Spatial variation in substrate composition, coral diversity and recruitment on Maldivian coral reefs, ten years since the 1997-98 mass bleaching event.

by

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CONTENTS

1. INTRODUCTION

Coral reefs are renowned for their complexity, biological diversity and high productivity, playing a pivotal role in shaping the ecosystems that dominate tropical oceans. The importance of coral reefs as a crucial source of income and resources reaffirms their economic and ecological significance to humanity. Correlative field studies have revealed that elevated sea surface temperatures (SSTs) have been responsible for triggering mass bleaching events (Glynn, 1993; Brown, 1997a), leading to extensive coral mortality (Glynn, 1993; Goreau *et al*, 2000) and ecological changes (McClanahan, 2000). The substantial loss of coral reefs following the 1997-98 mass bleaching event has been well documented (Wilkinson, 2002). Estimations of amounts and rates of subsequent recovery are important to predict future reef condition and to conservation management of the reef ecosystems (McClanahan *et al*, 2007). Recent surveys have highlighted extreme declines in coral cover leading to debates concerning the ability of reefs to recover from mass disturbance (Bruno and Selig, 2007; McClanahan *et al*, 2007). Evidence from the past 20 years suggests that corals and their zooxanthellae are not able to acclimatise or adapt fast enough to the short, sporadic thermal events typical of recent bleaching episodes (Hoegh-Guldberg, 1999). Globally, the current focus is to document the changes in coral reef assemblages through continuous monitoring at varying spatial and temporal scales. The present study aims to examine the extent of reef recovery in the Maldives

1.1 Disturbance on coral reefs

Impacts causing disturbance to coral reefs, both natural and anthropogenic, are best defined as any process that clears primary substratum, resetting an area to an earlier succession stage and allowing the cycle of recovery to begin again (Sebens, 1994). An intermediate disturbance will allow the greatest number of species to co-exist. Too little disturbance, however, allows only a few opportunistic species with high rates of reproduction to colonise the newly available space, compared with too much disturbance which will restrict many species from recruiting and growing fast enough to persist (Sebens, 1994). Disturbance has shaped coral reefs as organisms have adapted and evolved within a spectrum of disturbances at varying scales. Due to predicted global climate change and the increased fluctuations of natural events, coral reefs are being pushed beyond their current physiological limits. There are varying levels of degradation which can be observed on coral reefs, from the extreme and obvious (mortality) to more sublime changes in characteristics, including competitive dominance among organisms, decreased growth rates, breakdown of organismal associations, reduced fecundity, reproductive failure and declining recruitment of larvae (Nyström *et al,* 2000). The present study will document the existing composition of four Maldivian coral reefs situated in Baa atoll which were subjected to intense bleaching in 1997-98 (Stevens, pers. comm.).

1.2 El Niño Southern Oscillation events

Six major episodes of mass bleaching of corals, coincident with El Niño Southern Oscillations (ENSO) events, have been reported since 1979 (Hoegh-Guldberg, 1999). The strongest El Niño event was recorded in 1997-98, when mass bleaching caused devastation to many reef ecosystems. The development of El Niño in 1997 was so rapid from June to December that a new monthly record high was set for SSTs in the eastern equatorial Pacific (McPhaden, 1999). At the height of the event in December 1997, temperatures of 28-29 °C were reported in the equatorial basin (McPhaden, 1999). The mass bleaching of coral reefs occurred at geographical scales which involved entire reefs systems (Goreau and Hayes, 1994). Considerable mortality occurred on the reefs of Sri Lanka, the Maldives, India, Kenya, Tanzania and the Seychelles, with mortalities of up to 90% in many shallow areas (Wilkinson, 2002). Approximately 50% of coral reefs in other parts of the Indian Ocean or in waters below 20m experienced bleaching. Hence, coral death during 1997-98 was unprecedented in severity (Wilkinson, 1999). In the central atolls of the Maldives in 1998, data showed monthly mean SSTs ranged from 1.2- 4.0 °C above average during the warmest months (March-June), with the greatest anomaly of 2.1 °C in May. The substantial loss of coral reefs in the western Indian Ocean occurred against a background of little information.

1.3 Extent of bleaching damage

The depth to which corals were affected by bleaching-induced mortality varied geographically. In the Seychelles, the evidence showed that bleaching and bleaching-induced mortality increased with depth, and corals in deeper water bleached first, only followed later by shallow water coral colonies (Spencer *et al,* 2000). Previous studies (Spencer *et al,* 2000, McClanahan, 2000) had shown that in 1997-1998 shallow water corals (3-10m) were more temperature tolerant than corals in deeper water (10-20m) which usually experience a more constant temperature regime (Spencer *et al,* 2000). In the Chagos, the lowest coral cover was reported down to 30-35m (Sheppard *et al*, 2002). Northern atolls in the Chagos were worst affected at 5m, but less affected below 10-15m (Sheppard *et al*, 2002). In the Maldives, the cover of live coral on shallow reefs declined to almost 20 times lower than that recorded prior to the 1997-98 bleaching event. However, the deeper reefs (>12m) appear to be in better condition (Zahir, 2000). Coral reefs are likely to show varying patterns of recovery as bleaching-induced mortality was reported to have varied with depth. Coral recruitment can be affected by physical factors such as stability of the substrate and abrasion (Fox *et al*, 2003), and biological factors such as predation (Colgan, 1987) and competition for space (Chesson, 1998). The current study will examine the composition of substrate and coral diversity at various depths to determine the extent of recovery on the reefs.

1.4 Anthropogenic impacts on coral reefs

Coral reefs provide a major impetus for tourist development throughout the western Indian Ocean. Anthropogenic impacts have been shown to prevent reef recovery from mass disturbance by changing both physical and biological factors which restrict natural development. The series of coral reefs surveyed in this study are important to Maldivian economy, as they are used for recreational activities by tourists. The four reefs are used daily for snorkelling and SCUBA diving excursions from two of the largest resorts in Baa Atoll (Four Seasons Resort and Reethi Beach Resort). The location of the reefs makes them easily accessible to the resorts, and provides sheltered conditions favourable to tourists. Physical destruction can cause damage to live corals, reducing productivity of the coral and the 3-dimensional structure of the reef. Marked differences in coral community structure at dive sites shows that divers can have effects other than breaking corals (Hawkins *et al*, 1998). Higher diversity, lower coral cover and a greater proportion of branching corals at frequently visited dive sites have been reported as a consequence of opening up space through disturbance (Hawkins *et al*, 1998). Previous studies on the effect of recreational activities on Maldivian reefs indicated a significantly higher abundance of damaged or dead coral structures on frequently visited reefs in comparison to less frequented reefs (Allison, 1996). The physical damage caused by tourism is typically concentrated in the shallow areas of the reef, where repetitive contact with the reef occurs. A higher percentage of loose fragments of living coral have been shown in shallow areas of the reefs in comparison to deeper and less frequently used areas of the reef (Hawkins *et al*, 1998). Chronic disturbances, such as tourism, have been shown to promote reef degradation and reduce recovery, particularly after episodic disturbances such as bleaching events (Done, 1992).

Surfaces of recently dead tabular corals have been shown to create suitable surfaces for coral recruits to settle (Loch *et al,* 2004) and, therefore, damaging such structures could possibly reduce recruitment by limiting surfaces for attachment. Settlements on table groups of dead *Acropora hyacinthus* and *A.clathrata* have been examined and, on average, high densities of 25.9 colonies per m^2 of table surfaces were dominated by recruits (Loch *et al,* 2004). Similarly, *Acropora* tables have been found to attract significantly more recruits than any other substrate in the Chagos, in particular *Acropora* juveniles themselves (Sheppard *et al*, 2002). If such disturbances can be controlled, limiting them to be more episodic and acute or removing the stress altogether, reefs can and will recover (Nyström, 2001). Chronic disturbance by tourists may, therefore, not only be affecting present but also future coral communities, thereby hindering recovery in this region on Baa Atoll. It is, therefore, important to monitor reefs with the aim of reducing such damage and allowing natural recovery to take place.

The reefs surveyed in the current study are not, at present, subjected to intense pressure from tourism, despite the popularity of the reefs to surrounding resorts. There are nearly 100 resort islands in the Maldives, with 50 more being built during the next three years (Tomasetti, pers.comm.). A new tourist resort, the Anantara Resort & Spa on Kihavah Huravalhi Island, is planned for 2010 (http://www.poole-associates.com). Kihavah Huravalhi Island (5 17’49.94”N, 73 00’56.85”E) lies approximately.1.8km north of the coral reefs islands to be surveyed in the present study. The planned development has a recreational department which will inevitably use the nearby coral reef islands out of convenience for recreational activities. An increase in erosion, suspended sediment and coral damage has been shown around coral reefs surrounding numerous tourist resorts in the Maldives (Rajasuriya, 2000). Baseline surveys of the reefs are necessary so that monitoring of the reefs can be achieved to help prevent further degradation and encourage recovery.

1.5 Recovery of coral reefs

The recovery of coral-dominated ecosystems damaged by the strong El Niño event in 1997-98 was of the greatest concern as rapidly increasing human pressures were shown to hinder the recovery capacity of the perturbed coral communities (Glynn, 1994). Protection of coral reefs from human induced impacts is imperative, particularly in areas of high development. The main concern, however, is the synergistic impacts of both natural and anthropogenic disturbance on coral reefs, which is predicted to have the most devastating effects (Richmond, 2006). A study into the state of coral reefs in the Galápagos Islands revealed that destruction of the reefs was not only caused by the disturbances of El Niño in 1982-93, but also by human impacts on the corals from anchoring and fishing, which had collectively resulted in 95-99% coral mortality on the Islands (Glynn, 1994). Discrepancy within the literature is common as to whether or not anthropogenic disturbances are as pervasive as natural disturbances. However, what is certain is that the persistence of an anthropogenic impact after a natural disturbance will delay coral recovery. Large ecological changes have also been reported in areas with low levels of human influence, such as remote islands and reef atolls (Glynn, 1994; Allison, 1996; Sheppard, 1999a, b). The coral reefs of the Maldives-Chagos ridge are one of the areas with the lowest human influence in the western Indian Ocean. Many atolls are devoid of tourist developments, and many islands within atolls are presently uninhabited. Tourism is, however, intense within a small number of atolls and any anthropogenic disturbances are, therefore, likely to vary spatially. Consequently, recovery is likely to differ between atolls.

Coral reef recovery in South Asia over the ten years since the 1998 coral bleaching and mortality event has been highly variable (Zahir, 2008). Some severely bleached reefs, such as in the Chagos Archipelago and the western atoll chain of the Maldives, have returned to pre-bleaching coral cover and are making gradual process towards pre-bleaching population structure (Zahir, 2008). However, although coral cover is increasing at most sites in the Lakshadsweep islands, recovery is limited on several atolls. Localised and seasonal bleaching has been observed annually in the region since 1998, but bleaching related mortality has been very low (McClanahan *et al*, 2007). Surveys show reef status and recovery is better in areas where human interference and anthropogenic stress is low (Zahir, 2008). The combination of many factors can influence variation in reef recovery and it is, therefore, important to highlight such influences and document their impact on the coral reef community.

1.6 Ecological shifts on coral reefs

Ecologists are now considering the role of disturbance on coral reef ecosystem dynamics, as it has been shown to cause ecological changes to alternate states. The most familiar is a shift from a coral to algae dominated reef (Nyström, 2000; Belwood *et al*, 2004). However, recent studies have reported a shift from coral to corallimorph dominance (Tkachenko *et al,* 2007; Work *et al,* 2008). The persistence of dominating macroalgae can last a decade or more, as was shown along the north coast of Jamaica, where algal dominance persisted since damage associated with Hurricane Allen in 1980 (Hughes, 1994). Numerous reports from the Indian Ocean revealed shifts in species composition after mass bleaching in 1997-98. In the Chagos, 26% of coral skeletons were found encrusted in red algae (Sheppard *et al*, 2002). Similarly, in the Maldives, reefs were shown to be dominated by coralline and turf algae (68%) with the presence of erect fleshy algae and sponges being higher than previously reported on coral reefs (McClanahan, 2000). The loss of coral reef resilience can cause many changes within an ecosystem, resulting in dramatic shifts in species composition which may be detrimental to countries heavily reliant on coral reefs as an economic resource. The present survey will provide baseline data on four reefs which are important economically to the tourist islands within Baa atoll.

1.7 Coral Recruitment

Coral recruitment has long been recognised as fundamentally affecting the patterns of distribution and abundance of organisms within a coral reef ecosystem (Babcock and Mundy, 1996). Recruitment is dependent on the ability of coral larvae to identify an appropriate site for settlement and metamorphosis. The settlement of coral larvae on the appropriate substratum and orientation involves selection by coral planulae made on the basis of chemical signals (Babcock and Mundy, 1996). The pattern of settlement has been shown to play a significant role in creating different microhabitat distributions (Babcock and Mundy, 1996). Investigations into coral reproduction have revealed that life history strategies among corals may either constrain or enhance the rate of recruitment, and that post settlement mortality is also important in structuring coral populations (Smith, 1992). Natural rates of recruitment have an important role in shaping the overall dynamics and spatio-temporal patchiness in assemblages of species. Coral recruitment is shown to be spatially variable, dependent on physical environment factors and life history strategies such as method of reproduction.

Corals of isolated oceanic islands may be self seeding, or alternatively may be continually supplied with recruits advected from elsewhere by ocean currents. Larvae from species that spawn gametes are smaller, tend to disperse farther, and survive more poorly than do larvae from brooding species (Connell *et al*, 1997). As localised dispersal of larvae is found to supply reefs with new recruits, it is important to conserve and protect the coral reefs from anthropogenic impacts which may hinder reef recovery by destroying surviving corals which supply the recovering reefs with new recruits. The recruitment of corals may be affected after disturbance has occurred on a coral reef. It has been proposed that under conditions of environmental instability, where fatal disturbances occur at a high rate, a large number of motile propagules should be recorded, while clonal asexual growth will be favoured in stable conditions (Richmond and Hunter, 1990). Calculating the density of corals recruiting to the reefs post 1997-98 provided a good indicator of potential reef recovery and future ecological shifts.

The recruitment of corals onto artificial and natural reefs in central atolls of the Maldives has been examined with respect to elevated SST anomalies. In 1994, the coral community which had established on artificial reefs consisted of 95% branching corals and 5% massive corals. However, in 1999 post bleaching the composition changed, and was reported at 3% branching corals and 97% massive corals. Similarly, in 1999 McClanahan (2000) found coral recruits were sufficiently abundant at each site, an average of 29 individuals per m^2, but the most common recruits were in genera previously reported as subordinate genera, such as *Pavona* (11.7 individuals per m^2) and *Coscinarea* (4.4 individuals per m^2), whereas the previously dominant branching and encrusting species (*Acropora*, *Montipora* and *Pocillopora*) had recruit densities less than 0.65 individuals per m^2 (McClanahan, 2000). From these results it was predicted that unless there is significant compensation in growth and mortality, there may be future changes in coral species composition and benthic cover of these reefs (McClanahan, 2000). Recent studies, however, have shown that coral taxa that were the most susceptible to bleaching (acroporids and pocilloporids) have the largest increase in cover since 1998, while more resilient groups that survived the bleaching (e.g. agariciids and poritids) show a relative decrease in cover (Zahir, 2008). Recovery patterns, however, are shown to be variable between sites examined in the Maldives (Zahir, 2008). It is likely that the changes in generic composition observed immediately post bleaching may not be stable, but rather a temporary response to warm-water disturbances. As spatial differences in coral recovery throughout the Maldives are being reported (Zahir, 2002), the present study will provide essential baseline data on current composition on reefs in Baa atoll.

1.8 Economic importance of coral reefs

The Maldives is reliant on coral reefs as a resource. Therefore, their capacity to supply the residential population with ecological goods and services required must be secured (Moberg and Folke, 1999). Economically, coral reefs are important for the Maldives, primarily for tourism, followed by fisheries, coastal protection and the aquarium trade (Rajasuriya, 2000). Coral reef related tourism is of particular importance in the Maldives, where travel and tourism contribute around 56% to the national economy, and approximately 50% of the visitors are SCUBA divers (Westmacott *et al,* 2000). In an assessment evaluating the potential economic impact on tourism in the Maldives due to the mass mortality of corals in 1998, results suggested that the tourism industry was adversely affected by the coral morality (Westmacott *et al*, 2000). Loss of resilience of coral reef ecosystems will affect the quality and quantity of the goods and services currently provided by coral reefs. Due to the oceanic location of the Maldives, the islands have one of the lowest levels of human influences on coral reefs in the western Indian Ocean (McClanahan, 2000). Over 80% of the islands are less than 1–1.5 m above mean sea level and coral reefs play a vital role in sea defence, protecting the islands from storm damage and flooding (Pernetta and Sestini, 1989).

1.9 Current and future protection of the reefs

The total area of coral reefs in the Maldives covers 8,920 km^2, and the resources available for monitoring them are small (Zahir, 2002). Due to the proposed increase of tourist developments in Baa Atoll the Government of the Maldives, in cooperation with the United National Development Programme (UNDP), has initiated a project based on atoll ecosystem conservation of globally significant biological diversity in the Maldives. The objective of the 'Baa Atoll Project' is to promote the conservation and sustainable use of globally significant biological diversity in Baa Atoll. Atoll ecosystems in the Maldives provide the basis for the country's existence, as well as life supporting services such as shoreline protection and goods upon which the economy entirely depends (Rajasuriya, 2000). However, social and economic change is altering consumptive behaviour and livelihood strategies, outpacing institutional capacity and sectoral programs to adequately manage it. This in turn is threatening the natural endowment that is essential to maintaining the structure and function of atoll ecosystems, the viability of globally significant biological diversity, and the livelihoods and environmental security of the people (UNDP, 2008). To initiate the project, a basic rapid assessment of benthic composition of reefs in Baa atoll was conducted a month prior to the present survey, from which further and more detailed coral surveys are proposed on the most resourceful reefs in the atoll (Guignard, pers. comm). Efforts underway seek to improve reef monitoring that increasingly incorporates social and economic aspects, strengthening the research agenda and supporting uptake into management policy. It is, therefore, imperative that smaller scale baseline surveys are conducted on reefs with both ecological and economic importance to Baa atoll and tourist development in the region.

1.10 Aim of the project and specific objectives

Like most central Indian Ocean reefs, the reefs of the Maldives exhibited significant degradation following the mass bleaching event in 1997-98, where reports of mortality up to 90% was shown in many shallow areas (Wilkinson, 2002). Since the major bleaching event, the response of coral reefs to this disturbance has been shown to be highly variable due to a combination of biological and physical factors which affect recovery and development of the reefs. The location of the disturbed reefs, local oceanographic factors and depth have been shown to affect reef recovery. The location of the reefs is important to their recovery, as anthropogenic impacts have been shown to prevent development through pollution and substrate disturbance. More successful recovery has been shown in reefs exposed to ocean waters, where substrates have become stable, allowing the settlement colonisation of coral recruits. By reporting the existing state of the reef during recovery, the necessary protection can be afforded to maintain the reefs as a vital resource. With the projected increase in tourism within Baa Atoll, it is imperative that such surveys are performed in order to gain initial assessments from which future surveys can be based.

In the present study, surveys will be conducted to measure the extent of recovery on 4 reefs during a 3 month survey in Baa Atoll, Republic of Maldives. The surveys aim to assess spatial variation in recovery between the exposed northern slopes of these reefs and to investigate variation with increasing depth. The surveys intend to:

- Assess the composition of the substrate along transect lines at depths of 1 m, 5 m, 12 m and 18 m on each reef, in order to investigate the proportion of live coral and dead coral assemblages and the amount of substrate available for recruitment colonisation.

- Investigate the density and composition of coral recruits between reefs at depths of 5 m, 12 m and 18 m, in order to assess the success of coral recruits colonising the reefs.

- Investigate the abundance, diversity and richness of Anthozoan corals between reefs at depths of 1 m, 5 m, 12 m and 18 m, in order to assess the current variety in coral assemblages present on the recovering reefs.

- Assess the abundance of large tabular *Acropora* corals at 5m on the reef slopes as an indication of recent and current stressors impacting the reefs and to examine the type of physical damage occurring on the corals structures.

2. METHODOLOGY

Substrate composition, coral recruitment, coral diversity and assessments abundance of damage to tabular *Acropora* corals (>50 cm in diameter) were studied at four survey sites; Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo, in Baa Atoll within the Republic of Maldives, from 7th June to the 20th August 2008. Prior to initiating the survey, to aid in planning and experimental design, reconnaissance trips were undertaken on the 5th and 6th June.

2.1. Equipment

All the equipment used is listed in *Appendix 1*.

2.2. Survey Site Location

The Republic of Maldives is located in the central part of the Indian Ocean, and forms the largest part of the Laccadive–Chagos ridge. The Maldives is an approximately 700km long chain of 26 distinct geographical atoll formations, which are distributed in a north-south direction between a latitude of 7°6’30”N and 0°42’30”S and a longitude of 72°32’30”E to 73°46’15”E (Figure 1). The present study was undertaken in Baa Atoll, which is situated on the north-west of the Republic of Maldives (Figure 1). In the north of Baa Atoll, the four survey sites are located on the southern side of Kuda Kanduolhi. The Kuda Kanduolhi channel is 1.8 km wide and 0.25 km deep, and cuts through the atoll from east to west. Within the atoll the depth ranges from 45-55 m and the coral islands lie approximately 1 m below sea level.

