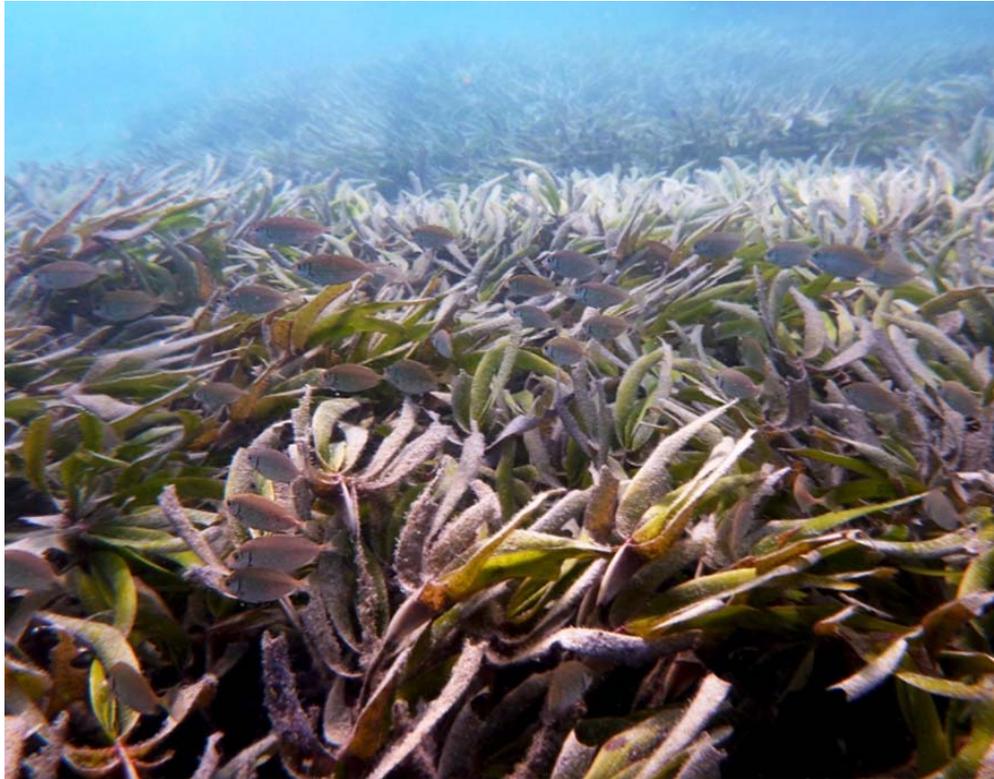


Influence of landscape configuration and within-patch variation on fish abundance, size and functional groups in tropical seagrass beds



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Master Degree Project Thesis 60 hp

November 2013

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TABLE OF CONTENTS

Abstract	4
Introduction	4
Aim	6
Methods	7
Location	7
Study species	8
Fish Census	8
Habitat mapping	10
Data processing	10
Juvenile and adult fish.....	10
Schooling fish	11
Functional groups	11
GPS-coordinates.....	11
Defining seascapes.....	11
Creation of a habitat map and integration with fish census.....	11
Statistical analysis	12
Results	12
Fish census	12
Factors and scales affecting fish abundance	13
Differences among sites	13
Within-patch variables affecting fish abundance.....	15
Large scale variables affecting fish abundance	16
Factors and scales affecting functional groups	17
Differences among sites	17
Within-patch predictors affecting fish abundance within different functional groups	19
Large scale predictors affecting fish abundance of different functional groups	20
Discussion	22
Large scale Effects on fish abundance	23
Large scale effects on functional groups	23
Within-patch variables affecting fish abundance	24
Within-patch variables affecting functional groups	24
Sources of error and suggestions of improvement	25
Surveyor bias.....	25
Map accuracy.....	25

Assumption of seagrass homogeneity	25
Visual census	25
Not evaluated variables.....	26
Conclusion and management implications	26
Acknowledgements	27
References	28

ABSTRACT

The tropical seascape consists of coral reefs, mangroves and seagrass beds that are connected via migration of organisms (fish in particular) and abiotic factors such as hydroecological flow. It is therefore important to view the whole seascape as an entity when examining only one part of it, in this case seagrass beds. The tropical seascape is of high value to local fishers and proper evaluation is the key for sustainable resource management. In the present study, it was proposed that large scale spatial variables, such as landscape configuration, will be of equal if not even larger importance than smaller within-patch variables, such as seagrass structural complexity, to determine fish community patterns in seagrass beds. Visual fish census was carried out in 15 *Thalassodendron ciliatum* seagrass beds around Zanzibar, Tanzania, in combination with bottom habitat mapping using maximum likelihood classification and Landsat satellite images. Fish observed was then divided into juveniles and adults, and assigned a functional group. It was established that fish abundance and assemblage structure can be affected by large scale environmental factors as well as small scale, within-patch factors. Regarding the small scale variables, depth influenced adult fish, whereas canopy height affected juvenile fish abundance. Herbivorous fish preferred middle habitats contrary to predatory and omnivorous fish that preferred edge habitats. Large scale assessment showed that proximity to mangroves and high amount of algae increased juvenile fish abundance, whereas adult fish abundance increased with amount deep water and coral. Herbivores resided to higher degree in areas close to mangroves whereas omnivores and corallivores increased with amount of deep water. Patterns were much stronger for all large scale variables compared to the within-patch variables. The findings of this study indicate a strong need to incorporate landscape scale studies when evaluating the variability of seagrass fish communities.

INTRODUCTION

The term “tropical seascape” refers to areas in shallow tropical waters where mangroves, seagrass beds and coral reefs are closely intertwined like a mosaic (Ogden 1988). This type of structural matrix of habitats allows for habitat connectivity, meaning cross-habitat migration of animals (Nagelkerken *et al.* 2000; Berkström *et al.* 2013). The proximity of the different habitats will also allow for ecological connectivity (Berkström *et al.* 2012), which includes disturbance processes and hydroecological flows, whereas habitat connectivity solely focuses on the connectedness between suitable habitat patches for any given species (Fischer & Lindenmayer 2007). For instance, coral reefs act as wave breakers and help to create the calm and protected environment in mangrove and seagrass habitats, and in turn mangroves and seagrass beds accumulate pollutants, organic material, and offset freshwater runoff for coral reefs (Harborne *et al.* 2006). Coral reefs may also provide clear oceanic water from deeper areas which would increase abundance of zooplankton, fish larvae and predatory fish in seagrass beds (Kochzius 1997; Unsworth *et al.* 2008). Low energy environments (with limited currents, waves, sedimentation events and winds) tend to result in more homogeneous seascapes whereas high energy environments result in patchier seascapes (Boström *et al.* 2006). These variations in environmental settings, or large scale variables, may affect local faunal species composition. The faunal species composition may also in turn affect the habitat itself, since some species are known to migrate and thus transfer energy between habitats or habitat patches. Grunts for instance feed in seagrass beds at night and transfer energy to the coral reef by fecal matter or by being predated upon during days (Nagelkerken *et al.* 2000; Appeldoorn *et al.* 2009). Grunt excretion has been shown to double the amount of some

nutrients on coral reefs (Meyer & Shultz 1985) and increase the growth rate of coral specimens (Meyer *et al.* 1983). The importance of ecosystem interactions in marine environments is still to the most part speculative due to a low number of quantitative studies (Beets *et al.* 2003), but recently landscape ecology theory has started to be applied to tropical seascapes (e.g. Gullström *et al.* 2008, 2011; Berkström *et al.* 2013), which is a way to assess this issue.

Seagrass beds are acknowledged as one of the most diverse ecosystems on earth and are highly productive (Hemminga & Duarte 2000). They are found in most shallow nearshore areas around the world (Green & Short 2003) where they have a number of functions, e.g. to modify currents and waves, and to filter nutrients and store sediments (Hemminga & Duarte 2000; Green & Short 2003). In the Indo-Pacific region, seagrass ecosystems show a high abundance of juvenile fish (e.g. Parrish 1989; Nagelkerken 2001; Nagelkerken *et al.* 2009), which is a reason why they are considered nursery grounds for fish (Nagelkerken *et al.* 2009). Seagrass beds provide shelter from predators and are a central source of food for many taxa, two factors which may increase the probability of juvenile survival (Heck & Orth 2006; Horinouchi 2007). Once the fish increase in body size the preference of habitat may shift as a tradeoff between food availability and predation risk (Dahlgren & Eggleston 2000).

In the Western Indian Ocean a great part of the livelihood of local people is immediately dependent on ecosystem services provided by the heterogeneous tropical seascape, and seagrass beds in particular (Jiddawi & Öhman 2002; Nordlund 2012; Cullen-Unsworth *et al.* 2013). For instance, in Zanzibar, it has been estimated in year 2000 that approximately 23 000 fishers were active, catching about 15 000 tons of fish (Jiddawi & Öhman 2002). In addition to fishing, collection of invertebrates from shallow seagrass areas in the intertidal zone and algal farming are important sources of food and income for many Zanzibaris (Bergman *et al.* 2001; de la Torre-Castro & Rönnbäck 2004; Gössling *et al.* 2004; Nordlund *et al.* 2010). Seagrasses all over the world are affected by human activities and are constantly decreasing (Green & Short 2003; Orth *et al.* 2006). Large-scale impacts on seagrasses include eutrophication, aquaculture and coastal development (Ruiz & Romero 2003; Pergent *et al.* 2006; Burkholder *et al.* 2007), while more local-scale impacts are for instance dredging, destructive fishing methods and boat anchoring (Erfetmeijer & Lewis 2006; Orth *et al.* 2006). A reduction of seagrass areas may be devastating to the local people (Hemminga & Duarte 2000; Waycott *et al.* 2009).

For a healthy and resilient seascape certain types of fish may be more important than others. Just as different habitats provide different services, so does different functional groups of fish. Bellwood *et al.* (2004) and Mumby *et al.* (2006) among others found that micro-algal feeding fish (i.e. grazers) increase the resilience of coral reefs and help them stay healthy. If a phase shift has occurred and reefs are covered in macroalgae, it is the macro-algal feeders which have the means to reverse this change, whereas herbivores which feed on algal-microfilms are of little help (Bellwood *et al.* 2004). It is possible that similar mechanisms are important in seagrass areas where algal-films need to be kept off the seagrass in order to keep a healthy environment, but seagrass areas are far less studied in this context than coral reefs.

