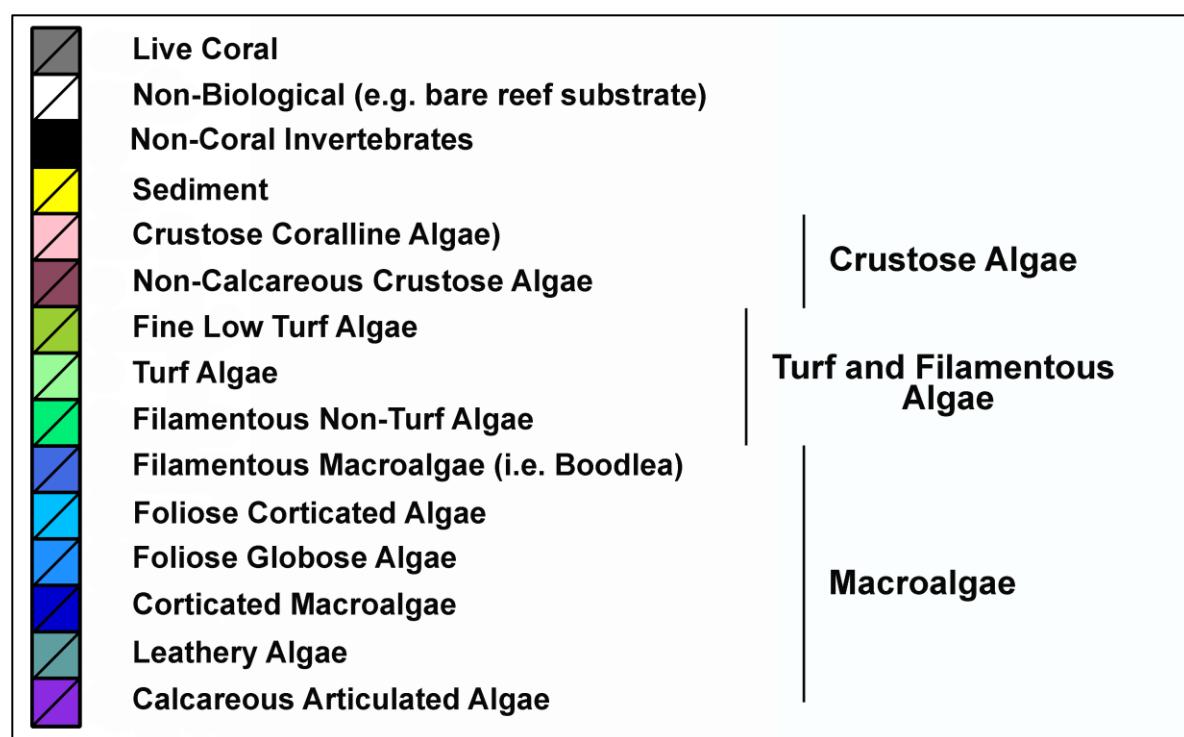
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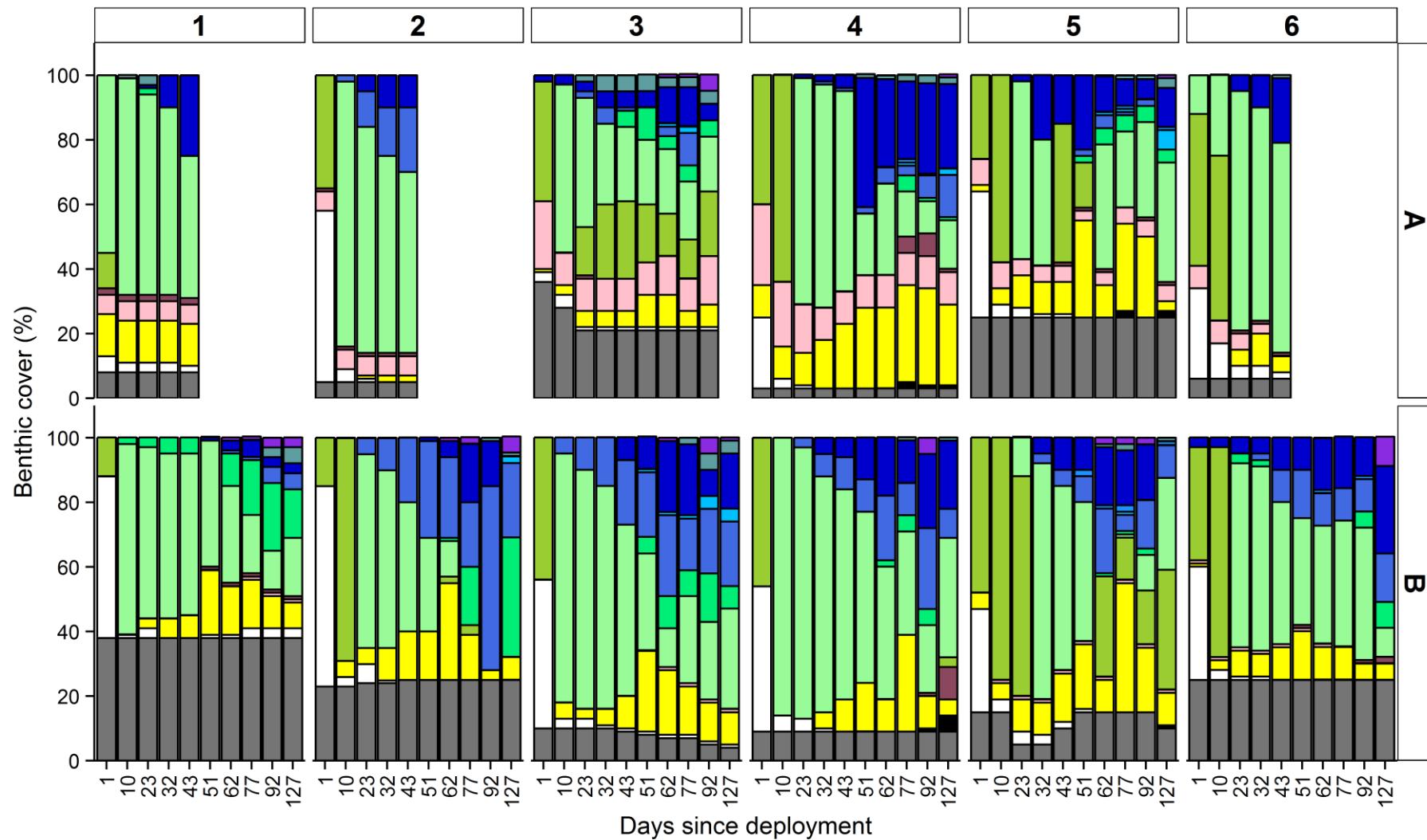
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