The survey sites are aligned in a chain formation from east to west, residing 7.66-10.18 km west from Landaa Giraavaru (the nearest resort island) and 1.2 km east from Kendhoo (the nearest inhabited island). The survey sites are outer edge carbonate atoll reefs which slope at an approximate angle of 45° to a sandy ledge at 20 m, which extends approximately 20-25 m away from the reef subsequently dropping steeply into waters in excess of 200 m. The total distance of the sequence of survey sites is 2.97 km, with an average of 0.35 km between each adjacent island (Figure 3). Sampling was undertaken on the outer exposed northern edges of each of the four reefs, adjacent to Kuda Kanduolhi channel. The specific locations of the reefs were identified using satellite images and the northern faces of the survey sites were identified. The total lengths of the survey sites at Undoodhoo, Funadhoo, Hulhoodhoo and Gemendhoo were recorded in situ and measured as 120 m, 160 m, 130 m and 140 m respectively. During reconnaissance trips, the boundaries of the survey sites were marked using the handheld Garmin GPS. Above and below water visual references were made and photographed to mark the boundaries of the northern faces at each survey site.

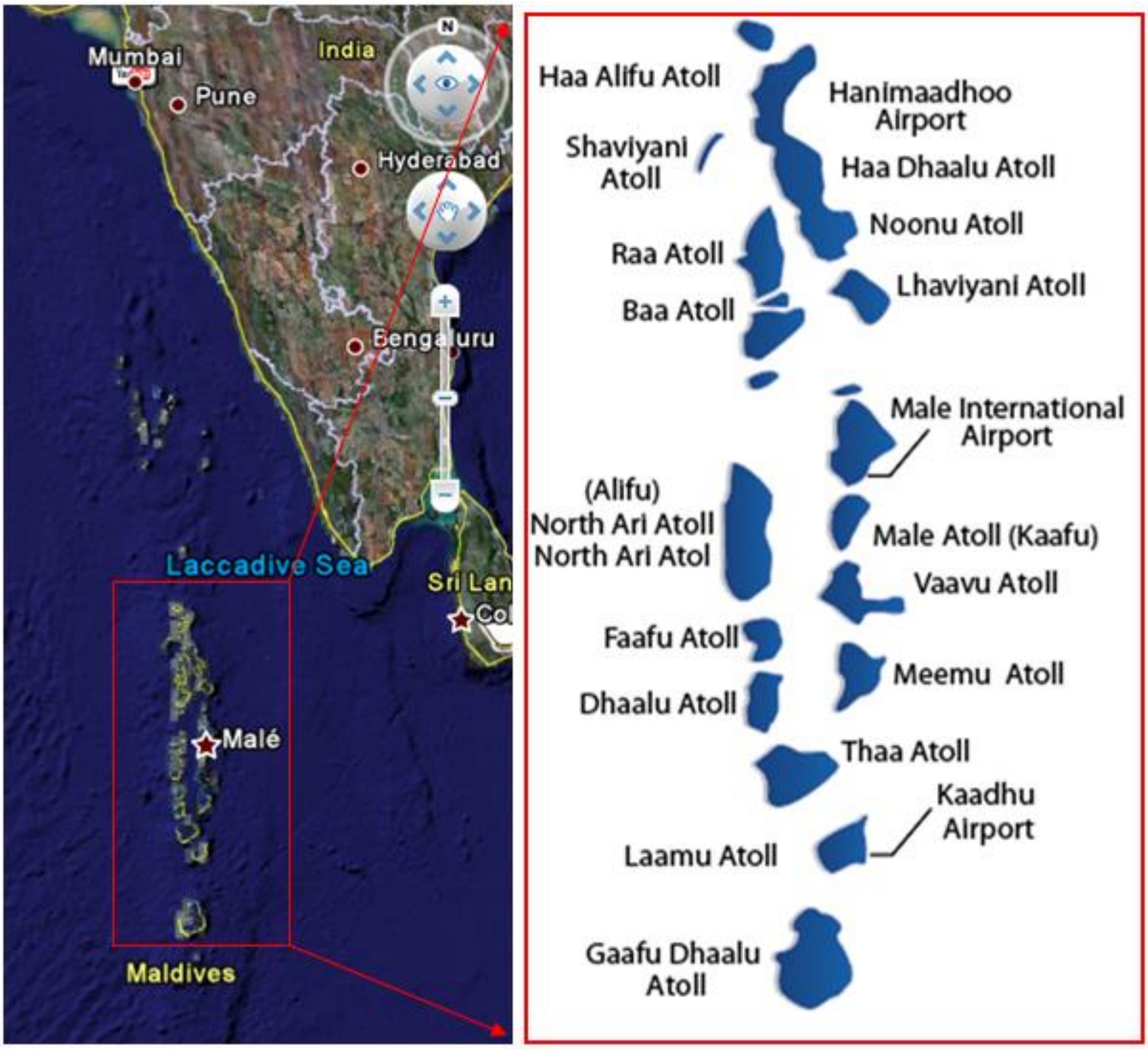


Figure 1: A satellite image of the Republic of Maldives (situated approximately 700 km south-west of Sri Lanka in the Laccadive Sea of Indian Ocean) and the formation of the 26 atolls within the Maldivian territory (http://earth.google.com).

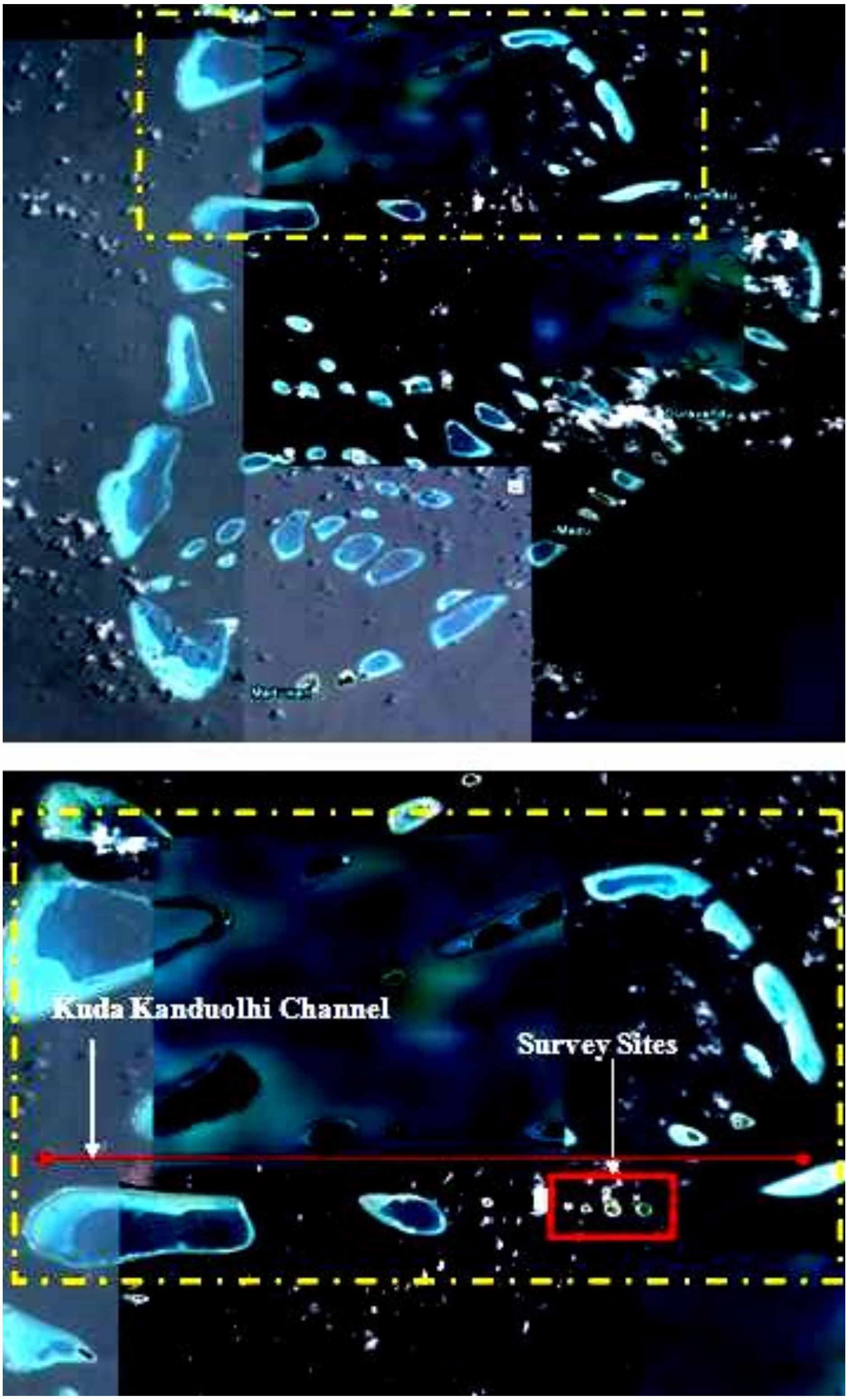


Figure 2: Satellite images of Baa Atoll, Republic of Maldives. Survey sites are situated south of the Kuda Kanduolhi Channel which divides Baa atoll from east to west (http://earth.google.com).

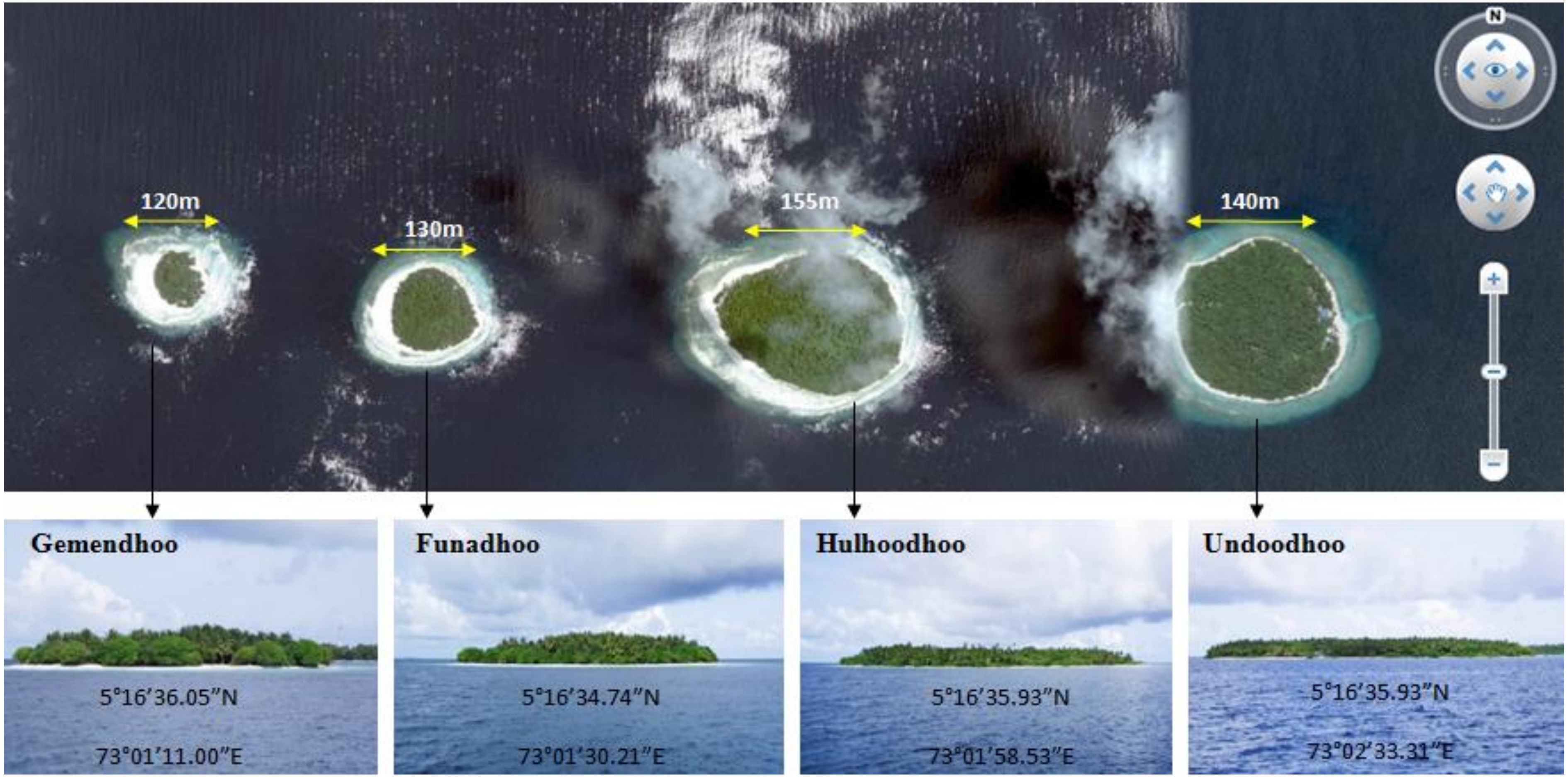


Figure 3: Satellite images (http://earth.google.com).and above water photographs of the survey sites (Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo). The survey site distances are marked at each site and GPS reading for each site are presented.

2.3 Survey techniques

The surveys were conducted using a combination of SCUBA diving and snorkelling techniques. The assessment of coral diversity and substrate cover was conducted within four depth categories; 1 m, 5 m, 12 m and 18 m at each survey site. The assessment of coral recruitment was conducted within three depth categories; 5 m, 12 m and 18 m at each survey site. A minimum of 5 x 20 m transect lines were placed randomly within each depth category and positioned horizontally along the reef slope. Along each transect line the substrate cover, coral recruitment and coral diversity was recorded.

2.3.1 Recording substrate composition

Substrate cover was recorded in situ every 0.5 m along the 20 m transect line. Points under the line were categorized into eight groups that included live hard coral, recently dead coral (a white skeleton with no live coral tissue on it), old dead coral, coralline and turf algae, fine sand, coral rubble, soft coral and an ‘others’ group for any observation not fitting into the above categories.

2.3.2 Assessing coral recruitment

Coral recruitment was assessed by placing a 1 m^2 quadrat every 2 m along the transect line. Recruits were categorised as individual isolated corals less than 5 cm in diameter. The abundance of recruits residing within the quadrats was recorded and identified to the level of family. High resolution macro photographs were taken when the identification of the recruit in situ was not possible and subsequently identified ex situ.

2.3.3 Assessing coral diversity

To assess coral diversity, 1 m^2 photoquadrats were taken at a 45° angle to the reef at 1m intervals along the 20 m transect line. A minimum of 5 replicate transects were placed within each depth category. Photoquadrats were taken using a 12 mega pixel Sea and Sea camera. Photoquadrats were placed above and below the transect line generating 40 x 1 m^2 frames per transect for analysis. Photoquadrats were analysed ex situ and images were subsequently uploaded and run through the Coral Point Count with excel extensions (CPCe) programme. Using CPCe, 1 m^2 borders were marked on each image, 12 points were randomly generated and coral lying beneath each point was visually identified. The same coral code file used in the CPCe program was used for all analyses and was developed and adjusted specifically for Maldivian coral reefs (Appendix 2). The coded data for each frame was stored and accumulated data of several frames were combined and saved as a whole transect dataset. The CPCe outputs generated excel worksheets with abundance estimates of corals present within each replicate transect at each survey site were produced.

2.3.4 Assessing the abundance and damage to Acropora corals

To assess the abundance of *Acropora* species greater than 50 cm in diameter; a 20 m transect line was placed randomly at 5 m (± 2 m). A minimum of 5 replicate transects were used at each site. *Acropora* species encountered within the 60 m^2 area belt transect were photographed. From these photographs the following details were recorded; the abundance of live and dead *Acropora* species, the number of individual *Acropora* displaying physical damage and the size of each individual coral was calculated using the scaled photographs.

2.4 Analysis

Basic statistics, graphs and tables were generated using Microsoft Office Excel (2007). Univariate analysis was entered into Minitab (version 14) and multivariate analysis was entered into Plymouth Routines In Multivariate Ecological Research (PRIMER) program (version 6).

2.4.1 Analysing substrate composition

The mean percentage cover for each substrate category was calculated from a minimum of 5 replicate transects in each of the 4 depth categories. Data was entered into PRIMER, square root transformed and a resemblance matrix was created using Bray-Curtis similarity. To test for differences in substrate compositions between depths at each site, and between depths across all sites, Analyses of Similarity (ANOSIMs) were performed. Pairwise tests were executed to identify at which depth and site comparisons cause differences in substrate composition. A SIMPER (Similarity Percentages) analysis was used to identify the key substrates responsible for dissimilarities and similarities between depths and sites.

2.4.2 Analysing coral recruitment

Coral recruitment abundance was recorded in 10 x 1 m^2 quadrats along the transect line, replicated a minimum of 5 times to produce an average abundance of recruits at each depth and at each survey site. The percentage composition of coral recruits within each family classification was calculated. Data was entered into PRIMER, square root transformed and a resemblance matrix was created using Bray-Curtis similarity. ANOSIMs were used to test for differences in the abundance of coral recruits between depths at each site, and between depths across all sites. Pairwise tests were performed to identify which depths and which site comparisons cause differences in coral recruitment abundance between each depth categories and at each site and between depths across all sites. A SIMPER analysis was used to identify the families responsible for the dissimilarity and similarity between depths and between sites. The diversity of coral recruits was calculated using Shannon Weiner diversity indices and evenness indices were calculated using Pielou's evenness index, both generated by PRIMER. Each data set was tested for normality and equal variance to meet the assumptions of Analysis of Variance (ANOVA). ANOVAs were used to analyse differences between coral diversity, evenness and richness between depths at each site, and between depths across all sites.

2.4.3 Analysing coral diversity

To analyse coral diversity photoquadrats were run through the CPCe program and converted into excel files. The percentage composition of corals belonging to each Order encountered was calculated. A Multi-Dimensional Scaling (MDS) plot was used to show the clustering based on the similarity between genera belonging to the class Anthozoa, in each depth category (1 m, 5 m, 12 m and 18 m) at each survey site. Using PRIMER diversity indices and richness was calculated for each depth category at each site. The data was square root transformed and was tested for equal variance to meet the assumptions of ANOVA. ANOVAs were performed to test for differences between depth and site, and Tukey's Pairwise Comparisons were performed to test for significant differences between depth and site comparisons.

The diversity, richness and evenness within the order Scleractinia was analysed further. Using PRIMER the Shannon-Weiner diversity indices, Pielou's evenness index and richness of Scleractinian genera was calculated for each depth category within every survey site. Data undertook square root transformation and was tested for equal variance to meet the assumptions of ANOVA. The indices were subjected to ANOVAs to test for differences between depths at each site and differences between depths across the survey sites. Tukey's Pairwise Comparisons tested for significant differences between sites and depths. SIMPER analysis was used to identify genera causing dissimilarities and similarities between depths at each site and between depths across all sites. Scleractinian genera identified as contributing to similarities between sites were used in further analysis and SIMPER analysis was used to assess which species were responsible for differences between depth at each site and between depths across all survey sites.

2.4.4 Analysing the abundance of Acropora species (>50 cm)

Acropora species (>50 cm) were recorded along 20 m transect line at 5 m (±2 m) and a minimum of 5 replicate transects were recorded to gain an average abundance of *Acropora* per 60 m^2. Each data set was tested for normality and equal variance to meet the assumptions of ANOVA. ANOVAs were used to test for differences between sites and the total abundance of *Acropora*, the abundance of live, dead and physically damaged *Acropora*. Tukey's Pairwise Comparisons were used to test for comparisons between depth categories and survey sites. Ratios between live and dead *Acropora* species encountered were calculated for each site.

3. RESULTS

3.1 Examining substrate composition of the coral reefs

3.1.1 Substrate composition

The substrate composition of the coral reefs was designated into one of the following eight categories; sand, coral rubble, live coral, recently dead coral, old dead coral, coralline and turf algae, soft coral and other. The percentage cover of each substrate category recorded at all sampling depths (1 m, 5 m, 12 m and 18 m) at each survey site (Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo) is presented in Figure 4. Figure 4 shows live coral cover contributes the highest percentage (42 ± 4.9%) to the overall substrate composition at each site; however variation between depths is apparent. The proportion of old dead coral was shown to be 23 ± 9.3 % on average across all depth categories at each site, however variation between depths and between sites is evident.

Recently dead coral contributes 8.5 ± 2.7 % on average across all depth categories at each site and is shown to be relatively uniform between depths. The proportion of old dead coral was shown to be 14 ± 8.5% on average more abundant than recently dead coral at each site. Coralline and turf algae were present at each depth at each site where cover ranged from 4.5-9%, excluding Undoodhoo and Funadhoo where percentage cover was 25.5% and 21% respectively at 1 m (Figures 4a and 4c respectively). Soft coral was not recorded at all sites and was shown to be highly variable with depth. The average proportion of soft coral ranged from 1-3.75%. Sand and rubble were recorded with great variation each depth and site, excluding Funadhoo, where neither sand or rubble were recorded at 5 m (Figure 4c).