Although configuration of a seascape may influence fish abundance and composition, factors at smaller scales may also be important. Such factors could for instance be depth, canopy height and seagrass shoot density (Koch 2001; Gullström *et al.* 2008, 2011). To better understand and assess effects of factors at different scales on fish community patterns there is a need to evaluate small- and large-scale factors together, and in addition, focusing on

functional groups to be able to evaluate effects of different environments and localized conditions.

AIM

The overall aim of this study was to apply a landscape ecology approach to assess the effects of seascape configuration, plant structure and environmental variables on fish abundance, size, composition and functional groups in seagrass beds around Zanzibar, Tanzania.

The specific questions of this study were:

- Which factors and scales (within-patch scale or landscape scale) are the most important predictors of fish abundance, composition and size?
- How do abundance and distribution of fish within different functional groups vary depending on small- and large-scale factors?

METHODS

LOCATION

The fieldwork was divided into two main parts, habitat mapping and fish census, which were conducted from November 2012 to January 2013 at Unguja (also known as Zanzibar Island or Zanzibar), the main island of the Zanzibar archipelago, Tanzania. Zanzibar is located approximately 40 km from the mainland of Tanzania and has an area of about 1650 km² (Siex 2011). Zanzibar is a developing area which has around one million inhabitants (National Bureau of Statistics & Ministry of Finance 2011), and the local people are highly dependent on fishing and tourism (Jiddawi & Öhman 2002).

Fish census was performed at 15 different sites in the shallow coastal waters around the island (Figure 1), while habitat mapping was performed in shallow waters, in mangroves and on land. Each of the 15 sites consisted of a continuous or patchy seagrass bed dominated by the seagrass species *Thalassodendron ciliatum*.



Figure 1. Locations of the fifteen study sites on Zanzibar Island, Tanzania.

Zanzibar contains a large number of marine conservation areas. The sites in Chakati and Marumbi are located in Chwaka Bay, a sheltered area protected by a reef system stretching along the coastline, within the Chwaka Bay marine conservation area (Department of fisheries and marine resources 2010). On the landward side of Chwaka Bay, there is a dense mangrove forest of approximately 3000 ha (Mohammed *et al.* 1995), the largest one in Zanzibar (Department of fisheries and marine resources 2010). Chwaka Bay also contains vast areas of seagrass, algae and sponge communities with conservation priority (Department of fisheries

and marine resources 2010). In Marumbi net fishing is not allowed and rangers frequently patrol the area. Machango and Mchangamle are situated relatively close to large mangrove areas and Mchangamle is also located adjacent to a large coral reef area. Chukwani is located close to a small mangrove forest (within hundreds of meters) (Department of fisheries and marine resources 2010). The site at Chumbe Island, a no take marine protected area, hosts one of the most pristine coral reefs in East Africa, and the no take regulations are heavily enforced by the rangers stationed on the island (Nordlund *et al.* 2013). All other sites are also found within marine conservation areas, but the level of enforcement is questionable.

STUDY SPECIES

Around the island of Zanzibar there are 13 known species of seagrass (Knudby & Nordlund 2011). In this study, *Thalassodendron ciliatum* was chosen as study species because it is one of the largest seagrasses, i.e. with high seagrass structural complexity, creating “forests” with great opportunity for fish to hide and feed (Figure 2). Several studies have suggested that seagrass structural complexity is an important factor for regulation of fish assemblages (Bell & Westoby 1986; Hyndes *et al.* 2003; Horinouchi 2007; Gullström *et al.* 2008).

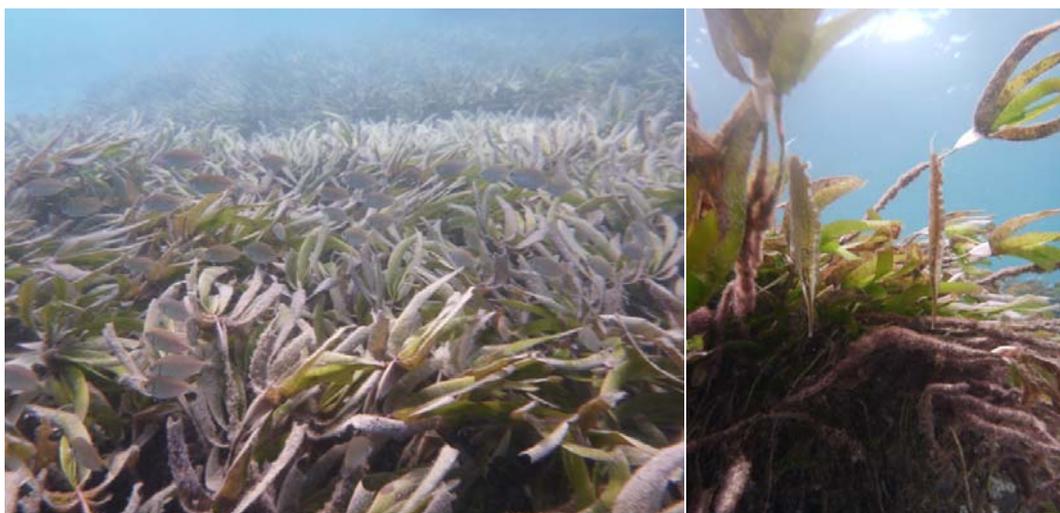


Figure 2. A school of juvenile specimens of *Siganus fuscescens* (left) and two specimens of *Aoliscus punctulatus* (right) in a *Thalassodendron ciliatum* bed. Photos: Karolina Wikström, Gustav Palmqvist.

FISH CENSUS

In each of the 15 fish census sites (Figure 1), observations of fish were carried out along twelve 25 x 4 meter belt transects, six placed in the meadow centre and six places in the edge zone (Figure 3), resulting in a total of 180 transects around Zanzibar. Usually the placement resulted in an encirclement of the middle transects by the edge transects, but in some cases the *T. ciliatum* bed was so large that all edge transects were placed on only one or two sides of the area. All transects were placed haphazardly within the area, but always within large patches of *T. ciliatum*. If the seagrass bed was patchy a minimum of 60% of each transect line had to be within the *T. ciliatum* covered area. This was to ensure a minimum patch size in combination with a maximum patch distance. The edge transects were placed as close to one meter inside the actual edge of the seagrass bed as possible. All transects had to be placed at a minimum of 10 meters apart.

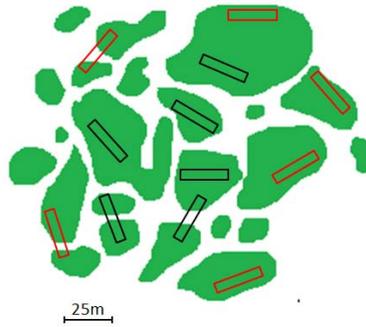


Figure 3. Illustrative example of a typical patchy *Thalassodendron ciliatum* site where fish census was conducted. Red squares indicate edge transects and black squares indicate middle transects. Transects were 25 x 4 m in size.

GPS-coordinates, depth, time and date were noted at both ends of each transect line. Mean seagrass canopy height was calculated by taking 10 height measurements haphazardly distributed along the transect line (always by the same person). The two tallest shoots were removed when calculating the mean canopy height per transect following Duarte & Kirkman (2001). Seagrass shoot density was estimated by counting all shoots in a 25 x 25 cm quadrat next to one of the 5 m nodes. Dead shoots were not counted and forked shoots were counted as one (although they were relatively rare). The same person conducted all density measurements in all sites. Canopy height and shoot density were included in the study since they have been shown to influence fish abundance (e.g. Hyndes *et al.* 2003, Gullström *et al.* 2008; 2011).

Fish census was conducted along each belt transect during 5 minutes. All fish were identified to species level and put in one of the following size classes for total length: 0<4 cm, 4<8 cm, 8<12 cm, 12<16 cm, 16<20 cm, 20<30 cm 30<40 cm 40<50 cm 50<60 cm and >60 cm. The number of individuals in large schools was roughly estimated, and subsequently all schooling fish were removed from the analyses. If an unknown fish species was encountered a quick drawing was made and the equivalent time added to the five minutes. All fish counts were conducted at water depths of approximately 3 m. More than 80% of the transects had a depth deviation of ± 0.5 m or less and only two transects (1.1%) were outside the ± 1 m interval. Due to the depth being set as a constant in the analyses, some transects were censused at high tide and some at low tide. Fish counts were, however, only conducted on days when the overall difference between low and high tide did not exceed 3 m, usually the days during, or close to, neap tide.

Before the fish census commenced the two observers (KW and GP) spent one month learning to identify common fish species and fish families around Zanzibar, via images online and various fish books. Their identification skills were of equal levels throughout the study as they continuously updated their fish repertoire. They both conducted equal numbers of transects and equal numbers of edges and middles. Of the 7969 fish counted (schooling fish removed) GP counted 57.4%. The proportion of the fish sizes 12<16, 16<20 and 20<30 cm was larger in KW's counts than GP's, but only the size class 20<30 cm showed a significant difference ($p < 0.01$, Figure 4). It has been acknowledged that the visual census technique may result in a large underestimation of fish, especially small cryptic species hiding in seagrass areas and

species known to migrate to seagrass areas nocturnally (Recksiek *et al.* 1991; Beets *et al.* 2003; Unsworth *et al.* 2007; Appeldoorn *et al.* 2009).

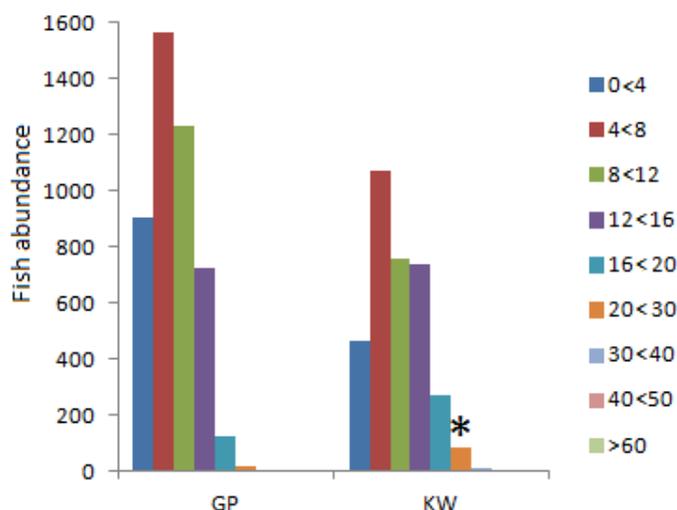


Figure 4. Number of fish specimens per size class counted by the two observers GP and KW. The y-axis shows fish abundance corresponding to fish per m². A star shows significant surveyor bias between GP and KW.