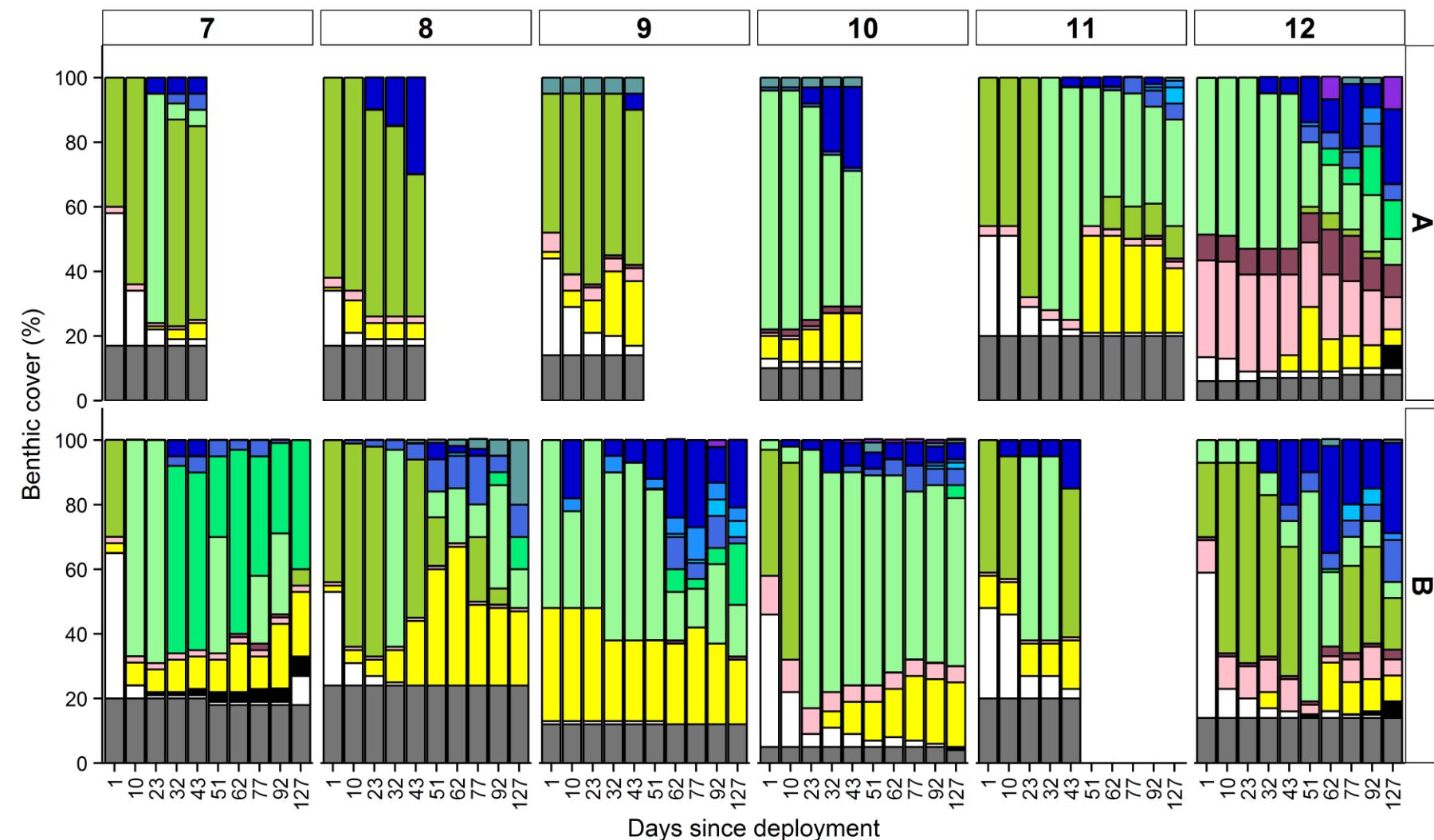
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## **Appendix A – Supplementary information for Chapter 2**

