

Calcium carbonate production and the response of calcifying organisms to natural and anthropogenic threats on the shallow platform of Zanzibar, Tanzania

A dissertation presented by

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In partial fulfillment of the requirements for the degree of

Doctor of natural sciences (Dr. rer. nat.)

Faculty of Geosciences,

University of Bremen

Germany

June 2017

The present work was conducted from June 2013 to June 2017 at the Leibniz Center for Tropical Marine Research (ZMT) in Bremen as part of the interdisciplinary SUTAS Leibniz Graduate School.



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Colloquium date: 29th September 2017

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All dwelling in one house are strange brothers three, as unlike as any three brothers could be, yet try as you may to tell brother from brother, you'll find that the trio resemble each other. The first isn't there, though he'll come beyond doubt. The second's departed, so he's not about.

The third and the smallest is right on the spot, and manage without him the others could not. Yet the third is a factor with which to be reckoned because the first brother turns into the second. You cannot stand back and observe number three, for one of the others is all you will see.

So tell me, my child, are the three of them one? Or are there but two? Or could there be none? Just name them, and you will at once realize that each rules a kingdom of infinite size. They rule it together and are it as well. In that, they're alike, so where, do they dwell?

— Michael Ende, Momo



Learn what is to be taken seriously and laugh at the rest.

— Hermann Hesse

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Acknowledgements

I would first like to thank the founding institutes, which granted this project in the frame of SUTAS Leibniz Graduate School. I cannot fail to offer my deep gratitude to Prof. Dr. Hildegard Westphal, for your unreserved support, for trusting me on this project, for making the SUTAS Leibniz Graduate School possible and above all for giving me the opportunity to specialize on the fascinating carbonate sedimentology research field. Thanks to Prof. Dr. Matthias Wolff, father and coordinator of the SUTAS project. Throughout these four years, we were all a Solid Unique Tropical Adorable Strain. I would like to thank Prof. Dr. Freiwald, Dr. Jahnerjahn and Dr. Reuter for your guidance and support. This project would not have been possible without the experience of our local partners Prof. Dr. Muhando, Prof. Dr. Narriman Jiddawi, Prof. Dr. Shaghude and Dr. Mukaka. Thank you to ALL the SUTAS crew for the exciting time on the field and particularly to Dieuwke and Fay, which made the first field trip an unforgettable adventure full of *Dafus*. Thanks to Dr. Rehren also called Jenni pho, for being a great SUTAS colleague. I am very glad to count with you as a friend. To Alonso del Solar for the tasty fish and *octopi* (you are a provider), to Tobias Mildenberger and Andreas Eich for all the wonderful whale-dives (some blast-dives too). Thanks to the *Zanzibaris* I had the pleasure to meet, for having such a free spirit. Particularly to Yusuf and Muhadini for your good will. Also to the anonymous *Dafu man* who was selecting the best coconuts in the whole island for us (precious electrolytes...).

This thesis would not have been possible without the scientific atmosphere created by every member of the Geoecology and Carbonate Sedimentology workgroup. Claire Reymond and Gita Narayan always had wise suggestions, literally always. I learned so much from you and we shared unforgettable time in the field and “soft skills seminar’s” on Wednesdays that I would never forget those chapters of my life. I would like to particularly thank Peter Müller and Kim Vane, the best officemates I could ever think of! I should acknowledge big André

and small André for your expertise and consistency. Thanks to Sebastian Flotow, Marleen Stuhr, Thomas Mann and Therese for your uncomplicated good vibes. To the past and present members of the Sea Level and Coastal Changes group, Dr. Rovere, Dr. Casella, Dr. Harris and Thomas Lorscheid for sharing inspiring and refreshing experiences in the field (I wish I would meet Mike Fanning too). I should share that I never thought that I would find seagrass intriguing, but since we were working on one of the most diverse seagrass spots in the world, seagrasses are certainly growing on me. I also have to admit that wavy-hand (*Thalassodendron*) and dirty-skirt (*Cymodocea rotundata*) are cute (OK, *Halodule* too). I thank for all this knowledge to the ZMT-Seagrass workgroup. Thanks to Agustin Moreira Saporiti and Ínes González Viana for getting me *teletransported* to the north of Spain to withstand homesick feelings, for laughing about not-important-things, for being so genuine... The wonderful Hawaiian experience shared with Yi Guan was certainly one gorgeous highlight. Thanks to Dino and Rebecca or should I say Dinava?...Well, Kiki and Lucy Gillis; you are so authentic! Thanks for that too.

Thanks to all my family. I would like to dedicate this thesis to my grandparents Ramon Herrán and José Navarro, my godmother and auntie Amelia Herrán and Rocío Navarro, because all of you saw how delighted I was when I started this project and I truly know that you are up there supporting me, always with me... Even though I do not say it often enough, thanks to my Mum, Dad (and his engineer perspective of the marine environment) and sister. You are always supportive and proud of me, without your love, nothing could ever be accomplished.

Thanks to those friends who encouraged me (from thousands of kilometers far away) and gave me the feeling that I was doing something remarkable. The king was gone but not forgotten, dear Thiago, we should play original songs of *sounds of the city* again. Thank you Thorin, my former roommate and friend, for a great time. Gracias a las *personajas* de

Bremen por ser tan *personajas*. Diese letzten vier Jahre wären nicht dieselben gewesen ohne die tiefe Freundschaft mit Karla, Simon und Selmi. Einen Riesendank an alle Gärtner*innen Heiko, Jessie, Gabriele, Almut und vor allem herzlichen Dank an meine Bremer Familie Anne, Gulliver, Jacob, Vincent, Fabian und Ava.

Abbreviations

ADCP	<u>a</u> coustic <u>D</u> oppler <u>c</u> urrent <u>p</u> rofiler
$\delta^{13}\text{C}$ or d13C	ratio of the stable isotopes $^{13}\text{C} : ^{12}\text{C}$
$\delta^{15}\text{N}$ or d15N	ratio of the two stable isotopes of nitrogen, $^{15}\text{N} : ^{14}\text{N}$
μCT	<u>m</u> icro <u>c</u> omputed <u>t</u> omography
% N	<u>n</u> itrogen content of suspended or sedimentary particulate matter
% POC	organic <u>c</u> arbon content of suspended or sedimentary particulate matter
ANOSIM	<u>a</u> nalysis of <u>s</u> imilarity
ANOVA	<u>a</u> nalysis of <u>v</u> ariance
BSE	<u>b</u> ack- <u>s</u> cattered <u>e</u> lectron
C	<u>c</u> arbon
CaCO_3	calcium carbonate
CHLa	chlorophyll a
CO_2	carbon dioxide
CCA	<u>c</u> rustose <u>c</u> oralline <u>a</u> lgae
CHIRP	<u>c</u> ompressed <u>h</u> igh <u>i</u> ntensity <u>r</u> adiated <u>p</u> ulse
CHICOP	<u>C</u> humbe <u>I</u> sland <u>C</u> oral <u>P</u> ark
C/N ratio	ratio of carbon to nitrogen
C3 plant	plant that solely does C_3 carbon fixation in photosynthesis
DBD	<u>d</u> ry <u>b</u> ulk <u>d</u> ensity
EACC	<u>E</u> ast <u>A</u> frican <u>C</u> oastal <u>C</u> urrent
GCP	gross <u>c</u> arbonate <u>p</u> roduction
H_2O_2	hydrogen peroxide
HSD	<u>H</u> onest <u>S</u> ignificant <u>D</u> ifference
IMS	<u>I</u> nstitute of <u>M</u> arine <u>S</u> cience, Zanzibar
K (or KD)	light attenuation

keV	<u>k</u> ilo <u>e</u> lectron <u>v</u> olts
LIT	<u>l</u> ine <u>i</u> ntercept <u>t</u> ransect method
mbsl	<u>m</u> eters <u>b</u> elow <u>s</u> ea <u>l</u> evel
Mg/Ca ratio	ratio of magnesium to calcium
MPA	<u>m</u> arine <u>p</u> rotected <u>a</u> rea
N	<u>n</u> umber of samples or <u>n</u> itrogen
NMDS	<u>N</u> onmetric <u>M</u> ultidimensional <u>S</u> caling
OC	<u>o</u> rganic <u>c</u> arbon <u>c</u> ontent
OM	<u>o</u> rganic <u>m</u> atter
Ph.D	<u>P</u> hilosophiae <u>D</u> octor
POC	particulate <u>o</u> rganic <u>c</u> arbon
POM	particulate <u>o</u> rganic <u>m</u> atter
PP	primary production / <u>p</u> rimarily <u>p</u> roducers
PRIMER-E	<u>P</u> lymouth <u>R</u> outines <u>I</u> n <u>M</u> ultivariate <u>E</u> cological <u>R</u> esearch
PSM	particular <u>s</u> suspended <u>m</u> atter
ROMS	<u>R</u> egional <u>O</u> ceanic <u>M</u> odeling <u>S</u> ystems
SD	standard <u>d</u> eviation of the mean
SE	<u>s</u> econdary <u>e</u> lectron
SEM	<u>s</u> canning <u>e</u> lectron <u>m</u> icroscopy
SIMPER	<u>s</u> imilarity <u>p</u> ercentage
SPM	<u>s</u> suspended <u>p</u> articulate <u>m</u> atter
SUTAS	<u>S</u> ustainable <u>U</u> se of <u>T</u> ropical <u>A</u> quatic <u>S</u> ystems
TC	total <u>c</u> arbon
WIO	<u>W</u> estern <u>I</u> ndian <u>O</u> cean
ZMT	Leibniz- <u>Z</u> entrum für <u>M</u> arine <u>T</u> ropenforschung, Bremen

Abstract

Biologically produced calcium carbonate (CaCO_3) structures are the foundation of coral reefs ecosystems and associated landforms. Produced by the growth and decay of hermatypic scleractinian corals and reef dwelling organisms (e.g. calcifying macroalgae, bryozoans, crustose coralline algae, mollusks, etc.), constructive and destructive processes typically occur on an individual scale. Over time collectively they control the reef framework accretion (on a long-term, reef-spatial scale) and the development of sedimentary deposits (e.g. coral cays and sandbanks). Also, the supply of reef-derived sediments supports other associated shallow water marine ecosystems (e.g. seagrass beds), and the reef framework roughness supports large amounts of biomass on coral reefs, which are among the most diverse ecosystems in the world. However, adverse effects of natural (e.g. marine snow, storms and earthquakes, water temperature rise, coral bleaching, and Crown-of-Thorns) and anthropogenic (e.g. sewage, nutrient loading, overfishing, tourists, mangrove cutting, construction and sedimentation) impacts on benthic community composition affect coral reef functionality and CaCO_3 production, among others, over a variety of spatial and temporal scales.

The objective of this work is to investigate the biophysical interactions that affect calcifying organisms (hard corals, crustose coralline algae, and calcifying macroalgae) and modify fringing reefs. With an emphasis on overall ecosystem health and the relevance of conservation areas, this study focuses on unprotected fringing reefs and a marine protected area, located in the Archipelago of Zanzibar, Tanzania. We assessed the status of the coral ecosystem and its function to produce CaCO_3 and maintain complex reef structures, using a range of multidisciplinary approaches, from ecological census-based methods, biogeochemistry and hydrodynamic measurements to morphological and sedimentological surveys. Traditional ecological census surveys provided a good estimation of the structural

complexity, which ranged from $(1.18\pm 0.13$ to 1.51 ± 0.24 m/m) and community structure of the ecosystem, which pointed hard coral as major CaCO_3 producers (8.47 ± 4.37 to 16.90 ± 9.70 $\text{KgCaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$) and the dominant benthic taxa (>50% coverage). However, sedimentological approaches provide a broad understanding of time-averaged, coral-derived sediment sources shaping the landscape. With the use of biogeochemical approaches, we measured the concentration of suspended particular matter (18.2 to 36.4 mgL^{-1}) and characterized the composition of its organic fraction (particular organic matter). The organic fraction shows that untreated sewage reaches coral reefs adjacent to Stone Town ($\delta^{15}\text{N}$, $10.28\pm 0.9\text{‰}$ on surface waters). Also, turbidity and associated shading effects control bathymetrically coral reef formations to 16 ± 2 meters. Moreover, since no baseline studies are available in the literature, we compared our findings with estimates from a local marine protected area, Chumbe Island Coral Park, to better understand potential negative effects of natural and anthropogenic impacts on the natural ecosystem. Despite that Zanzibarian reefs show on average a healthy reef condition, CaCO_3 produced on Chumbe Island Coral Park shows doubled production in comparison to CaCO_3 produced on more degraded reefs. So far Chumbe Island Coral Park shows the highest CaCO_3 budget globally, although scored similar values to other marine protected areas in the Caribbean, which highlighted the importance of conservation areas to keep corals functionality.

Zusammenfassung

Biologisch entstandene Strukturen aus Kalziumkarbonat (CaCO_3) stellen die Grundlage für Korallenriffe und die damit verbundenen Landschaftsformen dar. Sie entstehen durch das Wachstum und den Zerfall von hermatypischen Korallen und anderen Riffbildenden Organismen (z.B. kalzifizierende Makroalgen, Bryozoa / Moostierchen, Krustenalgen, Mollusken). Zwar finden die konstruktiven und destruktiven Prozesse charakteristischer Weise auf der Ebene eines Individuums statt, aber zusammengenommen kontrollieren sie langfristig den Zuwachs der Riffstruktur und die Entwicklung von Sedimentablagerungen (z.B. Koralleninseln und Sandbänke). Des Weiteren ist die Zufuhr von Riffsedimenten wichtig für andere Flachwasserökosysteme (z.B. Seegraswiesen) und die Rauigkeit der Riffstruktur fördert die Bildung großer Mengen an Biomasse.

Negative Auswirkungen natürlicher (z.B. Meeresschnee, Stürme, Erdbeben, Anstieg der Wassertemperatur, Korallenbleiche, Prädatoren) und anthropogener Einflüsse (z.B. Abwässer, Eutrophierung, Überfischung, Abholzung von Mangroven, Küstenbebauung und Sedimenteintrag) auf die Artenzusammensetzung der benthischen Lebensgemeinschaft beeinträchtigen unter anderem die Funktionalität von Korallenriffen und die Produktion von CaCO_3 .

Die vorliegende Studie hat daher als übergreifendes Ziel die biophysikalischen Wirkungsmechanismen zu untersuchen, die einen Einfluss auf kalzifizierende Organismen (Steinkorallen, krustende Korallenalgen und kalzifizierende Makroalgen) haben und somit zur Bildung von Saumriffen beitragen. Hierzu konzentriert sich unsere Studie auf den Gesundheitszustand von vier Saumriffen innerhalb des Sansibar-Archipels, Tansania, und auf die Bedeutung des Meeresschutzgebiets Chumbe Island Marine Park für die Erhaltung gesunder Riffstrukturen.

Der Zustand der einzelnen Korallenriffe wurde untersucht und ihre Rolle in der CaCO_3 Produktion, sowie in der Erhaltung von komplexen Riffstrukturen, wurde beurteilt. Hierzu wurde eine Reihe multidisziplinärer Ansätze verwendet: ökologische Erhebungen, biogeochemische und hydrodynamische Messungen, sowie morphologische und sedimentologische Untersuchungen. Die konventionellen ökologischen Erhebungen lieferten eine gute Einschätzung der strukturellen Komplexität (1.18 ± 0.13 bis 1.51 ± 0.24 m/m) und der Gemeinschaftsstruktur der untersuchten Saumriffe. Diese zeigten, dass Steinkorallen die Hauptproduzenten von Kalziumkarbonat darstellen (8.47 ± 4.37 bis 16.90 ± 9.70 kg CaCO_3 m^{-2} yr^{-1}) und die benthische Gemeinschaft dominieren (>50% der Flächendeckung).

Die sedimentologischen Untersuchungen lieferten ein umfassendes Verständnis über den Ursprung der langfristigen korallenbasierten Sedimentquellen. Anhand von biogeochemischen Methoden wurde die Konzentration von Schwebstoffen gemessen (18.2 bis 36.4 mgL^{-1}) und die Zusammensetzung des organischen Anteils bestimmt. Die Untersuchung des organischen Anteils hat ergeben, dass unbehandeltes Abwasser bis an die Korallenriffe vor Stone Town gelangt ($\delta^{15}\text{N}$, 10.28 ± 0.9 im Oberflächenwasser). Außerdem hat sich gezeigt, dass Trübheit und die damit verbundenen Abschattungseffekte die Riffbildung (bis zu 16 ± 2 Meter Wassertiefe) steuern. Aufgrund des Mangels an vergleichbaren Grundlagenstudien wurde das naturgeschützte Riff im Chumbe Island Marine Park als Kontrolle vergleichend herangezogen, um die negativen Auswirkungen von natürlichen und anthropogenen Einflüssen auf das Ökosystem besser zu verstehen. Es war erkennbar, dass das naturgeschützte Riff im Chumbe Island Marine Park doppelt so viel Kalziumkarbonat produziert im Vergleich zu den ungeschützten Riffen, welche näher an Stone Town lokalisiert sind.

Overview of publications and manuscripts

The Present dissertation is a cumulative thesis that consists in three submitted manuscripts (Chapter 2-3 and 5) and one further manuscript (Chapter 4). An extended abstract, introduction (Chapter 1) and discussion (Chapter 6) are framing the manuscripts.

Chapter 2 – Natalia N. HERRÁN, Gita R. NARAYAN, Claire REYMOND and Hildegard WESTPHAL (subm.): Calcium carbonate budget and coral reef structure along a distance gradient from Stone Town, Zanzibar – Submitted to *Frontiers in Marine Science* in June 2017.

Hildegard Westphal conceived the project; Natalia Herrán, Gita Narayan and Claire Reymond collected the data and performed the research. Natalia Herrán, Gita Narayan, Claire Reymond and Hildegard Westphal wrote the manuscript.

Chapter 3 – Natalia N. HERRÁN, André KLICPERA, André FREIWALD and Hildegard WESTPHAL (subm.): A moving partnership: New insights into semi-mobile solitary coral-tubeworm association offshore Zanzibar (East Africa) – Submitted to *Invertebrate Biology* in February 2017

André Freiwald and Hildegard Westphal conceived the project. André Klicpera and Natalia Herrán developed the concepts on this manuscript. Natalia Herrán collected the data and performed the research. Natalia Herrán, André Klicpera, André Freiwald and Hildegard Westphal wrote the manuscript.

Chapter 4 – Natalia N. HERRÁN, Silas MUKAKA and Hildegard WESTPHAL (in prep.): How do fine-size particle dynamics in tropical shallow waters influence coral reef geomorphology?

Hildegard Westphal conceived the project; Natalia Herrán developed the concepts on this manuscript. Natalia Herrán and Silas Mukaka collected the data on the field. Natalia Herrán and Hildegard Westphal wrote the manuscript.