HABITAT MAPPING

In order to map the bottom habitat a GPS coordinate was taken for a specific point, and the 4 x 4 m surrounding square was categorized using maximum-likelihood estimation following Knudby & Nordlund (2011). The following habitat classes were used: Dense seagrass, Sparse seagrass, Coral, Mangrove, Algae, Sand, Pavement, Building and Coastal forest. “Dense seagrass” was defined as seagrass coverage over 40%, and “Sparse seagrass” as seagrass coverage between 10 and 40%. The time, date and depth at each point were also noted to be able to adjust the depth at the same coordinates in a Landsat satellite image. A total of 19 representative areas scattered around Zanzibar were visited and between 20 and 70 points were taken at each site, resulting in a total of 720 points. The mean horizontal accuracy of these points was 6 m. Additional points were later added from the raw data in Knudby & Nordlund (2011). Most points were collected by walking in the intertidal zone (including mangroves and coastal forests) during low tide, although some points were taken whilst swimming or by boat. Buildings or other human-built structures such as jetties were included to act as reference points.

DATA PROCESSING

JUVENILE AND ADULT FISH

Using the maximum total length of fish species (Froese & Pauly 2013), encountered specimens could be divided into number of adults and juveniles. A fish was considered juvenile when it was one third or less of its maximum total length (Nagelkerken & van der Velde 2002). This methodology has also been applied by e.g. Lugendo *et al.* (2005), Dorenbosch *et al.* (2006) and Unsworth *et al.* (2008). Fish larger than one third of the total length was considered adult. The size border between juvenile and adult fish will here be

called the “juvenile-adult-boundary”. The juvenile-adult-boundary often occurred in the middle of one of the size classes which were distinguished in the field, and it was hence difficult to determine if an individual was adult or juvenile in retrospect. This problem was bypassed by assuming equal survival rate of all age classes. The number of individuals encountered in the border size class was thus divided proportionally into juveniles and adults depending on the specific juvenile-adult-boundary for each specific species. Five species of schooling fish (see next paragraph) as well as all unidentified species were removed from these calculations.

SCHOOLING FISH

Some fish species were almost exclusively seen in schools too large to be counted accurately. These species were *Plotosus lineatus*, *Hyporamphus dussumeri*, *Sphyreanidae* spp. and two unidentified small silvery fish species (perhaps *Engrualidae*, *Atherinopsidae* or juvenile *Gerres oyena*). These five species/families were excluded from all statistics that concerned abundance since they would skew the results with their large and unpredictable numbers.

FUNCTIONAL GROUPS

All fishes were assigned to functional groups according to Froese & Pauly (2013), including herbivores, algal herbivores, omnivores, invertivores, invertivores/piscivores, corallivores and cleaners.

GPS-COORDINATES

Approximately 51% of the GPS-coordinates were taken using a Panasonic camera (lumix FT4) in the geodetic datum WGS 84 Lat/Long, and subsequently converted into UTM zone 37M. This transformation was performed using Gtrans version 3.63 supplied by Lantmäteriet, the National Land Survey of Sweden. Sites affected by coordinate transformations were Marumbi, Chakati, Machango, Mchangamle, Dimbani North, Dimbani South, Chumbe, Chukwani and Muyuni North. The remaining 49% of coordinates were taken using a Garmin GPS and did not need transformation. A few GPS points, taken using a proper Garmin GPS as well as with the Panasonic camera, were clearly misplaced when entering the points into the geographic information system (GIS) program ArcGIS. In total fifteen points were removed due to such problems.

DEFINING SEASCAPES

In order to turn the fifteen sites into fifteen seascapes, a mean coordinate point was calculated in the middle of the site using ArcGIS. A circular area with a diameter of 1 km was then created around each centroid point, and thus defining a seascape. Two seascapes, Dimbani North and Dimbani South overlapped slightly. All other seascapes had a minimum distance of 500 m in between them.

CREATION OF A HABITAT MAP AND INTEGRATION WITH FISH CENSUS

The habitat data points in combination with the extra habitat points gained from the raw data of Knudby & Nordlund (2011) were paired with a depth, a pixel colour and brightness on a Landsat satellite image with 30 x 30 m resolution. This was done using the maximum likelihood classification in accordance with Knudby & Nordlund (2011). The influence of clouds and the shadows they cast, as well as sensory malfunction causing blind spots in the Landsat data were avoided by combining twenty different images to make a more accurate prediction. The location of cloud shadows was calculated using the date, time of day, angle of the sun and the height of the clouds. In order to correct the miscalculation of algae as seagrass the data was balanced creating equal numbers of all observations, and by creating a “distance to land” category a majority of the incorrectly labeled coral points were correctly turned into

deep sea. Coral was also sometimes miscalculated as land in low tide images when the reef crest was emerged. This was solved by using an 80% rule, i.e. only pixels which were classified as land in over 80% of the images were considered land in the final map. This rule also solved the issue of the shallow emerged area in low tide being incorrectly labeled as land. The results were extrapolated to cover the whole area of Zanzibar, giving a complete bottom habitat map of the island with an accuracy of 69%. This map was used as a raster in ArcGIS to identify the amount of seagrass, coral and other habitat types within a seascape, as well as the distance from the seascape centroid to the closest mangrove area. To evaluate the importance of mangrove, two categories were created: area of mangroves within a 6 km radius and distance to closest mangrove (from the centroid point). This distance was chosen since the input of nutrients, organic matter and outwelling are believed to be negligible at these distances (Unsworth *et al.* 2008).

STATISTICAL ANALYSIS

All statistics were performed using the R system for statistical computing. Before analyzing, the assumption of homogeneity of variances was examined using Levene's test, and checks for normal distribution performed. Data were square-root transformed when needed, and if the assumptions were met it was tested with an analysis of variance (ANOVA). Data which failed to meet the assumptions were tested using Welsh test. The significance level was set to 5% in all tests. When analyzing within-patch scale response variables, 180 samples were used (each transect) and for large scale response variables only 15 samples were used (each seascape). Rows containing N/A were removed from the analysis since they go against the assumptions of the tests (only relevant for small scale variables).

Stepwise multiple linear regression technique was used to explore the relative importance of both small- and large scale predictor variables on total fish abundance as well as juvenile and adult fish abundances separately. Prior to the analyses, the predictor variables were checked for collinearity. The acceptable VIF-value was set to ≤ 10 , which called for removal of Dense seagrass, Pavement and Sand (based on the AIC-values and ecological knowledge).

When analyzing fish composition and functional groups only the fish constituting 1% or more of the total abundance were included in the CCA analysis in order to de-clutter the graph.

RESULTS

FISH CENSUS

In total 7967 fish individuals were counted during the fish census (schools removed). These individuals included 129 identified species, 26 unidentified species within known families, 4 known family categories where species could not be distinguished and 8 unidentified categories where neither species nor family could be identified. A total of 25 species had an abundance higher than 1% of the total fish abundance (Table 1). A high proportion, 97 taxa (58% including unidentified), were rare and had an abundance of less than 10 individuals. The most encountered species were *Siganus fuscescens*, *Ctenochaetus striatus* and *Leptoscarus vaigiensis*. *Siganus fuscescens*, *L. vaigiensis* and *Cheilio inermis* were the only three species encountered in all fifteen seascapes but *Thalassoma hebraicum*, *Labroides dimidiatus* and *Stethojulus albobittata* were also very common and seen in fourteen of the sites. The species presented in Table 1 were the most abundant species driving most patterns observed throughout the study.

Table 1: Fish species with a minimum abundance of 1% of the total abundance in total numbers and percentages (in parenthesis), juvenile abundance, adult abundance, number of sites they were observed in and their functional group belongings. Fish were considered juvenile when they were one third or less of their maximum length (Nagelkerken & van der Welde 2002; Froese & Pauly 2013) and the juvenile/adult abundances were calculated by assuming equal survival rate of sizes within the size classes noted in the field. Functional groups: HA = Algal herbivores, O = Omnivores, I = Invertivores, IP = Invertivores/Piscivores, Clean = Cleaners, N/A = no known feeding preference.

Species	Total abundance	Juvenile abundance	Adult abundance	Observed in number of sites	Functional group
<i>Siganus fuscescens</i> (Sigafusc)	1661 (20.8%)	1381.3	279.7	15	HA
<i>Ctenochaetus striatus</i> (Ctenstrai)	665 (8.3%)	22.5	642.5	8	O
<i>Leptoscarus vaigiensis</i> (Leptvagi)	400 (5.0%)	156.3	243.7	15	H
<i>Scarus psittacus</i> (Scarpsti)	388 (4.9%)	329.5	58.5	11	HA
<i>Dasycyllus trimaculatus</i> (Dasctrim)	295 (3.8%)	96.3	198.8	10	O
<i>Chromis atripectoralis</i> (Chroatir)	256 (3.3%)	21.0	235.0	7	I
<i>Archamia mozambiquensis</i> (Arcamoza)	244 (3.1%)	14.8	229.2	7	N/A
<i>Amphiprion chrysopterus</i> (Amphchry)	218 (2.7%)	59.6	158.4	12	I
<i>Chromis weberi</i> (Chrowebe)	211 (2.6%)	16.6	194.4	6	I
<i>Chlorurus sordidus</i> (Chlosord)	187 (2.3%)	94.3	92.7	9	O
<i>Abudefduf sexfasciatus</i> (Abudsexf)	152 (1.9%)	31.7	120.3	12	O
<i>Thalassoma hebraicum</i> (Thalhebr)	151 (1.9%)	31.2	119.8	14	I
<i>Chromis viridis</i> (Chrovidi)	150 (1.9%)	75.3	74.7	5	O
<i>Thalassoma amblycephalum</i> (Thalamb)	145 (1.8%)	142.7	2.3	5	I
<i>Apogon nigripes</i> (Apognigr)	141 (1.8%)	71.2	69.8	5	N/A
<i>Dasycyllus aruanus</i> (Dascarua)	136 (1.7%)	40.8	95.2	4	O
<i>Chrysiptera annulata</i> (Chryannu)	129 (1.6%)	12.7	116.3	11	O
<i>Cheilio inermis</i> (Cheiiner)	110 (1.4%)	68.7	41.3	15	IP
<i>Labroides dimidiatus</i> (Labrdimi)	109 (1.4%)	40.0	69.0	14	Clean
<i>Chromis dimidiata</i> (Chrodimi)	103 (1.3%)	39.8	63.3	5	O
<i>Plectroglyphidodon lacrymatus</i> (Pleclacr)	99 (1.2%)	0.8	98.2	8	O
<i>Siganus sutor</i> (Sigasuto)	98 (1.2%)	93.3	4.8	11	H
<i>Pomacentrus trilineatus</i> (Pomatril)	95 (1.2%)	15.0	80.0	12	O
<i>Chromis nigrura</i> (Chronigr)	90 (1.1%)	30.5	59.5	3	N/A
<i>Stethojulis albivittata</i> (Stetalbo)	82 (1.0%)	19.8	62.2	14	O