**Fig. A1.** Composition of the benthic communities in the full (fine-mesh) exclusion cages, and changes in the relative abundance (expressed as percentages) of individual benthic groups over the whole experimental period, for each site and habitat separately. Sites are labelled 112 and those from the inner back-reef habitat are labelled as A and those from the outer back-reef habitat are labelled as B. The position of the sites and habitats can be seen in figure 3.5 in the Results section of Chapter 3. Macroalgae are presented in shades of blue, turf and filamentous algae in shades of green, and crustose algae in shades of pink.







## **Appendix B – Supplementary information for Chapter 3**

**Table B1 List of mean total lengths (TL), body depth to body length ratio, and body depth for each size group of each herbivore fish species. Body depth was used to determine which fish could enter the coarse-mesh cages.**

Species	Size group (cm)	TL (cm)	Body depth/TL ratio	Body depth (cm)
<i>Acanthurus gahhm</i>	10–15	12.5	0.32	4.0
	20–25	22.5	0.32	7.2
	25–30	27.5	0.32	8.8
	30–35	32.5	0.32	10.4
<i>Acanthurus leucosternon</i>	5–7.5	6.3	0.44	2.8
	10–15	12.5	0.44	5.5
<i>Acanthurus lineatus</i>	5–7.5	6.3	0.36	2.2
	25–30	27.5	0.36	9.8
<i>Acanthurus nigricauda</i>	10–15	12.5	0.35	4.4
	25–30	27.5	0.35	9.6
<i>Acanthurus tennentii</i>	20–25	22.5	0.36	8.0
<i>Acanthurus triostegus</i>	5–7.5	6.3	0.43	2.7
	15–20	17.5	0.43	7.5
<i>Chlorurus enneacanthus</i>	20–25	22.5	0.35	7.8
	30–35	27.5	0.35	9.6
<i>Chlorurus sordidus</i>	20–25	22.5	0.32	7.1
<i>Chlorurus strongylocephalus</i>	50–60	55.0	0.28	15.2
	90–100	95.0	0.28	26.2
<i>Ctenochaetus</i> spp.	5–7.5	6.3	0.40	2.5
	15–20	17.5	0.40	7.1
<i>Hipposcarus harid</i>	25–30	27.5	0.30	8.2
	35–40	37.5	0.30	11.2
	45–50	45.0	0.30	13.5
<i>Naso brachycentron</i>	50–60	55.0	0.32	17.5
	60–70	65.0	0.32	20.7

<i>Naso elegans</i>	7.5–10	8.8	0.35	3.0
	25–30	27.5	0.35	9.5
<i>Naso unicornis</i>	7.5–10	8.8	0.38	3.3
	35–40	37.5	0.38	14.1
	50–60	55.0	0.38	20.7
<i>Naso vlamingii</i>	5–7.5	6.3	0.36	2.2
<i>Naso</i> spp.	5–7.5	6.3	0.36	2.2
<i>Scarus frenatus</i>	10–15	12.5	0.31	3.9
	20–25	22.5	0.30	6.8
<i>Scarus ghobban</i>	45–50	47.5	0.33	15.7
<i>Scarus prasiognathus</i>	20–25	22.5	0.35	8.0
	25–30	27.5	0.30	8.2
<i>Scarus quoyi</i>	20–25	22.5	0.35	7.9
<i>Scarus rubroviolaceus</i>	15–20	17.5	0.29	5.1
	35–40	37.5	0.29	11.0
	45–50	47.5	0.29	13.9
	50–60	55.0	0.29	16.1
	60–70	65.0	0.29	19.0
<i>Scarus scaber</i>	2–3	2.5	0.29	0.7
	3–4	3.5	0.29	1.0
	10–15	12.5	0.29	3.7
	15–20	17.5	0.29	5.1
	20–25	22.5	0.29	6.6
<i>Scarus</i> spp.	2–3	2.5	0.29	0.7
	4–5	4.5	0.29	1.3
	5–7.5	6.3	0.29	1.8
	7.5–10	8.8	0.29	2.6
<i>Siganus lineatus</i>	7.5–10	8.8	0.37	3.2
	25–30	27.5	0.37	10.1
<i>Zebrasoma desjardinii</i>	10–15	12.5	0.42	5.2
	15–20	17.5	0.42	7.3
	25–30	27.5	0.42	11.5
<i>Zebrasoma scopas</i>	4–5	4.5	0.52	2.3
	7.5–10	8.8	0.52	4.5

## **Appendix C – Supplementary information for Chapter 4**

**Table C1 Number of cases used for the global herbivore-macroalgae comparisons from each location, reef type, depth, and year, including information on fish sizes used for the calculation of herbivore biomass; based on literature reviews.**

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## New record of five Butterflyfishes (Family: Chaetodontidae) from the Lakshadweep Archipelago, Western Indian Ocean, with notes on occurrence of four additional species

**K.K. Idreesbabu, N. H. Cernohorsky and S. Sureshkumar**

### Abstract

Five new records of Butterflyfishes (Family: Chaetodontidae), viz. *Chaetodon andamanensis*, *C. decussatus*, *C. guttatissimus*, *C. interruptus* and *C. lineolatus*, are reported from the atolls of Lakshadweep archipelago, India. The occurrence of four additional species viz. *C. madagascariensis*, *C. triangulum*, *Forcipiger longirostris* and *Heniochus pleurotaenia* were also confirmed. The extension of range of these coral reef associated fishes to these underexplored reefs points towards the need for an extensive scientific survey of fish biodiversity in Lakshadweep archipelago. A check list of the Butterflyfishes of the Lakshadweep Archipelago is also provided.