Chapter 5 – E. Fay BELSHE, Dieuwke HOEIJMAKERS, Natalia N. HERRÁN, Mirta TEICHBERG (subm.): Seagrass community-level controls over organic carbon storage are constrained by geophysical attributes within meadows of Zanzibar, Tanzania – Submitted to *Limnology and Oceanography* in May 2017

Mirta Teichberg conceived the project; Fay Belshe developed the concepts on this manuscript. Fay Belshe, Dieuwke Hoijsmakers and Natalia Herrán collected the data on the field. Fay Belshe, Natalia Herrán and Mirta Teichberg wrote the manuscript.

Gita R. NARAYAN, Natalia N. HERRÁN, Claire REYMOND, Yohanna W. SHAGHUDE, Hildegard WESTPHAL (in prep.): An assessment of the coastal water quality status off of Stone Town, Zanzibar, Tanzania – in preparation for submission

Hildegard Westphal conceived the project; Gita Narayan developed the concepts on this manuscript. Gita Narayan and Natalia Herrán collected the data on the field. Gita Narayan, Natalia Herrán and Hildegard Westphal wrote the manuscript.

1. General introduction

Coral reefs are one of the fewer ecosystems that is strongly defined by a geological component (Kleypas et al., 2001). Increasingly, the importance of coral reefs calcium carbonate structural complexity has come into focus, because the progressive loss of fish biomass (Cinner et al., 2009), marine biodiversity (Mumby and Steneck, 2008) and the loss of reefal associated ecosystem services (i.e. food provisioning, coastal protection or carbon storage) (Mazarrasa et al., 2015). Biophysical interactions within coral reef ecosystems regulate its internal ecological mechanisms and are ultimately the physical processes, which modify the reef structure and geomorphology by the readjustment of unconsolidated material (Kench 2010). Nevertheless, how changing physical factors interact with human-induced or natural disturbances is increasingly challenging due to the natural variability of controlling factors, such as water movement, temperature or light penetration, which drives coral reef community differences (Graham and Nash, 2013).

Biological calcification is an important process that builds coral reefs and associated depositional environments (e.g. reef islands, sandbanks, and beaches, among others). Calcium carbonate sediments account for about 25% of the marine surface sediments (Balch et al., 2005). A number of communities take part in the production and posterior accumulation of CaCO_3 debris, from planktonic pteropods (Fabry, 1990), coccolithophores (Andersson, 2013) to benthic organisms, such as calcareous algae (Milliman and Droxler, 1995), foraminifera (Langer et al., 1997), maerl beds (Bosence and Wilson, 2003) and coral reefs (Chave et al., 1972; Mallela and Perry, 2006; Morgan et al., 2016a; Perry et al., 2012; Smith, 1983; Vecsei, 2004). Therefore, the understanding of benthic community composition is of great importance to build and quantify census-base CaCO_3 budgets. Moreover, the lack

of individual carbonate production studies challenges climate modeling and the estimation of global reefal carbonate production that can only be crudely assessed (Vecsei, 2004).

1.1 Coral reefs as major bioengineers

Coral reefs are studied from many different perspectives. The classical ‘coral reef problem’ (Stoddart, 2008) concerns the geological relationships of reefs as major topographical features. Modern coral studies consider reefs both as complex biological systems of high productivity (Dubinsky, 2011) and as geological structures forming a framework for and being modified by coral growth (Stoddart, 2008). A large spectrum of benthic assemblages has fluctuated in the Earth geologic history due to the different environmental factors including biological evolution, substrate, water energy, water chemistry, light penetration, CO₂ concentrations and Mg/Ca ratios in the seawater (Westphal et al., 2010). *Bioengineers* tend to be the modern term to describe the processes behind each organism functioning regarding its contribution to the system. This concept describes essentially the capability of an organism to modulate the resources availability by a direct or indirect change in the biotic or abiotic materials. We classify into autogenic or allogenic engineers. Allogenic engineers or organisms change or modulate the living or non-living materials from one physical stage to another, commonly via mechanical action (Jones, 1994). Examples for allogenic engineers are woodpeckers, beavers or humans. In contrast corals or trees are good examples of autogenic organisms due to their capability to change the ecosystems via their physical structure producing a significant trophic effect in the environment.

1.1.1 CaCO₃ production: temporal and spatial variation

The net balance of physical, chemical and biological processes dictate net CaCO₃ produced and accumulated in coral reefs. Changes in any of those components alter the accretion potential of corals or/and reef associated sedimentary deposits. Based on key mechanisms,

we could define four conceptual models (Figure 1-1), which explain net reef production states (Kleypas et al., 2001):

1) Production-dominated reefs, where the dominant process is an accumulation of reefal CaCO_3 (Hubbard et al., 1990). 2) Import dominated reefs, much of the material found in those reefs does not proceed from the coral community, but from allochthonous material (i.e. siliciclastics, terrestrial, etc.) form the main reef structure. They also depend on this external supply to accrete. 3) Export-dominated reefs show high CaCO_3 accumulation, but the material is mostly exported. Those reefs are very productive, but they show low geological accretion. 4) Bioerosion-dominated reefs, where bioerosion rates exceed net CaCO_3 production. The difficulty in recognizing such reefs in the geological record would be greater as the CaCO_3 framework would be reduced to sediments and reef-building organisms would

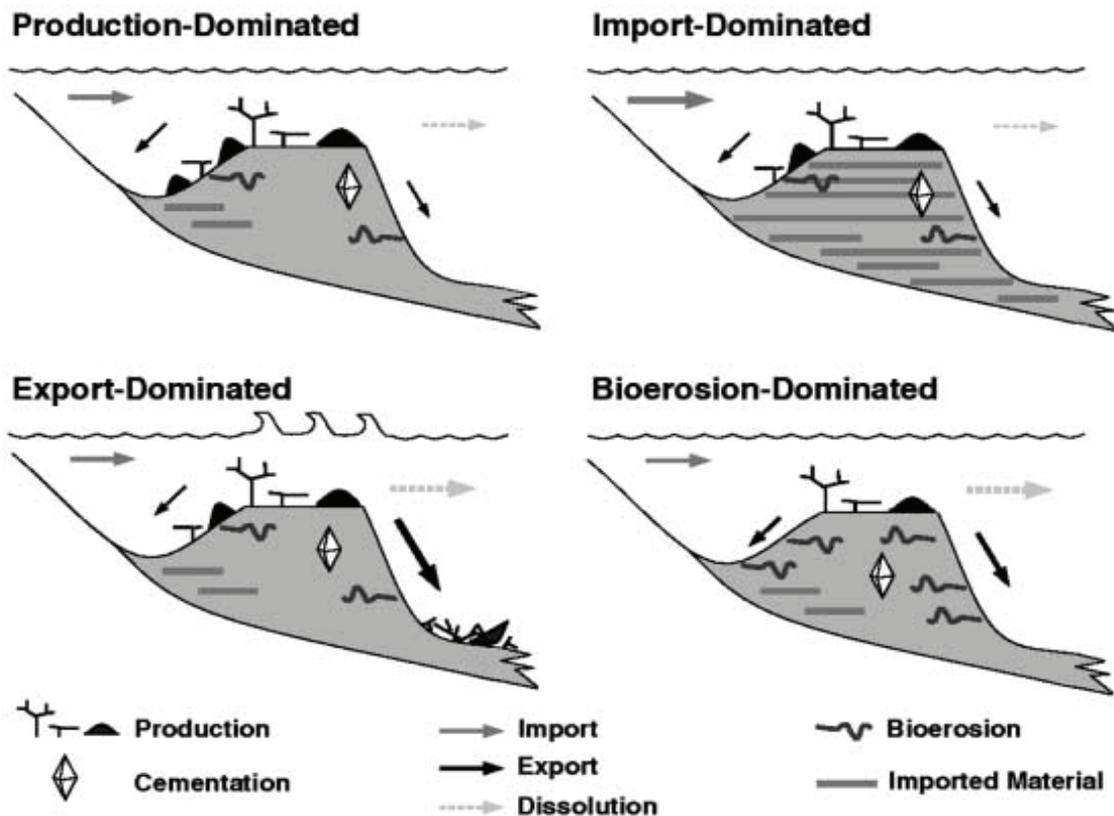


Figure 1-1 - Conceptual chart showing the main four reef types, based on major controls for calcium carbonate accumulation. The relative importance of

ecological and sedimentary processes is controlling the different reef states. Kleypas et al. (2001).

most likely not be found in living position. However, the interdependence of biological, physical and geological processes may change over time. Such changes may lead to shifts in the production state and change for example from production-dominant to bioerosion-dominant if an external pressure, e.g. nutrient input, Crown of Thorns outbreak..etc would break the natural balance.

1.1.2 Bioerosion and bioturbation

Bending large burrowing animals are well known to play a relevant role in benthic environments (Thayer, 1979; Lopez and Levinton, 1987) by burrowing and modifying solid structures. This alteration affects habitat suitability for other species. It is called trophic amensalism when large deposit feeders create unstable sediments, restricting the presence of suspension feeders and sessile fauna (Rhoads and Young, 1970; Meadows, 1991).

In that way bioeroders or bioturbators have effects in other organisms at different time or spatial scales, supporting different substrate composition (Jones, 1994). One example of evolutionary benthic crossover might have taken place during Devonian onwards where diversity of immobile suspension feeders on soft substrate suffered a diversification. Thayer (1979) explains this structural change from the benthic community by bioturbators or bioengineers that alter the media by fouling or burying. Increasing turnover rate of nutrients in sediments might have also lead to a phytoplanktonic (coccoliths, diatoms, and dinoflagellates) diversification during the Mesozoic and due to cascade trophic effect a corresponding zooplanktonic (radiolarian and foraminifera) diversification (Thayer, 1979).

On modern reef settings two major grazers are identify in the literature; sea urchins and parrot fish (Brown-Saracino et al., 2007; Mumby et al., 2006). They work as key stone species; they modulate reef morphology and control benthic biota (Hutchings, 1986; Perry et

al., 2012). Sea urchins graze on macroalgae and rasp mechanically the reef framework while grazing endolithic microalgae. Parrotfish also feed on macroalgae and turf algae attached/within dead/live coral (Adam et al., 2011). Both, urchins and parrotfish are important agents, that affect coral reef ecosystem by eroding reef structure and cleaning macroalgae and maintaining coral cover, which are main space competitors on tropical benthic systems (Coyer et al., 1993).

1.2 Reef formations in the Western Indian Ocean:

The distribution of coral reefs in the Western Indian Ocean (WIO) comprises different structural morphologies from fringing reefs developing along the east African coastline to fringing reefs growing attached to the flanks of the numerous islands. Barrier reefs are important formations in Madagascar coastal waters; ring-shaped atolls are abundant in Seychelles (e.g. Aldabra, Cosmoledo, Astove, Farquhar, St Joseph) and Mozambique channel (Europa, Bassas da India) so as the submerged atolls of Geyser and Zélée; Various coral and oceanic banks are found along the continental shoreline and Mascarene plateau. The total extension of productive reef areas in the WIO is 54000 km² (the third largest worldwide). The largest extension of productive reef areas is located in South-east Asia with 89000 km², and the second largest in the Pacific region with 67000 km² (Burke et al., 2011).

1.3 Anthropogenic threats in the Western Indian Ocean:

The autonomous archipelago of Zanzibar has been traditionally a fishing target due to the proximity to Tanzania mainland and its high biomass. Moreover, the archipelago has been proved to be one of the greatest marine biodiversity hotspots from Africa (Agnarsson, 2012). However, overfishing and baleful fishing practices like dynamite fishing, dragnets or seine fishing method, induce physical destruction along the seabed. These practices have been many times pointed like unsustainable (Callaway et al., 2007; Davies et al., 2007) and are currently banned in the Zanzibar Archipelago. However, they are common historically in the

Western Indian Ocean (WIO) region. Growing pollution, illegal fishing methods and coastal development (Brown 2006) seem to be some recurrent parameters which may fall into a figurate formula of unsustainability (Heal and Schlenker, 2008), but common in developing countries. Also, poverty, insufficient capacity for effective marine governance and enforcement, aggravated by lack of information, makes difficult to enforce measurements to get a sustainable environment and community. The recent growth of eco-tourism seems to be a great compromise, supporting local communities economically on one hand and on the other hand bringing natural resources into focus by establishing marine protected areas (MPA), which enables marine natural systems to develop without major anthropogenic disturbances.

1.4 Ecosystem health and its implications

This concept relies on the importance of the environmental description using two dimensions; the biological condition and the human disturbance (Karr, 2000). Interacting stressors operate on global (ocean acidification, ocean warming) and local scales (overfishing, sedimentation, pollution, algal blooms) affecting ultimately ecosystem health.

The environment condition can be cataloged as healthy or not healthy. A healthy environment can be considered an ecosystem, which has the capacity to provide a variety of functions to a diversity of organisms. A highly diverse system, builds up resilience, which is the ability to withstand stressors (e.g. chronic or abrupt events) and/or to fast recover to initial or functional condition. If so the ecosystem has reached a steady state in which the functionality is regulated by the biophysical interactions on the media (Bellwood et al., 2004). When influenced by human uses and activities, a healthy ecosystem can be disturbed by anthropogenic stressors in a way that shifts into a fragile system of a system with fewer functions and associated depauperate diversity.

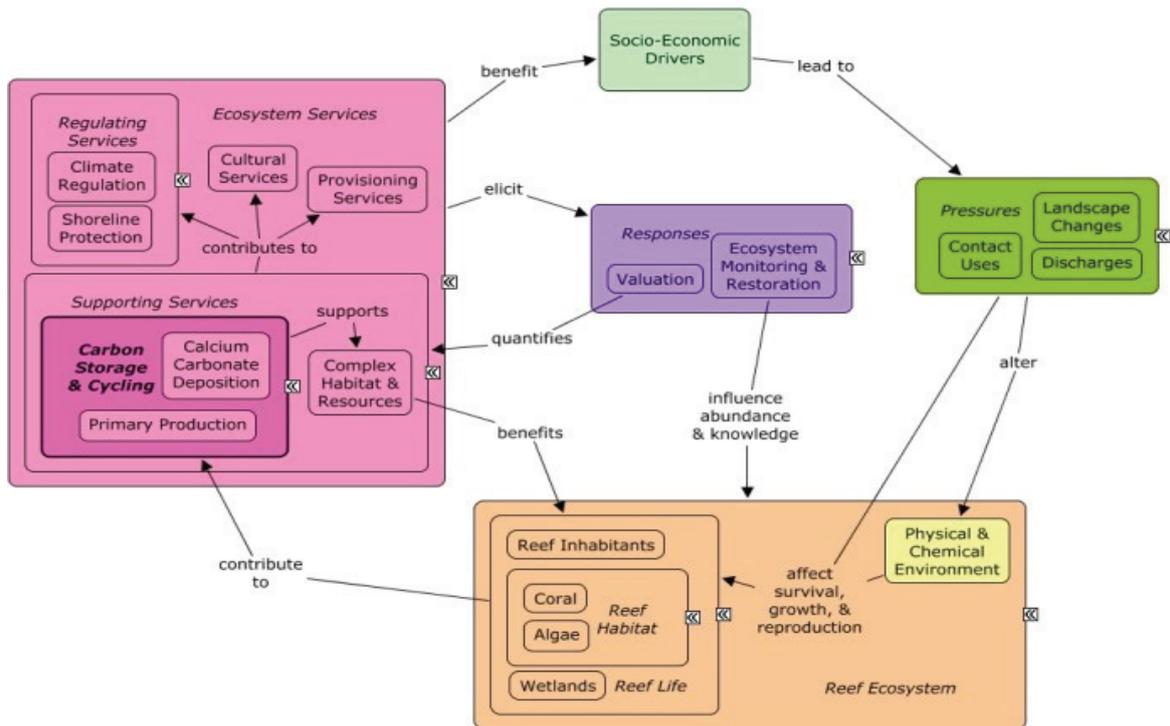


Figure 1-2 - Conceptual chart of coral reefs ecosystem services and the linkage socio-economic drivers and anthropogenic pressures. Cmap.

Therefore a healthy reef would provide a ecosystem ecosystem services (Figure 1-2). The reefal calcium carbonate production support and influence socio-economical drivers (Figure 1-2), which triggers human pressures affecting ultimately ecological parameters such as survival, growth, and reproduction of the reef inhabitants.

In the Zanzibar Archipelago, the most representative carbonate producers are algae, stony corals, and calcareous macroalgae. These bioengineers are the founding species that support and enhance biomass production (Lough and Barnes 1997), whereas foraminifera, echinoids, and coralline algae might gain importance while feeding sand barriers and provisioning sandy beaches (Shaghude 2002) important for the tourism in Zanzibar, Tanzania. In our study site, socioeconomic and natural systems are ineluctably linked, because local communities depend primarily on natural resources.

1.5 Research framework and objectives

The Ph.D. project “ Carbonate production and the response of calcifying organisms to natural and anthropogenic threats on the shallow platform of Zanzibar, Tanzania” is embedded in the SUTAS graduate program at the Leibniz Center for Tropical Marine Research (ZMT) in cooperation with the Institute of Marine Science (IMS) on Zanzibar. Funded by the Leibniz Association and with the support of the German Federal Government. This program is part of the ZMT mission of research towards science-based strategies for sustainable use of tropical coastal systems.

The present study examines from a holistic perspective the ecological value, status, production, breakdown and composition of coral reef in the Western Archipelago of Zanzibar. We used census-based field exploration to quantify the carbonate builders abundance and distribution to determine the relative contribution of different carbonate producers to the total net budget. We followed certain theoretical premises *sensu* Chave et al. (1977):

- 1) The measure of gross carbonate production (GCP) states for the collective carbonate producers in a reef scale.
- 2) The net calcium carbonate production, estimated the total CaCO_3 produced and potentially permanently retained within the reef system (i.e. the net balance of bioconstruction and bioerosion processes).

In addition, we assessed the dispersal of particulate sediment on adjacent reefs to Stone Town, in the western coast of the Zanzibar platform to estimate the extent of local human impacts (pollution). We also investigated the linkage between ecological processes and geomorphic formations, as physical factors re-work and transport carbonate material produced in the reefs, which ultimately can be utilized by other marine organisms. Therefore,

we also considered reef connectivity, because the ecosystem services coral reef provides (e.g. carbonate sediments) work as a foundation for other marine habitats, i.e. Seagrass beds.

Five general aspects would be addressed:

- Reef community composition and overall coral reefs status.
- CaCO_3 production and bioerosion
- Response, plasticity, and adaptation of the coral's inhabitants to turbid conditions
- Anthropogenic influences on reef geomorphology
- Carbon storage

1.6 Thesis outline

The research here presented provides an integrated view of coral reef geoecology. Several methodologies from different fields of knowledge (e.g. biogeochemistry, ecology, and geology) have been applied to approach the difficult question, on what is the relevance of calcium carbonate production, how much does reefs ecosystem produce and ultimately how humans affect coral reef systems and their functionality from a process-based approach. We have quantified the biologically driven carbonate production; the abundance, the biodiversity, and the distribution of carbonate secreting organisms (Chapter 2).