3.1.2 Substrate composition between depths at each site

Significant variation in substrate composition between 1 m, 5 m, 12 m and 18 m at Undoodhoo (Global R=0.598, P= 0.001), Funadhoo (Global R=0.843, P= 0.001) and Gemendhoo (Global R= 0.247, P= 0.003) was shown. No significant difference in substrate composition across all depths at Hulhoodhoo was shown (Global R= 0.102, P= 0.122). A SIMPER analysis indicates live coral, old dead coral and sand are driving similarities between depths at Hulhoodhoo, contributing 29.3%, 17.1% and 16.5% to the average similarity between depth categories.

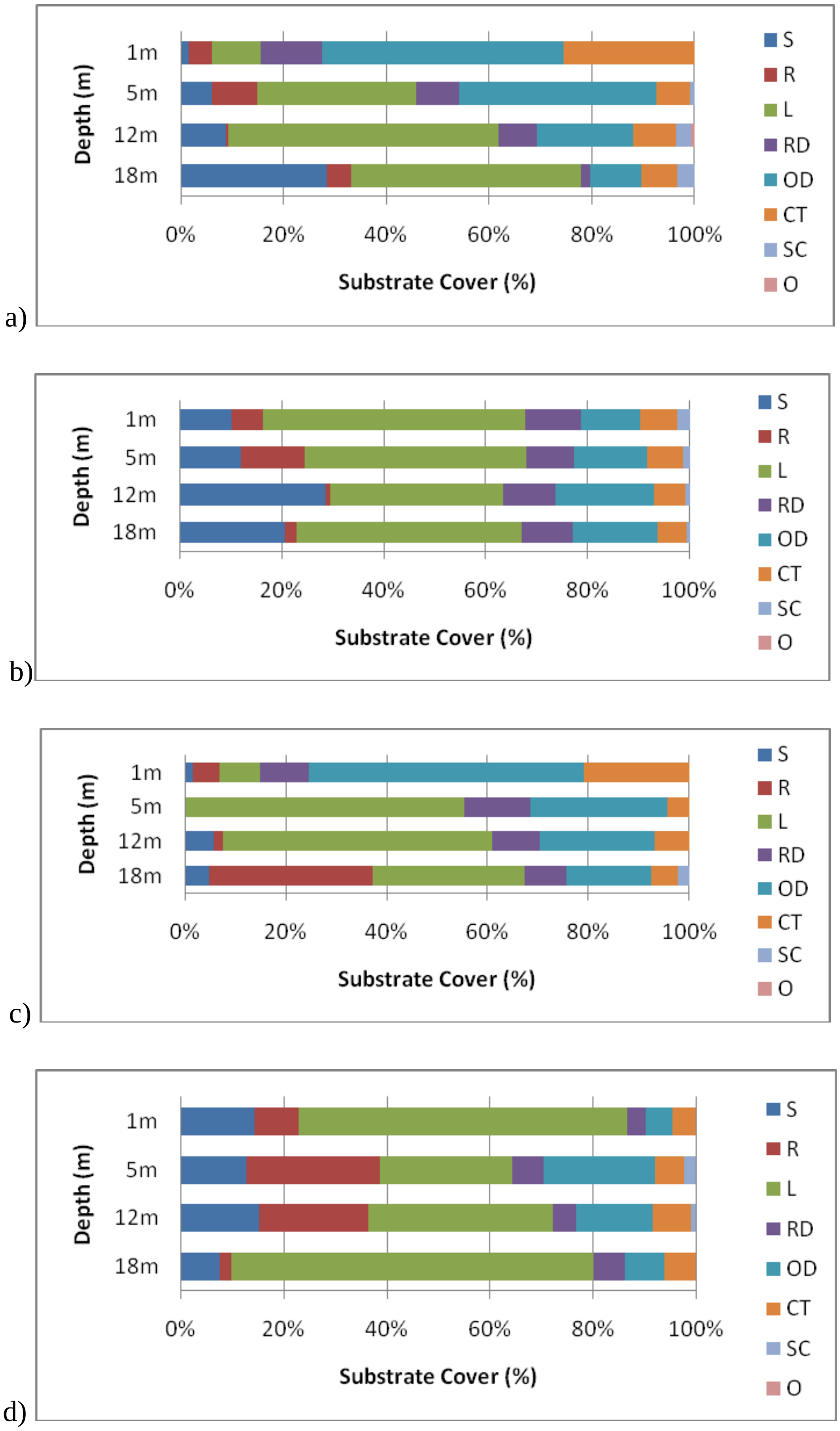


Figure 4: Mean percentage cover of sand (S), coral rubble (R), live coral (L), recently dead coral (RD), old dead coral (OD), coralline and turf algae (CT), soft coral (SC) and other (O), across all depth categories (1 m, 5 m, 12 m and 18 m) at Undoodhoo (Fig.4a), Hulhoodoo (Fig.4b), Funadhoo (Fig.4c) and Gemendhoo reefs (Fig.4d), Baa Atoll.

Table 1 presents the results from pairwise comparisons of substrate composition between depths at Undoodhoo, Funadhoo and Gemendhoo. No distinctive pattern in substrate composition between Undoodhoo, Funadhoo and Gemendhoo is shown and therefore variation in composition between depths is specific to each site. Table 1a shows the substrate composition at 12 m and 18 m is not significantly different at Undoodhoo, however, all other comparisons between depths indicate significant differences. At Funadhoo, a significant difference in substrate composition between all depths is shown (Table 1b). At Gemendhoo, substrate composition at 1 m is significantly different in comparison to all other depth categories (Table 1c).

Table 1: R values from pairwise comparisons of substrate composition between depths (1 m, 5 m, 12 m and 18 m) at Undoodhoo (Table 1a), Funadhoo (Table 1b) and Gemendhoo reefs (Table 1c), Baa Atoll (* indicates significance at the 5% level).

a)

	18 m	12 m	5 m
1 m	1.000*	0.772*	0.484*
5 m	0.563*	0.332*	
12 m	0.25		

b)

	18 m	12 m	5 m
1 m	0.988*	0.960*	0.992*
5 m	0.963*	0.660*	
12 m	0.719*		

c)

	18 m	12 m	5 m
1 m	0.431*	0.288*	0.536*
5 m	0.094	0.028	
12 m	0.1		

3.1.3 Substrate composition at each depth between survey sites

Substrate composition at each depth between sites showed significant differences at depths of 1 m (Global R=0.718, P=0.001), 5 m (Global R=0.435, P=0.001) and 18 m (Global R=0.334, P=0.04). No significant difference in the substrate composition at 12 m between each site was shown (Global R= 0.106, P= 9.30). A SIMPER analysis indicated that live coral, old dead coral and sand are the substrate categories driving the similarities in substrate composition between all sites at 12 m. Individually, live coral, old dead coral and sand contribute 31.3%, 21.3% and 14.5% respectively to the average similarity between all four survey sites at 12 m.

Table 2 presents the results from pairwise comparisons of the substrate composition at each depth category between each survey site. Table 2a shows the substrate composition at 1 m is significantly different at Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo. Table 2b and 2c show no significant difference between the substrate composition recorded at 5 m and 18 m at Hulhoodoo in comparison to the composition recorded at Gemendhoo and Undoodhoo.

Table 2: R values from pairwise comparisons between substrate composition recorded at 1 m (a), 5 m (b), 18 m (c) between Undoodhoo (U), Hulhoodhoo (H), Funadhoo (F) and Gemendhoo (G) reefs, Baa Atoll (*indicates significance at 5% level).

a)

	U	H	F
H	1*		
F	0.564*	1*	
G	1*	1*	0.484*

b)

	U	H	F
H	0.204		
F	0.672*	0.744*	
G	0.144*	0.048	0.736*

c)

	U	H	F
H	0.156		
F	0.583*	0.354*	
G	0.438	0.156	0.469*

3.2 Examining the abundance and diversity of coral recruitment

3.2.1 Abundance of coral recruitment

Coral recruitment was recorded at 5 m, 12 m and 18 m at Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo. Table 3 shows the mean abundance of coral recruits which indicates variation between sampling depths and survey sites. The greatest total abundance of recruits across all depths was recorded at Undoodhoo, which has approximately 100% more coral recruits per 1 m^2 in comparison to Hulhoodhoo and Funadhoo and 70% more recruits than Gemendhoo. In comparison to all other survey sites, the greatest mean abundance of recruits is shown at 12 m and 18 m at Undoodhoo (12.1 ± 1.8 and 10.7 ± 2.4 per 1 m^2 respectively).

Table 3: Mean abundance (with associated standard deviations) of coral recruits (individual isolate corals less than 5cm in diameter) per 1 m^2 at 5 m, 12 m and 18 m recorded at Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo reefs, Baa Atoll.

Depth (m)	Undoodhoo	Hulhoodhoo	Funadhoo	Gemendhoo
5	6.35 ± 1.3	5.6 ± 0.9	4.6 ± 0.9	6.8 ± 1.4
12	12.1 ± 1.8	6.4 ± 0.9	5.1 ± 1.1	3.2 ± 0.9
18	10.7 ± 2.4	3.9 ± 0.7	2.5 ± 0.8	6.4 ± 1.4
Total	29.2 ± 2.9	15.9 ± 1.3	13.9 ± 0.6	18.6 ± 1.2

3.2.2 Assessing the composition of coral recruitment community

Coral recruits were classified to seven families from the order Scleractinaria (Pocilloporidae, Poritidae, Fungiidae, Faviidae, Dendrophylliidae, Agariciidae and Acroporidae) and the class Demospongiae. Figure 5(a-d) shows the proportion that each family contributed to composition of coral recruits at each depth at each survey site. At Undoodhoo and Hulhoodhoo, Poritidae, Agariciidae and Demospongiae were recorded, however at Funadhoo and Gemendhoo these families were absent. At Undoodhoo, Acroporidae and Faviidae collectively represent 90.23% of the total composition at 5 m, however these families become less dominant at 12 m and 18 m (14.8% and 25.7% respectively) (Figure 5a). The proportion of Dendrophylliidae increases at 12 m and 18 m and contributes 40.9% and 63.9% respectively, of the total abundance of coral recruits at Undoodhoo.

Faviidae and Acroporidae cumulatively occupy 81.3% and 69.8% of the total abundance at 5 m and 12 m at Hulhoodhoo (Figure 5b). However at 18 m, Agariciidae and Dendrophylliidae represent 30.6% and 47.4% of the total abundance of recruits at Hulhoodhoo. Acroporidae represents 58.4%, 52.8% and 34.2% of the total recruitment abundance at 5 m, 12 m and 18 m respectively at Funadhoo (Figure 5c). Faviidae similarly represents a large proportion of the total abundance of recruits, contributing 25.7%, 40.6%

and 52.5% respectively to the recruitment composition at Funadhoo. Acroporidae and Faviidae cumulatively represent over 88.1 ± 4.9%. Dendrophylliidae, however, represents 4.2%, a comparably small proportion at 18 m at Funadhoo in comparison to other sites. At Gemendhoo, Acroporidae is found in low abundance (8%) at 5 m in comparisons to all other survey sites. Dendrophylliidae occupies over 43 ± 0.6% of the abundance of recruits at 5 m and at 18 m, however this family is present in low proportions (8.2%) at 12 m (Figure 5d). Demospongiae was not recorded at either Funadhoo or Gemendhoo, however, at Undoodhoo and Hulhoodhoo Demospongiae is present and comprises 16.6% and 14.8% of the coral recruitment composition at 12 m and 18 m.

3.2.3 Abundance of coral recruitment between sites

The abundance of coral recruitment at each site was shown to be significantly different (Global R =0.653 P=0.001). Pairwise comparisons indicate variation in the abundance of recruits between all survey sites (Table 4). A SIMPER analysis showed the dissimilarity between the abundance of coral recruitment at Gemendhoo in comparison to all remaining survey sites was driven by the families Dendrophylliidae, Faviidae and Acroporidae which collectively contribute over 80% to the dissimilarity between these sites. Similarly, a comparison between recruitment abundance at Undoodhoo with recruitment abundance at Hulhoodhoo and Funadhoo highlighted Dendrophylliidae and Demospongiae as the two main families collectively contributing over 65% to the dissimilarity between these comparisons.

Table 4: Pairwise comparisons between the abundance of coral recruits recorded at Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo reefs, Baa Atoll (* indicates significance at 5% level).

	Undoodhoo	Hulhoodoo	Funadhoo
Gemendhoo	0.860*	0.865*	0.544*
Funadhoo	0.794*	0.553*	
Hulhoodhoo	0.421*		

3.2.4 Abundance of coral recruitment between depths at each site

ANOSIMs were performed to test for differences between depths at each survey site independently. The abundance of coral recruits between 5 m, 12 m and 18 m was shown to be significantly different at Undoodhoo (Global R=0.689, P=0.002), Hulhoodhoo (Global R=0.802, P=0.001), Funadhoo (Global R=0.211, P=0.017) and Gemendhoo (Global R=0.449, P=0.003). Pairwise comparisons between abundance of recruits at Undoodhoo (Table 5a) and Hulhoodoo (Table 5b) indicated significant differences between 5 m, 12 m and 18 m. At Funadhoo, comparisons indicated a significant difference between the abundance of recruits at 5 m and 12 m and no significant difference between other depth comparisons (Table 5c). At Gemendhoo, no significant difference between the abundance of recruits at 5 m and 18 m is shown (Table 5d), however, significant differences between all other comparisons between depths is indicated. SIMPER analyses indicate the abundance of Dendrophylliidae, Demospongiae and Acroporidae recruits collectively contribute an average of 61.35 ± 3.4 % to the dissimilarity when comparing recruitment between each depth category.

Table 5: Pairwise comparisons between the abundance of coral recruits recorded at 5 m, 12 m and 18 m at Undoodhoo (a), Hulhoodhoo (b), Funadhoo (c) and Gemendhoo (d) reefs, Baa Atoll (*indicates significance at 5% level).

a)

	12 m	18 m
5 m	0.736*	1.00*
18 m	0.236*	

b)

	12 m	18 m
5 m	0.844*	1.00*
18 m	0.648*	

c)

	12 m	18 m
5 m	0.168*	0.248
18 m	0.196	

d)

	12 m	18 m
5 m	0.808*	-0.16
18 m	0.760*	

3.2.5 Diversity of coral recruitment

Diversity of coral recruits at 5 m, 12 m and 18 m at each station was calculated using the Shannon-Weiner diversity indices. The equitability is expressed as Pielou's evenness index which represents the variation the coral recruitment community. Richness was also calculated as the total number of families present at each station. Table 6 displays the results of these calculations found at each depth at every survey site.

Richness of coral recruitment composition ranged from 4 to 6 families across all sites (Table 6). Pielou's evenness indices were high across the majority of stations indicating low variation within the coral recruitment community. A significant difference in Pielou's evenness indices between Undoodhoo and Hulhoodhoo was indicated (Table 7). Shannon Weiner diversity indices ranged from 1.036 at Gemendhoo to 1.576 at Hulhoodoo, however little variation between depths at each station is shown (Table 6). No significant difference between the diversity of coral recruits between depths 5 m, 12 m and 18 m at Undoodhoo (df=2, F= 1.981, P= 0.180), Hulhoodhoo (df 2, F= 3.455, P= 0.065), Funadhoo (df=2, F=1.931, P=0.187) and Gemendhoo (df=2, F= 0.565, P=0.583) was shown. A significant difference in the diversity of coral recruits between sites is shown (df=3, F=10.51, P=0.004), however only diversity at Hulhoodhoo differs significantly when compared to recruitment at Funadhoo and Gemendhoo (Table 8).

Table 6: Richness (R), Pielou's evenness index (J') and Shannon-Weiner diversity indices (H'(loge)) of coral recruits at 5 m, 12 m, 18 m recorded within a 20m^2 area at Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo reefs, Baa Atoll.

Site	Depth	R	J'	H'(loge)
Undoodhoo	5	5	0.885	1.211
	12	5	0.900	1.290
	18	5	0.877	1.373
Hulhoodhoo	5	6	0.923	1.395
	12	6	0.937	1.576
	18	6	0.943	1.551
Funadhoo	5	4	0.929	1.123
	12	5	0.883	1.214
	18	6	0.926	1.344
Gemendhoo	5	4	0.930	1.125
	12	5	0.923	1.031
	18	4	0.912	1.155

Table 7: Tukey's Pairwise Comparison between the Pielou's evenness indices of coral recruitment at the classification level of Family between Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo reefs, Baa Atoll (*indicates significant at 5% level).

	Undoodhoo	Hulhoodoo	Funadhoo
Gemendhoo	2.640	-0.986	0.675
Funadhoo	1.965	-1.610	
Hulhoodhoo	3.626*		

Table 8: Tukey's Pairwise Comparison between the Shannon Weiner diversity indices of coral recruitment at the classification level of Family between Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo reefs, Baa Atoll (*indicates significant at 5% level).

	Undoodhoo	Hulhoodoo	Funadhoo
Gemendhoo	-2.547	-5.475*	-1.675
Funadhoo	-0.873	-3.800*	
Hulhoodhoo	2.928		

3.3 Examining coral diversity

3.3.1 Composition of corals within the class Anthozoa

Corals belonging to the orders Alcyonacea, Zoantharia, Actinaria, Anthipatharia, Corallimorpharia and Scleractinaria were recorded in varying abundance at Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo (Figure 6). Within the order Scleractinia 14 families were recorded from which 35 genera were identified. On average the order Scleractinia occupied 87.2 ± 7.2% of the total abundance of corals recorded between the four survey sites. Corals belonging to the order Alcyonacea were identified to 4 families, each family consisting of 1 genus of coral. Alcyonacea represented an average of 5.8 ± 1.5% at all survey sites. Actinaria (Stichodactyla species) and Zoanthidea (Palythoa species) are absent from all survey sites except Funadhoo, where they represent less than 1% of the total abundance of corals. Anthipatharia is present at all sites represent an average of 2.4 ± 1.4% of the total abundance. At Funadhoo, 17.1% of the abundance belongs to the order Corallimorpharia, whereas at all other sites the Corallimorpharia have an abundance of less than 1%.

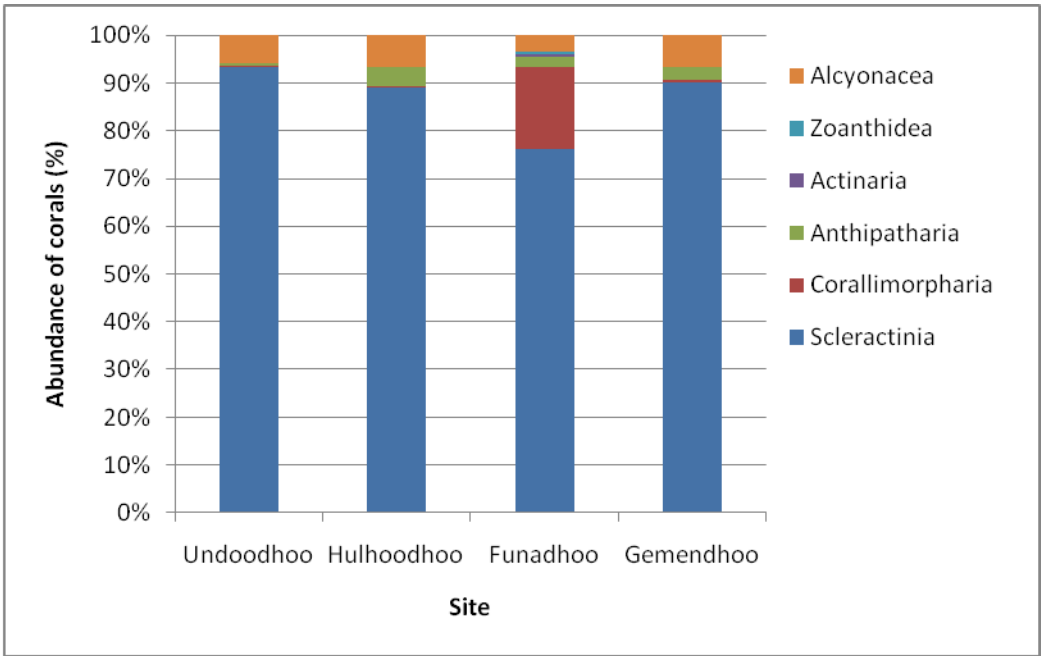


Figure 6: Percentage composition of corals (%) within the orders Alcyonacea, Zoantharia, Actinaria, Anthipatharia, Corallimorpharia and Scleractinaria recorded at 1 m, 5 m, 12 m and 18 m at Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo reefs, Baa Atoll.

3.3.2 Diversity within the class Anthozoa

An MDS plot showed the clustering based on the similarity between genera belonging to the class Anthozoa, in each depth category (1 m, 5 m, 12 m and 18 m) at each survey site (Figure 7). Two distinctive groups are formed at a 60% similarity showing likeness between Anthozoa recorded at Undoodhoo and Gemendhoo at 5 m, 12 m and 18 m. The MDS plot indicates similarities between genera within the 1 m depth categories across all sites. The stress level on the MDS plot is low (0.15), which allows the assumption that the 2-D plot is an accurate representation of the relationship between corals within the class Anthozoa within each depth category at each survey site.