**Keywords:** Arabian Sea, Chaetodontid, First record, Reef fishes, India.

### 1. Introduction

Lakshadweep archipelago, formerly known as the Laccadive Islands, is a Union territory of India and forms the northernmost segments of the Chagos – Maldives– Laccadive oceanic ridge. Due to its location and due to governmental restrictions it has been rather isolated from the rest of the world. This isolation has lead to greater protection from direct human impacts, but has also resulted in very few scientific studies being carried out in these waters. Although most of the studies that exist are focused on fish, in comparison to other coral reefs of the Indian Ocean, like Maldives, Seychelles, or the Chagos Archipelago, the fishes of Lakshadweep have still received far less attention, and Lakshadweep's fish fauna is yet to be fully discovered.

The first taxonomic study of fishes from these islands was done by Jones and Kumaran [1], which was based on samples acquired by commercial and sustenance fishing. However, most of the fishing gears used are inefficient in reef ecosystems and no *in situ* observation of the fishes using underwater devices was carried out. The more recent and complete work of Murty [2], done on reef fishes of Lakshadweep, was also based on samples collected through fishing operations. Although a few *in situ* fish studies using visual census methods exist, it still seems that these fish species-lists may be far from complete [3, 4, 5, 6]. During an ongoing research project on habitat selectivity and abundance of butterflyfish population in Lakshadweep, we found 28 species of Chaetodontids compared to the previous 18 species reported by earlier studies [2,4].

The fish populations of Lakshadweep have managed to stay very close to pristine due to its isolation and due to the local artisanal fisheries focusing predominantly on skipjack tuna, *Katsuwonus pelamis* (L.) which are caught using a traditional pole and line fishing method. The expected high biodiversity and good reef health in Lakshadweep waters are of great importance regarding the conservation of biodiversity in the Arabian Sea of Western Indian Ocean. Moreover the chance for the report of new species or extension of range of many fishes are expected if more intensive surveys are carried out in the archipelago using modern underwater technology. Hence an attempt to fully document the region is made.

## 2. Materials and Methods

Lakshadweep is an archipelago in the Arabian Sea ( $8^{\circ}$  and  $12^{\circ}30' N$ ,  $71^{\circ}$  and  $74^{\circ} E$ ) off the West Coast of India with  $20,000 \text{ km}^2$  of territorial water and  $400,000 \text{ km}^2$  of Exclusive Economic Zone. Lakshadweep Archipelago consists of 15 atolls and 5 submerged sand banks. These atolls constitute 11 inhabited, 16 uninhabited islands, and 3 submerged reefs. The total lagoon area for these atolls is  $4,200 \text{ km}^2$ . Belt transects [7] and timed swims techniques were used to record the occurrence and abundance of species of the family Chaetodontidae. Belt transects ( $20\text{m} \times 5\text{m}$ ) were placed horizontal to the reef flat in the shallow back-reef as well as on the outer-reef slope and observed to quantify the density of chaetodontids. Timed swims could cover large areas and were particularly useful to sample species that are unevenly distributed or occurred in low densities [8]. During the survey, fishes were photographed and video documented and specimens were collected to confirm correct identification. In the laboratory the species were identified primarily using standard references [9, 10]. The genus and species classification was done following Eschmeyer and Fricke [11]. Further validity and correct nomenclature of the fishes were checked in FishBase [12]. The fishes were identified up to species level and their abundance was recorded on underwater data sheets [13]. Data on occurrence alone are presented in this paper.

## 3. Results

This paper presents the occurrence of nine additional chaetodontidae species found from Lakshadweep of which five are new records: *Chaetodon andamanensis* Kuiter and Debelius 1999, *Chaetodon decussatus* Cuvier 1829, *Chaetodon guttatissimus* Bennett 1833, *Chaetodon interruptus* Ahl 1923, *Chaetodon lineolatus* Cuvier 1831. The other four species, *Chaetodon madagaskariensis* Ahl 1923, *Chaetodon triangulum* Cuvier 1831, *Forcipiger longirostris* (Broussonet 1782), and *Heniochus pleurotaenia* Ahl 1923 have been reported previously. However the basis for these reports is uncertain, as neither specimen deposits nor photographs exist. Therefore we present them here to confirm their occurrence in Lakshadweep. The photographs of the species are presented in figures and voucher specimens have been deposited in the reference collection of Western Ghats Regional Centre of Zoological Survey of India, Calicut [20]. For *Chaetodon interruptus*, *C. madagaskariensis*, *Forcipiger longirostris* and *Heniochus pleurotaenia*, we present only photographic evidence as no specimens could be collected. Table 1 provides the list of all species of the family reported from the Lakshadweep Islands.