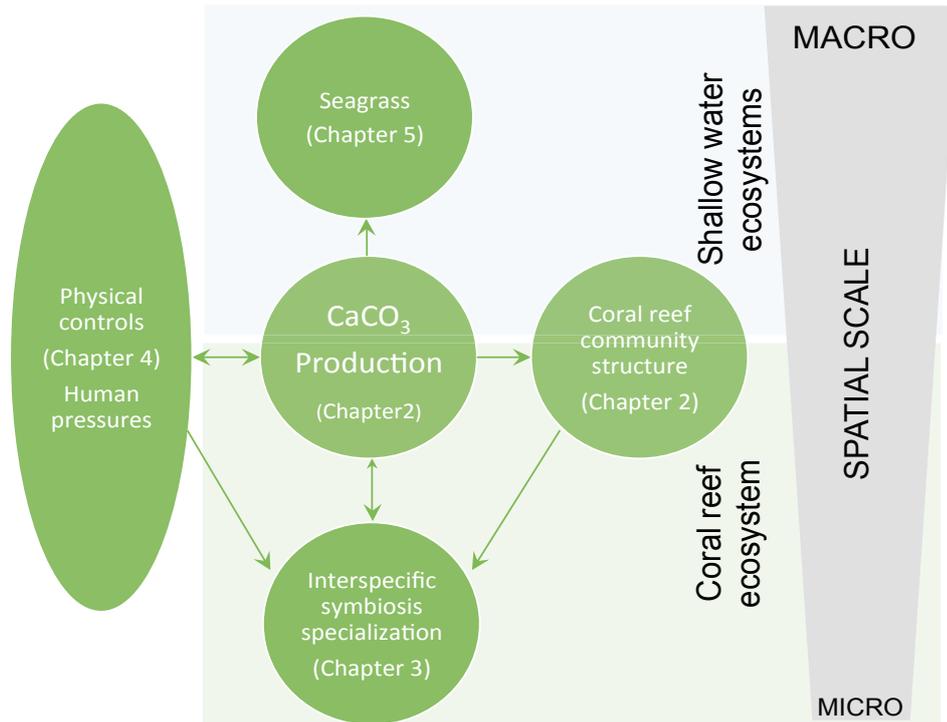
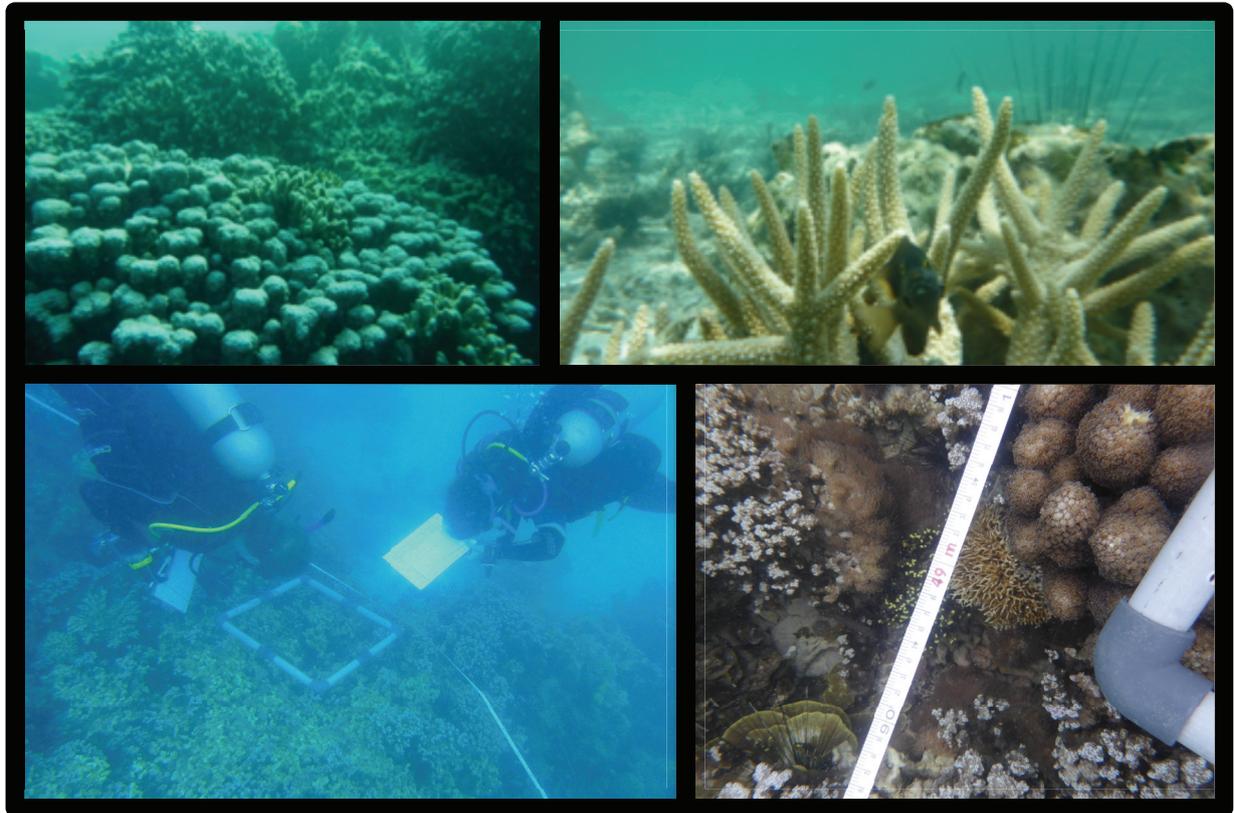


Figure 1-3 Concept of the chapters presented in this cumulative thesis indicating the central role of CaCO₃. The chart also highlights the different spatial scales which range from the individual micro scale (Chapter 3) to the reef scale (Chapter 2 and 3) and the linkage with other shallow marine ecosystems (macro scale – Chapter 5).

We investigated in detail, corals adaptation and specialization to environmental constraints (Chapter 3). We explored the effect of high sediment loads and human disturbances on coral reef morphology and reef development (Chapter 4). The chapter 5, is an interdisciplinary work on the assessment of seagrass beds ecosystem services, trapping and storing carbon (Chapter 5). The landscape and the substrate in which seagrass settled was characterized, as sediment availability worked as a key environmental driver. The last chapter is an extended discussion of the above mention chapters (Chapter 6).

2. Calcium carbonate budget and coral reef structure along a distance gradient from Stone Town, Zanzibar



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Keywords: Coral reefs; Environmental indicators; Bioerosion; Zanzibar Archipelago; Marine Biodiversity, Marine Protected Areas (MPA)

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2.1 Abstract

Photosymbiotic scleractinian corals are major bioengineers in tropical coastal waters, where they build structurally complex geological features and provide substrata for a manifold of macro and microhabitats. Ecological competition and physical parameters - natural as well as human-derived, drive species richness, biodiversity, and morphological adaptation on tropical coral reefs. Here, we compared four coral reefs in the Zanzibar Archipelago under different management regimes. To assess the ecological health of these reefs, calcium carbonate production, structural complexity, and biodiversity were determined. The reef located in a marine protected area showed the highest net calcium carbonate production (16.90 ± 9.70 Kg $\text{CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$), coral cover ($67.37 \pm 8.76\%$), and biodiversity (1.61 ± 0.24). Conversely, unprotected reefs in the direct vicinity of Stone Town, which are exposed to fishing pressure, land-derived pollution, unregulated tourism, and careless anchoring, showed the lowest calcium carbonate production (8.47 ± 4.37 Kg $\text{CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$), coral cover ($52.45 \pm 13.96\%$), and biodiversity (1.23 ± 0.52). However, in global comparison, the calcium carbonate production of all four reefs studied is high. Similarly, coral community structure differs significantly with distance from Stone Town, in that, the most homogenous reefs dominated by massive and submassive species (*Porites lobata* and *P. rus*) occurred the closest to Stone Town. This study highlights the dependence of coral reef functioning and biodiversity as reflected by reef health indices on use and protection.

2.2 Introduction

Local communities depend on coral reefs as they provide vital ecosystem services such as coastal protection, food acquisition and economic activities such as tourism (Bellwood et al., 2004). However, reefs are highly susceptible to local anthropogenic pressures (Mumby and Steneck, 2008) and are greatly threatened by human stressors such as coastal development, pollution and overfishing (Johnstone et al., 1998). The loss of reef structural complexity and the associated mechanics are a pressing topic, particularly in light of increasing anthropogenic threats (Graham and Nash, 2013; Hoegh-Guldberg et al., 2007; McClanahan et al., 2007). For instance, reefs affected by pollution show high framework bioerosion (Edinger, 1998; Holmes et al., 2000) and low skeleton density (Highsmith, 1981).

Tropical carbonate secreting benthic assemblages are major carbonate sediment producers (Graham and Nash, 2013). Yet, calcium carbonate (CaCO_3) produced within coral reefs accounts for more than 25% of the total CaCO_3 buried in marine sediments globally (Jones et al., 2015). Calcium carbonate sediments are highly important in tropical marine environments because they contribute to reef islands, sand banks and beaches. A number of physical parameters, such as wave exposure, currents and temperature, control the development of coral reefs, its biodiversity (Roberts et al., 2002) and reef morphology (e.g. hard coral morphological strategies) (Mallela et al., 2004; Perry et al., 2013; Webb and Kench, 2010). For instance, platy coral morphologies are more successful on deep fore reef sites, due to their ability to harvest light (Todd, 2008), whereas more robust, boulder corals are generally found in the reef crest under moderate to high hydrodynamic regimes (Storlazzi et al., 2002). Hydrozoans, octocorals, sponges and some hexacorals modify their morphology according to the nutrient, sediment, light or energy regimes in which they occur (Kaandorp and Kluijver 1992; Lesser et al. 1994; Sebens, Witting, and Helmuth 1997; Kaandorp 1999; Kaandorp et al. 2005; Kim et al. 2004; Kruszyński, Kaandorp, and Van Liere 2007). It is because of their

response to surrounding environmental constraints, that corals morphological strategies are used as a bioindicators of water quality (Roberts et al. 2002; Hallock et al. 2004), ecosystem health (Veron et al. 2009), ecological value and conservation priority (Edinger and Risk 2000). High-resolution standardized census-based datasets can provide further information on corals demography, the population dynamics affecting calcifiers demography, abundance (Jones et al. 2015) and ecosystem functions (i.e. shelter for marine organisms, coastline protection, nutrient fixation and cycling) (Ferrario et al., 2014; Jones et al., 2015; Perry et al., 2012). In addition, regional, high-resolution datasets are essential for the overall assessment of reef conditions in a changing ecosystem (Dubinsky and Stambler, 1996).

Here we examine coral reef multiplicity (intrinsic factors i.e. biodiversity and structural complexity) in some of the less studied reefs in the world (Johnstone et al., 1998). The aim of our study is to determine the role of a locally managed Marine Protected Area (MPA) compared to non-protected high use coral reefs. To achieve this we aim to: (1) measure the benthic community composition and associated spatial variability, (2) examine the reef structural complexity; (3) determine the net calcium carbonate budget; and (4) use bio-indicators (e.g. biodiversity indices, coral structural complexity, CaCO₃ production and bioerosion rates) on a distant gradient to highly populated areas, to estimate the overall reef complexity within the western Zanzibar reefs.

2.3 Material and methods

2.3.1 Study site

The Western Indian Ocean (WIO) region is known to support approximately 21.6 % of the global tropical coral reef area (Burke et al 2011). Of the total coral reef coverage, 1.2% is found in Tanzania, along the East Coast of Africa (UNEP-WCMC 2011). The Zanzibar Archipelago, off continental Tanzania, consists of three major islands including Pemba in the

CHAPTER 2

North and Zanzibar (Unguja) and Mafia Islands to the South (Figure 2-1A). The Zanzibar channel acts as a physical barrier, isolating Zanzibar Archipelago from Tanzanian coastal waters (Muzuka et al., 2010) and terrigenous sediments coming from mainland river discharges (Shaghude et al., 2002a). Within the region, the annual air temperature ranges between 27 and 35 °C (Shaghude, 2000) with annual average rainfall of 1600 mm on Zanzibar Island (Mgaya, 1997). Southwest-driven monsoonal rains and high currents occur between March to May, while low precipitation and northeastern currents are typical between November and March (Newell, 1957). ROMS models (Regional Oceanic Modeling Systems) show that the semidiurnal mesotidal regime, triggers strong tidal currents from the north and south entrance along the Zanzibar Channel, converging off of Stone Town (Lwiza and Bigendako 1988, Mukaka 2014).

Fringing reefs off Stone Town (Figure 2-1C), located in the western shoreline of Zanzibar Island, exposed to sewage outfall waters that discharge into coastal waters. The main outfall, located adjacent to the Port of Stone Town, discharges an estimated 2.2×10^6 L d⁻¹ of untreated sewage (Moynihan et al. 2012). Tidal currents canalize the flow of wastewater in a northward direction away from Stone Town towards three nearby reef sites that are important artisanal fishing grounds and tourist destinations (Johnstone et al., 1998; Mohammed and Mgaya, 2001; Mukaka, 2014).

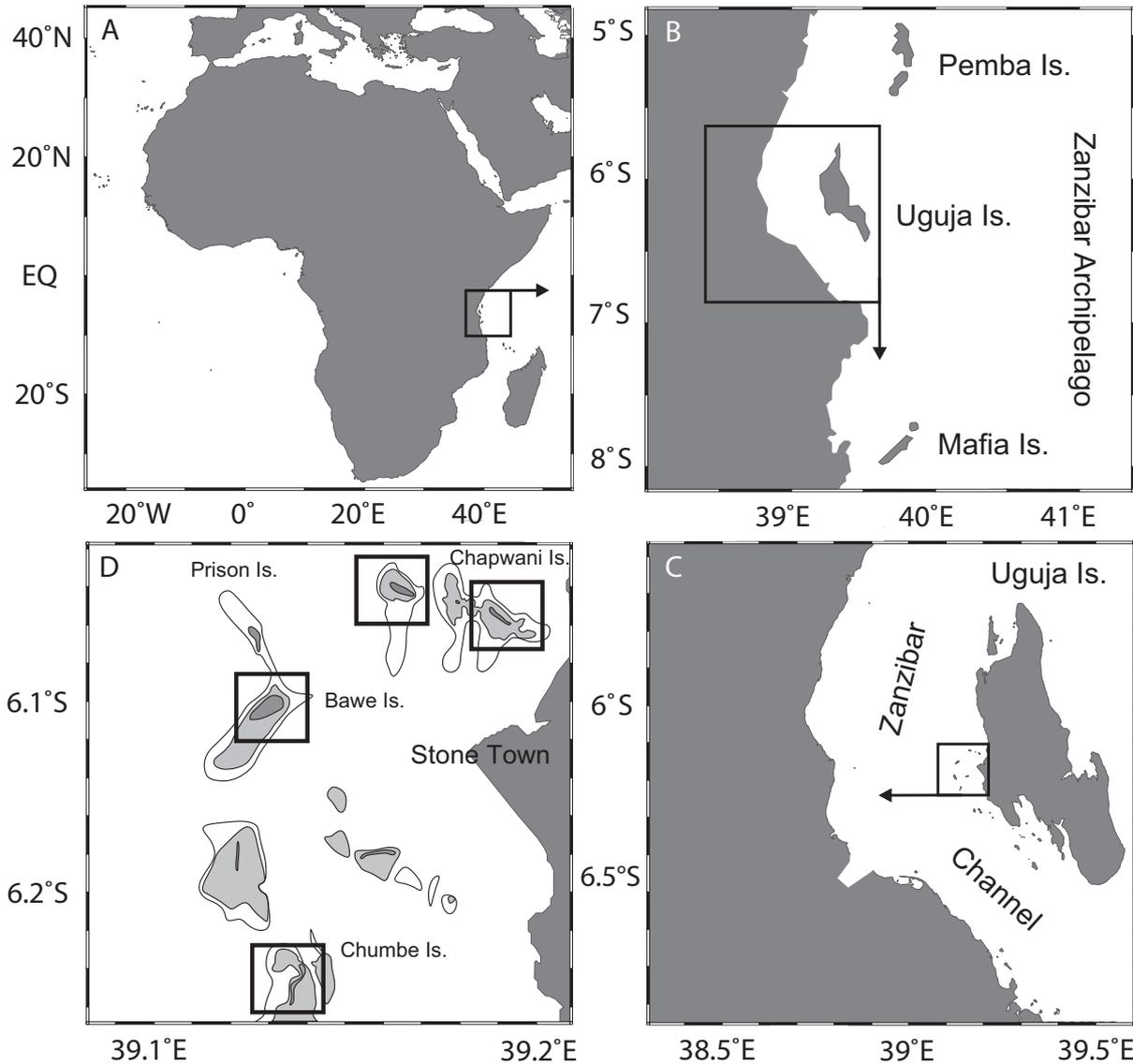


Figure 2-1 - Location of the study area showing A) the African continent; B) Zanzibar (Unguja) Island; C) the Zanzibar Archipelago, off of Tanzania; and D) the Zanzibar island chain and location of our study sites.

Four of these fringing reefs off to Stone Town are in the focus of the present study (Figure 2-1D). Chapwani Reef ($6^{\circ}7'35.89''\text{S}$, $39^{\circ}11'32.13''\text{E}$), Prison Reef ($6^{\circ}7'7.57''\text{S}$, $39^{\circ}9'58.90''\text{E}$), Bawe Reef ($6^{\circ}8'56.72''\text{S}$, $39^{\circ}7'57.04''\text{E}$) and Chumbe Island Coral Park (CHICOP) ($6^{\circ}16'42.32''\text{S}$, $39^{\circ}10'40.29''\text{E}$) are located at increasing distance to Stone Town (approx. 3, 5, 6 and 13 km, respectively). Bawe and Chapwani reefs possess a well-developed

fringing reef along its southern flank, whereas Prison reef main fringing reef faces the northwestern side of the Island. Prison and Bawe reefs are separated from Stone Town by a tidal channel (approx. 20-30 m deep) characterized by strong tidal currents (Mohammed and Mgaya, 2001). CHICOP is an ecological sanctuary and marine protected area (MPA) since 1994. CHICOP is a strictly non-take reef zone area, stretching along the western flank of the Island. Activities include sustainable eco-tourism and marine education among others, with a *zero waste* policy (Riedmiller, 1998).

2.3.2 Ecological surveys

To determine the species composition, coral reef status (e.g. biodiversity metrics) and calcium carbonate production in our study sites, we applied the line intercept transect method (LIT) (English et al 1997) and *ReefBudget* Method (Perry et al., 2012), respectively. By convention, six 10 meter transects were randomly placed and independently recorded by SCUBA divers in the reef-slope of each study site at shallow (5 ± 2 meters) and deep (10 ± 2 meters) areas. With the exception of Chapwani Reef, where transects were only recorded at 5 meters, as the reef slope was bathymetrically constrained to approx. 7 meters. The identification was made upon the genera level, species level when possible. We also recorded the following benthic categories: coralline algae, sponge, corallimorpharians, others (e.g. seagrass, zoanthids, clams etc.), sub-category 1 (i.e. dead coral and rubble) and sub-category 2 (i.e. sand, mud and silt).