The diversity within the class Anthozoa is represented by Shannon-Weiner diversity indices at each depth at each survey site which is displayed in Figure 8. Diversity at 1 m is lower than diversity shown at 5 m, 12 m and 18 m. No significant difference in diversity between sites were shown (df=3, F=1.00, P=0.26), however a highly significant difference in diversity between depths is shown (df=3, F=7.90, P=0.004). Pairwise comparisons show diversity of corals at 1 m differs significantly from that at 5 m, 12 m and 18 m (Table 9).

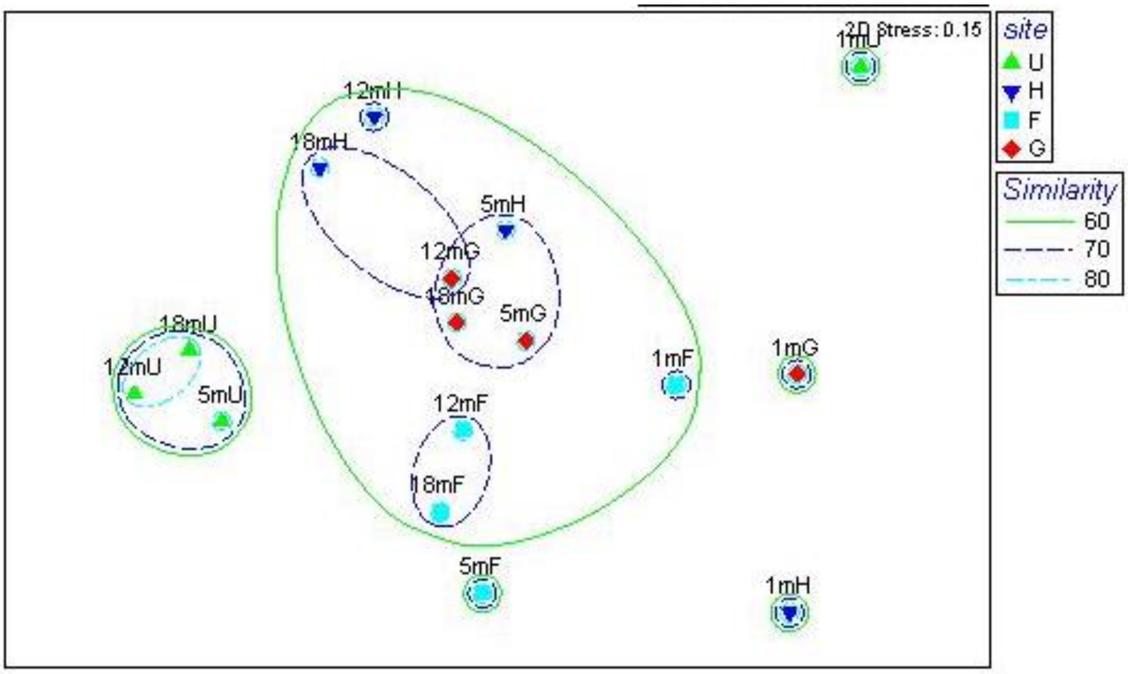


Figure 7: Two dimensional MDS ordination plot representing the similarity of corals within the class Anthozoa at different 1 m, 5 m, 12 and 18 m at Undoodhoo (U), Hulhoodhoo (H), Funadhoo (F), Gemendhoo (G) reefs, Baa Atoll (2D Stress = 0.15).

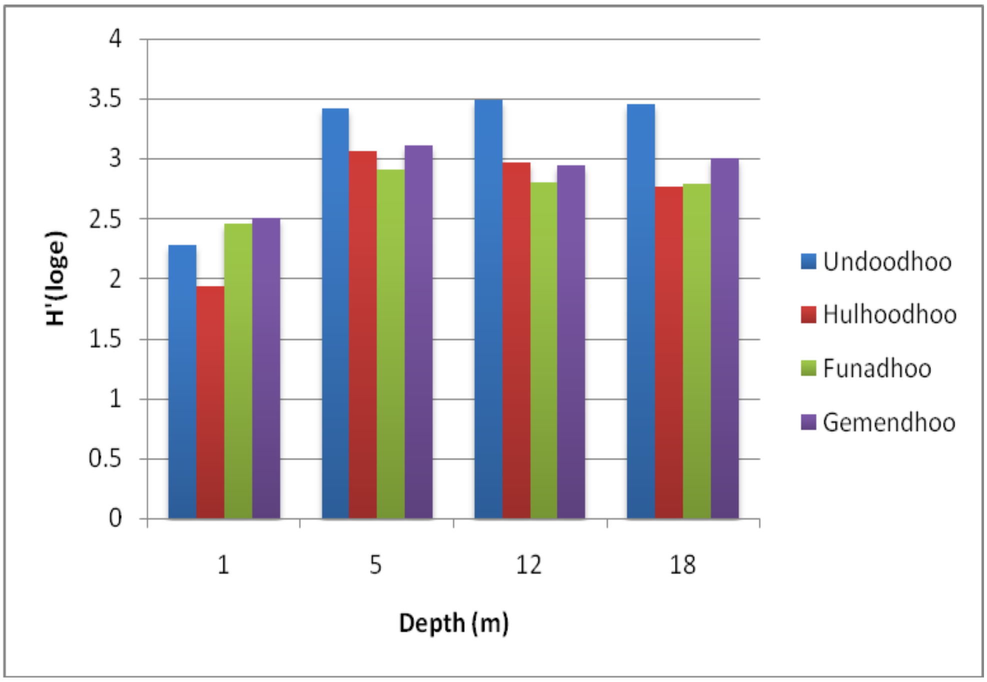


Figure 8: Shannon-Weiner diversity indices (H'(loge)) for the class Anthozoa recorded at 1 m, 5 m, 12 m and 18 m at Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo reefs, Baa Atoll.

Table 9: T-values from Tukey's pairwise comparisons of diversity between depths of 1 m, 5 m, 12 m and 18 m at Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo reefs, Baa Atoll (*indicates significance at 5% level).

5 m	4.28*		
12 m	3.89*	0.39	
18 m	3.65*	0.63	0.24
	1 m	5 m	12 m

3.3.3 Richness of corals within the class Anthozoa

The total number of genera recorded within each depth category at each survey site is displayed in Table 10. Richness is shown to increase from 1 m to 5 m by over 90% at all survey sites. At 5 m, richness is shown to be the highest in comparison to that found at 12 m and 18 m. Richness between 12 m and 18 m shows little variability between depths. At 5 m, 12 m and 18 m richness is shown to be the greatest at Undoodhoo in comparison to all remaining survey sites. However, no significant difference in richness between survey sites or depth is indicated (df= 3, F= 4.57, P= 0.023).

Table 10: Richness of corals within the class Anthozoa at 1 m, 5 m, 12 m and 18 m recorded at Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo reefs, Baa Atoll.

Depth	Undoodhoo	Hulhoodhoo	Funadhoo	Gemendhoo
1 m	10	8	13	13
5 m	37	24	23	26
12 m	34	22	18	20
18 m	35	18	18	21

3.3.4 Diversity within the Order Scleractinia

Further analysis into the order Scleractinia was performed as the group occupied the greatest average proportion (87.2 ± 7.2%) within the class Anthozoa. Scleractinian corals were classified to genus and the mean abundance was used to calculate richness, diversity and evenness of the coral community. Diversity within the Scleractinian coral community at 1 m, 5 m, 12 m and 18 m at each site was calculated using the Shannon-Weiner diversity indices. The equitability is expressed as Pielou's evenness index which represents the variation within the coral community. Richness was also calculated as the total number of genera recorded at 1 m, 5 m, 12 m and 18 m at all survey sites.

3.3.5 Richness of coral within the order Scleractinia

Figure 9 indicates little variation in the richness of coral genera at 1 m between sites, which ranged from 6 to 12 genera. At 5 m, 12 m and 18 m little variation is shown in richness of the coral community between Hulhoodhoo, Funadhoo and Gemendhoo ranging from 12 to 21 genera. Richness at Undoodhoo, however, is approximately 100% more at 5 m, 12 m and 18 m in comparison to the other survey sites, which ranged from 30 to 34 genera. A highly significant difference between the richness of the coral community between depths (df= 3, F=12.38, P= <0.001) and sites (df=3, F= 19.51, P=<0.001) was shown. Table 11a shows pairwise comparisons which identified a significant difference between the richness found at 1 m in comparison to that found at 5 m, 12 m and 18 m, however, no significant difference between 5 m, 12 m and 18 m was indicated. Table 11b shows the richness of coral genera at Undoodhoo differed significantly in comparison to all other sites, and no significant difference between Hulhoodhoo, Funadhoo and Gemendhoo was identified.

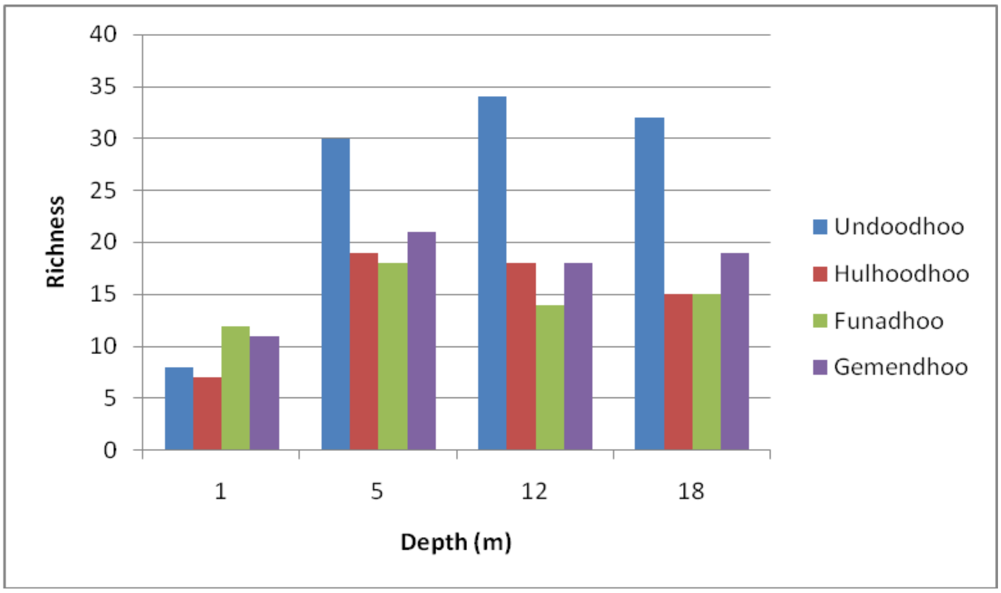


Figure 9: Mean richness of Scleractinian corals (total number of genera) recorded at 1 m, 5 m, 12 m and 18 m at Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo reefs, Baa Atoll.

Table 11: T-values from Tukey's pairwise comparisons of richness of Scleractinian corals between 1 m, 5 m, 12 m and 18 m (Table 11a) and between Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo reefs, Baa Atoll (Table 11b) (*indicates significance at 5% level).

a)

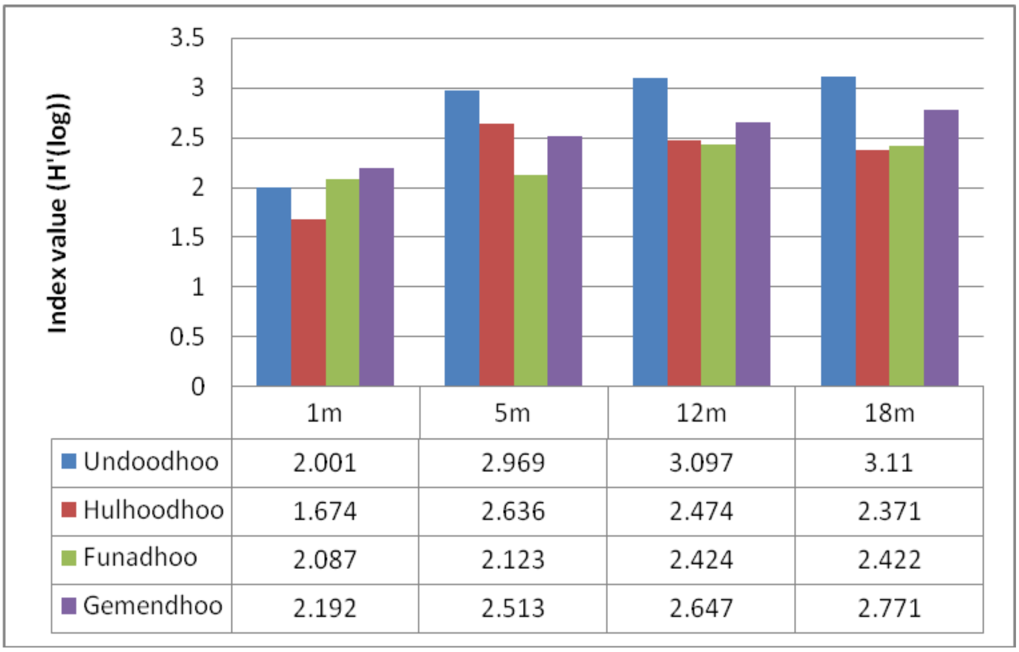
5 m	5.306*		
12 m	5.062*	-0.2594	
18 m	4.939*	-0.389	-0.1297
	1 m	5 m	12 m

b)

Hulhoodhoo	6.431*		
Funadhoo	6.751*	-0.3201	
Gemendhoo	4.976*	1.4549	1.775
	Undoodhoo	Hulhoodhoo	Funadhoo

3.3.6 Diversity of coral within the Order Scleractinia

Figure 10 indicates little variation in Shannon Weiner diversity indices at 1 m, 5 m, 12 m and 18 m at each survey site. The lowest Shannon Weiner diversity index was shown at 1 m at all survey sites ranging from 1.67 at Hulhoodhoo to 2.19 at Gemendhoo. Undoodhoo has the highest diversity index of corals at 5 m (2.97), 12 m (3.1) and 18 m (3.1). Figure 10 indicates an increase in diversity from 1 m to 18 m at Undoodhoo and Gemendhoo, whereas diversity at Hulhoodhoo peaks at 5 m and declines at 12 m and 18 m. Shannon Weiner diversity indices at Funadhoo show little variation between all depths. A significant difference between diversity of coral genera between depths (df=3, f=16.43, p=<0.001) and between sites (df=3, f=12.38, p=<0.001) was shown. Table 12a indicates that diversity at 1 m is significantly different from diversity at other depths. Table 12b shows diversity at Undoodhoo is significantly different from diversity at Hulhoodhoo, Funadhoo and Gemendhoo.



	1m	5m	12m	18m
🟦 Undoodhoo	2.001	2.969	3.097	3.11
🟥 Hulhoodhoo	1.674	2.636	2.474	2.371
🟩 Funadhoo	2.087	2.123	2.424	2.422
🟪 Gemendhoo	2.192	2.513	2.647	2.771

Figure 10: Shannon-Weiner diversity indices (H'(loge)) for Scleractinian corals recorded at 1 m, 5 m 12 m and 18 m depth categories at Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo reefs, Baa Atoll.

Table 12: T-values from Tukey's pairwise comparisons of diversity between 1 m, 5 m, 12 m and 18 m (Table 12a) and between Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo reefs, Baa Atoll (Table 12b)(*indicates significance at 5% level).

a)

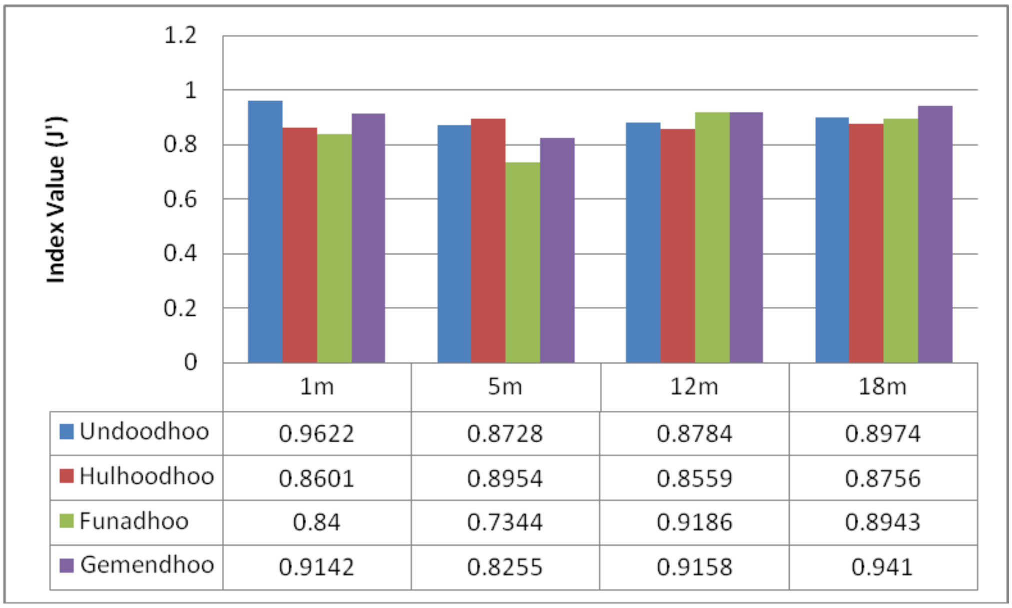
	1 m	5 m	12 m
5 m	4.995*		
12 m	6.074*	1.145	
18 m	6.232*	1.312	0.1674

b)

	Undoodhoo	Hulhoodhoo	Funadhoo
Hulhoodhoo	4.969*		
Funadhoo	5.502*	-0.5324	
Gemendhoo	3.039*	1.9298	2.462

3.3.7 Evenness of coral within the Order Scleractinia

Figure 11 shows the Pielou's evenness index for the coral community at each depth at every survey site. Little variation is indicated between depth and between sites. Pielou's evenness indices do not differ significantly between depths (df=3, F= 6.72, P= 0.09) or between sites (df=3, F=3.47, P=0.21) therefore indicating similar variation within the Scleractinian coral community.



	1m	5m	12m	18m
🟦 Undoodhoo	0.9622	0.8728	0.8784	0.8974
🟥 Hulhoodhoo	0.8601	0.8954	0.8559	0.8756
🟩 Funadhoo	0.84	0.7344	0.9186	0.8943
🟪 Gemendhoo	0.9142	0.8255	0.9158	0.941

Figure 11: Pielou's evenness indices for the community of Scleractinian corals recorded at 1 m, 5 m, 12 m and 18 m at Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo reefs, Baa Atoll.

3.3.8 Diversity of Scleractinian coral at 1m in comparison to 5m, 12m and 18m

As diversity within the order Scleractinia was shown to differ significantly between 1 m in comparison to all other depth categories (5 m, 12 m, 18 m) a SIMPER analysis was performed to assess the genera contributing to the dissimilarity between these depths. Table 13 indicates 13 genera which cumulatively contributed over 50% to the total dissimilarity at 1 m in comparison to 5 m, 12 m and 18 m. *Tubastrea* is absent at 1 m, however it is present at 5 m, 12 m and 18 m which causes the major dissimilarity between depths and therefore contributes the highest total percentage of dissimilarity at 5 m, 12 m and 18 m. *Diploastrea* is absent at 1 m yet is present at 12 m which increases the dissimilarity between these two depths. *Acropora*, *Montipora*, *Pavona*, *Pocillopora*, *Stylophora* and *Tubastrea* are 6 main genera which contribute over 15% to the total dissimilarity genera recorded at 1 m in comparison to those recorded within the 5 m, 12 m and 18 m depth categories. The highest abundance of corals recorded at 1 m were *Acropora* and *Pocillopora*, and in comparison at 5 m, 12 m and 18 m, there are fewer of these genera on average which contributes to the dissimilarity between depths.

Table 13: SIMPER analysis to assess the genera contributing to the dissimilarity between Scleractinian coral at 1 m in comparison to 5 m, 12 m and 18 m across Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo reefs, Baa Atoll (*indicates zero abundance).

	1 m	5 m		12 m		18 m		Total
Genus	Abun	Abun	Contrib	Abun	Contrib	Abun	Contrib	Contrib
Acropora	7.3	6.7	4.6	6	4.4	4.5	6.4	15.4
Diploastrea	0	*	*	2.3	4.1	*	*	4.1
Favites	2.9	*	*	*	*	4	4.9	4.9
Goniastrea	1.9	*	*	3	4.2	3	4.1	8.3
Montipora	1.9	2.5	6.8	1.4	5	1.5	5.1	16.8
Pachyseris	2	2.6	4.8	*	*	3.4	4.7	9.5
Pavona	1.4	1.9	5.3	1.9	4.7	3	6	16
Platygyra	2.7	1.4	4.6	*	*	*	*	4.6
Pocillopora	7	5	5	3.6	6.7	3.7	7.1	18.8
Seriatopora	1	2.2	4.6	2.5	4.6	*	*	9.2
Siderastrea	2	1.2	5.7	0.6	4.3	*	*	9.9
Stylophora	3.2	2.2	4.8	1.3	5.2	0.8	5.9	15.8
Tubastrea	0	2.1	4.9	3.9	7.7	4.5	9.2	21.7
Total	33.2	27.6	51	26.5	50.8	28.4	53.3	

3.3.9 Similarities between Scleractinian genera at 5 m, 12 m and 18 m

As there are no significant differences in diversity between 5 m, 12 m and 18 m further analyses was performed to assess the similarities between these depths. A SIMPER analysis indicated 11 genera which contributed to the similarity between coral composition at 5 m, 12 m and 18 m. Table 14 shows the average abundance of the genera and the percentage the genera contribute to the overall similarity within each depth group. SIMPER analysis showed *Goniastrea* (7.05%) contributes towards the similarity between all sites at 5 m, similarly *Pachyseris* (8.75%) contributes towards the similarity between all sites at 18 m. However, *Goniastrea* and *Pachyseris* do not contribute to the overall similarity between 5 m, 12 m and 18 m. Genera contributing a high total percentage similarity at each depth (across all sites) are *Acropora* (38.65%), Porites (32.8%), *Pocillopora* (28.13%), Favites (25.61%), *Tubastrea* (24.77%). These genera, therefore, drive similarities between 5 m, 12 m and 18 m at each site and further analysis was performed to determine any differences between species driving these similarities.