**Table 1:** Check list of the butterflyfish of the Lakshadweep Archipelago

Sl. No.	Scientific Name	Reference
1	<i>Chaetodon andamanensis</i> Kuiter and Debelius, 1999	Present study
2	<i>C. auriga</i> Forsskål, 1775	[1]
3	<i>C. bennetti</i> Cuvier, 1831	[1]
4	<i>C. citrinellus</i> Cuvier, 1831	[1]
5	<i>C. collare</i> Bloch, 1787	[1]
6	<i>C. decussatus</i> Cuvier, 1829	Present study
7	<i>C. fulcula</i> Bloch, 1795	[1]
8	<i>C. guttatissimus</i> Bennett, 1833	Present study
9	<i>C. interruptus</i> Ahl, 1923	Present study
10	<i>C. kleinii</i> Bloch, 1790	[1]
11	<i>C. lineolatus</i> Cuvier, 1831	Present study
12	<i>C. lunula</i> (Lacepède, 1802)	[1]
13	<i>C. madagaskariensis</i> Ahl, 1923*	[16]
14	<i>C. melanotus</i> Bloch and Schneider, 1801	[1]
15	<i>C. meyeri</i> Bloch and Schneider, 1801	[1]
16	<i>C. trifascialis</i> Quoy and Gaimard, 1825	[1]
17	<i>C. triangulum</i> Cuvier, 1831*	[16]
18	<i>C. trifasciatus</i> Park, 1797	[1]
19	<i>C. vagabundus</i> Linnaeus, 1758	[1]
20	<i>C. xanthocephalus</i> Bleeker, 1853	[1]
21	<i>Forcipiger flavissimus</i> Jordan and McGregor, 1898	[21]
22	<i>F. longirostris</i> (Broussonet, 1782)*	[4]
23	<i>Heniochus acuminatus</i> (Linnaeus, 1758)	[1]
24	<i>H. dipherutes</i> Jordan, 1903	[2]
25	<i>H. monoceros</i> Cuvier, 1831	[1]
26	<i>H. pleurotaenia</i> Ahl, 1923*	[16]
27	<i>H. singularis</i> Smith and Radcliffe, 1911	[2]
28	<i>Hemitaurichthys zoster</i> (Bennett, 1831)	[1]
	*Confirmed in the present study	

### 3.1 New records of Butterflyfish from Lakshadweep archipelago

#### 3.1.1 *Chaetodon andamanensis* Kuiter and Debelius 1999



**Fig 1:** *Chaetodon andamanensis* in the lagoon of Agatti Atoll. The specimen collected and deposited in Zoological Survey of India, WGRC, Calicut (inset specimen Reg.No.ZSI/WGRC/IR.V.2496)

#### Material Examined

D.XIV, 17; A.IV, 14; P.14; V.I, 5. TL 104 mm, SL 89 mm, Body depth: 52 mm. A single specimen was collected from Agatti lagoon ( $10^{\circ}50'43.99''N$ ,  $72^{\circ} 9'23.08''E$ ), from the back-reef in 1.2m depth. The specimen is deposited in Zoological Survey of India, WGRC, Calicut with specimen number- ZSI/WGRC/IR.V.2496.

#### Diagnosis

Bright yellow body with brownish grey line running along horizontal scales rows on the body originating from behind head, darkest and thickest along upper side and fading ventrally; head with black vertical band across eye, with pale blue margin; black spot with pale blue margin on upper part of caudal peduncle; caudal fin yellow with transparent margin<sup>[14, 15]</sup>.

#### Distribution

In Eastern Indian Ocean: from the northern Sumatra and the Andaman Sea westward through Sri Lanka to the Maldives<sup>[15]</sup>.

**Remarks:** Two sightings were made on the backreef of Agatti Island ( $10^{\circ}50'57.64''N$ ,  $72^{\circ} 9'27.12''E$  and  $10^{\circ}50'43.99''N$ ,  $72^{\circ} 9'23.08''E$ ). It is unclear whether these were two separate individuals or the same individual as the locations of the two sightings were only 450 m apart. This species is considered a sibling species of *Chaetodon plebeius* from the Eastern West Pacific and these two are still often confused<sup>[15]</sup>. There are a few studies where *Chaetodon plebeius* has been reported from Lakshadweep<sup>[4, 16]</sup>. However, the species observed had most likely been *C. andamanensis*, which had been probably misidentified

as *Chaetodon plebeius*, despite the absence of the blue blotch on the upper sides of the body. Due to the character of the oceanic currents around Lakshadweep and the fact that *C. andamanensis* is very rare in Lakshadweep, it is quite plausible that it has spread to Lakshadweep from the Maldives only recently.

#### 3.1.2 *Chaetodon decussatus* Cuvier, 1829

**Material Examined:** D. XIII, 24; A.III, 20; P.14; V.I, 5. TL 95 mm, SL 76 mm, Body depth: 50 mm. A single specimen was collected from Kavaratti lagoon ( $10^{\circ}33'40.09''N$ ,  $72^{\circ}37'15.65''E$ ), from the back-reef in 2 m depth. The specimen is deposited in Zoological Survey of India, WGRC, Calicut with specimen number-ZSI/WGRC/IR.V.2507.

**Diagnosis:** Black area covering most of the back part of the dorsal fin and continuing down to the end of the anal fin; anal fin with yellow stripe; a dark bar through middle of caudal fin; a black band over eye connected at nap; tips of dorsal spine white.