FACTORS AND SCALES AFFECTING FISH ABUNDANCE

DIFFERENCES AMONG SITES

There were large differences in the abundance of fish censused in the fifteen sites (Figure 5). The highest fish abundance was seen in Mchangamle, 1006 individuals in total (schools removed), and the lowest abundance was found in Marumbi, 220 individuals. The difference between the twelve transects within a site was however large in several sites, with the highest variation in Mchangamle (Figure 5). Chumbe Island showed a generally high fish abundance, which was significantly greater than in Chakati, Muyuni N, Marumbi ($p < 0.001$, $df = 14$) and

Nungwi Proper ($p < 0.05$, $df = 14$). A significant difference was also seen between Sume Island and Marumbi ($p < 0.05$, $df = 14$).

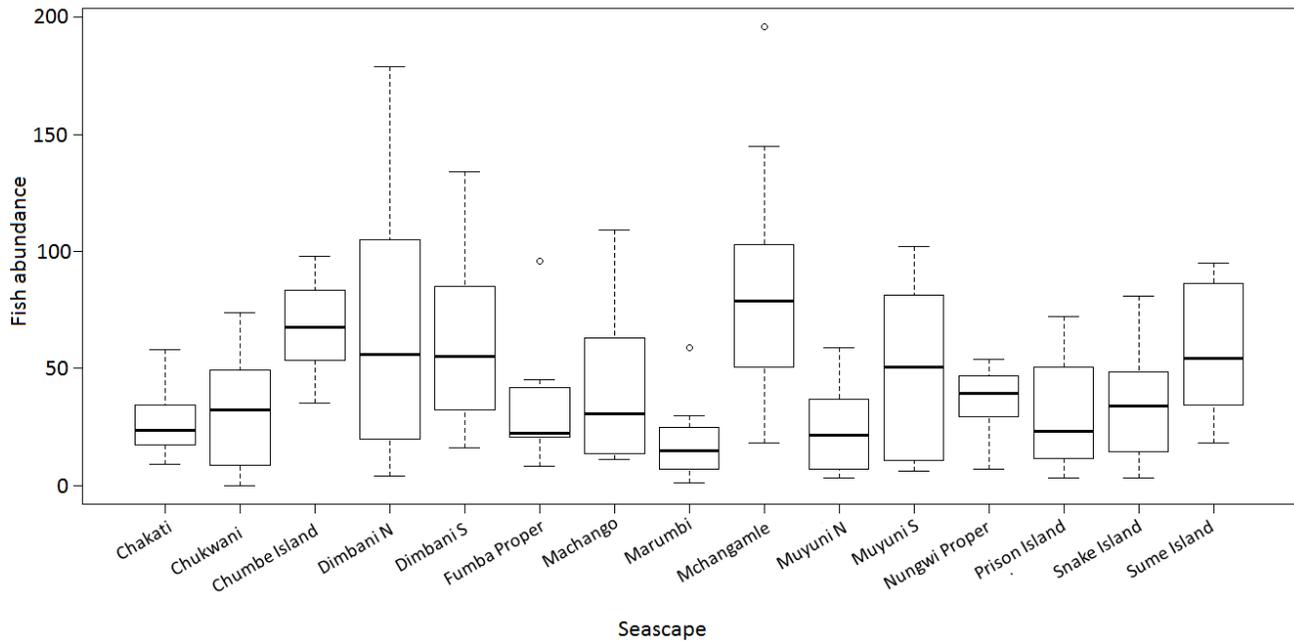


Figure 5: Fish abundance (n) in the fifteen study sites. Thick lines indicate median and boxes represent the interquartile range. Error bars indicate largest/smallest value or maximum 1.5 times the interquartile range. Circles are outliers.

The seascapes gave a broad spectrum of bottom habitat compositions (Figure 6). Some seascapes such as Dimbani North, Dimbani South and Muyuni South were examples of areas close to land and deep water, creating narrow habitable areas. Marumbi, on the other hand, is almost completely covered by dense seagrass, as was also the case in Nungwi proper even though not quite as much.

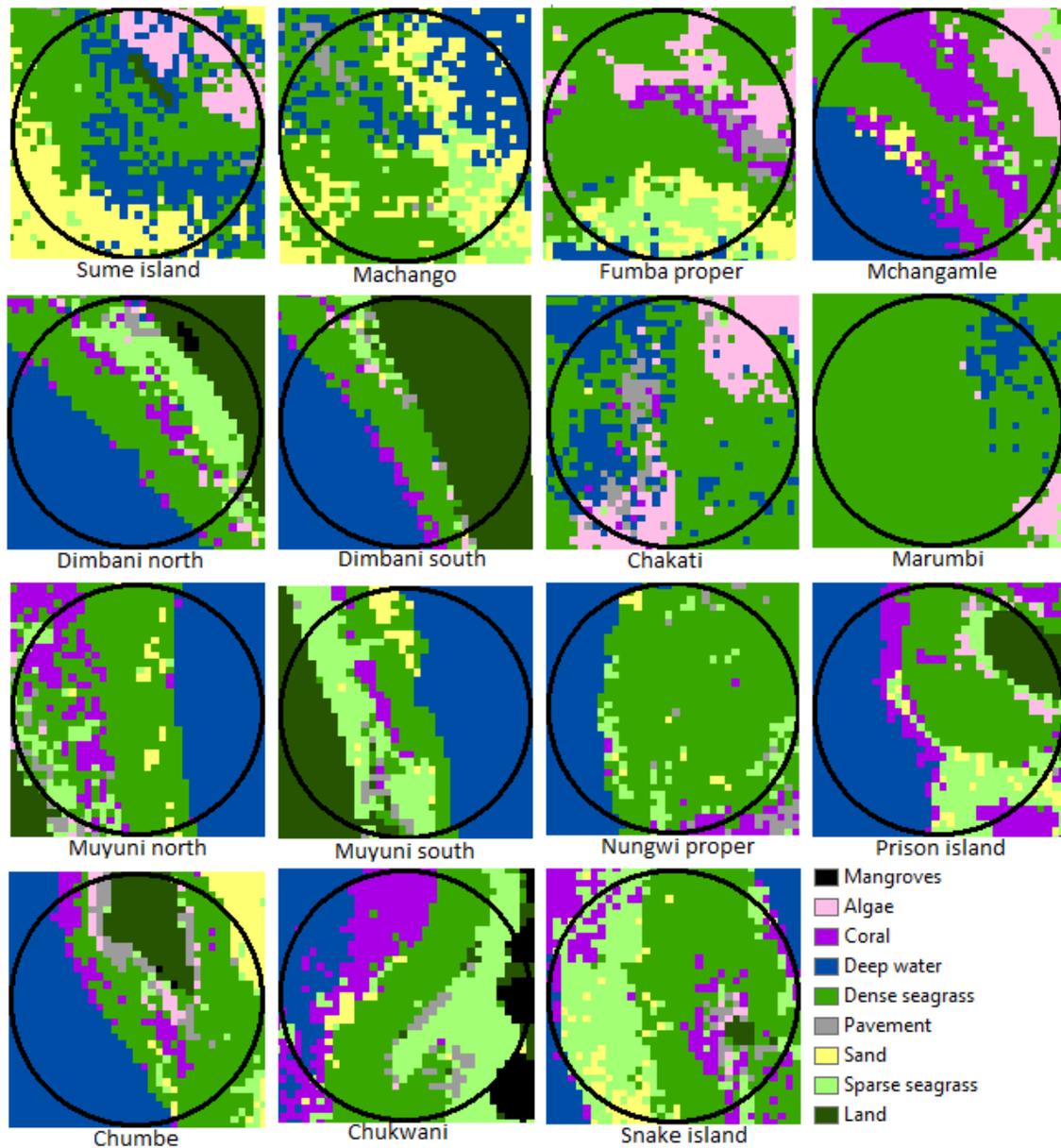


Figure 6. Habitat mapping of the fifteen seascapes. A circle presents an area of 500 m radius from a centroid point based on the transect layout within each seagrass bed.

WITHIN-PATCH VARIABLES AFFECTING FISH ABUNDANCE

Considering the entire fish community, no within-patch predictor could explain total fish abundance. However, when dividing the fish into adults and juveniles and the sites into edges and middles interesting correlation patterns arose (Figure 7). Depth was a significant predictor variable, but only for adult fish, and only in the edges of the sites ($p < 0.01$, $df=86$, $R^2=0.08$). For juveniles, canopy height was a significant predictor, but only for the middles of the sites ($p < 0.001$, $df=86$, $R^2=0.11$).