Table 14: Shows the average abundance (Av.Abun) of genera recorded and the percentage each genera contributes (Contrib %) to the similarity within the 5 m, 12 m and 18 m depth groups across all sites, Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo, Baa Atoll (* indicates no value).

Genera	5 m		12 m		18 m		Total
	Av.Abun	Contri%	Av.Abun	Contrib%	Av.Abund	Contrib%	
Acropora	6.66	14.78	5.97	14.6	4.53	9.27	38.65
Pocillopora	4.95	10.95	3.64	9.34	*	*	20.29
Porites	4.78	10.74	4.21	9.73	5.02	12.33	32.8
Favites	4.03	9.35	3.41	8.19	4.03	8.07	25.61
Goniastrea	2.99	7.05	*	*	*	*	7.05
Tubastrea	*	*	3.9	8.41	4.51	11	19.41
Pachyseris	*	*	*	*	3.44	8.75	8.75

3.3.10 Similarity between Scleractinian coral at 5 m, 12 m and 18 m at species level

SIMPER analysis indicated 8 species contributing to the similarity in coral diversity at 5 m, 12 m and 18 m between each survey site. Species typifying the coral reef at 5 m are *Tubastrea micranthus, Porites lobata* and *Favites abdit*a. *Tubastrea micranthus*, *Porites lobata* and *Favites abdita* are, therefore, the 3 key species which control the similarity between Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo at 5 m. Species characterising the coral reef at 12 m are *Acropora formosa, Pocillopora damicornis, Acropora digitifera, Porites lobata* and *Favites abdita,* they are, therefore, key species which control the similarity between the survey sites at 12 m. At 18 m, *Favites adbita*, *Porites lobata*, *Pocillopora damicornis* and *Acropora formosa* typify the coral reef at this depth, and are therefore key species which cause similarities between sites.

3.3.11 Similarities between Scleractinian coral at each site at the species level

Table 15 shows the species driving the similarities between depths at each site, and therefore, are the species characterising each site. At Undoodhoo, *Pocillopora damicornis* and *Acropora formosa* contribute cumulatively 41.67% of the total similarity across all depths. At Hulhoodoo, *Tubastrea micranthus* and *Porites lobata* contribute 47.3% of the total similarity across all depths. At Funadhoo and Gemendhoo, *Favites abdita* and *Acropora digitifera* contribute a consistently high percentage to the similarity across all depths.

Table 15: The average abundance and percentage contribution of species driving the similarities between each depth within Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo reefs, Baa Atoll.

Site	Species	Average Abundance	Contribution (%)
Undoodhoo	*Pocillopora damicornis*	11.73	21.90
	Acropora formosa	9.67	19.77
	Porites lobata	12.40	12.89
	Pocillopora verrucosa	6.07	10.94
Hulhoodhoo	*Tubastrea micranthus*	19.87	27.51
	Porites lobata	18.87	19.80
	Favites complanata	11.43	13.35
	Favites abdita	10.40	11.2
Funadhoo	*Favites abdita*	22.13	16.41
	Acropora digitifera	15.80	14.95
	Pocillopora damicornis	17.67	12.29
Gemendhoo	*Acropora formosa*	33.07	23.26
	Favites abdita	15.20	11.92
	Acropora digitifera	16.53	11.47

3.3.11 Abundance of Corallimorpharia

Corallimorphs belonging to the genus *Discosoma* were found in low abundance at all depths at Undoodhoo, Hulhoodhoo and Gemendhoo. At Funadhoo, within the 5 m depth category, 82 ± 2.3% of corals was dominated by *Discosoma* species. In comparison, the proportion of *Discosoma* species at all other depths and sites ranged from 0-4.9 %. Figures 12a and 12b show images of *Discosoma* species dominating the substrate at Funadhoo (at 5 m) forming a thick mat over the coral pavement. Figures 12c and 12d show *Discosoma* species present in degraded areas covering large boulders of old dead coral and pieces of large coral rubble.

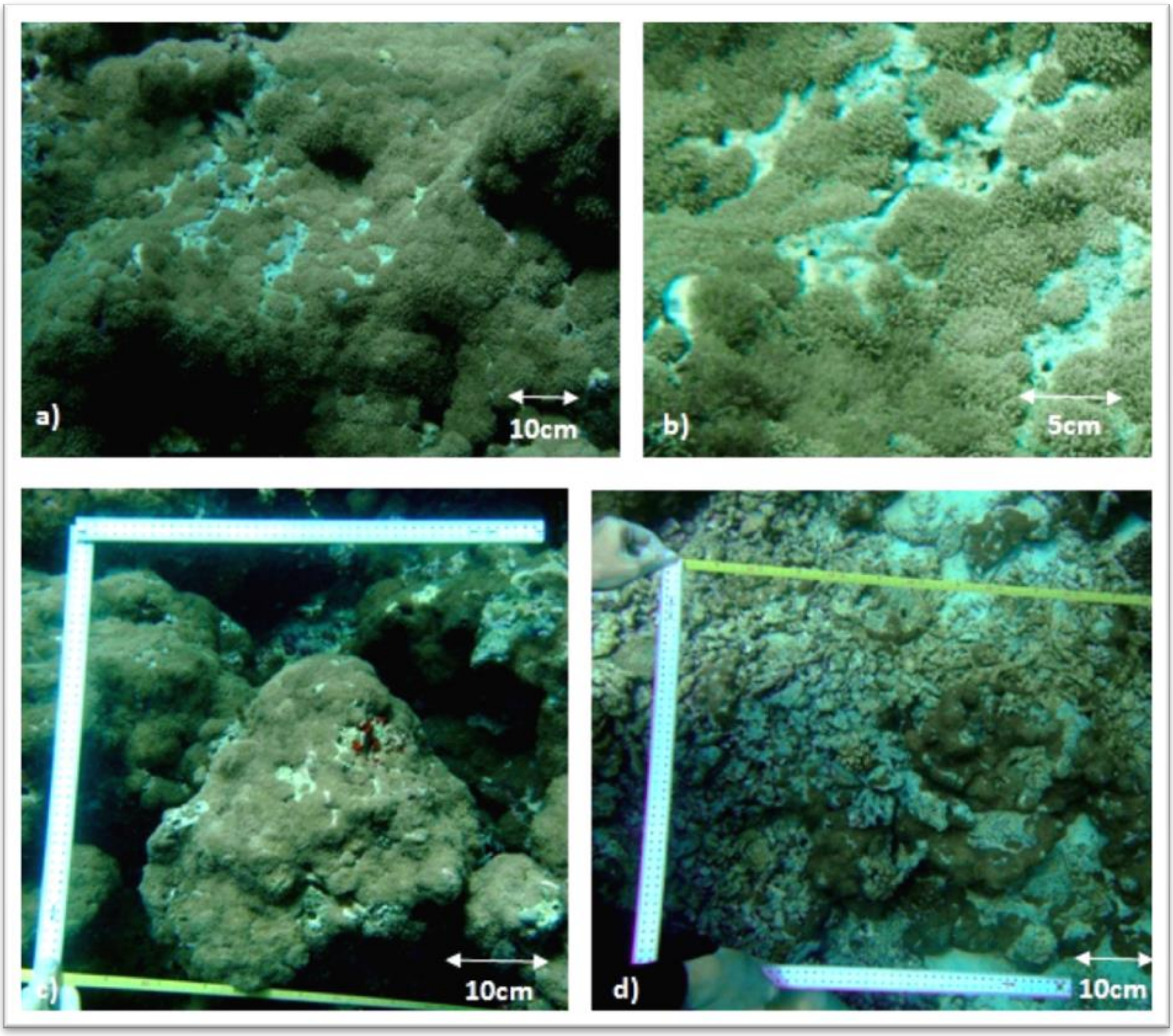


Figure 12: Photographs of *Discosoma* species found along a replicate transect at 5 m at Funadhoo covering large areas of coral pavement (a), found in dense aggregations (b), covering large boulders of stable old dead coral (c) and colonising areas of coral rubble (d).

3.4 Examining *Acropora* species greater than 50 cm in diameter

3.4.1 Abundance of Acropora *corals (>50 cm)*

The abundance of *Acropora* corals greater than 50 cm in diameter was recorded at 5 m (± 2m), the results of which are displayed in Figure 13. The greatest mean abundance of *Acropora* species was recorded at Funadhoo with 39.5 ± 2.9 individuals per 60m^2. The lowest abundance of *Acropora* was recorded at Undoodhoo with a mean abundance of 21 ± 4.5 individual corals per 60m^2, an approximate decrease of 50% in comparison to the abundance at Funadhoo. A highly significant difference (df=3, F=24.51, P= <0.001) in abundance of *Acropora* species (>50 cm) between survey sites is shown. Table 16 shows the results from a pairwise comparison between all survey sites which indicates the abundance of *Acropora* corals at Funadhoo is significantly different to the abundance at all remaining sites; however, there are no significant differences in comparisons between all other sites.

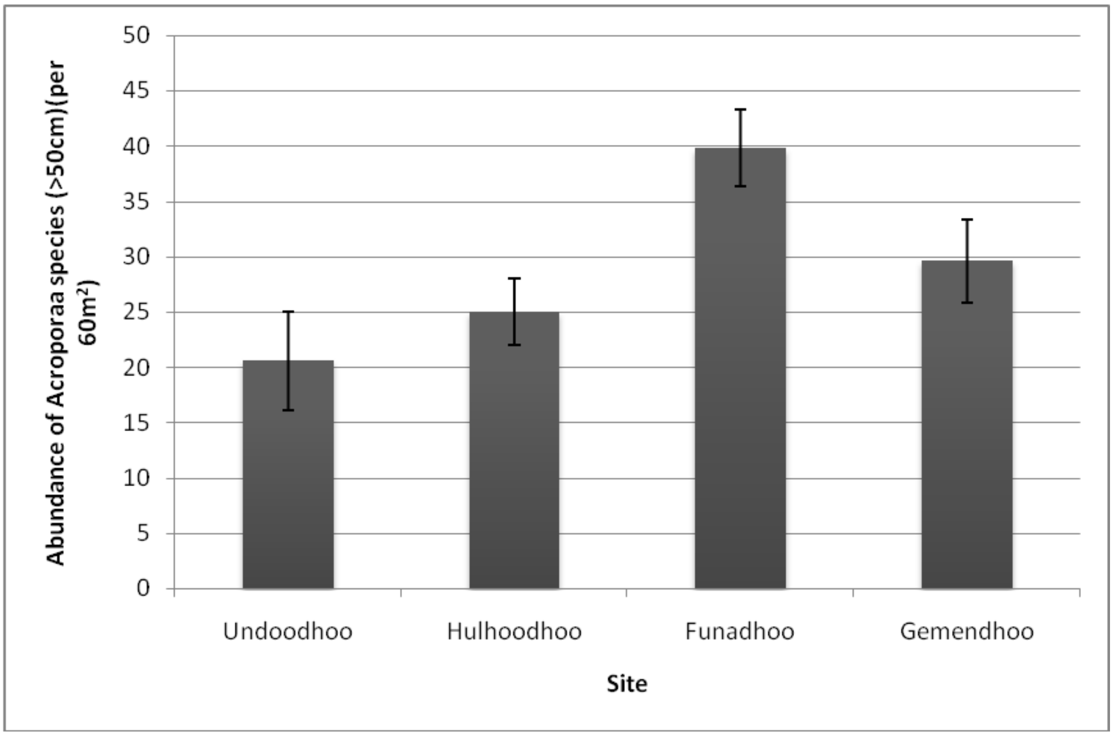


Figure 13: Mean abundance of *Acropora* corals greater than 50 cm in diameter (with associated standard deviations) per 60 m^2 at 5 m (±2m) at Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo reefs, Baa Atoll.

Table 16: T-values from Tukey's Pairwise Comparisons between the abundance of *Acropora* corals greater than 50 cm in diameter per 60 m^2 at 5 m (±2m) at Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo reefs, Baa Atoll (* indicates significance at 5% level).

	Undoodhoo	Hulhoodoo	Funadhoo
Gemendhoo	1.871	1.956	4.337*
Funadhoo	8.165*	6.294*	
Hulhoodhoo	1.871		

3.4.2 Proportion of live to dead Acropora *corals (>50 cm)*

Figure 15 shows the abundance of live and dead *Acropora* corals greater than 50 cm recorded at each survey site. The greatest abundance of live *Acropora* corals (<50 cm) was recorded at Funadhoo and Gemendhoo with 31 and 24 individuals respectively. In comparison, Undoodhoo and Hulhoodhoo show almost 50% lower abundance in live *Acropora* coral cover in comparison. A significant difference in the abundance of live *Acropora* corals was shown between sites (df= 3, F= 10.52, P= <0.001). Pairwise comparisons between sites indicate significant differences in the abundance of live *Acropora* coral at Undoodhoo in comparison to Gemendhoo and Funadhoo, and a significant difference between abundance at Hulhoodhoo and Funadhoo (Table 17). Figure 14 shows little variation in the abundance of dead *Acropora* corals and no significant difference between survey sites was indicated (df=3, F= 0.823, P= 0497). Table 18 shows the ratios of live to dead *Acropora* corals increases from Undoodhoo to Gemendhoo, with the majority of sites showing approximately 100% more live coral in comparison to dead coral. At Funadhoo and Gemendhoo the live coral is approximately 400% more abundant than dead coral.

Table 17: T-values from Tukey's Pairwise Comparisons of mean abundance of *Acropora* corals greater than 50 cm recorded per 60 m^2 at Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo reef, Baa Atoll.

	Undoodhoo	Hulhoodoo	Funadhoo
Gemendhoo	3.1217*	2.179	-2.003
Funadhoo	5.1243*	4.182*	
Hulhoodhoo	0.9424		

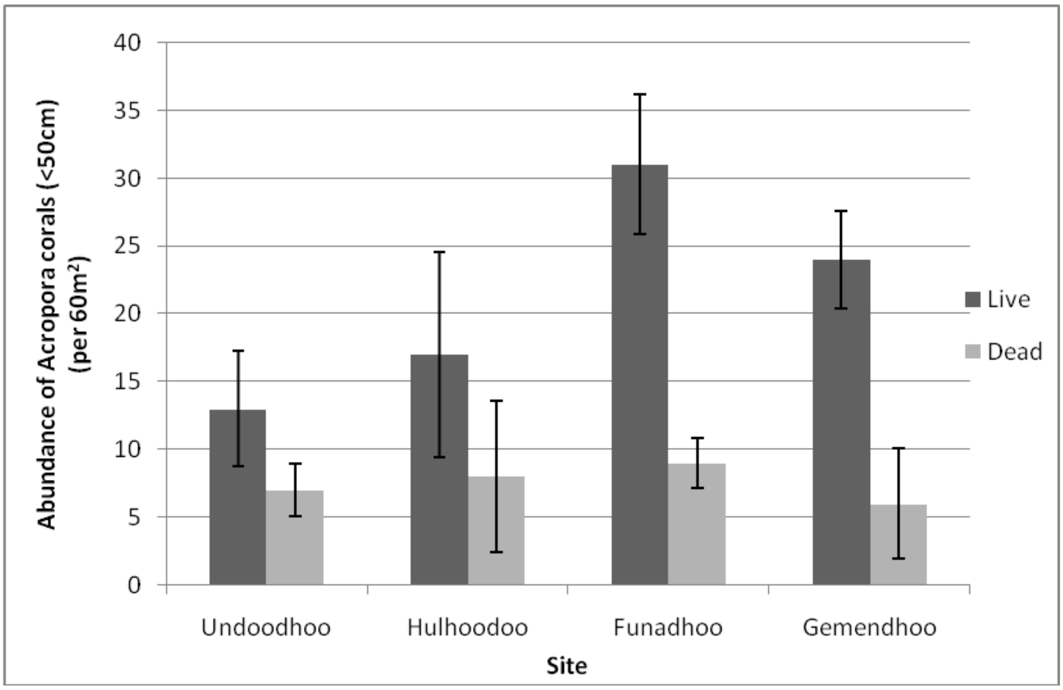


Figure 14: Mean abundance (an associated standard deviation) of live and dead *Acropora* corals greater than 50 cm in diameter recorded per 60 m^2 at Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo reefs, Baa Atoll.

Table 18: Abundance and associated ratio of live and dead *Acropora* coral greater than 50 cm recorded per 60 m^2 at Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo reefs, Baa Atoll.

Site	Live	Dead	Ratio of Live to Dead
Undoodhoo	13	7	1.91: 1
Hulhoodhoo	17	8	2.13: 1
Funadhoo	31	9	3.44: 1
Gemendhoo	24	6	4.00: 1

3.4.3 Assessing the abundance of physically damage Acropora *species (>50 cm)*

Physical damage to the *Acropora* coral skeleton was observed and recorded at Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo. In situ observations showed damaged was caused through physical destruction from storms, damage from Parrotfish (family Scaridae) and from contact from SCUBA divers and snorkellers. Figure 15 shows *Acropora* corals exhibit varying levels of physical damage, from broken edges of the coral in Figures 16b and 16c to sporadic surface damage caused by grazing organisms. Figure 16 shows high percentages of physically damaged corals were recorded at Gemendhoo where the mean percentage is approximately 15% higher in comparison to all other sites. The abundance of *Acropora* coral exhibiting varying degrees of physical damage is significantly different between sites (df 3, F= 5.70, P= 0.008). A Tukey's pairwise comparison indicates a significant difference between the abundance of physically damaged corals at Gemendhoo in comparison to all other sites (Table 19).

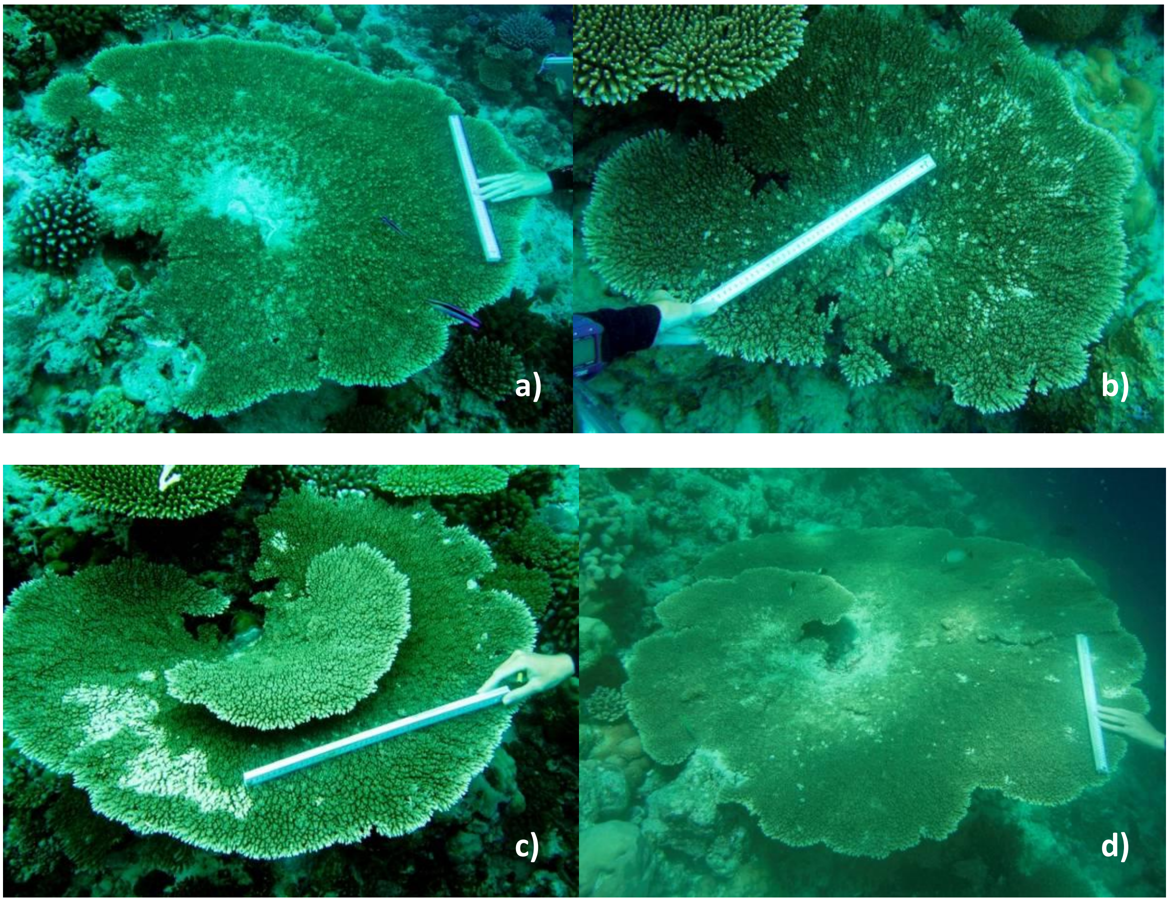


Figure 15: Photographs of *Acropora* table corals (>50 cm) located on Undoodhoo (a), Hulhoodhoo (b), Funadhoo (c) and Gemendhoo (d) reefs, Baa Atoll, each showing variation in physical damage which could be destruction from divers and snorkellers and damage from storms or grazers.