**Distribution:** throughout Indo - West Pacific, including Oman Maldives, India, Sri Lanka

**Remarks:** Both of these species are commonly found in the shallow lagoon and on the outer reef of Kavaratti and Agatti Island, especially in sites with high coralline algae cover. It was found at depths ranging from 1-25 meters. As *Chaetodon decussatus* resembles *C. vagabundus* Linnaeus, 1758 (Fig. 2), and both of these species are very common in the waters of Kavaratti and Agatti Island, previous studies<sup>[1, 2, 4, 5]</sup> which reported only *C. vagabundus*, had most likely misidentified *C. decussatus* as *C. vagabundus*.



**Fig 2:** Comparison of *Chaetodon decussatus* (A) and *C. vagabundus* (B) photographed and collected from the lagoon of Kavaratti Island. (insect specimen A Reg. No. ZSI/WGRC/IR.V.2499 and B Reg. No. ZSI/WGRC/IR.V.2507)

### 3.1.3 *Chaetodon guttatissimus* Bennett, 1833

**Material Examined:** D.XIII, 23; A. III, 18; P.14; V.I, 5. SL 80 mm, TL 96 mm. Body depth: 48 mm. A single specimen was collected from Agatti outer reef ( $10^{\circ}49'37.98''N$ ,  $72^{\circ} 9'18.83''E$ ), from 15 meter depth near the outer reef slope.

**Diagnosis:** Body pale to whitish with dense spotting over the body arranged in rows, spots extending on to dorsal and anal fin; a dark band around caudal peduncle; a black band from nape through eye to lower opercular margin; black

vertical bar at middle of caudal fin, margin of dorsal and anal fins light yellow. The specimen is deposited in Zoological Survey of India, WGRC, Calicut with specimen number- ZSI/WGRC/IR.V.2501.

**Distribution:** widespread Indian Ocean species.

**Remarks:** Eight pairs of *C. guttatissimus* were observed on the outer reef slope of Agatti at the depth ranging from 13-20 meters. This species is present on reefs of neighbouring countries such as the Maldives and Sri Lanka and was thus likely to be present in Lakshadweep as well.



**Fig 3:** *Chaetodon guttatissimus* photographed and collected from outer reef of Agatti Island. (inset specimen Reg. No. ZSI/WGRC/IR.V.2501)

### 3.1.4 *Chaetodon interruptus* Ahl, 1923



Fig 4: Photographic record of *Chaetodon interruptus* observed on the reef slope of Kavaratti Island

**Species description:** D.XIII, 22; A.III, 19; P.14; V.I, 5. SL 77 mm, TL 93 mm. Body depth: 45 mm. *C. interruptus* can be identified by their colour pattern of yellow body with black eye band, large black blotch below the dorsal fin, which spreads down and posterior black band with white posterior margin of dorsal and anal fins (Fig. 4).

**Distribution:** widespread in the Indian Ocean, including the Chagos Archipelago, Maldives and Sri Lanka.

**Remarks:** *C. Interruptus* was observed on the reef slope of Kavaratti Island at 20 meters ( $10^{\circ}34'35.42''N$ ,  $72^{\circ}38'50.93''E$ ) and was recently observed at two sites in Minicoy ( $8^{\circ}19'48.21''N$ ,  $73^{\circ}4'36.01''E$  and  $8^{\circ}18'42.73''N$ ,  $73^{\circ}4'21.26''E$ ) during Lakshadweep Department of Science and Technology Coral reef monitoring Survey 2011. It is a common species in India and throughout the islands of Maldives, and it is therefore not surprising its observation in Lakshadweep

### 3.1.5 *Chaetodon lineolatus* Cuvier, 1831

**Material Examined:** D. XI, 24; A. III, 21; P. 14; V.I, 5. SL 55 mm, TL 66 mm. Body depth: 32 mm. A single specimen was collected from Kavaratti lagoon ( $10^{\circ}33'32.71''N$ ,  $72^{\circ}37'24.34''E$ ), from a patch reef in 2 m depth. The specimen is deposited in Zoological Survey of India, WGRC, Calicut with specimen number-ZSI/WGRC/IR.V.2502.

**Diagnosis:** Body colour is white with a black elliptical marking along the edge of the posterior portion of the back extending across the caudal peduncle to the base of the posterior anal fin rays; broad black band overhead, partially interrupted in front above eye; The dorsal caudal and anal fins are bright yellow.

#### Distribution

Widespread throughout the Indo-Pacific. This species is also reported from Sri Lanka, Maldives, and the Chagos Archipelago.

#### Remarks

Two pairs of *C. lineolatus* were observed in the Kavaratti lagoon ( $10^{\circ}33'32.71''N$ ,  $72^{\circ}37'24.34''E$ ), at depths of 2-3 meters, on the outer reef of Kavaratti Island ( $10^{\circ}34'49.75''N$ ,  $72^{\circ}38'29.46''E$ ) at 9 meters, and outer reef of Agatti Island ( $10^{\circ}51'25.96''N$ ,  $72^{\circ}12'0.65''E$ ) at 10 meters. *C. lineolatus* was always found feeding along with *Heniochus monoceros*. Being the largest species of butterflyfish and common in the Maldives it is odd to not have been reported from the Lakshadweep archipelago previously.

Three of the nine species, *Chaetodon madagaskariensis*, *Chaetodon triangulum*, *Heniochus pleurotaenia*, have been mentioned in a Ph.D. thesis<sup>[16]</sup> but because the basis for these records is uncertain and due to the increased difficulty of accessing data from such studies, we have decided to present the three species here along with proper

photographic documentation and specimen details in order to confirm their presence on Lakshadweep reefs. Similarly the species *Forcipiger longirostris* has been briefly mentioned in an earlier study [4]. The identification is, however, ambiguous, which is supported by the fact that

"*Forcipiger* sp." has been used throughout their study. For this reason we also present this species in this paper with photographic evidence to confirm its occurrence in Lakshadweep reef ecosystems.