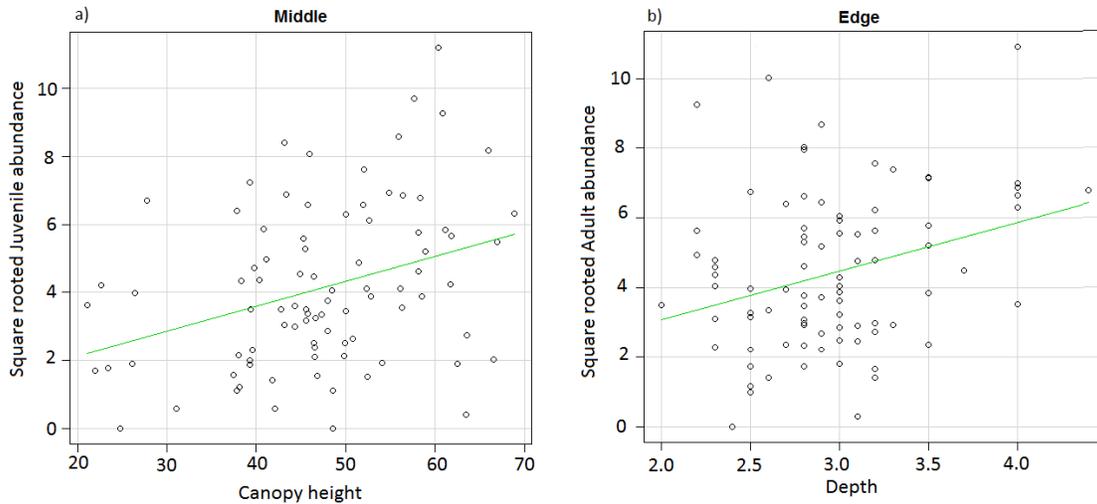


Figure 7. Correlations between (a) abundance of juvenile fish and canopy height, and (b) abundance of adult fish and depth.

LARGE SCALE VARIABLES AFFECTING FISH ABUNDANCE

The R^2 -values were much higher for all tests on the middle of the sites (0.75-0.87) compared to the edge habitats (0.38-0.51). This was the case for total abundance, juvenile abundance as well as adult abundance of fish.

Juvenile fish abundance in the middles of sites increases significantly with the amount of algae ($p < 0.01$, $df=5$, $R^2=0.87$) and the amount of mangrove in the seascape ($p < 0.05$; Figure 8a) and so does the adult abundance in the middle ($p < 0.05$, $df=6$, $R^2=0.76$; Figure 8b). In the edge habitat, deep water and distance to mangrove were positively related to juvenile fish abundance, whereas amount of mangroves was negatively correlated ($p < 0.05$, $df=7$, $R^2=0.40$; Figure 8c). The abundance of adult fish in the edge habitat was positively related to the amount of coral ($p < 0.01$, $df=8$, $R^2=0.51$) the amount of deep water ($p < 0.05$, $df=8$, $R^2=0.51$) and negatively related to the amount of mangrove ($p < 0.01$, $df=8$, $R^2=0.51$; Figure 8d).

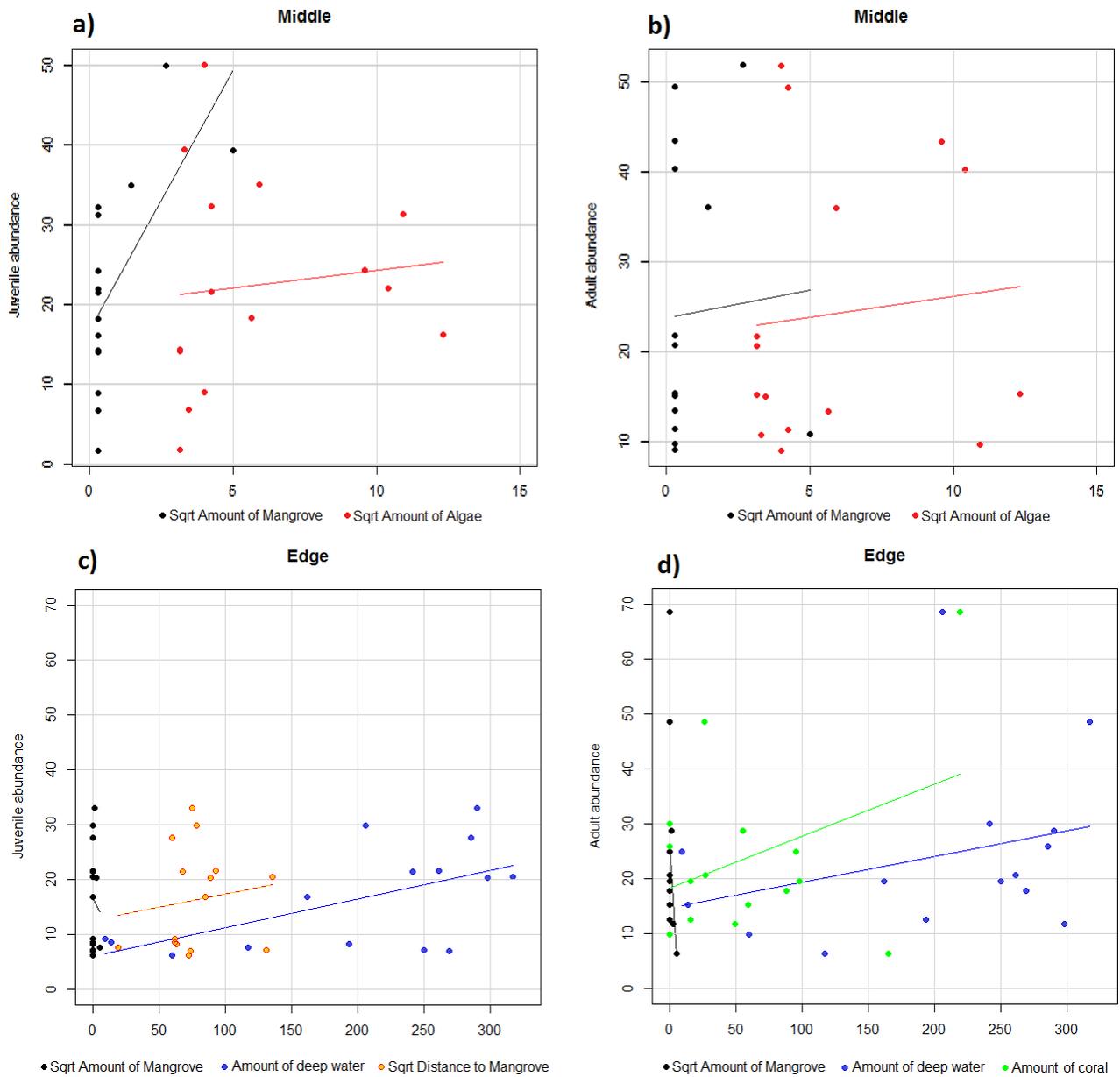


Figure 8. Landscape-scale predictor variables, which significantly affected juvenile or adult fish abundance in a multiple regression, were correlated to (a) juvenile fish abundance in the middles of sites, (b) adult fish abundance in the middles of sites, (c) juvenile fish abundance in the edges of sites, and (d) adult fish abundance in the edges of sites.

FACTORS AND SCALES AFFECTING FUNCTIONAL GROUPS

DIFFERENCES AMONG SITES

Omnivores (O) was the most abundant functional group throughout the fifteen sites, constituting 34% of the total fish abundance. Algal herbivores (HA) was the second most important group and made up 27% of the abundance, while invertivores (I) made up 15%. Corallivores (C) were very rare in all sites, whereas the abundance of cleaners varied among

sites. The abundance of fish within different functional groups differed greatly among different sites. In Chukwani, Chumbe Island, Fumba proper, Snake Island and Prison Island, the majority of fish was HA (65%, 42%, 42%, 38% and 28%, respectively; Figure 9). In contrast, omnivores were the dominant group in Muyuni South, Machango, Dimbani North, Dimbani South, Chakati and Sume (71%, 64%, 34%, 46%, 42%, and 34%, respectively). Mchangamle stands out with the highest abundance of I (32%) and the second highest of O (29%). Nungwi proper had a relatively high abundance of I (26%), HA (26%) and O (30%). Sume Island stands out in the aspect that it is the only site with a fairly high abundance (20%) of herbivores. Marumbi has the majority of fish in the N/A category (44%), while the second largest functional group (18%) was invertivores/piscivores (IP), a result only shared by Snake Island, which also showed a high IP abundance (26%).

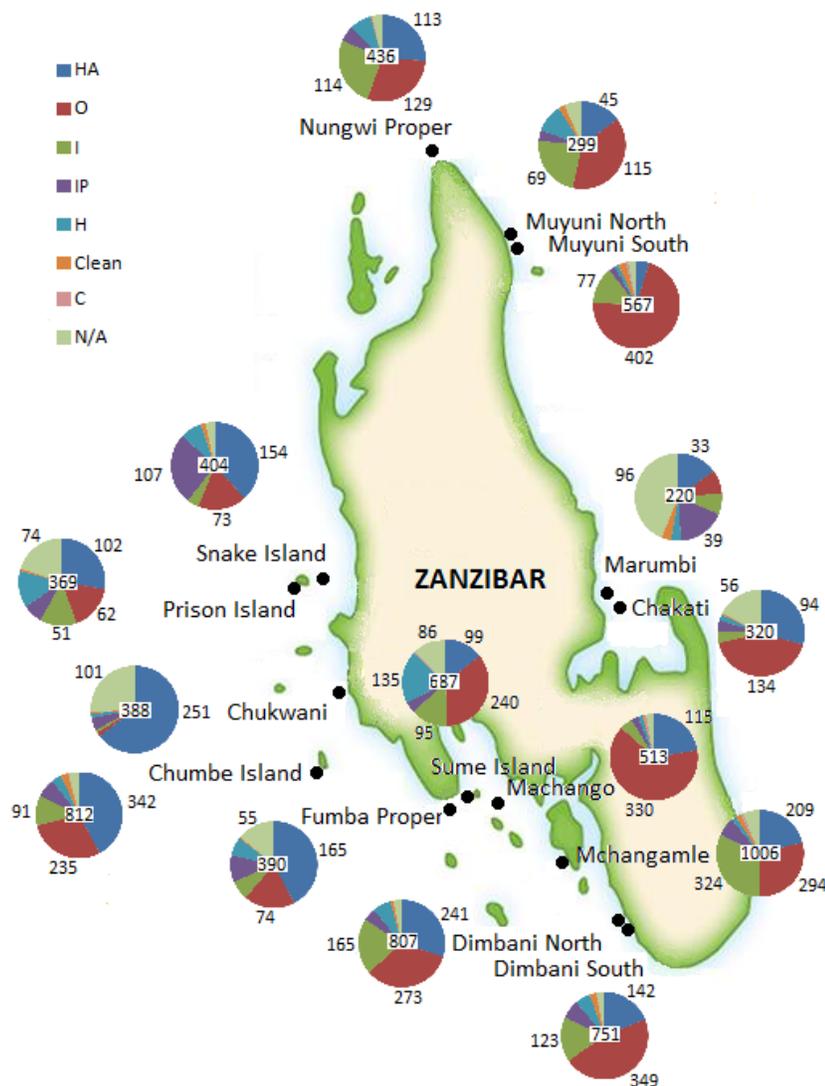


Figure 9. The total abundance of fish (center square) observed in each site and within different functional groups. HA = algal herbivores, O = omnivores, I = Invertivores, IP = Invertivores/piscivores, H = herbivores, Clean = cleaners, C = corallivores and N/A = fish which were not identified to species level or species with no known feeding preference.