The relative percentage cover of each benthic category was calculated by the relative fraction it occupies (X_i) [cm] divided by the total transect (TL) [cm] multiplied by a factor of 100. In order to quantify the calcium carbonate production and reef structural complexity, we measured the substrata, benthic taxa and habitat, making use of a high-resolution substrate analysis (English et al 1997) and the *ReefBudget* Method (Perry et al. 2012) to the morphological level. Following the *ReefBudget* methodology, four morphological classes

were distinguished; branching, platy, massive and submassive. We applied density and calcification rates of each morphological group accordingly. We measured 5 (50 x 50 cm) quadrants per transect to measure boring sponge, urchin and crustose coralline algae (CCA) abundance and coverage, to quantify corresponding bioerosion rates following Perry et. al. (2012). Thereafter, we measured net or total calcium carbonate production rates (gross calcium carbonate rates produced by carbonate secreting organisms, e.g. hard corals, CCA and calcifying macroalgae, minus, bioerosion rates of parrotfish, sea urchin, boring sponge and micro-bioeroders).

The roughness, reef structural complexity or reef architecture, here define as the three dimensionality property of the reef framework, was calculated as $D1/D2$ [m/m], where D1 is the contour measured of each substratum or feature and D2 the planar distance covered by the substratum (Harney and Fletcher, 2003; Hubbard et al., 1990; Mallela and Perry, 2006; Perry et al., 2012).

2.3.3 Data analysis: Statistical test

To correlate the variance between multiple reef components (e.g. biodiversity indices, reef complexity, coral morphologies and carbonate production rates) to location, distance and depth, a two-way-ANOVA was performed. The Tukey's Honest Significant Difference (HSD) post-hoc test and pairwise comparison t-test was used to determine differences between the reefs. To determine how representative the sampling method was and to validate the sampling strategy used in this study, we computed a rarefaction curve of the abundance data using Kindt's exact method described in Oksanen (2015). The alpha diversity (Biodiversity) is given as Shannon-Wiener natural log (Fedor and Spellerberg, 2013) and Margalef species richness *sensu* Gamito (2010). All those analysis were computed with R software (R development Core Team 2010). We used the following packages: Vegan

(Oksanen 2015), Companion to Applied Regression package (Fox and Weisberg 2011), BiodiversityR (Kindt 2005), tcltk (R core team 2014), ggplot2 (Wickham 2009) and Modern Applied Statistics with S (Venables and Ripley (2002).

To describe the benthic beta diversity (distribution patterns of the biodiversity between sites) and to describe the community composition, we run MDS (non-metric multidimensional scaling), ANOSIM (analysis of similarity), SIMPER (similarity percentage) analyses from the hard coral relative abundance data (Clarke, 1993). Such analyses were computed with PRIMER-E software v.6 (Plymouth Routines In Multivariate Ecological Research).

2.4 Results

2.4.1 Community structure and alpha diversity

Our study sites showed high live coral cover (>50%). Live coral cover in shallow reef-slope areas (5±2 meters) ranges (Mean±SD, n=6) from 52.45±13.96%, 65.83±10.64%, 72.72±15.05% to 67.37± 8.76% for Chapwani, Prison, Bawe and Chumbe reefs, respectively. Deeper areas (10±2 meters) also show high live percentage cover; 74.48±13.26%, 71.51±12.81% and 57.63±17.93% for Prison, Bawe and Chumbe reefs, respectively. Overall, there were significant differences of live cover between depths in Prison Reef (one-way-ANOVA, $F_{1,4}=19.74$, $p=0.011$) and Chumbe Reef (one-way-ANOVA, $F_{1,4}=10.31$, $p=0.032$), but not in Bawe Reef ($p>0.05$). The second more abundant benthic category was dead coral and coral rubble (Sub-category 1, >12%), but in Chapwani and Prison Reef the second dominant benthic category in shallow reef-slope areas was *Hexacorallia*, order *Corallimorpharia* (Stephenson, 1937). In total 35 hard coral taxon were observed when all transects together were pooled (S.1). At Chapwani Reef 11 hard coral taxa were observed, whereas in Prison, Bawe and Chumbe reefs a total of 22, 21 and 27 taxa were observed, respectively. Biodiversity and richness increased southwards from Chapwani Reef to Chumbe Reef (Table 1). In addition, deeper areas showed lower biodiversity than shallower

areas, with the exception of Prison Reef (Table 1). Chumbe Reef has the highest biodiversity (1.82 ± 0.21 and 1.61 ± 0.24 at 5 and 10 meters, respectively) and richness values (2.53 ± 0.47 and 2.08 ± 0.35 at 5 and 10 meters, respectively). However, no significant difference in biodiversity or richness was found between reefs and depths (two-way-ANOVA, $F_{3,35} = 2.324, p = 0.0918$).

Chapwani, Prison and Bawe reefs were dominated by *Porites rus* (*synaraea*) (Forskål, 1775), accounting for 50.7%, 40.8 % and 47.4 % of the relative abundance, respectively (Table S.1 ANNEX 1). *Galaxea* spp. (Oken, 1815) was the second most relevant taxon in Prison Reef and third most relevant taxon in Bawe Reef (S.1). Relatively high abundance of *Pocillopora* spp. in Bawe (6.4%) and Chapwani (6%) showed similarities between the two reefs. Branching coral *Acropora* spp. (Oken, 1815) was the most abundant taxon in Chumbe Reef, accounting for 31.6% of the total relative abundance. *Porites lobata*, *Acropora* spp. and *Porites rus* along with *Seriatopora* sp. and *Fungia* spp. were found in the shallow reef areas, whereas *Galaxea* spp., *Pocillopora* spp. and *Porites porites* were found generally in deep reef areas (Table S.1). No significant differences were found between shallow and deep communities (55.77%).

At transect-scale, we identified five distinct benthic groups (Figure 2-2 A). Hard coral community composition in all locations is at least 20% similar (Bray-Curtis dissimilarity matrix) (Figure 2-2). Groups 1 and 2; were characterized by *Porites rus*, *Galaxea* spp. and *Porites porites* as dominant taxon. Group 3; was the largest transitional group, which clustered diverse range of species (*Seriatopora* and *Pocillopora*) from all locations. This group shared the occurrence of a large range of coral genera, without a clear dominant taxon. Groups 4 and 5; were dominated by *Acropora* spp. and large *Millepora* spp. colonies. Overall, in Chumbe Reef, extensive *Acropora* spp. fields and distinctive coral species drove dissimilarities in benthic community composition between the reefs (Figure 2-2).

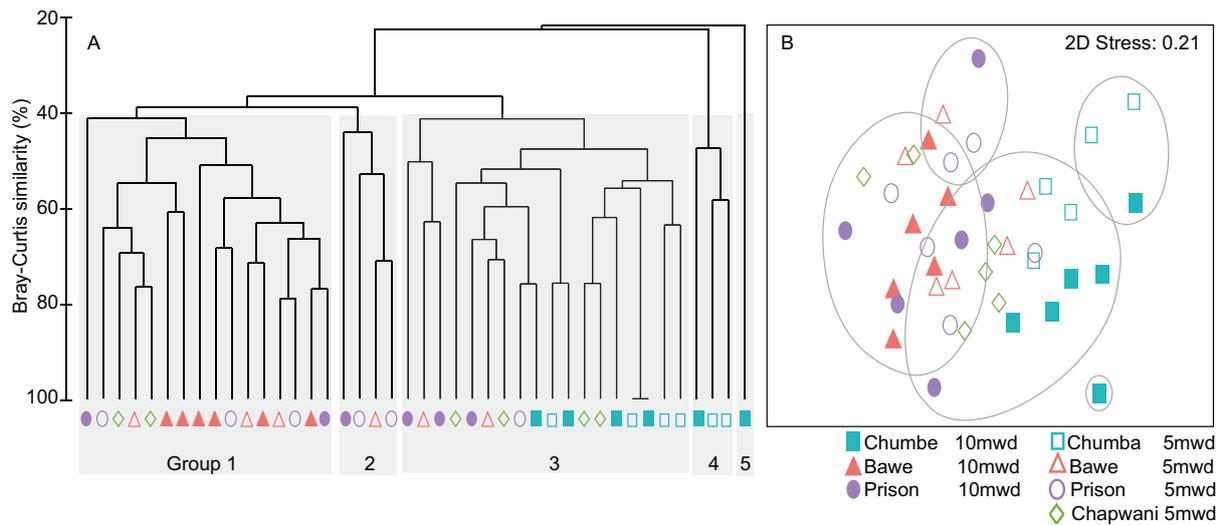


Figure 2-2 - A) Cluster analysis showing the different groups according to the hard coral composition analysis. B) The MDS ordination plot of the coral abundance data.

2.4.2 Morphological strategies and reef structural complexity

Platy corals were the scarcest morphotypes found in all locations (Figure 2-3). In Chapwani Reef this class was completely absent, whereas in Prison Reef small *Montipora* sp. and platy morphotypes of *Porites rus* were recorded (Figure 2-4). Pooled data show that platy corals coverage in Prison Reef is relatively low (1.05%) to other reefs where platy corals are more successful, for example in Bawe Reef (4.6%) and Chumbe Reef (5.2%). Massive and submassive corals were the most abundant morphotype among the reefs (Figure 2-3), with the exception of Chumbe reef where we find high branching coral percentage cover (47.70%).

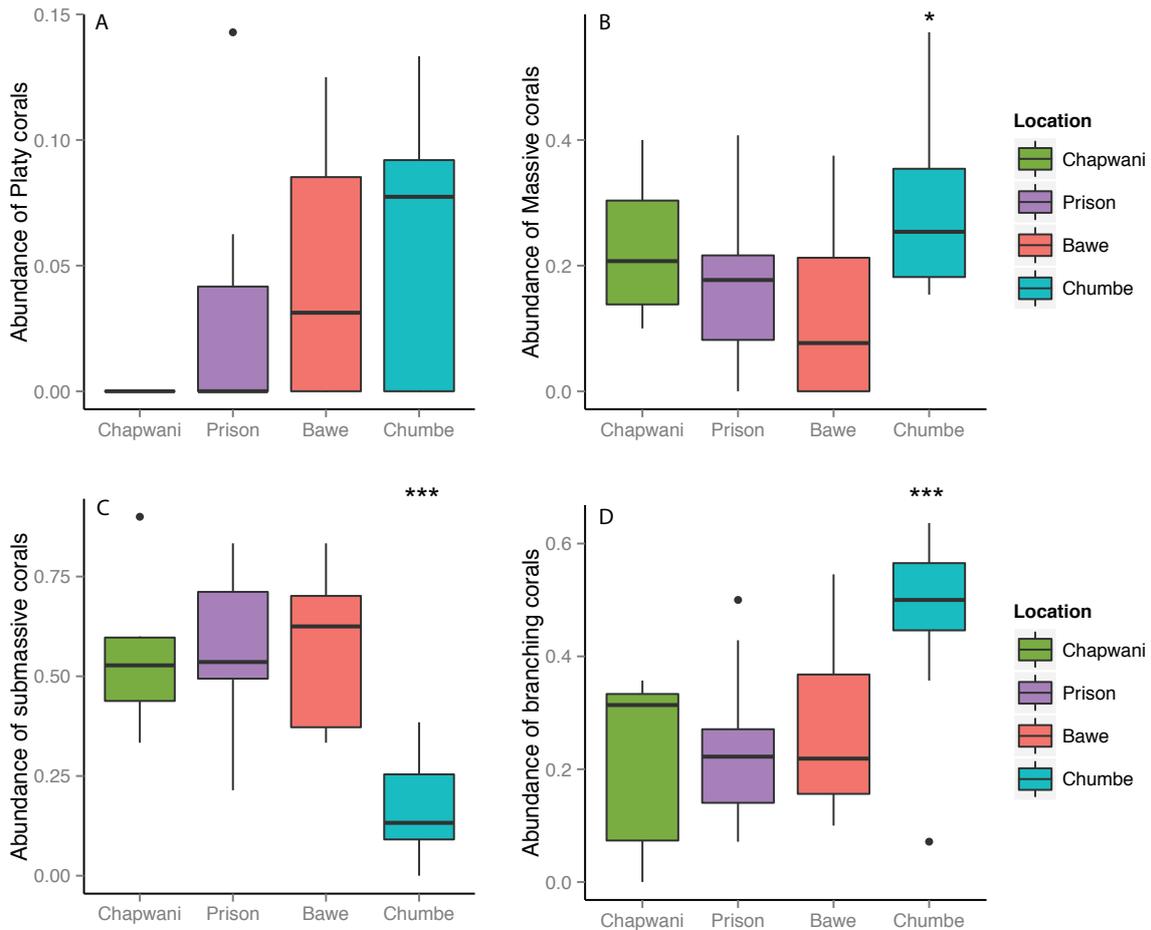


Figure 2-3 - Overview of the morphological categories of the different reefs. An analysis of variance showed significant differences between the massive, submassive and branching coral morphologies $F_{3-38}=4.257$, $p=0.0109$ *; $F_{3-38}=16.04$ $6.79e-07$ * and $F_{3-38}=7.197$, $p=0.00061$ *** respectively. However, the distribution of platy corals do not show strong spatial differences $F_{3-38}= 2.444$, $p=0.078$.**

We found significant spatial differences in hard coral morphological strategies between reefs (Figure 2-3). Among all sites, we found high abundance and large colonies (> 1-meter diameter) of massive corals *Porites* spp. Strong spatial distribution differences were recorded

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for submassive and branching corals, $F_{3,38}=16.04, p=6.79e-07$; $F_{3,38}=7.197, p=0.00061$, respectively (Figure 2-3, Figure 2-4).



Figure 2-4 - Representative quadrants (0.5 x 0.5 m) taken on Chapwani (*Porites rus*), Prison (*Porites rus*), Bawe (*Callyspongia* sp, *Pocillopora*, *Montipora*) and Chumbe (*Porites lobata*, *Acropora* sp, *Seriatopora* sp, *Montipora* sp, *Porites porites* and *Fungia ctenactis*) reef.

Reef structural complexity or reef architecture ranged from 1.18 to 1.51. Among all reefs, structural complexity was slightly higher at shallower rather than deeper areas of the reef slope. With the exception of Prison Reef, which presents higher reef complexity in deeper areas (1.47 ± 0.33 at 5 ± 2 meters and 1.51 ± 0.24 at 10 ± 2 meters). Prison Reef shows the highest reef structural complexity followed by Chumbe, Bawe, and Chapwani reefs (1.38 ± 0.12 , 1.35 ± 0.48 and 1.22 ± 0.28 , respectively at 5 meters; Table 2). The results of the two-way-ANOVA, to test if the reef complexity was significantly different by location and by depth, but no significant differences were established ($F_{3,35}=1.763, p=0.172$).

2.4.3 Bioeroders

The major bioeroder was the corallivores (Table 3). A large variability of parrotfish bioerosion rates was recorded between and within reefs, which ranged from $(0.44 \pm 0.8$ to $4.97 \pm 8.00 \text{ Kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1})$. We surveyed parrotfish presence, sea urchin abundance and boring sponge density. The relatively high sponge abundance and cover were found in Bawe ($2.52 \pm 3.61\%$) and Prison ($2.52 \pm 3.02\%$) reefs, contrasts with the relatively low sponge coverage found at Chumbe ($1.30 \pm 1.84\%$) (Figure 2-5) and Chapwani ($1.05 \pm 1.80\%$) reefs. There were no significant differences between bioerosion rates of boring sponge in Prison and Bawe reef, which show similar bioerosion rates; 0.46 ± 0.19 and $0.46 \pm 0.19 \text{ Kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$, respectively. However, Chapwani Reef presents very low coverage and subsequent erosion of boring sponge ($0.02 \pm 0.01 \text{ Kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$; Figure 2-5, Table 3). Conversely, Chapwani Reef showed very high sea urchin abundance and bioerosion rates ($1.33 \pm 0.18 \text{ Kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$), which was significantly different to sea urchin abundance and bioerosion rates in Prison ($p < 0.001$), Bawe ($p < 0.001$) and Chumbe reefs ($p < 0.001$) (Figure 2-5). Micro-bioerosion rates ($< 0.0001 \text{ Kg m}^{-2} \text{ yr}^{-1}$) are very low when compared to the rates calculated for macro-bioeroders on a reef-scale (Figure 2-5)

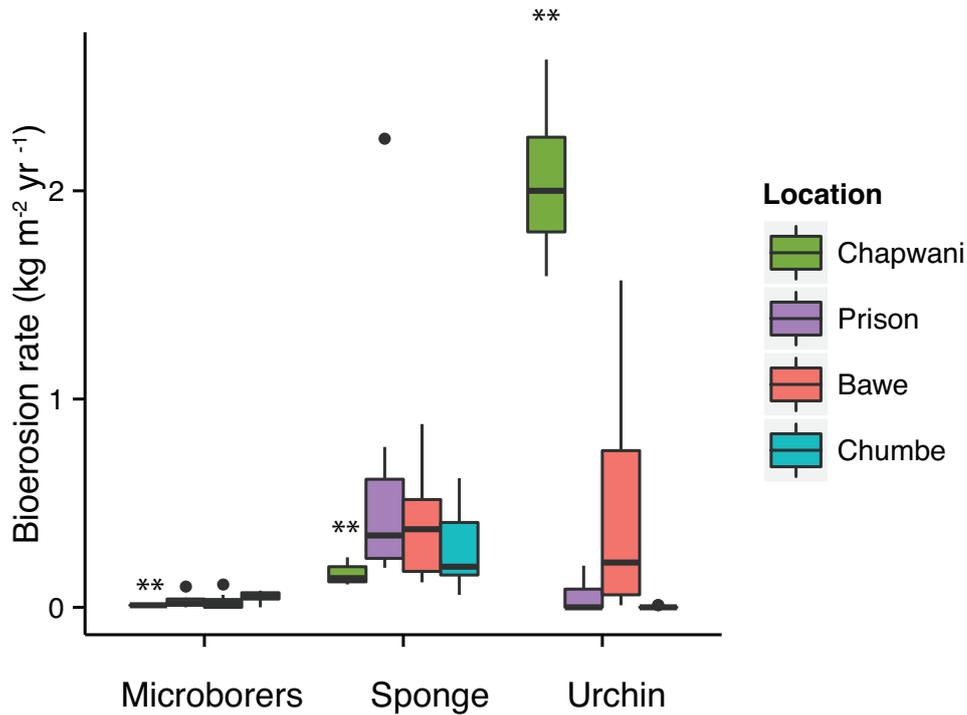


Figure 2-5 - Boxplots showing the bioerosion rates calculated for the different biogenic groups. The locations include Chapwani (green), Prison (purple), Bawe (red) and Chumbe (blue).

2.4.4 Calcium carbonate production

Along the western coast of Zanzibar, primary carbonate producers are photosynthetic hermatypic corals. We saw very little secondary production from crustose coralline algae (CCA's) and almost no carbonate production from calcifying algae. The reef with the highest CCA percentage cover was Chumbe Reef (approx. 2%). Negligible occurrence was recorded in the other reefs.