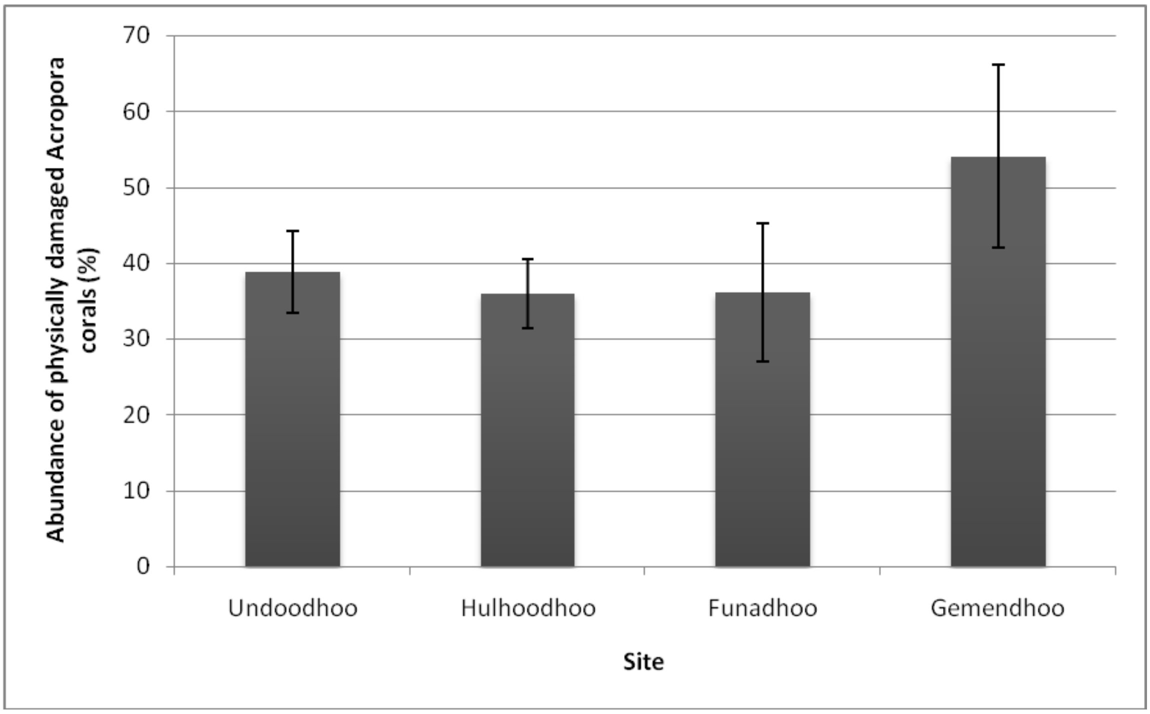


Figure 16: Percentage of physically damaged *Acropora* corals (>50 cm) (with associated standard deviation) relative to the total abundance recorded at within a 60 m^2 at Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo reefs, Baa Atoll.

Table 19: T-values from a Tukey's Pairwise Comparison of the abundance of physically damaged *Acropora* corals (>50 cm) recorded within a 60 m^2 area, between Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo reefs, Baa Atoll (* indicates significance at 5% level).

	Undoodhoo	Hulhoodoo	Funadhoo
Gemendhoo	3.0504*	3.53785*	3.458*
Funadhoo	-0.4072	0.08022	
Hulhoodhoo	-0.4874		

3.4.4 Size range of Acropora *species (>50 cm)*

Table 20 shows the mean size (with associated standard deviation) and size range of *Acropora* species (>50 cm in diameter) recorded at Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo. At Undoodhoo, a large standard deviation and a large size range of *Acropora* indicates high variation within the corals recorded in comparison to all other survey sites. In comparison, Funadhoo has a low standard deviation and small size range of corals which indicates little variation within the size of *Acropora*. A significant difference (df 3, F=5.79, P=0.007) between the size of *Acropora* coral encountered was shown. The mean size of *Acropora* corals recorded varied from 66.8 cm at Funadhoo to 83.0 cm at Hulhoodhoo. A Tukey's pairwise comparison indicates the mean size of corals recorded at Funadhoo and Hulhoodoo are significantly different (Table 21).

Table 20: The mean size (cm) of adult *Acropora* corals (<50 cm in diameter) with associated standard deviation (cm) and associated size range (cm) recorded at Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo reefs, Baa Atoll.

Site	Average Size	Standard Deviation	Size Range
Undoodhoo	77.0	9.46	64-84
Hulhoodhoo	83.0	6.40	82-94
Funadhoo	66.8	1.48	65-69
Gemendhoo	75.8	4.66	70-81

Table 21: T-values from Tukey's Pairwise Comparison between the mean size of *Acropora* corals (<50 cm) recorded at Undoodhoo, Hulhoodhoo, Funadhoo and Gemendhoo reefs, Baa Atoll (*indicates significance at 5% level).

	Undoodhoo	Hulhoodoo	Funadhoo
Gemendhoo	-0.305	-1.832	2.290
Funadhoo	-2.596	-4.123*	
Hulhoodhoo	1.527		

4. DISCUSSION

4.1 Substrate composition

4.1.1 Predominance of live coral on the reefs

The results of the present study show that live coral cover across all survey sites contributes an average of 42% (± 4.9%) to the overall substrate composition. Concepts such as 'ecosystem health' and 'coral-reef-health' are used by both scientists and environmental managers as an operational property that can be assessed and acted upon (Downs *et al*, 2005). The percentage cover of living benthos has often been used to infer the 'health' of a coral reef. Similar estimates of live coral cover of 40% in eastern central Maldivian atolls prior to the 1997-98 mass bleaching event have been recorded (McClanahan, 2000). It is imperative to consider the decline in live coral cover in 1997-98 in order to gain an appreciation of the results shown in the present study. A decline of approximately 95% of live corals was reported after the bleaching event, which was confirmed in numerous post bleaching studies on Maldivian coral reefs (Edwards *et al*, 2000; McClanahan, 2000; Loch *et al*, 2002). Indications that mean cover of live coral had declined to 2.1%, and ranged between 1.0% and 3.1% among the different atolls, has been reported (Zahir, 2000).

No surveys immediately post 1997-98 were conducted in Baa atoll. However, McClanahan (2000) studied the reefs in 3 atolls in the central Maldives (Felidu, Mulaku and South Malé). The study reported a decline in live coral cover to approximately 2%, 3-6 months post bleaching, which was shown to have increased to 8% 11 months post bleaching (McClanahan, 2000). A more limited survey focused on one atoll at this time indicated the presence of 5% living coral cover (Loch *et al*, 2002) which is in accordance with the findings of Edwards *et al* (2001) who reported 7% live coral cover in shallow water (<10m depth). Schumacher (2005) reported gradual increases in live coral cover of 8% 2000, 18% in 2001, 22% in 2002 and 27% in 2004, which surpass values in the majority of other studies (McClanahan, 2000; Edwards *et al*, 2000). Variation in estimates of live coral cover is likely between studies due to spatial variation between survey locations. However, the surveys conducted by McClanahan (2000) and Edwards *et al* (2000) are based in atolls neighbouring Baa atoll.

High densities of coral recruiting to reefs after the bleaching event in 1997-98 were recorded (McClanahan, 2000). Despite initial shifts in species composition of recruits, the reefs had the potential to recover from the bleaching event. Albeit the estimates of live coral coverage in the present study are comparable to those reported prior to 1997-98 (McClanahan, 2000), it is imperative to note that McClanahan's (2000) estimates were based on reefs which were subjected to numerous acute disturbances. Continuous changes in benthic assemblages have been documented since 1958, which is typical of reef ecosystems. Benthic surveys conducted on Maldivian reefs in 1958, 1964, 1992 and 1999 reported declines in hard coral cover from 60% to 8%, with the majority of change occurring after 1964 (McClanahan, 2000). Disturbances occurring prior to 1997-98 have been recorded, but few studies examined the effect on Maldivian coral reefs. The abundance of live coral cover reported in the present study is encouraging ten years post 1997-98, considering the devastation that occurred on Maldivian coral reefs.

The present study is hindered by the lack of baseline data on coral reefs within the entirety of Baa atoll. Since the development of a nearby local island, Kendhoo, which is situated approximately 500m from the survey sites, the reefs have been frequented by local Maldivians on a daily basis (Stevens, pers. comm). Observations made during 1997-98 confirmed that mass mortality had occurred on the sites surveyed in this study and throughout neighbouring atolls. In the Philippines, the time taken for a coral community to develop 50% live coral cover after disturbance, with successful colonisation by 30 species of coral at depths of 16-23m, was estimated to be 15 years. The reefs in the present study have had ten years to recover from intensive bleaching, and an average live coral cover of 42% is an encouraging assessment for reefs severely affected by elevated sea surface temperatures.

4.1.2 Spatial variability between the surveyed reefs

Spatial variability between coral reef recovery can be attributed to interactions between the biological and physical factors which affect the reefs. Between the reefs surveyed in the present study, variations in the percentages of live coral cover at 1m were shown, with the lowest reported estimate of live coral of 3.2% recorded at Undoodhoo reef, and the greatest percentage of 24.8% recorded at Gemendhoo reef. In one of the few recent surveys conducted in 3 central atolls (South Male, Felidhoo, Ari), 8 years after the 1998 coral mass mortality, estimates of live coral cover in shallow water have shown significant variation between sites, ranging from 12% to 37% (Lasagna *et al*, 2008). The high spatial variability of live coral cover among sites suggests that Maldivian reefs are still in an ongoing process of re-colonisation. Spatial variation on coral reefs in the Chagos archipelago prior to

1997-98 was shown, as live coral on sea ward slopes ranged from 50 to 95%, declining to an average of 12% and even to zero between 0-5m in some shallow areas (Sheppard *et al*, 1999b). Similarly, in the Chagos archipelago estimates of live coral cover between atolls was highly variable eight years after very heavy mortality (Sheppard *et al,* 2008). Variations in live coral cover values of less than 20% were recorded at 3 atolls, compared to reports of over 100% live coral coverage to 10m depth at other sites in the Chagos, indicating patchy recovery of the reefs (Sheppard *et al,* 2008). Variation in live coral cover between sites on a small spatial scale is, therefore, not uncommonly shown in reefs systems in archipelagos, and could possibly be attributed to a variety of natural biological or physical factors as well as either chronic or acute anthropogenic impacts acting on the reefs throughout the recovery process.

The results of the present study indicates that Undoodhoo and Funadhoo reefs have lower percentages of live coral cover at 1m in comparison to Hulhoodhoo and Gemendhoo reefs. The variation shown between the reefs within such a small spatial scale may be attributable to localised anthropogenic impacts inhibiting the recovery of Undoodhoo and Funadhoo reefs. Undoodhoo and Funadhoo reefs are visited daily by guests from two nearby tourist resorts (Four Seasons Resort and Reethi Beach Resort), whereas Hulhoodhoo and Gemendhoo are rarely frequented. At the shallow depth of 1m, physical damage caused by snorkellers, through unnecessary contact with the corals on a regular basis, was observed on the affected reefs. The distribution of broken corals has been shown to correlate positively to the abundance of snorkellers using Maldivian reefs in north Malé atoll (Allison, 1996). Snorkellers and SCUBA divers have been found to inadvertently damage corals by clambering over them, by kicking them accidentally with their fins, or by stirring up silt that suffocates the corals (Hawkins *et al*, 1999). Barker and Roberts (2004) recently demonstrated (in St Lucia) that this damage was virtually impossible to avoid. However, close supervision of divers and snorkellers reduced the number of reef contacts. In situ observations also showed that damage to large *Acropora* colonies was not only caused by SCUBA divers and snorkellers, but also by physical destruction from storms and damage from the feeding activities of Parrotfish (family Scaridae). The frequent disruption occurring on Undoodhoo and Funadhoo reefs may be resulting in substrate composition being dominated by old dead coral and coral rubble at 1m which was reported in the present survey. It is possible, therefore, that recovery of the reefs is being inhibited by constant disturbance from anthropogenic impacts.

4.1.3 Variation in substrate composition with depth on each reef

In the present study, significant variation in substrate composition between all depths was shown on all surveyed reefs excluding Hulhoodhoo. Variation in substrate composition with depth is not similar between Undoodhoo, Funadhoo and Gemendhoo and therefore there is no general pattern in substrate composition with depth between these reefs. Substrate composition will have an effect on the future development of the reefs as this will affect the colonisation of coral recruits. In contrast, in the Chagos, it was reported that there is no marked pattern of change in either coral cover or total colony density with depth (Sheppard *et al*, 2008). An exception was reported in Egmont atoll, which showed lower live coral coverage at all depths where old dead colonies dominated shallow water (Sheppard *et al,* 2008). Low values of <20% were frequent at 3 atolls and at all depths, this pattern suggests that some depths and atolls show greater variability or different patterns to the other, emphasising the patchiness in the extent to which sites recover (Sheppard *et al,* 2008). The extent of substrate variation may have profound influences on the development of the reefs and will therefore determine the amount of variation in reef recovery.

4.1.4 Presence of coralline and turf algae on the reefs

Coralline and turf algae were present at each depth on each surveyed reef, cover ranging from 4.5-9%. At Undoodhoo and Funadhoo, however, the percentage cover of coralline and turf algae was high, reported as 25.5% and 21% respectively at 1m. Typically, degraded reefs have reported phase shifts from coral to macroalgae dominated reefs. Spatial patterns of algal composition and production are strongly influenced by patterns of grazing, disturbance and competition with corals. There also appears to be a systematic causative relationship between the intensity of grazing from scraping and denuding herbivores and the structure of algal assemblages. Algae on the reefs in the present study are not the dominant form of benthic cover, and it is possible that these disturbed areas of Undoodhoo and Funadhoo reefs can recolonise without passing through a macroalgae phase. Conditions on the remainder of the reefs at the depths surveyed do not favour conditions preferable for algal growth over coral cover and, therefore, there is a high probability that the corals on the surveyed reefs will recover in a coral dominated community.

4.2 Coral recruitment

4.2.1 Density of coral recruits settling on the reef

The 1997-98 mass bleaching event occurred against a background of little baseline information on the natural rates of recruitment on Maldivian coral reefs. Since 1998, research into the rate and composition of new coral recruits on both natural and artificial bare substrate post-bleaching has been the focus of most recent research (McClanahan, 2000; Edwards *et al,* 2001; Sheppard *et al*, 2002). The results of the present study show that the mean abundance of recruits ranged from 2.5 to 12.1m^{-2} across all depths and between the surveyed sites in Baa atoll. Prior to the mass bleaching event, recruitment to artificial structures located in north Male atoll was estimated at an average of 12.6 recruits per m$^{-2,}$ which were reported to have settled between 1991 and 1994 (Clark and Edwards, 1995). Recruits belonged to species of *Acropora* or *Pocillopora,* which were shown to have settled on vertical or near vertical surfaces where densities reached a maximum of 18m^{-2} (Clark and Edwards, 1995). The recruitment densities reported in this present study are similar to the results shown by Clark and Edwards (1995) conducted prior to 1997-98, both of which show that Maldivian reefs are not recruitment limited.

In April 1999, McClanahan (2000) reported recruitment densities from 11 study sites in the eastern central atolls, and showed mean abundance to be 29 individual recruits per m^{-2} on outer exposed edges of natural reefs. In a more limited study of recruitment onto artificial structures, a similar result was reported by Edwards *et al* (2002), showing densities of 23.2 individual recruits per m^{-2}. In both of these studies recruitment densities are shown to be higher post bleaching for recruits settling on both artificial and natural reefs in comparison to the densities recorded in this study. The results of the present survey are also comparable to those reported by Loch *et al* (2002) 21 months post bleaching in 1997-98, which recorded a mean density of 4.4 colonies per m^{-2} onto the reef. In the Seychelles (Aldabra), Stobart *et al* (2005) stated that coral recruitment was ‘consistently high from 2001-2003’, where average numbers of recruits were between 7-9m^{-2} at 10m depth and 4-6m^{-2} at 20m depth. The present survey, therefore, shows corals are recruiting to the surveyed reefs, and recruitment densities in Baa atoll are similar to those recorded post bleaching in the north Malé atoll (Maldives) by Loch *et al* (2002) and more recently in Aldabra (Seychelles) by Stobart *et al* (2005). The present study also shows that despite present recruitment densities not being similar to those recorded immediately post bleaching, the surveyed reefs in Baa atoll are not recruitment limited.

4.2.2 Spatial variation in coral recruitment between reefs

Numerous studies have demonstrated that coral recruitment in open systems is highly variable in space and time (Connell *et al*, 1997, Hughes and Connell, 1999). A limitation to numerous studies based in the Maldives is the lack of information on coral recruitment at several scales. Spatial variation in the densities of corals recruitment between the surveyed reefs was shown in the present study. The distances between the reefs are small (~200-300m) in comparison to many studies which have concentrated on recruitment over larger spatial scales, particularly on the Great Barrier Reef (~1km) (Dustan and Johnson, 1998). In regard to spatial scale, Connell *et al* (1997) found that recruitment varied in samples close together in the same habitat on reefs up to 300m apart. In the present study, variation of recruitment within transects on each reef was low. However, high variation in density of recruits between reefs was indicated. This finding is supported by Connell *et al* (1997), who found that recruitment densities at two smaller spatial scales (1-5m and 40-300m between samples) were similar, whereas significant variation in densities between survey sites up 300m apart was indicated. Mechanisms that affect recruitment (e.g. physical and biotic characteristics of the substrate) may also be operating at a much larger spatial scale. The most likely causes of spatial variation in recruitment rates acting on the reefs in the present study include differences among study areas in 1) supply of larvae from the plankton, 2) suitability of the substratum for settlement, and 3) mortality during the period between settlement and the time the recruits were first censured. The supply of planktonic larvae to the reefs is likely to be more similar within a habitat than at widely separated sites in different habitats, and this could produce the observed spatial pattern of variation in recruitment.

It has been suggested that reefs within archipelagos such as the Maldives and Chagos received a supply of planktonic larvae from corals in deeper water which survived the mass bleaching event in 1997-98. The studies by McClanahan (2000) and Edwards *et al* (2001) also showed that there were large numbers of *Acropora* and *Pocillopora* larvae arriving to settle on the reefs, despite observations that all the shallow water parent stock had died in 1998. Suggestions that emergency broadcast spawning occurred prior to the elevation in sea surface temperature have been put forward (Loch *et al*, 2004). Sources of larvae may also include adults that have a refuge in depth on seaward slopes, whereas non local recruitment is likely to be much slower. The isolation of the reefs in Baa atoll may be a reason for the low abundance of recruits recorded in the present study. An almost complete failure of coral recruitment at Scott and Seringapatam Reefs in western Australia since 1998 has been shown, and has been attributed to their extreme isolation. It was suggested that reefs like Scott and Seringapatam are self seeding and would, therefore, take decades or longer to recover from disturbance. Consequently, recovery from the 1998 bleaching event could take decades or longer. Graham *et al* (2006) suggests that the inner Seychelles and the Maldives will be largely reliant on self recruitment. The small and disconnected brood stocks of many species of coral (particularly fast growing branching species) will likely reduce the rate of recovery. It is possible that with the high abundance of live coral cover, mainly *Acropora* on the shallow reefs, the future densities of recruits on the reefs my increase.

Coral recruitment has previously been shown to vary among zones within reefs (Harriot, 1985; Babcock, 1988) and between reefs (Harriot and Fisk, 1988). Spatial variation in the density of coral recruitment between survey sites was recorded in this present study. High spatial variation in coral recruitment at the level of regional atolls in the Maldives has been shown from densities of 12 individuals per m^2 in south Ari atoll to estimate over 26 individuals per m^2 in north Male atoll (Zahir, 2002). In the Seychelles, two years after mass mortality, low densities of *Acropora* and *Pocillopora* recruits were reported, and recruitment to the degraded reefs was patchy, 35% of the sites surveyed showing no recruitment (Turner *et al,* 2000). In Chagos, patchy yet strong recovery is clear in terms of number of colonies, coral cover, and number of recruits (Sheppard *et al,* 2008). Such spatial variations in recruitment density may be having a profound effect on the long term recovery from the 1998 bleaching event in the Maldives and surrounding archipelagos, which may explain the low densities of recruits reported in the present study.