A large number of fish species contributed to the abundance patterns around Zanzibar (Table 1). The herbivore (H) functional group was made up entirely by *Leptoscarus vaigiensis* and a few *Siganus sutor* (8%). For instance, Sume Island showed a high abundance of H (and hence *L. Vaigiensis*; Figure 9), which was considerably higher than the H fish abundance in several of the other sites.

For the functional group HA the result is also fairly conclusive with high abundance of *Siganus fuscescens* being the main contributor in all cases, but several other species giving minor contributions. In Machango and Dimbani North *Scarus psittacus* also contributed greatly to the HA abundance in addition to *S. fuscescens*. Considerable differences can be seen between Chumbe Island and four other sites.

For the omnivores the pattern was less clear and the main contributors varied among sites. For Muyuni North and Muyuni South, *Ctenochaetus striatus* comprised the bulk of abundance in combination with *Chlorurus sordidus* in Dimbani South. The other sites with high omnivore abundance diverge from this pattern. In Chakati, *C. striatus* was not found, and the omnivore abundance was due to a high abundance of *Abudefduf sexfasciatus* and *Chrysiptera annulata*. Nor in Machango were there any *C. striatus*, and the O abundance was created by *Chromis vidiris*, *Dascyllus aruanus* and *Plectroglyphidodon lacrymatus*. On Sume *D. aruanus* and *P. lacrymatus* were also the most important contributors. Chukwani and Marumbi showed the lowest Omnivore abundance, which differed markedly from several other sites.

The high invertivore abundance found in Mchangamle is solely due to very high abundances of *Chromis atripectoralis* and *Chromis weberi*. This site is very different from several others. In Marumbi, the two most abundant species were *Archamia mocambiquensis* and *Apogon nigripes*, both species unfortunately without information about their feeding preferences.

WITHIN-PATCH PREDICTORS AFFECTING FISH ABUNDANCE WITHIN DIFFERENT FUNCTIONAL GROUPS

When comparing the abundance of fish of different functional groups in the edges and middle habitats a clear pattern arose. Herbivores (H and HA) were more common in the middle of the seagrass sites than in the edges, whereas corallivores, invertivores/piscivores, invertivores and omnivores were more common in the edge habitats (Figure 10). The great difference in HA abundance between edges and middles ($p < 0.001$) was due to the large number of *Siganus fuscescens* and *Scarus psittacus* encountered in the middles. Seventy percent of all *S. fuscescens* were found in the middles and almost 66% of these were juveniles. Noteworthy, the smallest size class (0-4 cm) was rare in the edges with only 30 observations compared to 335 observations in the middle. A similar pattern could be seen for *S. psittacus*, where 70% of all individuals were encountered in the middle of patches and out of those 90% were juveniles.

Invertivores/piscivores was the only other group that showed significant differences between edges and middles ($p < 0.01$), with 68% of all fish observed in the edge habitats. Out of the 25 species belonging to this functional group, 20 were more commonly seen in the edges. The most striking species in this regard was *Lutjanus fulviflamma*, which was seen 64 times in the edges and only twice in the middle. *Apogon cyanosoma* was also quite important with 28 observations in the edges and only 6 in the middle habitats. Six species of

invertivores/piscivores were only encountered in the edges, but these species were all rare, with an average abundance between 1 and 4 individuals.

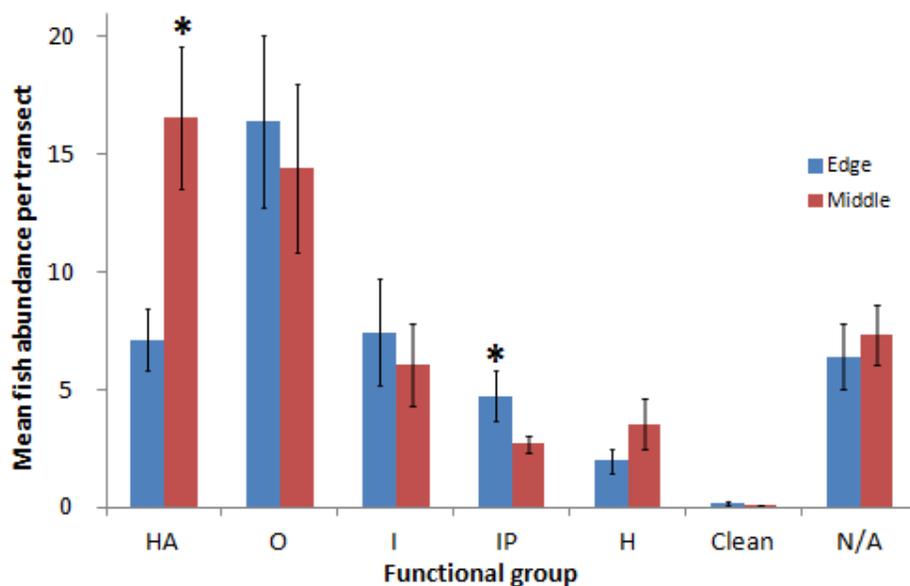


Figure 10. Mean abundance of fish observed in the edge and middle habitats, divided into functional groups. HA = Algal herbivores, O = Omnivores, I = Invertivores, IP = Invertivores/piscivores, H = Herbivores (only seagrass), Clean = Cleaners, N/A = all fish not identified to species and species with no known feeding preference. Corallivores (C) are excluded from the graph due to their very low abundance. Stars indicate significant differences between edge and middle. Error bars show standard error. Information about functional groups is taken from Froese & Pauly (2013).

LARGE SCALE PREDICTORS AFFECTING FISH ABUNDANCE OF DIFFERENT FUNCTIONAL GROUPS

The different functional groups were affected by different predictors determining the fish abundance. Corallivores and Omnivores were positively affected by amount of deep water ($p(\text{Corallivores}) < 0.05$, $df=11$, $R^2=0.33$; $p(\text{Omnivores}) < 0.01$, $df=13$, $R^2=0.49$; Figure 11a and b). *Ctenochaetus striatus*, which was the most abundant omnivore in Muyuni North, Muyuni South, Dimbani North and Dimbani South, was mostly driven by amount of deep water, presence of land and distance to mangrove (Figure 12). *Abudefduf sexfasciatus* and *Chrysiptera annulata*, on the other hand, seem to be driven by area of mangrove (Figure 12). The other omnivorous pomacentrids predominately found in Sume and Machango (*Chromis vidiris*, *Dascyllus aruanus* and *Plectroglyphidodon lacrymatus*) seem to prefer areas with lots of algae (Figure 12). Algal herbivores were positively correlated to amount of deep water and negatively correlated to distance to mangrove ($p(\text{Deep water}) < 0.05$, $p(\text{Dist}) < 0.01$, $df=6$, $R^2=0.57$; Figure 11c). Invertivore/Piscivore abundance increased with amount of coral, and decreased with amount of mangrove ($p < 0.05$, $df=10$, $R^2=0.41$; Figure 11d). Herbivore abundance decreased with amount of mangrove and depth ($p < 0.01$, $df=6$, $R^2=0.60$; Figure 11e). The two herbivorous species *Leptoscarus vaigiensis* and *Siganus sutor* are placed close to all three of these variables in the CCA-plot (Figure 12). Invertivores was the only functional group affected by amount of sparse seagrass ($p < 0.01$, $df=9$, $R^2=0.54$; Figure 11f) and as seen in Figure 12 all invertivores encircle sparse seagrass which is located close to the middle in the CCA-plot. In Mchanganle the most abundant fish were *Chromis atripectoralis* and

Chromis Weberi, both species belonging to the invertivores/piscivores functional group, and likely reacting positively to the amount of coral (Figure 12).