Our study sites scored consistently high gross calcium carbonate production rates, 10.7 ± 4.09 , 10.43 ± 2.37 , 15.03 ± 7.76 and 18.95 ± 9.70 $\text{KgCaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$, for Chapwani, Prison, Bawe, and Chumbe, respectively. The results showed that the gross calcium carbonate production increased with distance from Stone Town (Figure 2-6) and was significantly different

between reef sites ($F_{3,35}=3.459$, $p=0.0266$), but carbonate budgets were not significantly different when shallow and deep areas were compared ($F_{1,35}=0.066$, $p=0.7986$). When, we compared one to one gross calcium carbonate production rates, Chumbe Reef production differs significantly from the production recorded in Prison Reef and Chapwani Reef ($p=0.004$ and $p=0.020$, respectively). However, when we compared production rates found in Bawe Reef to those found in Chumbe or Prison reefs we did not see significant differences ($p=0.161$ and $p=0.114$, respectively).

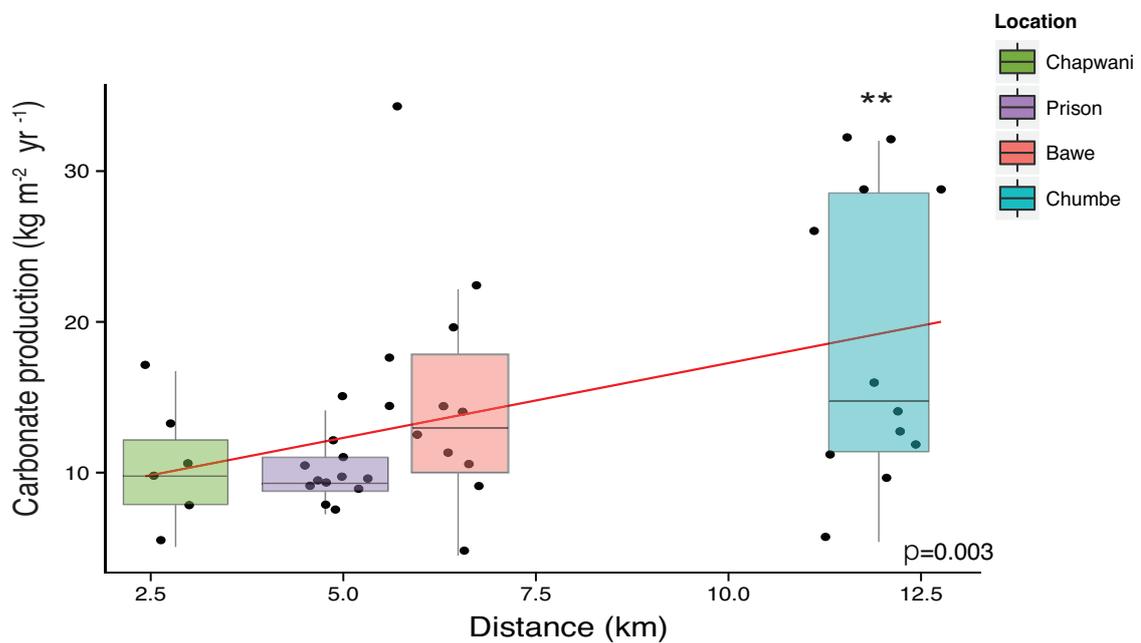


Figure 2-6 - Boxplot showing the net calcium carbonate production per reef at 5 m and 10 m. Solid red line shows the correlation between the calcium carbonate production and distance to shore.

Our study sites show high net calcium carbonate production rates (Gross production rates – bioerosion rates), range from 8.03 ± 4.37 to 16.90 ± 9.70 Kg $\text{CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$. The CaCO_3 production was positively correlated to biodiversity ($p = 0.010$) (Figure 2-7) and increased with increasing distance to Stone Town ($p=0.003$) (Figure 2-6). Chapwani, Prison and Bawe reefs dominated by massive and submassive species (Table 4) show high net carbonate production rates 8.03 ± 4.37 ; 9.8 ± 2.4 and 14.11 ± 7.36 Kg $\text{CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$, respectively.

However, the non-take zone of Chumbe Reef, dominated by branching ramose *Acropora* spp shows the largest net calcium carbonate production (Figure 2-8).

2.5 Discussion

2.5.1 Community composition

Chronic stress has conspicuous consequences towards coral reef community structure, recovery and resilience (Nyström and Folke, 2001) and can be exacerbated by compounding local pressures including nutrients, sedimentation, and temperature anomalies. Previous studies have suggested that nutrient levels control primarily coral community structure (Fabricius, 2005; Lapointe et al., 2011), however, nutrient variability is high and concentrations are low in western Zanzibar reefs (Narayan pers comm. 2017). Sedimentation resuspension observed in the reefs is a possible cause of regular boat traffic (based on field observations) on the Zanzibar Archipelago. Additionally, recent temperature anomalies have seen massive die backs since the 1998 bleaching event throughout the Zanzibar Archipelago (Muhando and Lanshammar, 2008). However the proximity to source pollution and marine management practices could have significant influence on the current community structure and future resilience to local and global stresses.

The community composition of corals found in the reefs adjacent to Stone Town are depauperate and dominated by *Porites rus*. This could be related to similar local stressors, *i.e.* land-based pollution and unregulated tourism (Moynihan et al., 2012). Chapwani Reef showed the lowest coral cover ($52.45 \pm 13.96\%$), biodiversity (1.23 ± 0.52) and calcium carbonate production ($8.47 \pm 4.37 \text{ Kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$). In addition, Chapwani Reef showed low CCA relative abundance ($< 0.05\%$), which is known to limit coral larvae settlement (Vermeij et al., 2011), reef calcification (Fabricius and De'ath, 2001), and overall coral reef recovery. Consistent to our findings, low CCA occurrence has been reported (Szmant, 2002) at

Chapwani reefs. In combination with impoverished benthic diversity, indicates suboptimal (e.g. turbid or polluted waters) coral reef conditions (Szmant, 2002) and/or high sediment stress (Fabricius and De'ath, 2001).

In 1998 and 2005 Chumbe Reef was heavily affected during both bleaching events (Muhando and Lanshammar, 2008). In 1998, 90% of the branching corals (mainly *Porites porites* and *Acropora* spp.) were affected and 50% were reported dead (Mohammed et al., 2001; Muhando and Lanshammar, 2008; Muhando, 1999). In 2005, shallow *Acropora* fields were also strongly impacted, as *Acropora* spp. is known to be less resilient to bleaching (McClanahan et al., 2007). However, in a few years corals recovered their functionality and community structure at Chumbe Reef (McClanahan et al., 2007). Whereas, limited recovery was found generally on heavily exploited reefs globally, after the 1998 bleaching event on reefs subjected to fishing pressures and/or pollution (Wilkinson, 2008).

The conspicuous plasticity of *Porites rus* favors the dominance of this particular coral species in Chapwani Reef, Prison Reef and to a certain extent at Bawe Reef (Figure 2-3, Figure 2-4). This coral species has been found in their submassive, branching, and platy form in all three locations, proving to be the most resilient coral species in this region. Presumably, corals adjust their skeletal shape to the main constraining environmental factors that control morphological specialization in corals, e.g. light intensity, water movement and sedimentation rates (Todd, 2008). Furthermore, our findings suggest that this mechanism drives beta diversity in our study sites as we found small scale (colony level) differences on the morphological strategies among sites (Figure 2-3). We propose a top-down controlled primarily by shading effect of suspended particulate matter and sedimentation processes. Wave movement should have a minor effect as there are no substantial differences between reefs due to the nature of tidal-currents in our study site. Tidal-induced currents are highly energetic (5 to 20 cms^{-1}), however all locations are protected from swells (Shaghude et al.,

2002b) and wave energy may control corals morphology through mechanical damage (Todd, 2008).

Chumbe Reef showed the highest biodiversity values (1.82 ± 0.21) whereas Chapwani and Prison reefs scored consistently low (1.23 ± 0.52) to medium (1.39 ± 0.52) biodiversity values when compared to other studies. For example, Madang lagoon in Papua New Guinea is considered to have medium-high biodiversity (1.11), whereas Bunaken National Park has high biodiversity (1.65) (Fuad, 2010) and high coral cover (46%), and biodiversity values that are similar to CHICOP. Other studies considered high structural complexity threshold of > 0.5 [m/m] (Friedlander et al., 2008; Fuad, 2010), whereas in our study sites we found consistently high structural complexity among sites, > 1 [m/m].

We propose the use of biodiversity indices over live percentage coral cover or structural complexity (discussed above) as a discrete proxy for ecosystem health in the Western Indian Ocean, as high coral cover triggered by benthic ecological competition due to limited accommodation space is characteristic of turbid reef settings. Similar results were found in nearshore reefs, where hard coral cover was two times higher than mid- and outer-shelf reefs (Morgan et al., 2016a). However, biodiversity indices gave us a finer overview, supported and correlated with other multifactor approaches (e.g. calcium carbonate budget).

Overall, the reefs studied showed mid to excellent health; outstanding reef condition was estimated in CHICOP coral reef and proved to be in agreement to other studies (McClanahan et al., 2007). CaCO_3 values ($16.90 \pm 9.70 \text{ Kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$), coral cover ($67.37 \pm 8.76\%$), reef structural complexity (1.36 ± 0.17) and medium-high biodiversity (1.82 ± 0.21 and 1.61 ± 0.24 at 5 and 10 meters, respectively) and richness (2.3 ± 0.41) could be used as baseline for inner shelf coral reefs in the Western Indian Ocean.

2.5.2 Calcium carbonate production and reef complexity

The model used to quantify calcium carbonate production, gave us a good overview of the different biogenic groups crucial to produce, maintain and shape coral reef framework. We were able to quantify and assess the main community composition and compare them with global reefs by using keystone species as ecological bio-indicators. Overall, we found a strong gradient that explained the calcium carbonate production in relation to distance to Stone Town (Figure 2-7). When compared to global carbonate budgets, Zanzibar's carbonate reefs are very productive (Figure 2-7, $> 8 \text{ Kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$). Among the reefs examined by this study, CHICOP (Chumbe Island Coral Park) marine protected area (MPA) stands out with high live percentage coral cover and high calcium carbonate production rate ($16.95 \text{ Kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$). Similar production rates have been reported within Caribbean MPA's. Bonaire, for instance, scored $16.68 \text{ Kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ (Figure 2-8).

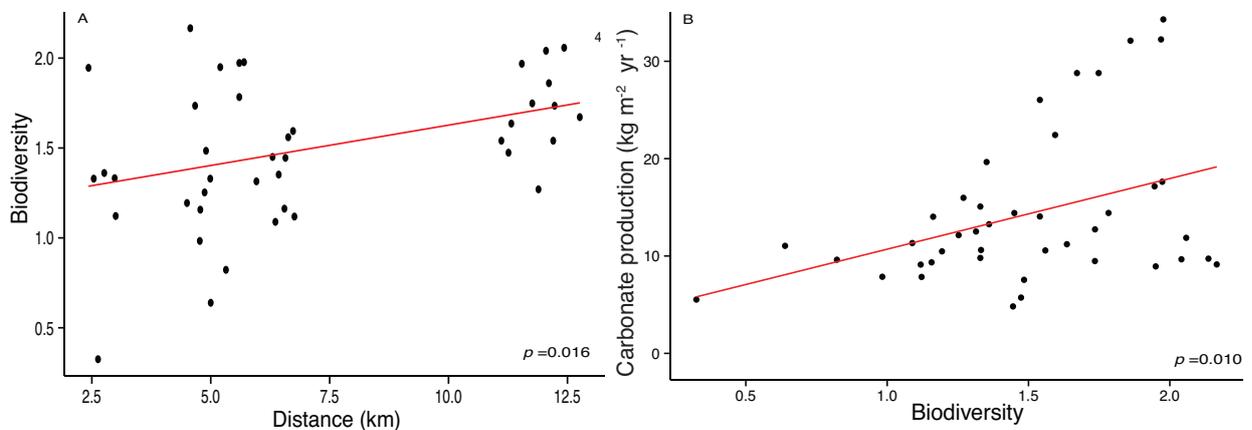


Figure 2-7 - Linear regression model showing the significant relationship ($p < 0.05$) between: A) biodiversity correlated to distance to Stone Town and B) calcium carbonate production and Shannon -Wiener biodiversity index.

Bioeroders play a significant role in shaping reef community structure (Mumby et al., 2006). The classification and quantification of bioeroders has been largely discussed in the literature

(Edinger et al., 2000; Glynn and Manzello, 2015; Highsmith, 1981; Holmes et al., 2000; Hutchings, 1986). Yet, the regional and high specificity of certain bioeroders (e.g. boring sponge) complicates the estimation of bioerosion on a large scale (> 2km). We measured primarily parrotfish, urchins and boring sponge as they strongly affect reef community structure and reef structural complexity (Graham and Nash, 2013; Perry et al., 2012). We also estimated the effect of microborers, but when compared to sea urchins and corallivore fish, their effect was negligible.

Among the reefs, Bawe Reef reflected high bioerosion by parrotfish and urchins. However, this reef showed high bioerosion variability and reef heterogeneity (Fig. 5). When we compared erosion rates in the deep areas of Bawe and Prison reefs, we found that the sponge abundance and bioerosion rates were identical 0.46 ± 0.19 and 0.45 ± 0.29 Kg $\text{CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ respectively. We observed mix patches with large sponge colonies and high sea urchin abundances at both sites. Large urchin die-offs have been reported in the Caribbean (Hughes, 1994; Mumby et al., 2006) following extremely high sea urchin densities (Liddell and Ohlhorst, 1986), which resulted in a massive loss of CCA's and live coral cover. Sea urchins are keystone species controlling benthic algal populations (Liddell and Ohlhorst, 1986). Filamentous red and green algal turf species endanger slow growing benthic biota due to their ability to compete for space (McCook, 2001). Ecological interactions and ultimately bioerosion are key processes, which shape reef geomorphology (Mallela et al., 2004). Prison Reef showed higher structural complexity than Bawe Reef, which suggests greater reef maturity (Graham and Nash, 2013). We observed some instability on the fore-reef slope in Prison Reef, followed by the collapse of non-cemented big coral colonies. This heterogeneous framework break-down affected the structural complexity measurements and likely masked potential reef calcification. Here, major topographic changes were not shaped by ecosystem engineers (Bruno and Bertness, 2001; Jones et al., 1994) but most likely

promoted by bioerosion. Therefore, crude measurements of structural complexity might lead to misleading ecosystem health interpretations, since we associate high structural complexities to healthy and functional reefs (Graham and Nash, 2013).

We observed that relatively high bioerosion and/or poorly cemented framework lead to high structural complexity through the break-down and disintegration of the reef framework. In addition, Zanzibar's fringing reefs are spatially constrained to areas that were previously colonized due to the limitation of coral larvae to settle on unconsolidated substrates (Fabricius, 2005; Wolanski et al., 2003). Thus, due to reduced recruitment, reef expansion in turbid settings takes place through the break-down and collapse of the fore-reef flank (Tudhope and Scoffin, 1994). We conclude that reef structural complexity is a key factor for measuring calcium carbonate productivity. Therefore, the resulting high Prison Reef carbonate budget could be misinterpreted for good coral reef health. We observed that the structural complexity scored higher when biodiversity metrics suggested intermediate disturbances (Table 1, 2). Yet, initial disturbances causing coral mortality does not necessarily affect reef structure immediately (Graham et al., 2009). Whether disturbances persist, reef complexity will be gradually lost. For example, structural changes after the 1998 bleaching event happened in a time span of 5-6 years (Graham et al. 2006, 2009). The intermediate disturbance hypothesis suggests that an unimodal pattern in the biodiversity metrics should be observed along a disturbance gradient (Connell, 1978; Grime, 1973). This would explain the large variability of the biodiversity indices showed at Prison Reef. By contrast Chumbe Reef scored consistently high biodiversity values and low standard deviations (Table 1).

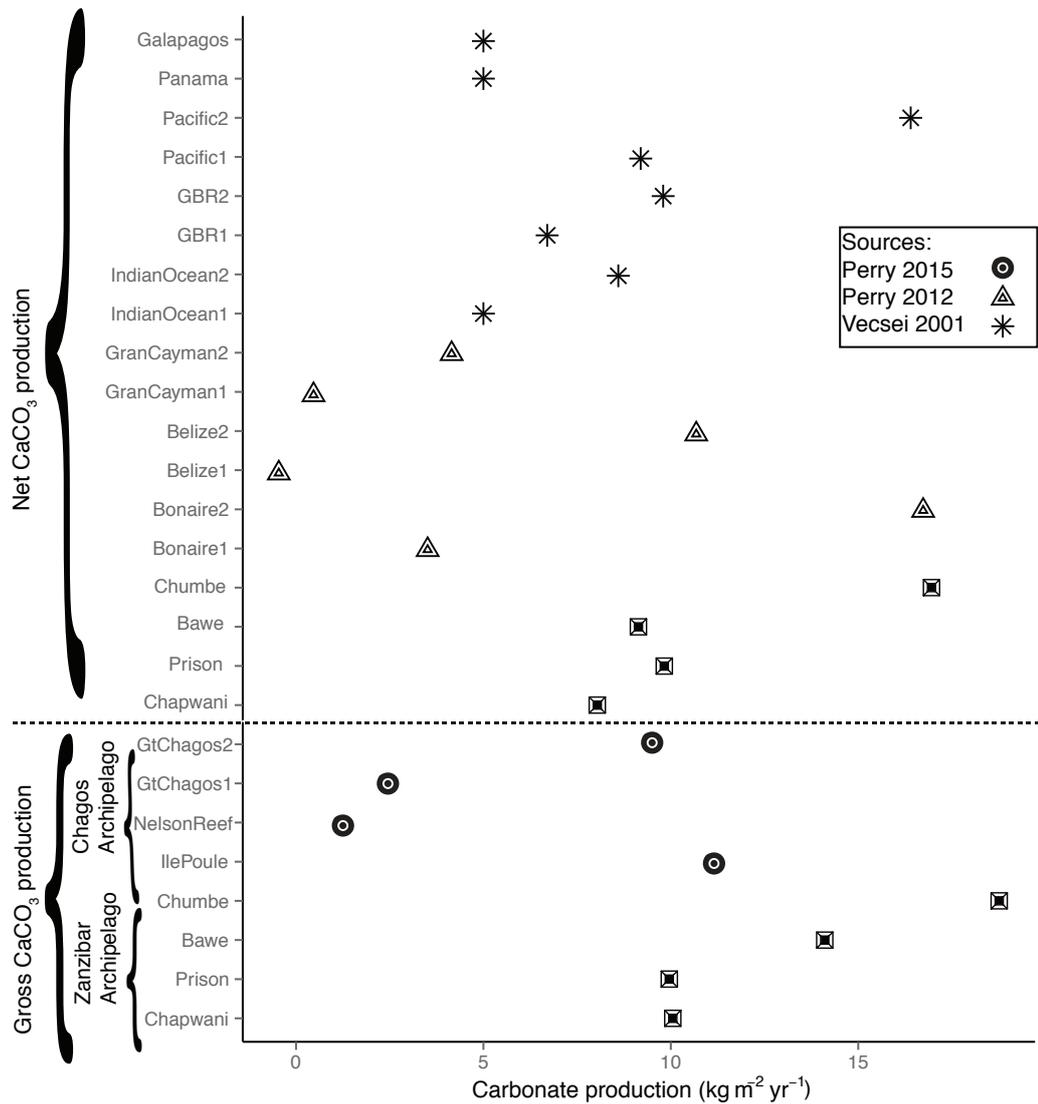


Figure 2-8 - Global comparison showing the CaCO₃ production at different locations. Filled dots present the gross calcium carbonate production in our study sites, squares show the gross calcium carbonate at Chagos Archipelago, as presented *sensu* Perry et al. 2015, triangles shows the net calcium carbonate according to Perry 2012. The numbering 1 and 2 indicate the minimum and maximum value. Asterisks represent the source Vecsei 2001. The numbering 1 and 2 remark the prevalent morphology of the reefs either low or high ramose coral.