Differences in coral recruitment between sites may be attributable to the local influences on each reef, such as competition and influences of post settlement mortality. Through an evolutionary time scale, sufficient dispersal occurs to ensure gene flow to reefs possibly thousands of km apart, but in the short term, however, coral reefs appear to be primarily self seeded with respect to coral larvae (Sammarco and Andrews, 1987). The supply of coral recruits to a reef is dependent on the water regimes circulating around the reef. Reefs within the central GBR have been shown to be biologically interconnected and interdependent, with considerable inter-reef dispersal of benthic invertebrate larvae (Williams *et al*, 1984). Corals of isolated oceanic islands may be self seeding, or alternatively may be continually supplied with recruits advected from elsewhere by ocean currents. On the Bermuda islands, the transport of larvae from distant source populations was found to be rare, and it was evident that populations are replenished via a pool of larvae that are spawned locally and retained in the vicinity of the Bermuda Islands (Schultz and Cowen, 1994).

The spatial variation of corals on groups of islands is dependent on the circulation of water, transporting larval recruits from neighbouring islands in a localised vicinity (Schultz and Cowen, 1994). Larvae from species that spawn gametes are smaller, tend to disperse further, and survive more poorly than larvae from brooding species (Connell *et al,* 1997). Similarly, on Tanguisson reef in GBR, Colgan (1987) suggests that the sources of coral recruits were in situ spawning colonies, which explains the accelerated recovery displayed. Similarly, on Molasses Reef in Florida (USA), heavily damaged areas were surveyed and studied for 27 months and the highest recruitment was shown by previously dominant species whose adult colonies had survived the physical damage (Gittings *et al*, 1988). Strong correlations between adult and juvenile colonies were shown on this reef in recovery, due to reproductive strategies and environmental restrictions for coral planulae (Colgan, 1987). The fact that *Acropora* recruits dominated the reefs in the present study suggests that parent stocks are being replenished in Baa atoll.

4.2.3 Variation in coral recruitment between depths on each reef

In the present study, variation in recruitment abundance between 5 m, 12 m and 18 m was shown on all surveyed reefs. Variation in recruitment present at each depth is likely to have an effect on the future development of the reefs. Substrate composition is likely to affect the density of recruits settling on the reefs. In comparison, studies of recruitment in the Chagos archipelago have shown no differences between recruitment densities in general with depth (5 m, 15 m and 25 m) or spatial variation between atolls (Sheppard *et al,* 2008). However, by taking each genus of juveniles in turn, many genera showed a marked depth preference. In the Chagos, thirteen genera were reported to have shown the depth preference and since recruitment was onto substrates that largely lacked both coelenterates and significant macroalgae, it was suggested that there is strong depth selection at the juvenile stage by many genera (Sheppard *et al,* 2008). The variation in recruitment density between depths may be due to the variation shown in substrate composition, which will consequently affect the settlement of coral recruits on the reefs. A combination of biological and physical factors will influence the recruits, influencing post settlement mortality and consequently affecting the abundance of the recruits at various depths.

4.2.4 Post Settlement mortality due to the abundance of coral rubble

The low abundance of coral recruits at some depths may be attributable to post settlement mortality due to the lack of stable, sediment-free surfaces for colonisation. Areas with high proportions of coral rubble were shown to correlate to low densities of coral recruitment in the present study. A significantly lower abundance of recruits have been shown to attach to an unstable chain-link fencing structure in comparison to a more stable artificial structure in the same area (Clark and Edwards, 1995). All recruits subsequently died, due to their low elevation and the abrasive action of the mobile rubble and sediment (Clark and Edwards, 1995). It is, therefore, possible that areas of the reef with high abundance of coral rubble will have less future coral development, due to the prohibition of settling corals. Algae were shown to cover patches of coral rubble on the surveyed reefs (personal observation). In a study by Heyward and Negri (1999), active biochemical inducers appear to be present in calcareous substrates, where live crustose algae are not apparent such as non-encrusted coral rubble. In the Maldives, after mass bleaching, the survivorship of recruits on a reef and small juveniles corals within permanent quadrats located in north Male atoll was high (>80%), and did not differ significantly over the survey period between February 2000 and July 2002 (Zahir, 2002). This indicates that recruits faired well after the bleaching and, therefore, had the ability to establish themselves on the coral reef within the community. As the coral community develops and becomes increasingly stable, it is likely that coral recruitment densities will increase on the survey sites. However, this requires continuous monitoring to assess future patterns in coral recovery.

4.2.5 Temporal variation in coral recruitment

Temporal variation in the abundance of coral recruits has been reported in many studies (Wallace, 1985; Harrison *et al*, 1984, Fisk and Harriot, 1990, Smith, 1992). Within the present study, the abundance of recruits over the sampling period was not designed to determine temporal variation; however the low abundance of recruits may be attributable to seasonal or inter annual variation in coral recruitment. Information on temporal variation in the abundance of coral recruitment in the Maldives is limited to a few sites located in two atolls (Zahir, 2000). From the limited literature on Maldivian reefs, recruitment densities and size frequency distributions for sampling sites in Malé atoll were shown to be consistent between years, therefore indicating no temporal variation at these sites (Zahir, 2000). Coral recruitment, however, has been shown to vary temporally in Australia, where peak recruitment was shown to have occurred in 2 spring-summer periods (Oct-Feb), and minimal recruitment in the winter-spring periods (Jun/Jul-Oct) (Wallace, 1985). Wallace (1985) reported high densities of recruits at all sites in spring-summer, but the numbers recruiting to the slopes changes little from one spring-summer to the next (Wallace, 1985). Wallace (1985) found that most coral larvae settle out of the plankton during a single limited time period each year. This strong seasonal pattern is obvious at all sites during the present study, confirming observations from the Great Barrier Reef (Wallace, 1985). Literature is sparse for estimates of coral recruitment in the Maldives, but an abundance of literature reported post bleaching recruitment. However, it has been noted that an usually high abundance of recruits was shown post bleaching, due to an unusual spawning episode prior to 1997-98 event. This phenomena has been reported in Moorea, French Polynesia where a large increase in recruitment immediately preceded a bleaching event (Gleason, 1996). Therefore, comparisons with immediately post bleaching recruitment data should be examined with caution.

4.2.6 Taxonomic diversity within the coral recruits

The results of the present study indicate that the greatest abundance of coral recruits were identified as belonging to Acroporidae and Faviidae at 5m and 12m. Despite the reported decimation of 98% of shallow water branching species during 1997-98, 67% of post-bleaching recruits were shown to belong to the Acroporidae and Pocilloporidae communities (Edwards *et al*, 2001). The genus *Acropora* has been transformed from being the most abundant coral genus in the Indian Ocean to one of relative scarcity and low diversity. *Acropora* was among the genera most susceptible to mortality in 1998 (Obura, 2001) and low recruits for the first 2 years after that for several areas, particularly the Maldives (McClanahan, 2000). However, from 2000 onwards juvenile *Acropora* became abundant among newly recruiting species in the Chagos (Sheppard *et al*, 2002). The influx of recruits for recovery was coming from corals in deeper water that were not as severely affected. The possibility of year to year variation in community composition has provided encouragement of recovery via high recruitment (McClanahan, 2000). Similarly on reefs in the Chagos Archipelago, *Acropora* was the most commonly found recruit, followed by *Montipora*, *Pavona*, all Faviids and *Porites*, which together accounted for 76% of juveniles recorded (Sheppard *et al*, 2002). The successful recruitment of *Acropora* juveniles to reefs in the Chagos in 2001, was reflected in the high cover of *A.cytherea* and *A.palifera* reported in 2006 (Sheppard *et al*, 2008). If Edwards' study (2002) is an accurate reflection of post bleaching recruitment it is expected that the present study would indicate an abundance of species belonging to the genera *Acropora* (*A.formosa* and *A.digitifera)* on the surveyed reefs. Davies *et al* (1971) were able to distinguish several biological zones on the Maldivian reefs, one of which was an *Acropora formosa* zone, which was described as a mixed zone between 5-10m characterised by the presence of forests of *Acropora,* dominated by *Acropora formosa* (UNEP, 1986). Similarly, species belonging to the family Faviidae (*F. complanata* and *F. abdita)* were found to drive similarities between coral assemblages found at each depth. In Aldabra and Cosmoledo in the Seychelles, the most successful recruitment of new coral was said to be the Faviids (Sheppard and Obura, 2005). The Faviids were found to remain sparse above the 'critical depth', but have a high diversity below it, albeit with low or moderate cover, because they exist today mainly as many small, young colonies in the Seychelles (Sheppard and Obura, 2005). The situation before the 1998 mortality event cannot be known for certain, but inferences can be made from present conditions and from the expanses of recently dead coral.

Disturbance cause by El Niño 1997-98 was shown to significantly affect many dominant corals in a variety of ways. Due to the high mortality of adult colonies, recovery is reliant on successful larval recruitment, which is likely to be reduced both by a reduction in the abundance of gravid colonies and the loss of a higher proportion of large colonies than would be expected in other types of disturbance (Baird and Marshall 2002). Environmental factors, therefore, affect the recruitment of corals, and spatial and temporal variation in recruitment is also displayed. The ability for corals to recover from disturbance is dependent on the survival of recruits already attached to the reef, and the successful recruitment of new corals on substratum. Physical damage, such as tropical storms and cyclones can create uninhabitable areas where coral planulae attachment is not preferable. Elevated SSTs can create areas of dead coral structures on which coral recruits can colonise. On Maldivian coral reefs the upper surfaces of dead *Acropora* structures were reported to provide a suitable substratum for recruitment colonisation (Edwards *et al*, 2001). However, elevated SSTs can also reduce the survival of planulae. Many studies comment on the recruitment of corals post disturbance with no information of the natural rate of recruitment prior to disturbance, and few studies monitor long term recruitment patterns on reefs. It is, therefore, imperative that reefs affected by frequent disturbance are continuously monitored, to gain a better understanding of rates and changes in recruitment patterns.

4.3 Coral diversity

4.3.1 Variation in coral diversity with depth

In the present study coral diversity at 1m was shown to be significantly lower than diversity recorded at all other depths. Diversity on coral reefs in the Maldives has been shown to be typically low near the surface and increases to a maximum to 15m and 30m (McClanahan, 2000). *Acropora* and *Pocillopora* were shown to have recruitment densities less than 0.65 individuals per m^2 in a rapid assessment in 3 Maldivian atolls in 1999 (McClanahan, 2000). However, densities of recruits belonging to these two genera were shown to increase in 2002 (Loch *et al*, 2004). In the present study *Acropora* and *Pocillopora* dominated the reef at 1m and were recorded at a significantly lower abundance at 5m, 12m and 18m. The rapidly growing (10-15cm yr^{-1}) branching species (*Acropora, Stylophora, Pocillopora*) are most sensitive to exposure, but their fast growth compensates for the higher survival of the slowly growing (a few mm yr^{-1}) massive forms. The shallow reef is typically low in diversity. However, if no continuous disturbance occurs, then this is likely to encourage few species to monopolise the reef at 1m. Glynn (1999) found a similar effect on reef flats on the Pacific side of Panama, where extreme tidal exposure killed 40-60% of the dominant species of *Pocillopora*, and had a diversifying effect on the reef flat. Similarly, in the Eastern Indian Ocean the reef edge has been shown to be totally dominated by dense ramose-growth forms of many *Acropora* species and *Pocillopora damicornis* (Huston, 1985). The ability of *Acropora* and *Pocillopora* to take on growth forms which maximise wave turbulence in this zone, and thus prevents siltation, may be a reason for their abundance on the shallow reef crest on the survey sites in the present study.

4.3.2 Similarity in coral diversity between 5 m, 12 m and 18 m.

The reefs in the present study showed no significant difference in coral diversity at 5m, 12m and 18m. The survey was designed to ascertain a ‘critical depth’ to which mass mortality extended on the survey sites and affected diversity on the coral reefs within Baa atoll. Within the Indian Ocean, severe mortality affected reefs to a specific depth, beneath which coral survival was much greater (McClanahan, 2000, Spencer *et al*, 2000; Wilkinson, 2000; Sheppard *et al*, 2002). A post bleaching study in March 1999 indicated all *Acropora* tabular corals down to a depth of 10m had been killed. At that time no living polyps were recorded and no new settlements were detected (Loch *et al*, 2002). The critical depth in the Maldives was, therefore, said to be around 10-12m (Loch *et al*, 2002). However, other studies have suggested that the critical depth varies between reefs and regions in the Maldives dependent on local thermoclines during the El Niño event (Edwards *et al,* 2001). The critical depth, however, was shown not to apply equally to all coral families. Therefore variations between depths would be expected.

In the present study, the 5m, 12m and 18m depth categories did not differ significantly from each other in terms of species diversity; however, they did differ significantly from the diversity in the extreme shallow water. In deeper water, coral assemblages are dominated by *Porites*, *Favites* and *Tubastrea*, as has been the case elsewhere in the Indian Ocean (Obura, 2001; Riegl, 2002; Sheppard and Loughland, 2002) due to the removal of the more sensitive groups in shallow water. On the surveyed sites in the present study, this has been shown to be the case at 5m, 12m and 18m, therefore suggesting that the reefs surveyed were affected by the mass bleaching event down to 18m. Sheppard and Loughland (2002) predicted a Faviid and *Porites* dominated reef system based on the condition of sites in the Arabian Gulf, and this has been shown to be occurring on Cosmoledo and Aldabra in the Seychelles. In situ observation recognised an abundance of coral rubble belonged to the *Acropora* species, indicating the importance of this group here previously. The abundance of typical *Acropora* species (*A.formosa*) in this study therefore indicates the recovery of species that were reportedly killed during the 1997-98 bleaching event. The critical depth in the Seychelles is variable between atolls and other reefs in the region, these atolls of 8-10m being fairly shallow when compared with many atolls and other reefs in the region, where transition from extremely heavy to partial mortality is considerably deeper at 30-40m. Monitoring is continuing as part of the Coral Reef Degradation in the Indian Ocean (CORDIO) programme. It is imperative that such monitoring is conducted to assess how the community structure changes over time.

4.3.4 Abundance of Dendrophyllidae at 18m on all reefs

The results of this study show an abundance of Dendrophyllidae recruits on each survey site. The most common species within the Dendrophyllidae family is recorded in the Maldives and is the azooxanthellate coral *Tubastrea micrantha*, which has been recorded on reefs subject to strong currents, including both wall reefs and exposed fringing reefs (Edinger, 2000). Only *Tubastrea micrantha* is capable of forming tall structures, and only in highly protected habitats where its faster growing competitors have been eliminated by

Acanthaster predation (Edinger, 2000). In a survey on Maldivian reefs in north Malé atoll, *Tubastrea micrantha* constituted the majority of fauna in 2002. They had not, however, proliferated and their number was significantly reduced in repeated surveys in 2004. An abundance of *Tubastrea micrantha* recruits was also recorded on the survey sites, particularly at 18m, suggesting that unlike in previous reports *T.micrantha* is still proliferating on the coral reefs in this region.

*4.3.5 Abundance of Corallimorpharian (*Discosoma spp*) at Funadhoo reef at 5 m.*

The results from this study show a great abundance of Corallimorpharia (*Discosoma* spp), which have formed dense mats in the shallows of Funadhoo reef. Earlier molecular phylogenetic analyses indicate that the corallimorpharians appear to fall either within the Scleractinia (Fautin and Lowenstein, 1992) or within a separate group that includes the Actinaria (Chen *et al*, 1995a). Medina *et al* (2006) performed a complete mitochondrial genome comparison and showed one clade of scleractinians is more closely related to corallimorpharians that it is to another clade of scleractinians. The outcome suggests that the Discosomatidae (represented by *Discosoma* and *Ricordea*) are derived from within another corallimorpharian group, which supports the notion that corallimorpharians are monophyletic (Medina *et al,* 2006).

One of the most dominant corallimorpharians in the Indian Ocean is *Discosoma* (*Rhodactis) rhodostoma* (Ehrenberg, 1934), which has been reported to form dense aggregations in shallow coral reef environments (den Hartog, 1980; Chadwick-Furman & Spiegel, 2000). Large aggregations of *Discosoma* polyps have been reported on coral reefs in the Caribbean (den Hartog, 1980), Malaysia (Ridzwan, 1993), and Taiwan (Chen *et al,* 1995a). Aggregations or colonies of soft bodied benthic cnidarians, such as sea anemones and soft corals, may occupy large areas of hard substrate and thus compete for space with stony corals on tropical reefs (Chadwick-Furman and Spiegel, 2000). The ability for corallimorpharians to form dense aggregations, as reported in this study, is imperative if they are to become a dominant group occupying the shallow coral reef. Corallimorpharian life history strategies have been shown to favour rapid clonal replication on hard marine substrates on tropical coral reefs (den Hartog, 1980), as well as in temperate kelp forests (Chadwick, 1991).

Several of the estimated 18 species in the tropical corallimorpharian genus *Discosoma* are known to replicate clonally (Elliot and Cook, 1989). *Discosoma* are thought to derive little energy through heterotrophy (Elliot and Cook, 1989) as their tentacles lack the musculature required for zooplankton capture (Chadwick-Furman and Spiegel, 2000). Instead, members of this genus have shown much of their energy is obtained via photosynthesis using endosymbiotic zooxanthellae (den Hartog, 1980). The polyps of many tropical zooxanthellae anthozoans have been reported to grow and replicate fastest when light and/or temperature levels are highest, thus facilitating maximal photosynthetic energy production by their zooxanthellae (Chadwick-Furman and Spiegel, 2000). The ability for *Discosoma* to colonise and grow rapidly on Funadhoo reef allows the formation of dense aggregations to monopolise the shallows of the coral reef.

The results of this study show aggregations of *Discosoma* spp are only present in high densities at 5m on Funadhoo reef, and were reported as absent or in low density in comparison at deeper depths. Studies have shown Corallimorpharian distribution is influenced by environmental conditions and restricted to the shallow areas of the reefs. Dense aggregations of *Discosoma* were reported on the shallow reef flats in Eilat, northern Red Sea (Chadwick-Furman and Spiegel, 2000) and similarly in the shallows on numerous reefs in Tanzania (Muhando *et al,* 2002). In *Discosoma rhodostoma* and in other anthozoans, clonal growth has appeared to be controlled by both exogenous as well as endogenous factors (Chadwick-Furman and Spiegel, 2000). Chadwick-Furnman and Spiegel (2000) suggested corallimorpharians were able to tolerate conditions that are characteristic of shallow waters in the tropics, i.e. high temperatures and UV radiation. In Tanzania, the ability of corallimorpharians to withstand raised temperatures and UV radiation conforms with observations in the Red Sea (Muhando *et al*, 2002), where *Discosoma rhodostoma* showed strong resistance to dehydration and exposure to air for several hours during midday (Chadwick-Furnam and Spiegel, 2000). The tolerance of *Discosoma* spp to withstand such conditions in shallow water presents them with a competitive advantage over other cnidarians. Polyp size of corallimorpharians on coral reefs in Eilat, northern Red Sea, has also been shown to relate to environmental conditions (Chadwick-Furman and Spiegel, 2000). Studies have reported a significantly larger size of polyps in vertical rather than horizontal orientations, which may be due to less exposure to environmental stressors such as ultraviolet radiation and sedimentation on vertical reef surfaces (Chadwick-Furman and Spiegel, 2000).

Results of the present study show spatial variation in the distribution of *Discosoma* spp between survey sites; dense aggregations were only recorded on Funadhoo reef only. It is suggested that this variation is related to competitive abilities and environmental factors, with water conditions and depth playing a vital role (Kuguru *et al*, 2004). Variation in abundance of corallimorpharians among and within reefs in close proximity has been reported on Tanzanian reefs (Kuguru *et al*, 2004). Spatial variation in the abundance and distribution of *Discosoma* spp may also be related to disturbance-generated elements of overlying gradients of change in species composition and diversity within reef communities (Ninio and Meekan, 2002). It is likely, therefore, that corallimorpharians have responded to disturbance on Funadhoo reef, and that conditions were favourable to support rapid colonisation and, therefore, dominance of this species in shallow water. Competition for space may limit growth of typically dominant corals such as *Acropora* and thus change the rates in which the reef becomes dominated by xeniid soft corals or corallimorpharians (Ninio and Meekan, 2002). It is suggested that coral reef communities experiencing such spatial variation may be due to mosaic dynamics, which has been shown in studies at Tiao-Shi reef in Tanzania that have reported variation in shifts in dominance by coral species (Muhando *et al*, 2002). However, studies have shown that during a single mass disturbance such as a cyclone or a COTS outbreak, this is a sufficiently widespread disturbance to affect all reefs in a particular locality within 10s of kilometres (Ninio *et al*, 2000).

The formation of dense aggregations of *Discosoma* spp on Funadhoo reef is a result of rapid replication. Polyps of *Discosoma rhodostome* have been shown to replicate clonally by at least 3 distinct modes at a rate that permits them to rapidly monopolize large areas of space on some reefs (Chadwick-Furman and Spiegel, 2000). In the tropical corallimorpharian *Rhodactis indosinensis*, replication rate also varies between clones, and depends on seasonal changes in seawater temperature (Chen *et al*, 1995a). Clonal replication in Corallimorphs use several distinct modes per species, including pedal laceration, fission (den Hartog, 1980), and budding (Chen *et al*, 1995a).