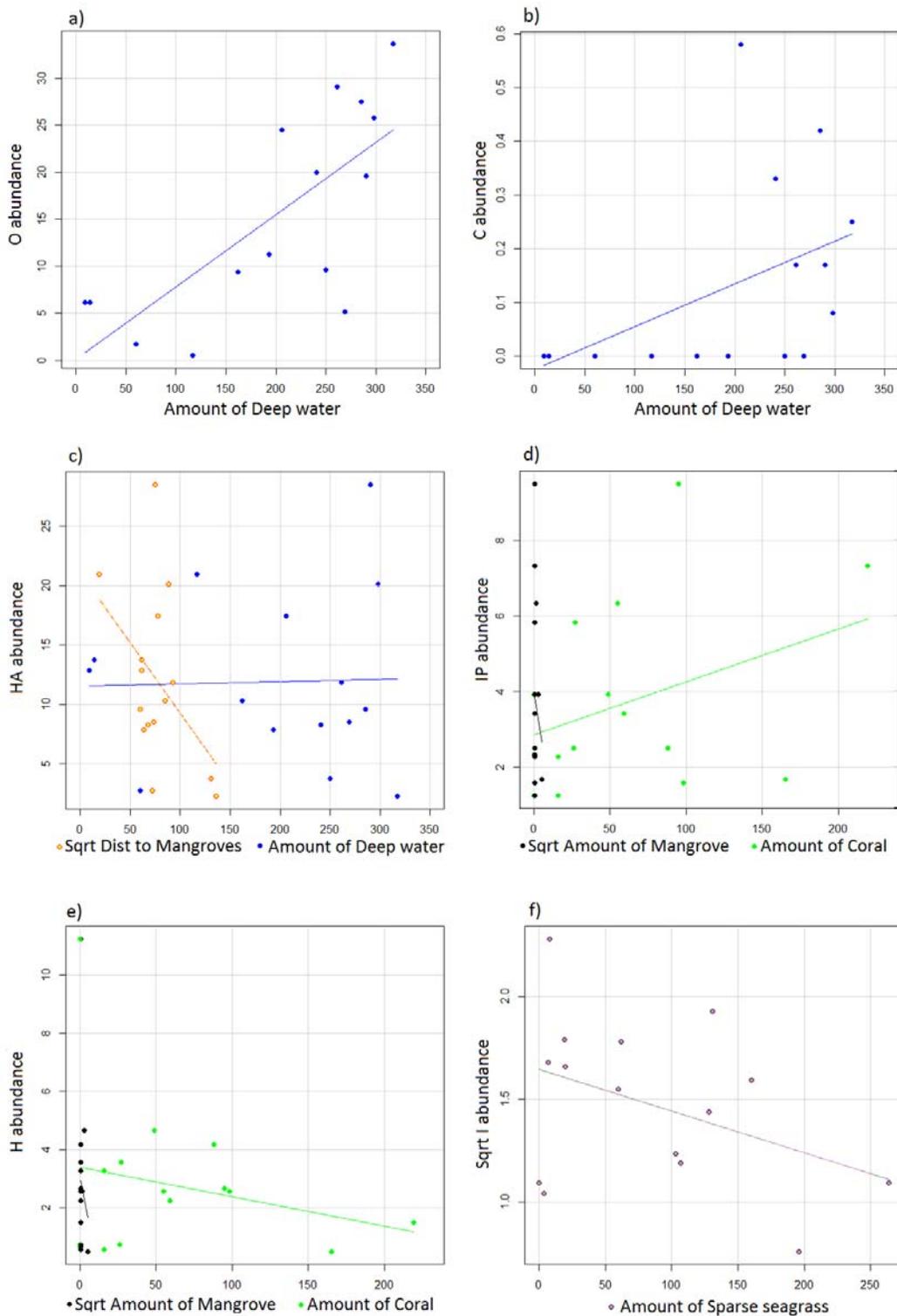


Figure 11. All large scale variables which significantly affect the fish abundance in the different functional groups. a) Corallivores. b) Omnivores. c) Algal herbivores. d) Invertivore/Piscivores. e) Herbivores. f) Invertivores.

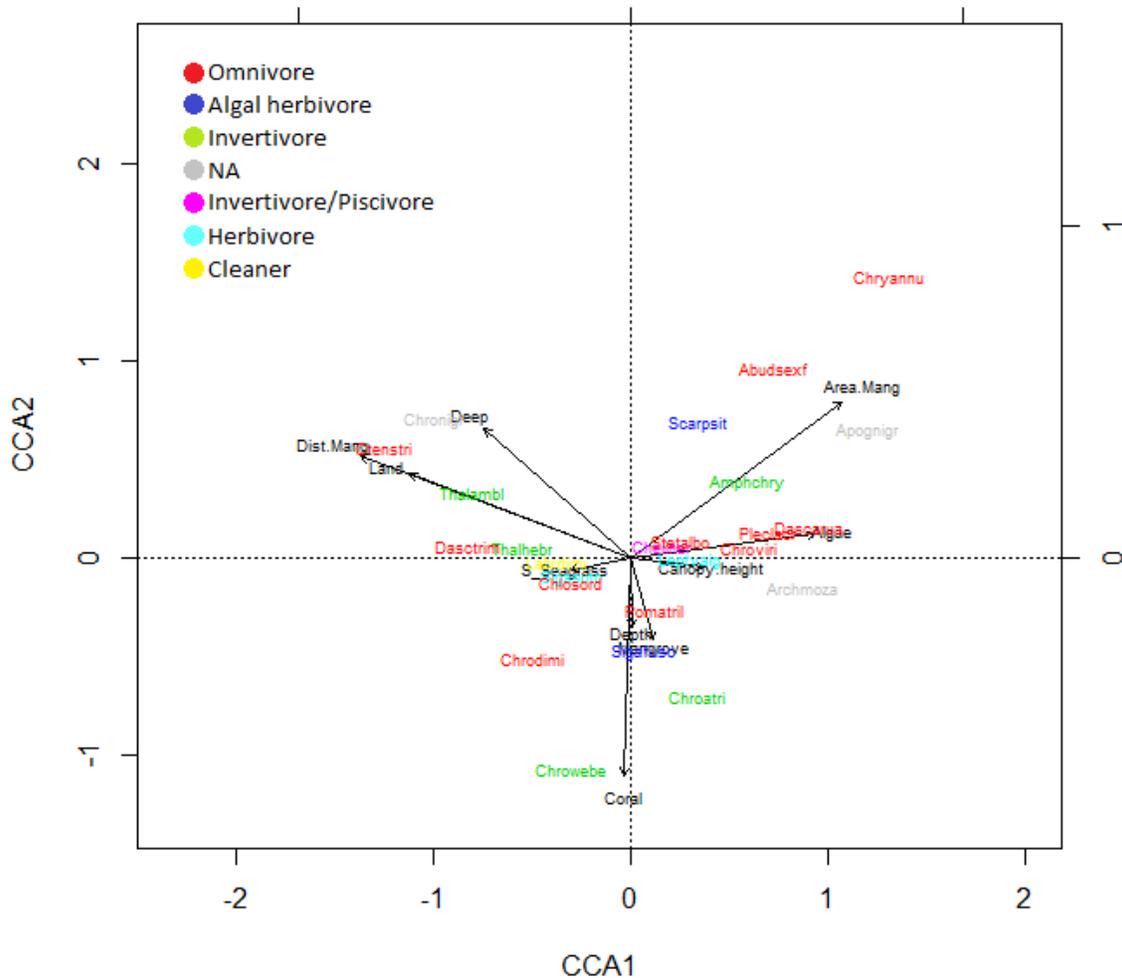


Figure 12. CCA-plot showing variables affecting species with abundance larger than 1% of the total abundance. Deep = amount of deep water in the seascape, Area.Mang = square-rooted area of mangroves (within a 6000 m radius), Algae = amount of algae in the seascape, Canopy.height = the mean height of the seagrass canopy in the seascape, Depth = the mean depth at the site where fish census was performed, Mangrove = the amount of mangrove in the seascape, Coral = the amount of coral in the seascape, S_Seagrass = the amount of sparse seagrass in the seascape, Land = the amount of land in the seascape, Dist.Mang = the square-rooted distance to mangroves from the center of the seascape. For species list see Table 1.

DISCUSSION

The results indicate that large scale seascape factors are of higher importance than small scale localized factors, such as structural complexity, for the overall composition of fish communities. It was also established that the variation in fish abundance in the middles of sites can be explained to a higher degree than the variation in the edge zones. This difference between edges and middles may be on account of the interior parts of seagrass beds being more commonly of homogenous character, whereas the edge zones mostly vary in appearance, a habitat differentiation which could cause larger variation in fish abundances in the edges. These findings indicate that general seascape formation needs to be given larger priority when evaluating the management needs in associated shallow-water areas.

LARGE SCALE EFFECTS ON FISH ABUNDANCE

Seascapes with lots of mangrove and algae had significantly more juvenile fish than other habitat types, whereas adult fish abundance decreased with increased amount of, and proximity to, mangroves. Adult fish seemed to prefer large areas of deep water and adults in the edge habitats also preferred areas with high coral content.

Several previous studies confirm the findings of positive relationships between juvenile fish abundance (Jelbert *et al.* 2007; Unsworth *et al.* 2008) or species richness /diversity (Nagelkerken *et al.* 2001; Lugendo *et al.* 2005; Berkström *et al.* 2012; Berkström *et al.* 2013) and proximity to mangroves. Mangrove areas are sheltered and safe environments for juvenile fish and are thus believed to function as nursery grounds (Nagelkerken *et al.* 2002). Once the fish reaches maturity an ontogenetic shift may occur, where they change habitat from nursery grounds to coral reefs (Dahlgren & Eggleston 2000; Nagelkerken *et al.* 2001). The distance to coral reefs has also been shown to affect fish abundance and species richness positively (e.g. Weinstein & Heck 1979; Appeldoorn *et al.* 2009), and especially adult fish (Dorenbosch *et al.* 2006) since they commonly migrate across the shallow-water landscape. Recent findings suggest that high seagrass cover within a distance of 100 m (Grober-Dunsmore *et al.* 2008) or 400 m (Kendall 2005) from a coral reef will increase coral reef fish diversity and abundance. In contrast to adults, juvenile fish are subjected to increased predation risks when migrating between coral reefs and seagrass beds (Dahlgren & Eggleston 2000), which may explain why only adults are positively affected by presence of coral in the present study. The predation risk for adult fish is also believed to be reduced in deeper water compared to shallow water (Schlosser 1991) and this might be a reason for the adult fish to prefer areas in close proximity to extensive deep habitats. Previous studies have shown that patchy, heterogeneous areas seem to attract fish with preferences both to vegetated and bare substrate, which should lead to higher species diversity (Leopold 1933; Salita *et al.* 2003). The present study did not show such a pattern, which might partly be due to the resolution of the map (30 x 30 m), which may be too low to reflect the total degree of patchiness in the seascape.

Both adult and juvenile fish abundances in the middle of the sites were positively affected by increased amounts of algae, whereas edge abundances were not affected by the amount of algae. This is surprising since the algae are not expected to be in close proximity to the middles of the sites. Increased fish abundances in the middle of seagrass beds could however be explained by high structural complexity. The opportunity to hide is presented in tall algal belts as well as in the center of seagrass patches. Fish may move in between these two areas and stay away from residing in the edges since these areas can be more dangerous, providing risks of being spotted by predators (Boström *et al.* 2006).

LARGE SCALE EFFECTS ON FUNCTIONAL GROUPS

All sites with a majority of algal herbivores (mainly *Siganus fuscescens*) were situated adjacent to each other and in close proximity to Zanzibar Town. The location of these sites could be a result of effective larval distribution due to favorable environmental conditions in these areas. Another possible explanation could be an increased fishing pressure close to Zanzibar Town due to the increase in population compared to other more rural areas around Zanzibar (National Bureau of Statistics & Ministry of Finance 2011). Fishers often target large, predatory fish, which could result in a cascading effect enhancing the survival of herbivores (Sala *et al.* 1998). A third possible explanation could be increased amounts of runoff from the city, which may alter the species composition compared to other areas (Fabricius 2005). Sites closer to mangrove had more algal herbivores but no relation between algal herbivores and coral reefs could be detected, a finding that previous studies have also

confirmed (Unsworth *et al.* 2008). Corallivores and omnivores were positively affected by the amount of deep water and for the omnivores it was especially *Ctenochaetus striatus* that drove the distribution patterns favoring the exposed sites. *Ctenochaetus striatus* appeared in very large schools and was usually of larger sizes than the omnivorous damselfish, a difference which may call for the need of increased food availability per unit of area. It also sweeps sediment on coral rock as a food source (Krone *et al.* 2008), and as seen in this study the exposed sites have a much higher coral content than the sheltered ones. The main omnivores in Sume and Machango (*Chromis vidiris*, *Dascyllus aruanus* and *Plectroglyphidodon lacrymatus*) preferred areas with more algae, which also is one of their main food items (Froese & Pauly 2013). The invertivores *Chromis weberi* and *Chromis atripectoralis* both feed on and prefer areas with lots of coral (Froese & Pauly 2013), which may explain their high abundances in Mchangamlee, where coral was plentiful.