2.5.3 MPA relevance and implication for management

A range of local stressors has been reported from our study site. From overfishing in Bawe Reef (Lokrantz et al., 2009), pollution in Chapwani and Prison reefs (Moynihan et al., 2012) to mechanical damage by destructive fishing methods like dragnets (Mohammed et al., 2001; Muhando, 1998) or careless anchoring (Mohammed et al., 2001; Muhando, 1998). At the same time, Zanzibar shows a rapid population growth rate (National Bureau of Statistics 2012) closely linked to the increase in resource demand and tourist infrastructure (Lange and Jiddawi, 2009). A negative outcome of coastal development is the increment of sediment load in the water column (Mumby et al 2006), which has a direct effect on coral community structure (Fabricius, 2005). Both natural and anthropogenic stressors including sedimentation stress, thermal stress, storm damage and overfishing, are constantly affecting reef health and community structure (Dubinsky and Stambler, 1996; Hatcher, 1997; Szmant, 2002).

Our results demonstrate significantly that the beta diversity is negatively correlated to the proximity to Stone Town. Moreover, the overall reef condition and the calcium carbonate production show a negative gradient towards Stone Town. Reef-scape degradation (loss of three-dimensional coral architecture, live coral cover and aesthetics) could have slow-to-reverse effects on Zanzibar's economy. Strategic conservation measures like fix-moorings or wastewater treatment plants would improve prospects for resilience by the reduction of particulate suspended solids, which in turn would maximize coral reef ecosystem functioning. When protected versus unprotected reefs were compared, CHICOP conservation area proved to be effective in preventing impacts from local human pressures on the reefs (Johnstone et al., 1998; Lokrantz et al., 2009). Consistent ecosystem differences have been found when protected and unprotected areas were compared. First of all, the biodiversity in CHICOP was higher than in the other study sites. Also, the branching coral genera that have high conservation value according to Edinger and Risk (2000), occurred in CHICOP. Secondly,

CHICOP showed very high calcium carbonate production values when compared globally. Lastly, the conservation area showed a high percentage coral cover and complex reef architecture.

Nevertheless, all indices of reef condition indicate that remediation and protection efforts are likely to succeed on Prison Reef and Bawe Reef. Prison Island is one of the key sites for the tourism industry in the vicinity of Stone Town. For this reason, the protection of the reef should receive the highest conservation priority. We propose the implementation of measures that avoid mechanical damage (e.g. careless anchoring, tourist walking on the reef flat). Moreover, conservation measurements should account for the subsistence needs of local people. Bawe Reef is an important fishing ground for local communities, because its intertidal platform provides women and children an area to harvest small invertebrates (Fröcklin et al., 2014), whereas fishermen use fishing-nets close to the reef. In addition, the easy access and location close to the main trade market makes this location attractive for seasonal fishermen (Jiddawi and Ohman, 2002). Therefore, the conservation effort should be in concordance to local community needs. It should ensure whole reef functioning by following a two-directional approach (ecological and social).

This study examined the ecological and structural traits that confer coral reef multiplicity. The good condition of the ecological and structural traits ensures the complete functionality of the ecosystem and the capacity to cope with natural and human-induced disturbances. Reef associated human activities, such as fisheries and tourism, substantially affect reef condition, development and health (Souter and Lindén, 2000). The negative effect of these activities is excluded in CHICOP, and yet we see a resilient reef ecosystem due to the functional biodiversity and the calcium carbonate budget. Large branching *Acropora* fields and large massive coral colonies found in CHICOP, are fundamental in resilient carbonate budgets (Januchowski-hartley et al., 2017). However, other human induced-disturbances (e.g.

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wastewater runoff) and the potential effect of untreated wastewater remain unclear. Such factors are extremely relevant because MPA's are unable to protect coral reef ecosystems from eutrophic or turbid waters. A better understanding of the biogeochemical properties of the water column, such as the seasonal variability is crucial in constraining the environmental factors that control benthic assemblages.

Table 1 - Comparative table showing the mean and standard deviation so as the minimum and maximum values for the Shannon-Wiener biodiversity index and Margalef richness index.

Location	Hard coral taxon (Mean±SD)			
	Shannon (Ln)	Range	Margalef	Range
Prison 5m	1.39±0.52	0.64-2.14	1.76±0.87	0.86-3.34
Prison 10m	1.57±0.46	0.98-2.166	2.17± 0.81	1.20-3.24
Bawe 5m	1.54±0.36	1.08-1.97	1.98± 0.58	1.30-2.88
Bawe 10m	1.27±0.29	0.82-1.594	1.64± 0.46	1.08-2.16
Chumbe 5m	1.82±0.21	1.54-2.06	2.53± 0.47	2.08-3.11
Chumbe 10m	1.61±0.24	1.27-1.96	2.08± 0.35	1.51-2.58
Chapwani	1.23±0.52	0.32-1.94	1.52± 0.75	0.43-2.65

Table 2 - Comparative table showing the reef structural complexity or rugosity measured at the study sites.

Location	Complexity Mean± SD	Depth
Prison	1.47±0.33	5
Prison	1.51±0.24	10
Bawe	1.35±0.48	5
Bawe	1.18±0.13	10
Chumbe	1.38±0.12	5
Chumbe	1.34±0.23	10
Chapwani	1.22±0.28	5

Table 3 - Key biogenic groups and microboring bioerosion rates.

Bioerosion rates [KgCaCO ₃ m ⁻² yr ⁻¹]	Prison 5m	Prison 10m	Bawe 5m	Bawe 10m	Chumbe 5m	Chumbe 10m	Chapwani
Sp. Bioerosion	0.63± 0.811	0.46±0.19	0.39±0.23	0.45±0.29	0.13±0.05	0.47±1.88	0.02±0.01
Urchin Bioerosion	0.03±0.04	0.03±0.05	0.76±0.61	0.14±0.16	0.00	0.00	1.33±0.18
Microbioeroders	0.04±0.04	0.02±0.03	0.04±0.04	0.03±0.02	0.05±0.01	0.06±0.02	0.10±0.03
Parrot bioerosion	0.55±1.75		4.97± 8.00		1.80±3.04		0.44±0.8

3. A moving partnership: New insights into semi-mobile solitary coral-tubeworm associations, Zanzibar (East Africa)



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Keywords: *Microstructural analysis, Heterocyathus sp., Heteropsammia sp., symbiosis, climate change, solitary coral, tropical carbonate system*

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3.1 Abstract

Turbid coral reef settings in Tanzania are bathymetrically constrained to approx. 16 meters below sea level. Deeper settings characterized by carbonate sand and mud along the shallow carbonate platform of Zanzibar are not suitable for reef-building corals to thrive. Here we report new insights into a multi-species symbiotic association that solitary sediment-dwelling corals establish with the tubeworm *Aspidosiphon cf. muelleri muelleri*, which enables the coral to move on or within the sediment. Furthermore, we highlight the complex interactions between both organisms, which are documented from a structural and morphological perspective. High-resolution techniques such as scanning electron microscopy (SEM) and micro computed tomography (μ CT) were applied to develop a detailed 3D model that provides insights into these complex morphological adaptations. A structural analysis shows striking morphological similarities between the two coral genera classified in separate families, namely *Heteropsammia* in the Dendrophylliidae, and *Heterocyathus* in the Caryophylliidae. These similarities suggest convergent co-evolution and similar adaptation strategies to environmental constraints. The larger size of *Heteropsammia cochlea* compared to *Heterocyathus aequicostatus* entails an advantage on hosting the fast-growing tubeworm-symbiont. The symbiotic interaction is further enriched by the presence of the commensal bivalve (*Jousseaumia* spp.) that was identified living within the tubeworm chamber inside the coral skeleton and whose detailed SEM pictures are completely new to science.

3.2 Introduction

Reefs cover only 0.2% of the ocean's sea-floor (Reaka-Kudla, 2005), yet they support high biodiversity; more than 4000 fish species (Spalding et al., 2001) and 95000 macro-species, which represent 5% of the species found in the world and 35% of known marine species (Reaka-Kudla, 2005). Currently, Holocene reef studies have focused on open-water and outer-shelf systems which show very little or no sediment input. Nonetheless, recent studies have begun to remark on the manifold range of atypical reef types and suggest that reef habitats are underestimated or “suboptimal” and act as projected future climate-change refugia scenarios (Morgan et al., 2016a). Increasingly, coral reef environments encounter high loads of suspended particulate matter (SPM) and therefore become nutrient enriched waters, which are associated with high turbidity, causing low transparency of the water column. This reduces ultimately coral growth rates and affect negatively coral larval settlement among others effects (Rogers 1983, 1990; Babcock and Smith 2002; Fabricius et al. 2013). However, contrary to numerous investigations of the influence of sedimentation on coral reef environments (Rogers 1990; Babcock and Smith 2000; Fabricius 2005; Junjie et al. 2014), only a few studies have so far described the adaptation strategies of solitary corals in symbiotic relationships with other marine organisms in naturally turbid and dynamic systems (Kennis and Fauna, 1920; Cutler, 1964; Gerth, 1952; Hoeksema and Best, 1991; Zibrowius, 1998). Such trade-offs, provide valuable information on ecological interactions for conservation agencies, habitat mapping and modelling.

We present new insights and evidence into the morphological adaptations of the symbiotic associations formed between solitary corals of the species *Heteropsammia cochlea* (Spengler, 1781), and *Heterocyathus aequicostatus* (Milne Edwards &

Haime, 1848), with sipunculid worms of the species *Aspidosiphon muelleri muelleri* (Diesing, 1851). In addition to the coral-tubeworm symbiotic association, we identified a rare commensal relationship: a cryptoendolithic bivalve (*Jousseaumia* spp.), which resides in the tubeworm cavity, the *Aspidosiphon* chamber. The present morphologic study provides new information on coral biodiversity and the distribution records of *Heterocyathus aequicostatus* and *Jousseaumia* spp. in the Western Indian Ocean (WIO).

3.3 Material and methods

3.3.1 Study site

The Zanzibar Archipelago consists of three larger islands (Pemba, Unguja-Zanzibar, and Mafia) and several smaller islands and islets, which are separated from the African mainland by the Zanzibar Channel, an approximately 50 km wide strait. This channel acts as a physical barrier and isolates the Zanzibar Archipelago. Water depths greater than 50 meters below sea level (mbsl) occur in the central channel where the currents flow southwards during the northeast monsoon (November to March) and northwards during the southern monsoon (May to September), with an increasing current intensity during the south-east monsoon (Shaghude and Wannäs 2000). The vertical motion of the tides, with a maximum range of 4.6 m (Mukaka, 2014) close to the Zanzibar shore, results in strong horizontal surface currents. A mixed and dominant semi-diurnal tide setting causes currents that ultimately shape the geomorphic features of the islands (Shaghude and Wannäs 2000). The study site was sheltered from wind and wave activity, which is typically found along the protected western coast of each of the three major islands.

A field study was conducted from September 2013 to October 2013 and from August 2014 to November 2014. We sampled along the fringing reefs of Bawe Island (6°

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9'19.08"S, 39° 8'10.25"E) and Changuu Island (6°7'7.57"S, 39° 9'58.90"E), each located approximately 5-7 km away from Stone Town. Bawe Island shows a clear reef zonation with a reef flat of approximately 100 m in width on the southern side of the island, while the northern side shows patchy coral colonies. At Bawe Island, a well-developed reef crest surrounds the reef-flat along the southeastern side, deepening from near sea level to water depths exceeding 30 mbsl. The relatively steep reef slope is composed of coarse-sandy substrate (e.g. coral rubble and sandy substrates from the reef flat) at depths from 16 mbsl onwards. The northern leeward side of Bawe Island presents a very shallow and patchy reef that is characterized by a gentle slope reaching a maximum water depth of approximately 16 mbsl. Changuu Island has a semi-enclosed back reef lagoon on the northern side, which is protected by a narrow reef crest. The reef crest leads to a steep fore-reef that presents high coral cover. The reef-base from the northern side of the island is bathymetrically limited to 10 mbsl. Changuu Island supports the development of extensive seagrass meadows and isolated clumps of stony corals along the southern sector. The island is confined between two dynamic tidal channels.

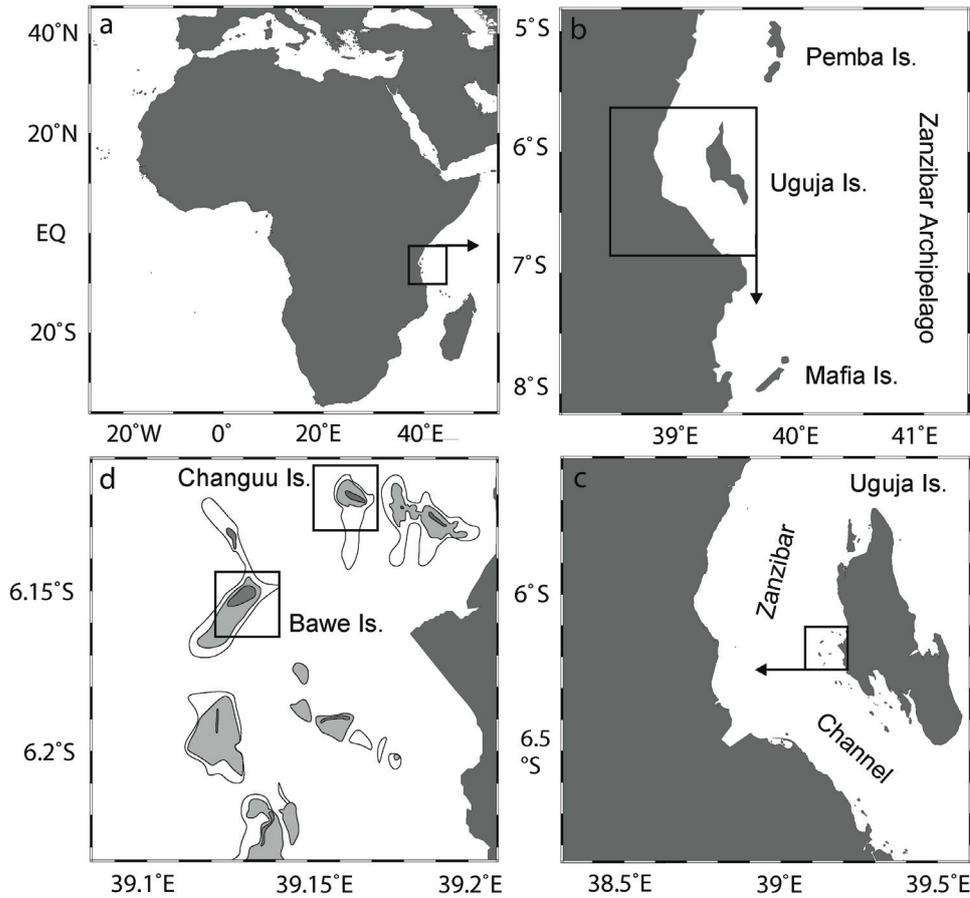


Figure 3-1 - Location of the study area. a) View of the African continent. b) Zanzibar (Unguja) Island. c) The Zanzibar Archipelago, off Tanzania. d) The Zanzibar island chain and our study sites (black square).

3.3.2 Field sampling

We used a stainless steel *Van Veen* grab sampler (3 mm plate 250 cm² - approx. 3l) to collect the upper 5-10 cm of substrate (N=85; bulk samples of 250 g each) in the vicinity of Changuu (Figure 3-1). The skeleton of the coral species *Heteropsammia cochlea* and *Heterocyathus aequicostatus* were directly isolated from the bulk sediments for morphological analysis.

In addition, SCUBA based exploration transects were conducted in order to locate free-living and semi-mobile corals at three different sites following a water depth gradient of 10 mbsl to 20 mbsl. Additional abundance data were extracted from photographic documentation. Several living solitary corals (N= 7) were collected from the fore-reef and reef slope for further analyses and carefully stored in seawater aquaria at IMS (Institute of Marine Sciences, Zanzibar) in order to keep the specimens in similar physical conditions. Upon arriving at the ZMT (Leibniz Center for Tropical Marine Ecology, Bremen) the corals were replaced in a seawater aquarium for several weeks for maintenance and a photographic documentation.

3.3.3 Pretreatment prior to structural analysis

Sedimentary samples were rinsed with clean freshwater in order to remove soluble components and dried at 40°C for at least 48h. Granulometric measurements were conducted on loose sediments which were sieved into the following grain-size fractions according to the classification of Wentworth (1922): gravel (>2000 µm), coarse sand (1000-2000 µm), medium sand (500-1000 µm), medium-fine sand (250-500 µm), fine sand (125-250 µm), and very fine sand to mud <125 µm. Using a binocular microscope, the gravel fraction (>2000 µm) was analyzed in order to identify the components of interest.

Living single polyp corals were first fixed in 40 ml of 99,8% Ethanol, then treated with H₂O₂ (90 %) for 48h to remove organic materials and to avoid biodegradation of carbonate material after death. To prepare the specimen for optimal reading under the micro CT scanner, the specimens were completely dried at 40 °C.

3.3.4 µCT, SEM scans, and microscope measurements

In order to conduct a high-resolution CT scan and to build a virtual 3D model of the sample specimen, a stand-alone micro-CT (µCT) scanner (Skyscan 1172) was used at

University Kiel, Germany providing a high power load (180 keV) to irradiate through the carbonate skeleton. Micro-CT scans obtained provide a nominal resolution of 5-8 μm per voxel, depending on magnification scale, and were scanned at angular increments of 0.9° rotation steps over a period of 3 to 11 hours. SEM images were taken with a Tescan[®] Vega 3 XMU SEM at 20 keV (SE detector). Back-scattered electron (BSE) images were taken at 15 keV in low-vacuum mode. For light microscopic images, a Keyence VHX- 5000 equipped with a VH-Z20R lens a VHX-5020 camera and XY-Stage VHX-S550E was used.

3.3.5 Thin sections

The best-preserved coral specimens (N=4) picked from the sediment samples were embedded in epoxy resin and carefully sliced following the longer edge through the center. Afterwards, the thin-sections were polished to approximately 35 μm thickness and gold sputtered for further SEM analysis. To obtain a optimal resolution and contrast, back-scattered electron scanning (BSE) and secondary electron (SE) was applied to the thin-sections at 10 to 15 keV.