**Fig 5:** *Chaetodon lineolatus* photographed and collected from the outer reef of Kavaratti Island. Juvenile of *C. lineolatus* (inset above) and adult (inset below) (Reg. No. ZSI/WGRC/IR.V.2502)

### 3.1.6 *Chaetodon madagaskariensis* Ahl, 1923



**Fig 6:** Photographic record of *Chaetodon madagaskariensis*, observed on the outer reef of Kavaratti Island

#### Species description

D.XII – XIII, 18 - 20; A.III, 15 - 17; P.14; V.I, 5. Maximum TL 130

mm. It is easily identified by its colour pattern. The body is silver at the head becoming white towards the tail, with a triangular orange

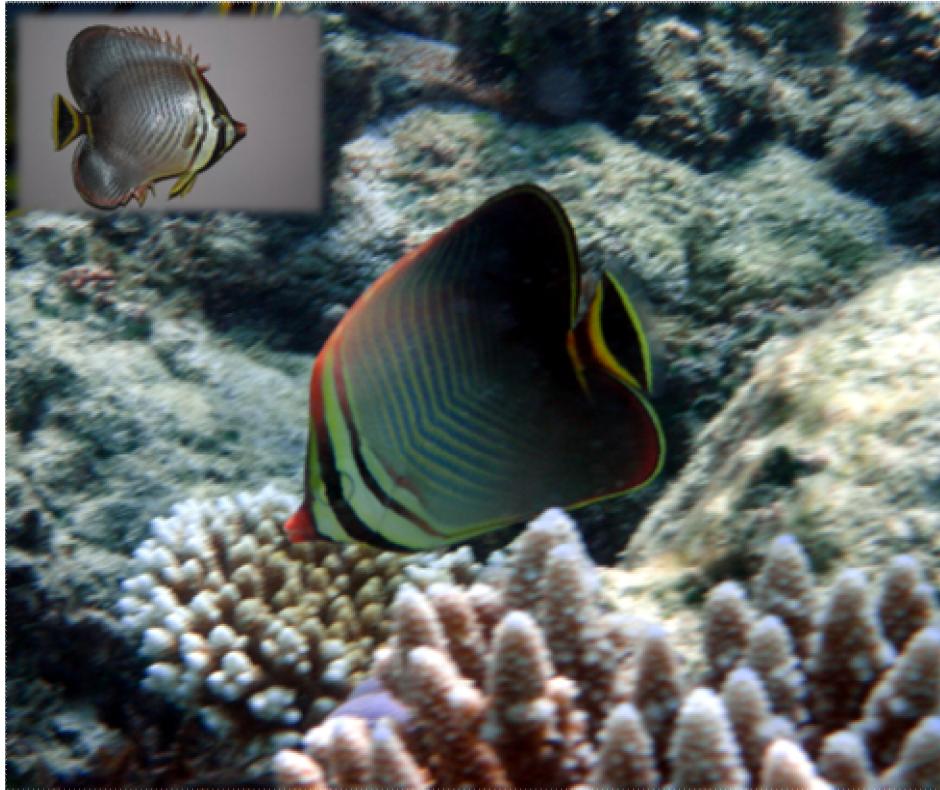
patch at posterior dorsal fin and the caudal peduncle. There are a series of about eight dark grey chevron lines on the sides of the body. Between the eyes and the start of the dorsal fin on the nape, there is a black patch rimmed with white. The base of the caudal fin is white, followed by an orange patch and a white rim. The dark band passing thought the eye also possesses white margins.

#### Distribution

This species is distributed along Indian Ocean including Sri Lanka, the Chagos Archipelago, and Maldives.

#### Remarks

*C. madagaskariensis* was found many times on the outer reefs of Kavaratti and Agatti atolls in groups of 2 - 5 individuals, at an average depth of 20 meters.



**Fig 7:** *Chaetodon triangulum*, photographed and collected from the leeward back-reef of Agatti Island. (inset specimen Reg. No. ZSI/WGRC/IR.V.2505)

### 3.1.7 *Chaetodon triangulum* Cuvier, 1831

#### Material Examined

D. XI, 23; A. III, 20; P. 20; V.I, 5. SL 85 mm, TL 105 mm. Body depth: 59 mm. A single specimen was collected from Agatti lagoon ( $10^{\circ}52'0.58''N$ ,  $72^{\circ}10'39.76''E$ ), in 2 m depth. The specimen is deposited in Zoological Survey of India, WGRC, Calicut with specimen number-ZSI//WGRC/IR.V.2505.

#### Diagnosis

Identified by deep body triangular in shape and black tail fin; snout short and prominent, body purplish brown with narrow cream coloured angularly bent bars on sides, three dark bars on head, a dark purplish bar with pale edge across caudal fin; edge of soft dorsal black; ventral fins light yellow.

#### Distribution

This species is distributed along the Indian Ocean; from the coast of East Africa to Christmas Island to the Andaman Sea. This species is also reported from the Chagos Archipelago and Maldives.