WITHIN-PATCH VARIABLES AFFECTING FISH ABUNDANCE

The results indicate that the seagrass canopy height influence juvenile fish abundance and that depth is an important predictor of adult fish, which is in line with recent research (Gullström *et al.* 2008). It is possible that juvenile fish prefer areas with higher canopy height, and thus larger structural complexity, because it increases their survival rate by enhanced sheltering capacity, as suggested by Heck & Orth (1980), and/or increases food availability (Connolly 1994a). Other studies have not found any conclusive results indicating that canopy height is an important factor for fish abundance (Bell & Westoby 1986, Sogard *et al.* 1987, Connolly 1994b), but these focused on less complex seagrass habitats. It is possible that the complexity of *Thalassodendron ciliatum*, with its stem and leafy crown, causes larger fish to have difficulties maneuvering and increase the camouflage ability for smaller fish compared to other, simpler types of seagrasses. Depth, on the other hand, may influence only adult fish since they are believed to have a preference for slightly deeper habitats (Schlosser 1991; Gullström *et al.* 2008). Gullström *et al.* (2008) also found shoot density to be an important factor affecting both juveniles and adults, a variable which did not show any significance in any of the tests performed in the present study.

WITHIN-PATCH VARIABLES AFFECTING FUNCTIONAL GROUPS

In the present study, trends were seen that herbivorous fish were observed in higher densities in the middle-site habitats, and that predatory and omnivorous fish were more common in the edge habitats. Algal herbivores were of higher abundances in the middles, and this pattern was predominantly created by juvenile *Siganus fuscescens*. These small fish will likely have a larger chance of survival in the middle due to increased hiding availability (Heck & Orth 2006; Horinouchi 2007). Invertivore/piscivores were significantly more common in the edges, a pattern created by 20 out of the 25 species of this functional group, *Lutjanus fulviflamma* and *Apogon cyanosoma* in particular. For *A. cyanosoma* this is not surprising since this species of cardinal fish stays in small or large aggregations and often hovers under ledges of coral bommies or rocks (Froese & Pauly 2013). Coral bommies were more commonly seen in the edges of seagrass patches and therefore it could be assumed that this species would be more common in the edge zones and the large aggregations caused the numbers to rise quickly. *Lutjanus fulviflamma* also most often occurred in large schools but was on occasion seen alone. The majority of observations were of adult individuals. Adult *L. fulviflamma* prefers coral reef habitats (Froese & Pauly 2013), which may be why they were residing in the edges. Bell *et al.* (2001) stated in a review that a clear majority of fish taxa do not show any relationship with edge effects as did Connolly & Hindell (2007), but neither of these studies divided taxa into functional groups. It is possible that predatory and omnivorous fish do have

higher food abundance in the edges where fish and invertebrates cannot hide as well as in the center of a seagrass bed.

SOURCES OF ERROR AND SUGGESTIONS OF IMPROVEMENT

SURVEYOR BIAS

The two surveyors were synchronized when it came to fish identification, but they both found it difficult to identify *Leptoscarus vaigiensis*. This particular species may in many cases in fact be *Calotomus spinidens*, a species known to exist in the area but never identified by either surveyor. This however is of no importance to the functional group data, since both species are herbivores (Gullström *et al.* 2008). Regarding the size estimations it was established that there was a significant difference in the estimations of the size class 20<30 cm. Only fish with their juvenile break in the size class 16<20 cm (assuming KW was incorrect in her size estimation) or the size class 30-40 cm (assuming GP was incorrect in his size estimation) could be affected, resulting in 14 possibly mislabeled species. This involves 192 individuals or 2.4% of the total fish abundance. Out of these 14 species only *Cheilio inermis* had a total abundance of $\geq 1\%$, while all other species were rare. It is unlikely that *C. inermis* would cause any major errors in the juvenile-adult fish ratio, and it is therefore safe to assume that differences in size estimations are not important for the overall abundance results.

MAP ACCURACY

It is important to remember that the map created has an estimated accuracy of 69%, meaning that almost every third pixel might be incorrect. All pixels are on the other hand not equally prone to error since some habitat classes are easier to determine than others. In particular dense seagrass is overestimated and those pixels could in fact be any other habitat type except deep water or land. Sand may be confused with pavement or very sparse seagrass, since they all look fairly similar. The risk of deep water to be labeled incorrectly is however fairly small, so all results showing significant results involving deep water are highly likely to be correct. It is however possible that some of the other results may change if the map were to be improved. Another possible point of improvement is the resolution of the map. The resolution used in the present study was 30x30m and it is obvious that the environment may not be completely homogenous within this large square. If the spatial resolution would be increased to 4 x 4 m for instance as it would be if using IKONOS satellite images instead of Landsat this would allow for much higher accuracy. Seagrasses in particular are often quite patchy (Borum *et al.* 2004), something not accounted for in the present study, where seagrass areas are mostly seen as large homogenous fields.

ASSUMPTION OF SEAGRASS HOMOGENEITY

Structural complexity may vary greatly among seagrass species and seasons, and hence the homogeneous seagrass areas might also differ (Boström *et al.* 2006). It would be of great value to be able to separate the target species *Thalassodendron ciliatum* from other types of seagrass. The reason why Dimbani South, Dimbani North, Mchangamle, Machango and Muyuni North showed such high fish abundances could in fact be continuous *T. ciliatum* found at these sites, whereas many other sites showed a more patchy distribution pattern of *T. ciliatum*.

VISUAL CENSUS

To decrease the risk of underestimation when using visual census, trap fishing could be used (Recksiek *et al.* 1991; Beets *et al.* 2003; Unsworth *et al.* 2007). Fishing could also have been carried out during nighttime to account for nocturnally migrating fish (Unsworth *et al.* 2007).

To be able to compare different sites/seascapes, a constant depth (3 m) was held; however, potentially influential factors like diel or tidal migrations (Gibson 2003; Appeldoorn *et al.* 2009) were not considered.

NOT EVALUATED VARIABLES

Three variables not examined are the influence of fishing pressure, the distance to coral reefs and the seagrass patch size. Patch size was excluded purposely since it has previously been shown to be of little importance to fish abundance (Conolly & Hindell 2007). Adding fishing pressure and distance to reefs, on the other hand, could have improved the study and possibly given an alternative explanation to the differences in fish abundance among sites. Seagrass areas in Chumbe and Mchangamle, the two sites with the highest fish abundances, are subjected to limited fishing activity and are found close to large coral reef areas. Several studies have shown these two factors may be of great importance (e.g. Kendall 2005; Valentine *et al.* 2008; Grober-Dunsmore *et al.* 2008).

CONCLUSION AND MANAGEMENT IMPLICATIONS

This study has shown that it is important to consider both localized factors and seascape context when evaluating the management needs of a shallow-water coastal area. Seascape configuration was shown to be of greater significance than the smaller within-patch variables for seagrass-associated fish abundance and assemblage composition.

Juvenile and adult fish as well as fish within different functional groups were shown to be affected in different ways to large- and small scale variables and it was hence important to separate these groups and study them individually. The influencing factors also differed depending on if the fish was observed in the edge or in the middle of a seagrass patch. Both juveniles and adults who preferred the middle of seagrass patches also favored areas with high mangrove and algae content, and juveniles did also prefer increased seagrass structural complexity. These fish were to high extent herbivores and algal herbivores and could be utilizing these areas mainly for protection from predation, and it is thus natural that they also favor algal belts and areas with high structural complexity where it is easy to hide. A similar pattern was also visible when studying these two feeding guilds (i.e. herbivores and algal herbivores) separately; they both preferred areas closer to mangroves. Since mangroves are viewed as a nursery ground (Nagelkerken *et al.* 2009) it is possible that the juvenile fish as well as the fish within herbivorous functional groups prefer seagrass areas in close proximity to mangroves which would decrease the predation risks during migration. In the edge habitat both juveniles and adults instead favored areas further away from mangroves, with increased amounts of deep water, and adults also preferring increased coral cover and depth. Fish which favored edge habitats were shown to be predatory to a higher extent and may take advantage of the more open areas in the edge habitats for hunting. Adult fish are more likely to migrate to the reef and utilize deeper areas for feeding purposes or to decrease the predation risks upon themselves (Schlosser 1991). Corallivores and omnivores were two of the functional groups which preferred areas with increased deep water content in particular. Different functional groups will have different impact on the resilience of the area and it is hence important to know the functional group arrangement to determine an area's specific management needs.

In order to facilitate fisheries management a recommendation would be to use a landscape approach and a fairly large scale to get a better understanding of fish assemblage composition and connectivity within the tropical seascape, a view shared by Boström *et al.* (2006),

Gullström *et al.* (2011) and Berkström *et al.* (2013) among others. Accurate benthic maps can work as a proxy for estimating species diversity and abundance (Gray 1997; Ward *et al.* 1999) and as seen in the present study such maps can be used to predict where fish of various functional groups and age classes may reside. This can aid in pinpointing locations in need of preservation (Kendall *et al.* 2004). In addition to evaluation on a seascape scale, localized scale examination could further improve the knowledge of variables affecting fish composition and abundance, and should therefore not be neglected. The shallow tropical seascape is highly essential and to preserve such environment is of the utmost importance of economical, cultural and ecological reasons.

ACKNOWLEDGEMENTS

I would like to thank Stockholm University and Sida for making this project possible and the Institute of Marine Sciences in Zanzibar for all the assistance in the field.

I would also like to thank my supervisor Martin Gullström and co-supervisors Lina Mtwana Nordlund and Regina Lindborg for all the help during the project. Thanks also to Narriman Jiddawi, our contact in Zanzibar, Anders Knudby, for his great work creating our habitat /seascape map and Olle Hjerne for helping with statistical questions.

Thanks to my co-workers Gustav Palmqvist and Alan Koliji for making the fieldwork so rewarding.

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