3.4 Results

3.4.1 Benthic assemblage and abundance

Solitary coral specimens of the genera *Heterocyathus* and *Heteropsammia* were identified in shallow waters between 16 mbsl to 21 mbsl. *Heterocyathus* and *Heteropsammia* prosper in the windward fringing reef flanks that extend up to 1.5 km off the southern side of Bawe Island. The benthic assemblage from which the sediment-dwelling corals were encountered, host several solitary coral species; *Cycloseris distorta* and *Cycloseris cyclolites*. However, the assemblage is clearly dominated by *Heteropsammia cochlea*. A similar community composition is known

from sandy inner shelf environments of some other Indo-West Pacific reefs (Fisk 1981, 1983; Goreau and Yonge 1968, Gill and Coates 1977). The reef slope substrate at Bawe Island is dominated by coral rubble and debris derived from the outer reef edge where *H. cochlea* inhabit up to 4 individuals per square meter (m^{-2}). Moreover, in the vicinity of Changuu, *Heteropsammia cochlea* was found in more scarce abundance (approx. 1 individuals $2m^{-2}$). However, no other solitary corals were identified inhabiting the eastern tidal channel of Changuu.

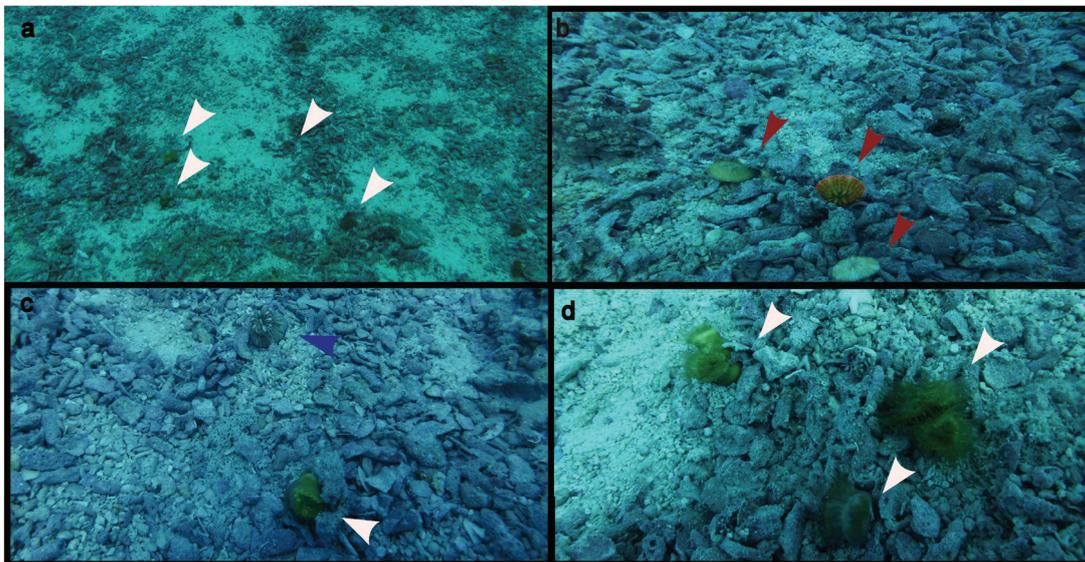


Figure 3-2 - Single polyp corals zooxanthellate and azooxanthellate species found at Bawe Island, Zanzibar. a) In situ overview of the study site dominated by *Heteropsammia cochlea* (white arrows). b) In situ assemblage form by two *Diaseris distorta* Michelin, 1842 (red arrow). c) Close up of *Heterocyathus aequicostatus* (blue arrow), *Heteropsammia cochlea* (white arrow). d) Two pluri-corallite individuals showing extended polyps (white arrow) and one individual (bottom white arrow) of the non-obligate zooxanthellate free living coral *Heteropsammia cochlea* without

the symbiont tubeworm. a) Field of view 3 x 2 meters. b) Field of view app. 0,60 x 0,40m. c, d) Field of view app. 0,40 x 0,15 m. Depth = 16-19mbsl.

Living *Heterocyathus aequicostatus* clusters were only encountered at Bawe Island in abundances 1 individuals m⁻² and altogether absent from Changuu Island. Nevertheless, *Heterocyathus aequicostatus* skeletons were present in the larger sediment fraction on the eastern and southern sides of Changuu Island.

3.4.2 Taxonomic identification and description

Heterocyathus aequicostatus Milne Edwards & Haime, 1848

The calices of four specimens identified as *Heterocyathus* ranged from 9 mm to 14 mm in length (Tab. 1). The living color of the specimens is pale to dark brown (Figure 3-2). The coral skeleton shows a corallum globoso: the corallum exhibits well-developed paliform lobes connected to thin, smooth and a very pronounced exert septum (Figure 3-3). The coral shape is subcircular, base slightly convex and shows an aperture of the tubeworm or foramen (1 mm diameter). Several pores of 328 µm in size are located along the aboral side. Edges of the corallum are smooth, with a roundish approximately 500 µm deep inclined calice. The imperforate theca shows one axis growing septa along the vertical axis, ornamented with small spike-like features and granulate texture. All of the examined specimens are observed living in a symbiosis of first order (dinoflagellate algae, zooxanthellae) and a close, obligatory symbiosis of second order (sipunculid worm of the species *Aspidosiphon m. muelleri*, Diesing 1859). Furthermore we observed a commensalistic relationship (symbiosis of third order) with a commensal bivalves *Jousseaumia* spp.

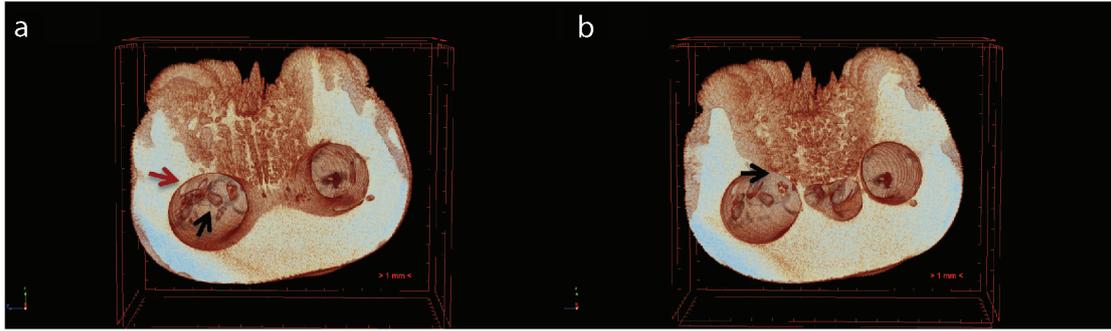


Figure 3-3 - *Heterocyathus aequicostatus* μ CT scans, upright position. a) Pore openings (Red arrow) and *Jousseaumia* specimens (Black arrow). b) Intrusion of the *Aspidosiphon* chamber on *Heterocyathus* septum and colummella (Black arrow).

***Heteropsammia cochlea* Spengler, 1781**

Heteropsammia cochlea shows a squat base, flat and oval calice, where the polyp emerges (Figure 3-4). The narrowed and sigmoidal calice, ranges in size from 7 mm to 17 mm. Those are highly polymorphic ranging in size and shape. *Heteropsammia cochlea* sustain a non-obligatory symbiosis of first order (dinoflagellate algae, zooxanthellae). However, the symbiosis of second order (sipunculid worm of the species *Aspidosiphon m. muelleri*, Diesing, 1859) is obligatory. *Heteropsammia cochlea* sustains a third order order symbiosis association with the opportunistic commensal and cryptoendolithic bivalve *Jousseaumia* spp. *Heteropsammia cochlea* can show more than one corallite. The budding takes place by elongation and later bipartition of the main corallite architecture. The budding happens in 38% of the specimens (N=29). Only the 3% (N=29) of *H. cochlea* showed more than 2 polyps.

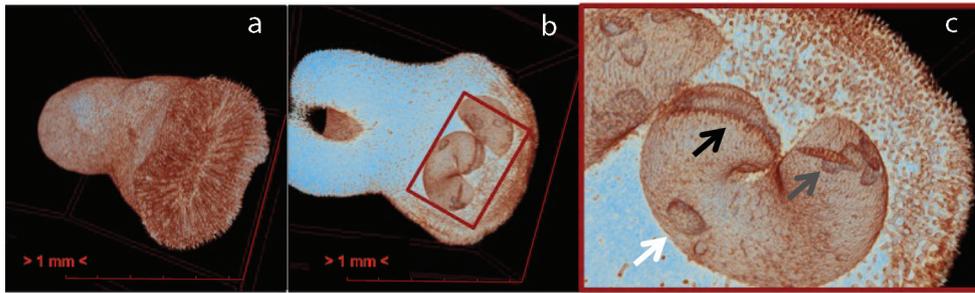


Figure 3-4 - *Heteropsammia cochlea* μ CT scans. a) Frontal view of the specimen. b) Ventral- intermediate layer, revealing bivalve shells on the walls. c) Detail of the internal chamber and the exposed bivalves, *Jousseaumia*, unknown artifact (grey arrow) and scratches (black arrow).

***Jousseaumia* spp. Bourne, 1906**

The bivalve (0.8 to 1.0 mm in length) belongs to the family Montacutidae which was previously classified into the order *Eulamellibranchia* by Bourne in 1906. He first described these commensal bivalves to inhabit the two semi-mobile coral species presented in this study. *Jousseaumia* spp. is bilaterally symmetrical, with a heterodont hinge lying in the sagittal plane (Figure 3-5). It presents two differently sized hinge teeth forms. A shorter anterior ill-defined tooth and a posterior cardinal tooth closer curving posteriorly (Figure 3-5 f).

A high abundance of bivalves was found within the skeletal cavity of *Heteropsammia cochlea* (Figure 3-4), which accounts for 10 individuals per coral specimen (N=1) and 14 individuals per coral unit (N=1) inhabiting the skeleton of the analog Caryophylliid coral (Figure 3-3).

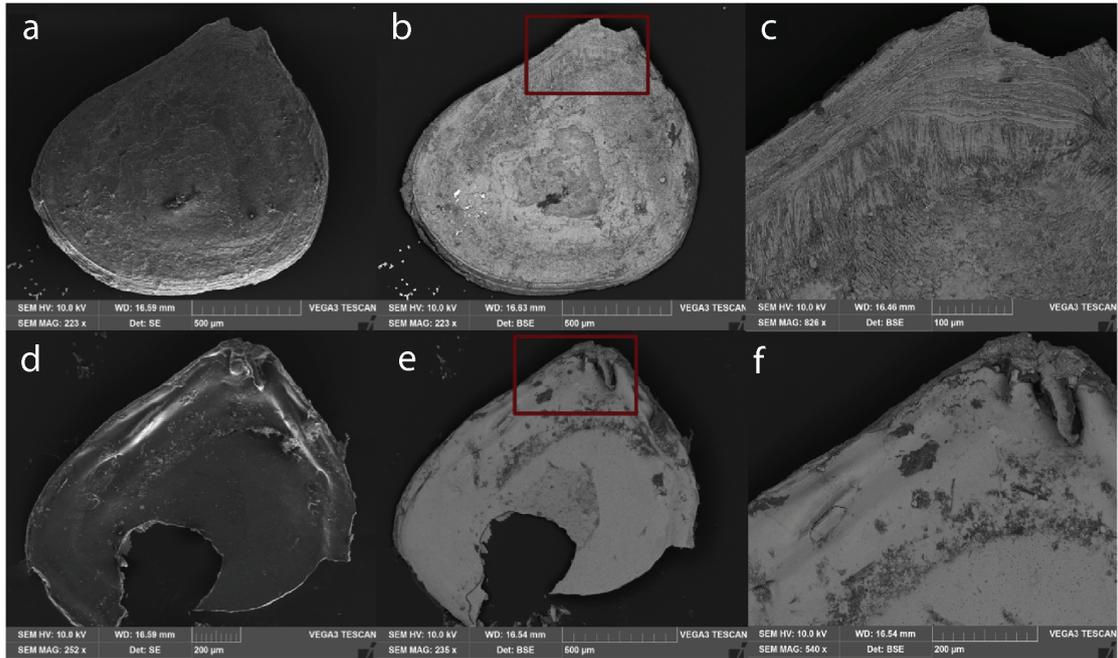


Figure 3-5 – a-f *Jousseaumia heterocyathi* length= 1328 μ m, height= 1191 μ m scanning electron microscope (SEM). a) Secondary electron (SE) images of exterior left valve. b) Backscatter electron image (BSE) from the exterior left valve. c) Close up of the beak. d) SE image of the interior right valve. e) BSE image of the interior valve. f) Close up of the dorsal side of the valve showing the hinge.

3.4.3 Morphological sub-components derived from the interspecific association

Heteropsammia cochlea and *Heterocyathus aequicostatus* present similar physical adaptations, since their ecological niche is similar and both species show a comparable life history (Hoeksema and Best, 1991). We have identified three relevant morphological subcomponents present in both coral genera: (1) the initial “relic” substrate (e.g. gastropod or scaphopod shell, carbonate grain) on which larvae of the species *Heteropsammia cochlea* and *Heterocyathus aequicostatus* can settle during their early life stage; (2) a morphological feature derived from the partnership

between the sipunculid worm and coral, forming the *Aspidosiphon living* chamber; (3) a morphological feature that originates from the multispecies interaction resulting in the development of lateral pores (small sized openings present in the horizontal axis of the coral body).

Initial substrate

Thin-section analysis of the adult sedimentary fraction (Figure 3-6 a) (*Heterocyathus aequicostatus*) did not reveal any trace of the initial substrate used by the coral larvae for initial settlement. Similar results were observed in the μ CT scans performed in the adult fractions from both species (Figure 3-3 b and Figure 3-4b,c). However, thin-sections prepared from nubbin and juvenile stages of both species (Figure 3-6 b-d) revealed that a gastropod shell in the innermost part of the *Aspidosiphon* chamber serve as initial substrate. The length of the major axis of the gastropod shell found in the core of *H. aequicostatus* was 1346 μ m and 469 μ m for the minor axis.

Aspidosiphon chamber

The hollow cavity inhabited by the sipunculid *Aspidosiphon muelleri muelleri* was here referred as the *Aspidosiphon* chamber – the ellipsoidal and basal internal chamber that sweeps through the coral frame in a spiral pattern and meets the aurea spiral proportion in the inner-most part. Grazing marks were identified on the walls of *Aspidosiphon* chamber (Figure 3-4c). We observed that the *Aspidosiphon* chamber could ingrain into the living tissue (mesenteries) of the coral polyp allocated in the columella, exclusively in *Heterocyathus aequicostatus* (Figure 3-3).

Our results show that *Jousseaumia* spp. and *Aspidosiphon m. muelleri* ultimately inhabit the same *Aspidosiphon* chamber. Therefore, three macro-organisms are involved in this complex biocoenotic association sustained by *H.cochlea* and *H. aequicostatus* (Figure 3-3, Figure 3-4).

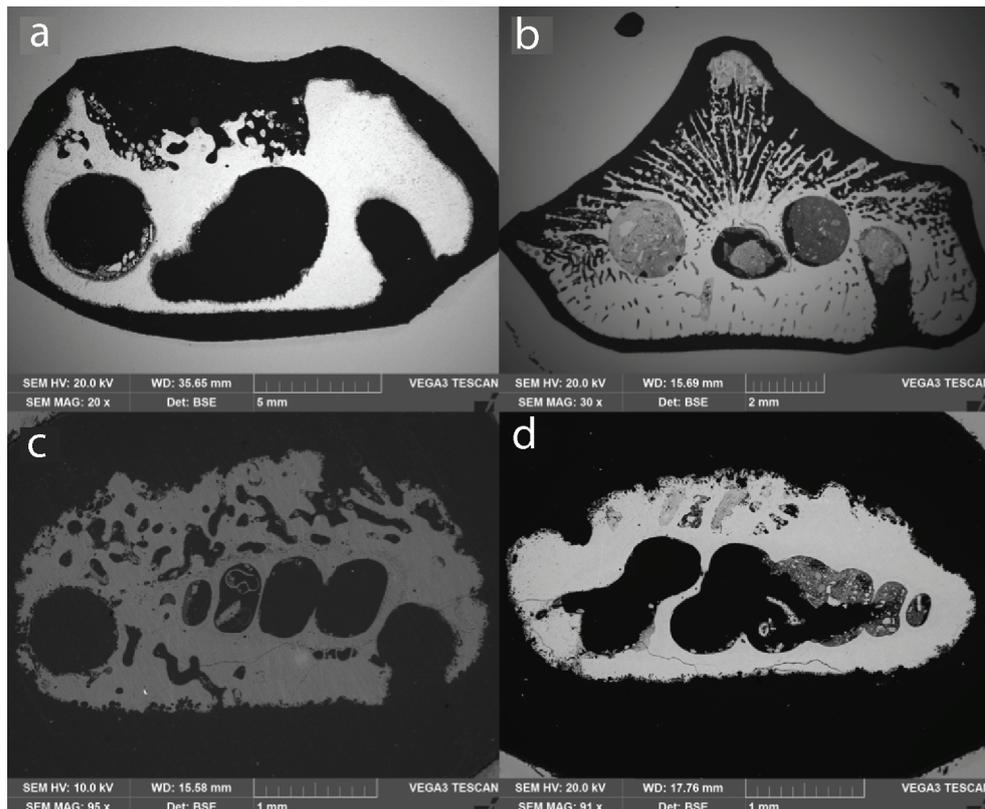


Figure 3-6 - Thin sections from the sedimentary material. a) Adult specimen of *Heterocyathus aequicostatus* without any sign of the gastropod shelf that serves as initial substrate. b) Juvenile *Heteropsammia cochlea* showing internal cementation and remains of the gastropod shell. c) and d) show the remains of gastropod shells located in the middle axis of the skeleton on nubbin stages of *Heterocyathus aequicostatus* and *Heteropsammia cochlea* respectively.

Lateral pores

The lateral pores are visible from external perspective showing a delineated pattern of the foramen which was examined in higher resolution by using CT scans. The mean aperture values of those lateral pores typically differ from *H. aequicostatus* to *H. cochlea*. However the openings are located in a similar location in the middle axis of the *Aspidosiphon* chamber. The openings size for *H. aequicostatus* N=7, Ave =

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328.29 μm . \pm 94.16. The peritheca and costae growth pattern follow the primary exert septum vertical axis. Whereas in *H. cochlea* the lateral apertures are less abundant and differ in dimensions, N=4, ave 285 μm \pm 86.17. The openings are on average smaller, the meandrous growth pattern of the peritheca and costae closes the openings.

Table 4 - Skeletal measurements of the living specimens (N=7) collected in the vicinity of Bawe and Changuu reefs.