#### Remarks

*C. triangulum* was encountered in the shallow lagoons of Agatti and Kavaratti atoll at the average depth of 2 meters. *C. triangulum* was found feeding on coral *Acropora* species along with *C. trifascialis* and *C. fulcula* in the Agatti lagoon.

### 3.1.8 *Forcipiger longirostris* (Broussonet, 1782)

#### Species description

D.X - XI, 24 - 28; A.III, 17 - 20; P.15 - 17; V.I, 5. Maximum TL: 22 mm. Distribution: This fish is present throughout the Indo-Pacific region.

#### Remarks

Four pairs of *F. longirostris* were encountered on the outer reef slope of Kavaratti Island ( $10^{\circ}34'49.59''N$ ,  $72^{\circ}38'29.29''E$ ) at the depth of 14 meters. The population in Lakshadweep may have decreased after the major bleaching event in 1998, but the population showed a slight increase recently (personal observation). This species may have previously been confused with *Forcipiger flavissimus* Jordan and McGregor 1898 due to the close resemblance of

*F. longirostris* and *F. flavissimus*.



**Fig 8:** Photographic record of *Forcipiger longirostris* observed on the outer reef slope of Kavaratti Island

### 3.1.9 *Heniochus pleurotaenia* Ahl, 1923



**Fig 9:** Photographic record of *Heniochus pleurotaenia* observed on the outer reef slope of Kavaratti Island

**Species description**

D.X, 23 - 25; A.III, 17 - 18; P.14 - 15; V.I, 5. Maximum TL: 17 mm.

**Distribution**

This species distribution is restricted to the north-eastern Indian Ocean and Andaman Sea; from Maldives, southern India, and Sri Lanka throughout the Andaman Sea, down along the western part of Sumatra to northern Java.

**Remarks**

A Pair of *H. pleurotaenia* was observed on the outer reef slopes of both Agatti and Kavaratti Island; 10°51'37.53"N, 72°12'6.30"E and 10°34'44.55"N, 72°38'38.64"E respectively, average depth 20 m. It was also observed later around Bangaram Island (10°55'56.01"N, 72°19'0.64"E). These records of *H. pleurotaenia* in Lakshadweep form the western most point of its distribution range.

**4. Discussion**

Up till now Lakshadweep was known to have only 18 species of butterflyfish [2, 4], but during a study on habitat selectivity and abundance of butterflyfish in Lakshadweep, we found 28 species of chaetodontids. Butterflyfishes are well known corallivores and thus in close association with corals among which they also rely on for shelter. However the coral communities changed in Lakshadweep after the 1998 massive bleaching event [17]. Therefore butterflyfish communities may have changed in response to the changing coral reef, providing a possible explanation for the new butterflyfish records. However, and more likely, these new records are due to low amount of scientific research done on Lakshadweep coral reefs. More fish species are expected to be encountered as more intensive fish surveys are carried out. The type of methodology used for the collection of data during this study may be the main reason for the five new butterflyfish species recorded from this region, as the majority of coral reef fish studies that have been carried out in Lakshadweep in the past have not obtained data based on underwater observations. They have acquired data from fishing and observations of landings. Gill nets and traps were often used to collect the fish species. Gill nets are, however, unsuitable for collecting many reef fishes as many of them hide among corals. Snorkelling and SCUBA diving with simultaneous recording by photography along the belt transects and timed swims, used in our study, are much more effective for the species composition and population assessment of butterflyfishes [18, 19]. The photographs of the species are presented and voucher specimens have been deposited as a primary documentation for further reference if required.

Another plausible explanation for why these species were not recorded before is that they may have been misidentified as other species. For example *Chaetodon decussatus* resembles *C. vagabundus* and both of these species are very common and coexisting in the waters of Kavaratti and Agatti Island, thus earlier researchers [1, 2, 4, 5] may have misidentified *C. decussatus* as *C. vagabundus*. In the present study we have collected both the species and accurately identified them. Similarly *C. andamanensis*, considered a sibling species of *Chaetodon plebeius* Cuvier, 1831 from the eastern West Pacific [15], may be confused with *C. plebeius*. There are a few studies [4, 16] where

*Chaetodon plebeius* has been reported from Lakshadweep. However the basis for these reports is uncertain, as neither specimen deposits nor photographs exist. Due to the characteristics of the oceanic currents around Lakshadweep and the fact that *C. andamanensis* is very rare in Lakshadweep, it is quite plausible that it has spread to Lakshadweep from the Maldives only recently. The presence of *C. andamanensis* in Lakshadweep is an extension of its geographic range, in which Lakshadweep (Agatti Island) now forms the most western point of its range of occurrence.

The report of five species new to the Lakshadweep waters points towards the urgent necessity of detailed investigation on the occurrence and population of this very important group of fishes. Due to the close tie between butterflyfish and corals the abundance and distribution of these fishes need to be studied to ensure correct future management. Most studies, including this one, have been carried out on reefs of a few densely populated islands. Exploration of other islands, especially uninhabited islands, using underwater surveys may add new records or perhaps even species to the current species list of the region. The high biodiversity and reef health in Lakshadweep are of high importance not only in terms of the very existence of the ecosystem but also in terms of conservation of biodiversity in the western Indian Ocean, as Lakshadweep may act as an important recruiting ground for many reef fishes. Therefore, further studies in this area are much warranted considering its ecological significance and incomplete documentation of underwater fauna.

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