Competition among sessile reef organisms may take different forms. For example, an organism might out-compete another organism by outgrowing it, by using available resources more efficiently such as light or food (exploitative competition), or by having a more effective reproductive strategy. The results of the present study show dense aggregations of *Discosoma* spp were found to colonise old and recently dead coral at Funadhoo reef. Corallimorpharians have been shown to rapidly colonise and cause aggressive damage to neighbours, allowing polyps of *R.rhodostoma* to become an alternate dominant to stony coral in some disturbed reefs (Chadwick-Furman & Spiegel, 2000). Chadwick-Furman & Spiegel (2000) found corallimorpharians monopolised large areas of reef space via clonal production of extensive aggregations, followed by aggressive damage to other benthic cnidarians (Langmead & Chadwick-Furnman, 1999b). These combinations of reproductive and competitive strategies contribute to the dominance of *R.rhodostoma* polyps in some shallow reef habitats in the Indo-Pacific region (Chadwick-Furman *et al,* 2000). Polyps that contact stony-coral competitors develop specialised marginal tentacles that damage their neighbours' tissues, after which the polyps move onto the coral skeletons and overgrow them (Langmead & Chadwick-Furman, 1999a).

Within sections of the inner reef flat at Eilat, dense aggregations of *R.rhodostoma* have become an alternate dominant to the stony corals that were major space occupiers before the disturbances (Chadwick-Furman and Spiegel (2000). The Caribbean corallimorpharian *Discosoma sanctithomae* uses inducible bulbous tentacles to kill stony corals and defend its space on coral reefs (den Hartog, 1980). In these species, the use of aggressive organs allows the corallimorpharians to damage competitors and overgrow them on hard substrata. In the Seychelles, polyps of *Discosoma howesii* have been observed to form patches of considerable size that overgrow and apparently kill stony corals (den Hartog, 1980). In an anecdotal report, Moosleitner (1989) termed *Rhodactis* as killer anemones due to their imputed ability to damage and overgrow corals in the Maldives (Langmead & Chadwick-Furman, 1999). Corallimorphs on Funadhoo reef are, therefore, not only dominating the reef due to rapid colonisation, but they also have the ability to actively competing for space using aggressive organs.

Observations in the Egyptian Red Sea indicate that *R.rhodostoma* polyps grow over the bases and sides of *Acropora* spp coral colonies, and in some cases completely cover their skeletons (Land and Chornesky, 1990). The interactive distances observed in the present study between corallimorpharians and stony corals are similar to those found from interactions among scleractinian corals (Sheppard, 1980). A study by Muhando *et al,* 2002 showed corallimorpharians tend to negatively affect scleractinian coral. Closer observations showed colonies of *Porites* spp and *Acropora* spp that were in contact had their edges bleached, indicating stress. The results show that the corallimorpharian wins during contact competition with encrusting algae sponges, hydrozoans corals and branching stony corals, but is unable to overgrow massive stony corals, actinian sea anemones and some soft corals.

R.rhodostoma appears to dominate patches effectively on the reef via exploitation of open space by asexual reproduction (Chadwick-Furman and Spiegel, 2000).

As well as competing with live scleractinian corals, several studies have reported anemones colonising areas of old dead coral and rubble. The corals *Discosoma dawydoffi* and *Discosoma howesii* were found to dominate the reef slopes of the Pulau islands in Malaysia, where both species colonised the collapsed, dead coral branches (mostly branching *Acropora* spp) and coral rubble forming extensive beds of contiguous aggregations (Tkachenko *et al,* 2007). In addition, rubble overgrown by anemones and corallimorpharians has been shown to inhibit hard coral survival and stabilize the alternate state (Tkachenko *et al,* 2007). The competition for space that coral rubble provides is evident on many coral reefs. Fox *et al* (2003) revealed that after clearing soft coral from the coral rubble, small scleractinian colonies were found below. These hard corals fared much better once the soft coral was removed, suggesting that although they had been surviving amid the soft coral, their growth was inhibited (Fox *et al,* 2003). The inhibition of settlement and development of scleractinian corals in the prevent study will have a profound effect on the recovery of the reefs.

4.3.6 Phase Shifts from coral to corallimorpharians

Numerous studies have shown sea anemones to be an alternative stage instead of algae in phase shifts following mortality of stony corals (Chadwick- Furman and Spiegel, 2000, Kuguru *et al*, 2004, Tkachenko *et al,* 2007). Tiao-Shi Reef, southern Taiwan has suffered from anthropogenic impacts and natural disturbance from typhoons, which has reduced diversity and has degraded reefs into vast areas of coral rubble (Tkachenko *et al,* 2007). Since the disturbance, *Acropora* rubble piles have been colonised by dense populations of solitary sea anemones *Condylactis* spp (Tkachenko *et al,* 2007). In recent years, the anemone dominated zone has become covered by *Discosoma indosinesis* as well as *Condylactis* spp. A coral recovery zone was occupied by *Montipora stellata,* which succeeded to dominant due to rapid development; however, a dramatic phase shift was seen to long term dominance by anemones with almost no coral recovery in the adjacent-dominated zone (Tkachenko *et al,* 2007). Studies on the coral reefs on the Great Barrier Reef (GBR) have shown that phase shifts are not always persistent. Disturbance on the reefs was initially followed by an increase in algal cover, soft corals and corallimorpharians; however, this was a transient stage. In order for it to become a permanent shift would require either failure of recruitment, high post settlement mortality of hard corals, or both (Ninio *et al*, 2000). With phase shifts to corallimorpharians the coral reefs may be composed of a mosaic of patches at different developmental stages, with each individual patch following a course which is influenced by local and regional processes (Bythell *et al*, 2000). Continued monitoring of the survey sites of this study should be implemented to assess whether the shift to *Discosoma* on the shallow reef at Funadhoo will be persistent or merely a stage in recovery to disturbance.

4.4 Acropora corals (>50 cm)

4.4.1 Abundance of Acropora coral (>50 cm) at 5 m on each reef

A high ratio of live to dead tabular *Acropora* coral (>50 cm) was recorded at Funadhoo and Gemendhoo (3.4:1 and 4:1 live to dead coral respectively). The high proportion of live tabular *Acropora* coral greater than 50 cm on the reefs indicates that this genus is becoming more predominant and stable within the reef ecosystem. The predominant post-bleaching settlers belonged to the families Agariciidae and initially Fungiidae. The loss of the previously dominant Acroporidae and Pocilloporidae lead to the preponderance of Agariciidae, and not until 6 years post bleaching was the typical shallow-water species shown to become more prominent (Schuhmacher *et al*, 2005). After the mass bleaching in 1997-98, *Acropora* tables which died during the mass bleaching in 1997-98 were reported to still be standing up until 2004, where respective tables were found to have completely collapsed (Schuhmacher *et al*, 2005). The dead tabular *Acropora* corals in the present study were recently dead and still maintained their shape and structure. The recent death of large *Acropora* corals may be due to their exposure to physical destruction from the southwest monsoon season. In the Maldives, the wet southwest monsoon lasts from the end of April to the end of October and brings strong winds and storms, which have the ability to disrupt the shallow water corals unable to withstand the conditions. The reduction in large *Acropora* not only reduces the parent stock on the reefs, but also reduces the three dimensional structure of the reef flat and crest, where tabular *Acropora* corals can no longer act to catch new settlers. The number of *Acropora* corals were recorded between 2000 and 2004 and divided by size groups (Schuhmacher *et al*, 2005). Whereas the smaller size groups (0-5, 5-10 and 10-20cm) doubled between 2000 and 2001, their number remained almost stable in the following years, and the larger size groups (20-50 and 50-100cm) showed only a slow linear increase (Schuhmacher *et al,* 2005). Individuals colonies of *Acropora clathrata*, were reported to have settled on the fragmented substrate and reached 25-30cm diameter by 2004, which, constituted the beginning restoration of the topography, but would not compensate the massive loss of reef framework. The high abundance of *Acropora* corals (>50 cm) in the present study indicates that conditions have been favourable for colonies to establish and grow, therefore, developing the reefs 3D formation, increasing parent stock and further enhancing coral recruitment.

4.4.2 Physical damage on Acropora coral (>50 cm) at 5 m on each reef

Examining corals greater than 50 cm gives an indication on the disturbance occurring on the reef since 1997-98. The number of new Acroporidae, which was conspicuously low up to 2002, was shown to increase in 2004, and was indicative of a return to their previous role in reef frame building (Schuhmacher *et al,* 2005). Based on data collected over the past 6 years and the behaviour of different species with respect to growth patterns, Schuhmacher *et al* (2005) predicted that Maldivian reefs cannot reach a pre-bleaching state in less than 30 years. The reduction in recruitment from 2001 to 2002 was from 25.9 to 16.5 colonies per m^2 of table surface, a possible explanation being that it is a competitive spread of algae displacing the young coral colonies. If this development should continue, the building of new stands of *Acropora* tables, typically characteristic of a healthy upper reef slope, will be considerably delayed. Loch *et al* (2004) showed that between 2001 and 2002 there was an actual decrease on *Acropora* tables and flattening of the growth curve in transects. It is encouraging that *Acropora* recruits were found in high abundance on the reefs in the present study, as their importance to the reef structure and future recruitment is unprecedented.

4.5 Future protection and management

India, Maldives and Sri Lanka together form the South Asia Node of the Global Coral Reef Monitoring Network (GCRMN), supported financially by the UK Department for International Development (DFID). The low lying atolls of the Maldives are particularly vulnerable to sea level rise and potential climate change impacts. Coastal inundation, saline intrusion of fresh groundwater and coastal erosion are among the most serious impacts. Sea level rise due to climate change, therefore, will adversely affect the cities and agricultural and industrial lands due to salt water intrusion. In 2000, up to 25 marine protected areas (MPAs) in the Maldives were declared under the Environment Act of the Maldives and administered by the Ministry of Home Affairs, Housing and Environment (MHHE). All are important dive sites for tourists. They are generally small, without specific assessment of biodiversity, except for flagship species such as sharks, rays and groupers. The main threats to these MPAs are from overfishing, anchor damage, coral mining and diver damage. This pro active approach is optimistic for environmental monitoring in the Maldives because as a country, they are reliant on the 'health' of coral ecosystems for numerous resources and high economic revenue.

As previously mentioned (see section 1.4) tourism in Baa atoll is increasing within the atoll, but more specifically a new resort is being constructed opposite the surveyed reefs. It is important through suitable education, that developers, tourists and local Maldivians understand the need to protect the reefs within the atoll, for economic as well as environmental purposes. As the reefs in the present study show variation in substrate composition, coral diversity and recruitment on small spatial scales it is imperative that monitoring of these reefs continues in order to protect the reefs and aid the recovery process. Further studies should aim to detail and incorporate a wider selection of reefs within Baa atoll to gain a true representation and appreciation for the status of coral reefs within the atoll.

Prior to 1997-98, literature on coral reef ecology in the central and western Indian was limited to few locations and few spatial scales. In the Maldives, literature focused on the destruction of reefs used in coral mining and the development of artificial structures to enhance reef recovery (Clark and Edwards, 1994). After the mass bleaching event in 1997-98, there was an increase in the abundance of literature which focused on detailing the damage caused by elevated SSTs (McClanahan, 2000; Edwards *et al,* 2002). Since 1998, monitoring programmes have been developed in areas with a high amount of tourism however these studies are restricted to few reefs within few atolls. To the present day, no studies conducted in the Maldives examine coral diversity at large spatial scales; therefore generalisations are commonly made on the 'health' of coral reefs in the Maldives. Further studies should be directed at examining Maldivian coral reefs on a larger spatial scale to provide an accurate representation of the state of reefs in the Maldives.

In Baa atoll, a recent rapid assessment of the biodiversity on the coral reefs reported large variation between islands, which was attributed to the reefs position and locality

(Guignard, pers. comm). In the present study only the northern sides of the reefs were examined due to resource and time limitations. Further study could examine the diversity and recruitment around the entirety of the coral reef islands which may differ due to typographical and hydrodynamic variation. Biological and physical factors which may differ on each side of the reefs may impact the abundance and composition of recruits, subsequently affecting reef recovery and development.

Many recruitment studies based in the Maldives have used settlement plates to assess the abundance and composition of recruits colonising the reefs (Loch *et al,* 2002; Schumacher *et al,* 2005). The settlement plates are secured underwater for at least 3 months to 2 years and therefore it takes a long time to collect data. In comparison, in the present study the abundance of recruits was recorded in situ and was not designed to examine any temporal variation in recruitment assemblages. Further experimentation, however, could examine the temporal variation in recruitment on the surveyed reefs which would help document and predict their future development. To further the study of recruitment on the reefs, it could be useful to identify the substrate on which the recruits are colonising. Post 1997-98, studies in the Maldives reported a significant number of recruits colonising dead *Acropora* tables and large, stable artificial structures (Loch *et al,* 2002). Determining the substrate on which recruits are settling would indicate a link between substrate composition and recruitment on the reefs. Further protection can be afforded with increased knowledge of how the reefs are recovering and developing after mass disturbance.

4.6 Conclusion

The present study aimed to assess features of Maldivian coral reefs in relation to small scale spatial variation and depth. Variation in substrate composition between depths and the majority of sites is reported; however, no distinctive pattern between depths is indicated. Differences in substrate composition is not uncommon in reef systems in archipelagos and can therefore be attributed to a variety of natural biological or physical factors as well as either chronic or acute anthropogenic impacts acting on the reefs throughout the 10 year recovery process. The high proportion of live coral cover (42%) reported in the present study is an encouraging indication on the recovery of Maldivian coral reefs in Baa atoll. Spatial variability in live coral cover between studies conducted in the Maldives should be expected during recovery of reefs as they are still in an ongoing process of re-colonisation.

Anthropogenic pressures are affecting the shallows of Undoodhoo and Funadhoo reefs which has been reflected in the lower percentage of live coral cover recorded at 1m. Such differences are imperative to document, so that continued monitoring can be achieved as the reefs face being subjected to an increase in tourism, which has the potential to limit reef recovery.

Significant variation in recruitment densities between depths and sites is reported, however no general pattern in densities between the reefs is shown. Acroporidae and Faviidae recruits were abundant on the reefs at 5m and 12m, and Dendrophylliidae at 18m, which are likely to have derived from the abundance of parent stock shown at the respective depths. The density of coral recruits recorded in the present study is encouraging as they show the survey sites are not recruitment limited. Scleractinians dominated the coral community at each depth on the reefs. Scleractinian coral diversity at 5 m, 12 m and 18 m did not differ significantly; however diversity was significantly different at 1 m. *Acropora* and *Pocillopora* dominated the reef at 1m and were recorded at a significantly lower abundance at depth. In deeper water, coral assemblages are dominated by *Porites*, *Favites* and *Tubastrea*. Similarities in coral diversity from 5 m to 18 m suggest that corals between these depths are in a similar process of recovery. The majority of sites are showing approximately 100% more live *Acropora* coral (>50 cm) in comparison to dead coral. In situ observations showed damaged was caused through physical destruction from storms, damage from Parrotfish (family Scaridae) and from contact from SCUBA divers and snorkellers.

The results of the present study indicate that recovery on Maldivian coral reefs is possible in 10 years following severe coral mortality; however spatial variation between reefs in close proximity has occurred in response to large scale disturbance. As such variation between reefs of close proximity is shown it is likely that local physical and biological factors are having an impact on reef recovery. Temperature projections, however, suggest that in approximately 20 years SST peaks will occur too frequently to permit recovery (Sheppard, 2003). The Maldivian government has recognised the need for base line information, and therefore the initiation of the Baa Atoll Project is an optimistic approach to conservation and monitoring within the atoll. Effective protection requires knowledge on the current state of the reefs, and with projected increases in tourism in the next few years' immediate action is required. An adaptive management approach should be used in order to fully protect the reefs from anthropogenic impacts which may hinder further reef recovery.

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Personal Communications

Guignard, 2008

Stevens, 2008

Tomasetti, 2008

7. APPENDIX

7.1 Appendix 1

Lists of scientific and diving/snorkelling equipment used during surveys and electronic equipment and programmes used during analysis and report writing.

Scientific equipment

- GARMIN GPS
- 50 m measuring tape
- 1 m^2 quadrat
- 2 underwater slates/pencils
- 1 x 10 mega pixel Sea & Sea DX-1G Digital underwater camera
- 1 x 8 mega pixel Olympus 850 SW Digital underwater camera (back up)
- 1 x mesh bag

Diving/snorkelling equipment

- Mares mask
- Aqua Lung regulators
- Aqua Lung fins
- Mares BCD
- Surface Marker Buoy
- O’Neill wetsuit

Electronic equipment and programmes

- HP Compaq 6720s laptop
- Coral Point Count with excel extensions (CPCe)
- Minitab version 14
- PRIMER version 6
- Microsoft Office Excel 2007
- Microsoft Office Word 2007

7.2 Appendix 2

Maldivian Coral Code for Coral Point Count with Excel extensions

"ACR","Acroporidae"

"AST","Astrocoeniidae"

"POC","Pocilloporidae"

"EUP","Euphyllidae"

"OCU","Oculindae"

"SIDE"," Siderasteridae"

"AGA","Agariciidae"

"FUN","Fungiidae"

"PEC","Pectiniidae"

"MER","Merulinidae"

"DEN","Dendrophylliidae"

"MUS","Mussidae"

"FAVI","Faviidae"

"POR","Poritidae"

"M","Corallimorphs"

"ALC","Alcyoniidae"

"THI","Anthipathidae"

"GORG"," Gorgoniidae"

"S","Sponges"

"MA","Macroalgae"

"DCA","Dead coral with Algae"

"CA","Coralline Algae"

"Z","Zoanthids"

"OL","Other live"

```
"SPR","Sand, pavement, rubble"
"TWS","Tape, wand, shadow"
"U","Unknowns"
"AM", "Montipora","ACR"
"AA", "Anacropora","ACR"
"AC", "Acropora","ACR"
"AS", "Astreopora","ACR"
"STY", "Stylocoeniella","AST"
"MAD", "Madracis","AST"
"POL", "Pocillopora","POC"
"PSTY", "Stylophora","POC"
"PSE", "Seriatopora","POC"
"EUP", "Euphyllia","EUP"
"PHY", "Physogyra","EUP"
"OG", "Galaxia","OCU"
"SID", "Siderastrea","SIDE"
"PSA", "Psammocora","SIDE"
"COS", "Coscinaraea","SIDE"
"AGAR", "Agariciidae","AGA"
"PV", "Pavona","AGA"
"LEP", "Leptoseris","AGA"
"PG", "Pachyseris","AGA"
"FN", "Fungia","FUN"
"ECH", "Echinopora","PEC"
"PP", "Pectinia","PEC"
"MU", "Merulina","MER"
"FY", "Tubastrea","DEN"
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"ACN", "Acanthastrea","MUS"
"LOB", "Lobophyllia","MUS"
"FA", "Favia","FAVI"
"FV", "Favites","FAVI"
"FG", "Goniastrea","FAVI"
"FP", "Platygyra","FAVI"
"OU", "Oulophyllia","FAVI"
"LE", "Leptoria","FAVI"
"FM", "Montastrea","FAVI"
"FD", "Diploastrea","FAVI"
"CY", "Cyphastrea","FAVI"
"EH", "Echinopora","FAVI"
"PO", "Porites","POR"
"PG", "Goniopora","POR"
"PA", "Alveopora","POR"
"MOR",  "Corallimorphs","M"
"ALCY",  "Alcyoniidae","ALC"
"ANTH", "Anthipathidae","THI"
"GOR",  "Gorgoniidae","GORG"
"IOP",  "Acarnus","S"
"MIC",  "Clatharia","S"
"CRAM",  "Monanchora","S"
"SPO",  "Amphimedon","S"
"DYS",  "Dysidea","S"
"SQUA",  "Squamariaceae","MA"
"POM",  "Chaetomorpha","MA"
"CHLO",  "Chlorodermis","MA"
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"AMP", "Amphiroa","MA"

"DICT", "Dictyota","MA"

"TURB", "Turbinaria","MA"

"PAD", "Padina","MA"

"TURF", "Turf","MA"

"DCA", "Dead coral with algae","DCA"

"ODC", "Old dead coral","DCA"

"RDC", "Recently dead coral","DCA"

"CALG", "Coralline algae","CA"

"PAL", "Palythoa sp.","Z"

"ZO", "Zoanthid","Z"

"ASC", "Ascidian","OL"

"O", "Other","OL"

"NEP", "Nephtheidae","OL"

"ALC", "Alcyoniidae","OL"

"ANE", "Stichodactylidae","OL"

"PLU", "Plumularidae","OL"

"BC", "Antipathidae","OL"

"NID", "Nidaliidae","OL"

"P", "Pavement","SPR"

"R", "Rubble","SPR"

"S", "Sand","SPR"

"TAPE", "Tape","TWS"

"WAND", "Wand","TWS"

"SHAD", "Shadow","TWS"

"UNK", "Unknown","U"