<i>Specimens</i>	<i>Calice Length a (mm)</i> <i>SD±0.1</i>	<i>Length b (mm)</i> <i>SD±0.1</i>	<i>Height (mm)</i> <i>SD±0.1</i>	<i>Weight (gr)</i> <i>SD±0.001</i>	<i>Polyp No</i>	<i>Pores No</i>	<i>Tissue color</i>	<i>Location</i>	<i>Substratum*</i>
Het-psa-1a	17.67	10.05	17.41	5.24	1	8	Brown	Changuu	Very fine sand
Het-psa-1b	Calice1 10.42	Calice1 10.30	12.53	10.16	2	3	Brown	Bawe	Fine pebbles
	Calice2 8.4.73	Calice2 8.62							
Het-cya-1a	12.49	10.81	10.44	2.87	1	7	Pale brown	Bawe	Fine pebbles
Het-cya-1b	11.48	10.27	8.87	3.25	1	8	Dark brown	Bawe	Fine pebbles
Het-cya-1c	14.02	11.38	10.62	2.662	1	8	Brown	Bawe	Fine pebbles
*Het-psa-1c-prot	13.25	7.29	14.98	5.08	1	10	Dark brown	Changuu	Very fine sand
*Het-cya-1d-compact	11.66	9.627	9.67	2.88	1	9	Dark brown	Bawe	Fine pebbles

3.5 Discussion

3.5.1 Interspecific symbiotic association of Caryophylliid and Dendrophilliid corals

Here we report *Heterocyathus aequicostatus* for first time in Tanzanian waters. This entails the expansion of the taxonomic family Caryophylliidae to Tanzanian wildlife archives. For the contrary *Heteropsammia cochlea* was already reported to grow in Tanzanian waters. Although both corals belong to two different genera, the morphological similarities between both species are striking.

The Caryophylliid coral specimens tend to be slightly smaller than dendrophilliidae corals. The corallite ranges between 1 to 2 cm diameter, but tends to be wider at the base, which shows prominent costal ribs on the flanks.

The dendrophilliid specimen *Heteropsammia cochlea*. has a similar appearance by showing a squat and oval aboral base coronate with a slightly narrowed calice. Adult specimens are typically larger than the caryophylliid *Heterocyathus*. The smaller and lighter skeleton of *Heterocyathus aequicostatus* is adapted to favor mobility. The symmetrical and round base ensures a stable upright position. However, the reduced space available within the coral compromises coral development, as *Aspidosiphon m. muelleri* length ranges between 5 to 30 mm (Cutler 1994) and *Jousseaumia's* ranges between 0.8 to 1 mm. For that reason, the tubeworm will seek space by scratching the walls and expanding the *Aspidosiphon* chamber.

The relationship between the coral host and its partner *Aspidosiphon m. muelleri* has been confirmed to be obligatory (Fisk, 1981, 1983; Goreau and Yonge, 1968; Hoeksema and Best, 1991). The coral gains mobility whereas the sipunculid worm gains protection against predators (e.g. reef fish, crabs, anemones, cephalopods and other invertebrates). Furthermore, similar symbiotic associations have been found in

the geological past (Schindewolf, 1959). The Cretaceous tabulate coral, *Pleurodictyum problematicum*, for example, is interpreted to have provided protection to its associated worm *Hicetes* sp.. Other modern examples of interspecific cooperation are the polychaete species *Eunice norvegica* which lives in association with the cold water coral species *Lophelia* sp.. The polychaete feeds on detritus, which benefits the coral by removing the particles from the coral tissue, favoring metabolic assimilation of the coral and consequently enhancing coral growth (Mueller et al. 2013).

However, based on previous studies the occurrence of a commensal bivalve has not been reported (Goreau and Yonge 1968, Gill and Coates 1977; Fisk 1982, 1983; Zibrowius 1998; Stolarski et al. 2001). Numerous recent studies report findings of new species of commensal bivalves living in complex associations with a variety of marine invertebrates (Goto et al., 2016; Oliver, 1993; Rotvit et al., 2007), this highlights that the plasticity of the opportunistic bivalve has been until now, underestimated.

3.5.2 Macromorphological structural analysis

Initial substrate

We report the absence of the primary initial substrate (i.e. skeletal grain, shell) in the mature stages of our specimens. Some authors report traces of the initial substrate were identified in adult specimens *sensu* Goreau and Yonge 1968, Gill and Coates 1977; Fisk 1982, 1983; Stolarski et al. 2001. In most cases, a gastropod was found to be the base-substrate (Fisk 1982, 1983; Goreau and Yonge 1968) or scaphopod shell (Zibrowius 1998). In our study, we only found gastropod shells in the innermost part of the *Aspidosiphon* chamber in nubbin stages of the coral. The gastropod shell

provides a valuable substrate for settlement in soft-sediment areas with limited availability of other types of hard substrate.

The lack of initial substrate in the mature coral stages could suggest dissolution; reabsorption and remineralization of the primary carbonate structure of the gastropod shell. Furthermore, pH depletion of the pore-water inside the *Aspidosiphon* chamber due to respiration or chemical burrowing may be plausible (Williams and Margolis, 1974) but rather improbable because it would negatively affect the coral, particularly when the *Aspidosiphon* chamber intrudes into the coral mesenteries. A straightforward explanation for the lack of the initial substrate is the mechanical removal by the sipunculid to expand the living space supported by the observation of internal scratch marks (Figure 3-4) and by the fact that *Aspidosiphon m. muelleri* is equipped with a powerful introvert fitted with abrasive structures like grooves and hooks (Antonelli et. al., 2015).

Aspidosiphon chamber and lateral pores

Stolarski et al. (2001) and Zibrowius (1998) subdivided the coral-sipuncula association in two morphological subclasses: 1) polyporous - numerous openings or pores in the lateral and 2) proximal side and monoporous – single pore opening plus main opening. In this study only polyporous specimens were encountered within our samples. Nonetheless, the lateral pores were not found in the proximal side of *Heterocyathus aequicostatus* as described by other authors (Stolarski et al. 2001; Figure 3-5). *Ex situ* observations in aquaria suggest that the pores tend to protrude. Only the bottom part of the base becomes buried in the sediment. The standing position is controlled by the sipunculid worm, which leaves the pores facing the sediment-water interface. In that way, the lateral pores provide extra exchanging ducts with the exterior favoring the water circulation, which may support the idea of low pH

due to respiration in the inner part of the *Aspidosiphon* chamber. In addition, the pore openings complement the extension of the internal *Aspidosiphon* chamber. Moreover, they show a thin coverage of thin endothelial coral tissue, which implies that the sipunculid creates and maintains the lateral pores. However, the high abundance of boring bivalves (*Jousseaumia spp.*), their location and the shell size suggest a secondary use of this lateral pores to enter the cavity. For example, the internal pores of the Cretaceous *Pleurodictyum problematicum* were found to be in-filled with worm excrements (Gerth 1952). In this case, the relatively large size of the coral colony, compared to the worm size, makes the exchange with the exterior inaccessible. Nevertheless, the disposal of fecal pellets through lateral pores is quite plausible.

The functionality of these pores has been previously discussed by Stolarskt et al. 2001; Zibrowius 1998; Fisk 1982, 1983; Goreau and Yonge 1968, Gill and Coates 1977. Thereby, primarily two main functions were suggested: 1) as water circulation facilitation and 2) as excrement releasing facilitation. Only two authors have proposed the possibility, which here is also favored by the authors, that these openings are potential footprints or traces of a “still unidentified boring organism” (Stolarskt 2001; Schindewolf 1959), the footprint of *Jousseaumia spp.*

3.5.3 Adaptation to environmental constraints

Heterosapmmia cochlea and *Heterocyathus aequicostatus* are two semi-mobile coral species that are well adapted to dynamic ecosystems found on turbid, shallow water, inner-shelf, reef platforms in Zanzibar. Here, suspended particles can drift large distances, transported by the tides and currents and can easily reach vulnerable coral reef environments. For example, non-cohesive particles derived from dredged material may migrate up to 100 km in the timespan of 2 or 3 days (Decrop et al., 2015) reaching flourishing coral reefs. The limited mobility of sediment dwelling

solitary corals suggests that migration may not be possible. This also implies that like its sessile congeners, solitary corals, are susceptible to extreme events (e.g. hurricanes). Nevertheless, likely “walking corals” can deal with damage produced by specific and short-term events (e.g. storms), inhabit dynamic environments (e.g. tidal channels) or withstand high sediment loads (Goreau and Yonge, 1968) . For instance, the species *H. aequicostatus*, due to its smaller size and better mobility is able to better cope with short-term extreme events.

At the study site, anthropogenic disturbances are range from increasing coastal pressures (Lange and Jiddawi, 2009; Muhando and Mohammed, 2002), overfishing (Lokrantz et al., 2009), dredging activities and land-based pollution (Moynihan et al., 2012). The construction of tourist infrastructure in our study area (i.e. holiday cabins built in Bawe Island in 2012 and restored in 2014) might influence the natural system. Actually, few studies have been undertaken describing the local anthropogenic factors, sediment distribution and high sediment fluxes as described *sensu* Muzuka et al. 2010 off of Stone Town (Shaghude and Nyandwi, 2000; Shaghude and Wannäs, 2000; Shaghude et al., 2002a; Shaghude, 2003). However, these studies provide essential information towards understanding the physical natural environment at our study site. For instance, the sediment flux ranges from 0.2 to 41.5 mg cm⁻² d⁻¹ (Muzuka et al 2010), which are just above the lethal limit of 10 mg cm⁻² d⁻¹ (Rogers 1990). However, the strong tidal currents, with a magnitude that ranges from 0.2 to 0.9 m s⁻¹(Muzuka et al 2010) induce the “cleaning off” of particles from coral tissues (Rogers, 1983).

Interspecific symbiosis ubiquitous in terrestrial environments have played a major role in the generation of biodiversity (Douglas 1994; Moran 2006). Those interactions are important catalysts of evolutionary processes. However, most studies approach

alternative ecological interactions as predation and competition, whereas the importance of symbiosis remains unclear. The mechanisms by which certain species have colonized new habitats can be explained by the role that symbiosis plays by facilitating niche expansion and species diversification (Joy 2013). However studies linking both processes remain scarce (Futuyma and Agrawal, 2009; Janson et al., 2009). More understanding of long-term species interaction and the linkage between diversification and niche expansion is critical to understand tradeoffs in coral reef environments.

Species interactions are essential and influence ecosystem functioning and structure. The understanding of those interactions is mandatory in order to understand and promote the conservation of endangered ecosystems. Full functioning of the entire ecosystem is known to be vital to sustain very sensitive ecosystems (Dubinsky and Stambler, 1996). For instance, in the case of the coral holobiont (coral-algae-bacteria symbiosis) the life habit of the host (i.e. scleractinian coral) is altered and it is this holobiont community that allows it to function as the major reef framework builder. Furthermore, the holobiont boosts its capacity to adapt under unfavorable conditions (Kelly et al., 2014). In a similar way, the inter-species symbiosis between a coral and a tubeworm, as presented by this study, is exemplary for the cooperation of two non-taxonomically related organisms to withstand major natural constraining factors (e.g. sediment load, food availability, predation and physical disturbances). Other sessile non-associative coral colonies fail to thrive when living singularly in this environment.

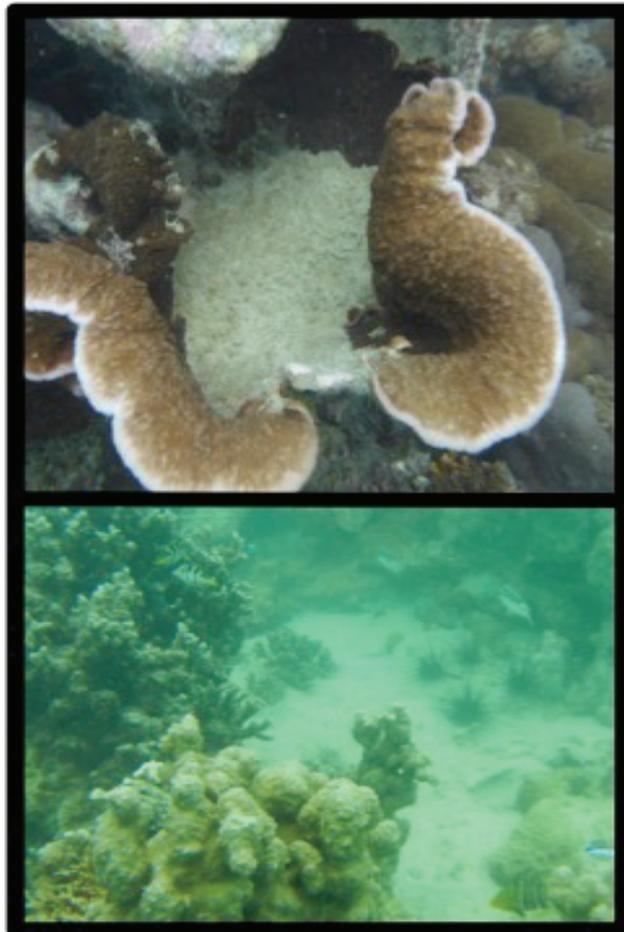
Our results confirm that *Heterocyathus aequicostatus* and *Heteropsammia cochlea* shows specific adaptation to high sediment fluxes and strong currents. It shows

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internal morphological adjustments such a hollow and light skeleton, which can be dragged by a tubeworm above the soft-bottom, but has a squat and flat base stable enough to be anchored under high-energy conditions. In addition, the optimal skeleton size provides enough space for a single tubeworm to inhabit the coral body. The association with the tubeworm *Aspidosiphon muelleri muelleri* provides a clear advantage in such environments including: 1) mobility to avoid burial in unconsolidated sediments; 2) a favorable upright position; 3) anchoring of the coral to soft substrates; and 4) assistance in cleaning by removing and/or feeding-on organic particles attached to coral tissue.

4. How do fine-size particle dynamics in tropical shallow waters influence coral reef geomorphology?

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Keywords: Tropical carbonate systems, coral reefs, geomorphology, suspended particulate matter.

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4.1 Abstract

Deterioration of sensitive habitats is a global-scale trend that has been enhanced during the last century. Tropical coralline islands are characterized by their rich marine biodiversity and their sensitivity against anthropogenic and environmental changes. It is proven that a decrease of light intensity is correlated with an increase of turbidity affecting directly corals growth rate and coral reefs ecosystem health overall. The measured high loads of suspended particles in the water column, which range from 18.3 to 31.7 mgL⁻¹. The composition of such particles in our locations differed significantly, Prison Reef showed particular organic matter prevention of marine primary producers and other undetected carbon sources. Bawe Reef showed enriched $\delta^{15}\text{N}$ values (>10 ‰), depleted $\delta^{13}\text{C}$ values and overall low C/N molar ratio. These findings reflect the impact of sewage waters on coral reefs. We correlate sedimentation of SPM to the reef slope geomorphology. We found that sedimentation and turbidity controlled outer reef geomorphology. Steeper reef slope was found on reefs showing sedimentation and gentler reef slope formation when reef development is controlled by turbidity.

4.2 Introduction

Coral reefs ecosystems are one of the most diverse of all ecosystems and valuable habitat for a multitude of marine organisms (Reaka-Kudla, 2005). Today, most tropical coastal-near environments are seriously threatened by natural- and anthropogenic-induced disturbances, often acting on a global scale (Browne, 2012; Graham et al., 2011; Hughes, 1994). Low water quality, enhanced sediment and nutrient input, rising sea surface temperatures are well-known key-drivers responsible for a continuous destruction of coral reef framework and changing biodiversity patterns (Mallela et al., 2004). As a result of a non-sustainable use of marine and terrestrial resources, enhanced hinterland agriculture, and deforestation of natural mangrove pre-filtering systems, most coral reef environments have to face an increasing load of suspended particulate matter (SPM) (Rogers, 1990), often associated with high turbidity causing low light penetrations into the water column (Fabricius, 2005). Most commonly coral reefs are found in oceanic tropical waters and they can grow up to greater depths >40 meters, but the shading effect of suspended particles in the water column limit their ability, constraining reefs to 10 meters depth (Yentsch et al., 2002). The causal effect of sediment and coral stress has been extensively documented (Babcock and Smith, 2000), as it has always been a probable cause of reef demise in the fossil record (Hallock and Schlager, 1986). However, the fundamental effect sediment supply and composition has on reef development has greatly challenge the field, because the intricate linkage between sediment input and nutrient increase acting in various time and spatial scales.

Whereas the role of long-term reef growth controls (e.g. sea level rise) is better understood (Kennedy and Woodroffe, 2002), short-term controls are underestimated. The relative rapid changes of reefal landscape on a geoscientific scale (Hopely et al.,

2007), challenges the understanding on the synergistic effects of natural and new anthropogenic controls. For example, natural or anthropogenic induced turbidity and associated sedimentation controls reef slope geomorphology, reducing the effective accommodation space (Tudhope and Scoffin, 1994; Hopely et al., 2007) and consequently coral larvae recruitment (Rogers, 1990). However, very scarce studies have focus on the solely effect of sedimentation and/or turbidity on reef slope geomorphology.

The main goal of this study was to investigate the concentration and composition of particulate material and its short-time dynamics (during a tidal cycle) and its potential geomorphological effect on the fore reef flanks of two distinct fringing reefs. We aim to assess the origin of particulate material in the water column to ultimately establish the threats affecting Zanzibar fringing reefs. To approach this objective we measured and characterized the concentration of suspended particular matter (SPM), we measured the chlorophyll content and the stable isotopic signature of suspended particular matter to better understand OM dynamics reaching daily the reef area. In addition, we characterize the coral reef front, combining sonar and imaging view, of two fringing reefs in order to determine the implications of chronic turbidity on reef development.

4.3 Material and methods

4.3.1 Study area and sampling

Tanzanian coastline is approximately 1424 km long, which is surrounded by highly diverse scleractinian corals, 150 coral species *sensu* Francis and Bryceson (2001). Fringing coral reefs protect Zanzibar coastline from wind- and storm- waves. Zanzibar posses a great variety of coastal environments including estuaries, mangroves and seagrass meadows (Jiddawi and Ohman, 2002). Zanzibar climate and

oceanographic setting is driven by the seasonal monsoonal seasons. The north-east monsoon (November to March), brings low-winds speeds, high temperatures and humidity. The southeast (SE) monsoon (April to September) brings lower temperatures and higher wind-speed up to 20 knots. Current intensity increases commonly during the SE monsoon (Shaghude and Wannäs, 2000). Torrential monsoonal rains occur between April and May, which supply half of Zanzibar's annual precipitation (Mahongo and Francis, 2010).

Zanzibar Archipelago consists of three main islands (Pemba, Unguja, and Mafia) and several smaller islands and islets. Unguja is separated from Tanzania mainland through the Zanzibar Channel, which is approximately 50 km wide. This channel represents a physical barrier between Unguja and Tanzania mainland. The first study site, Prison Reef, is located approx. 4 km far away from Zanzibar, capital city, Stone Town, located in Unguja Island. The main fringing reef is located on the northeastern side of Prison Island (6°7'9.27"S, 39° 9'58.30"E), which is relatively protected from waves and currents. The second site is in the southern sector of Bawe Island (6°9'19.00"S 39° 8'10.20"E), and uninhabited Island located approximately 7 km offshore of Stone Town (Figure 4-1). The investigated island shows a clear reef zonation. The southern flank of the reef presents a well-developed reef crests followed by a fore reef front, which deepens until approx. 30 meters. The northern side of Bawe Island presents a very shallow and patchy reef, which is characterized by a gentle slope that reaches a maximum depth of approx. 16 meters.

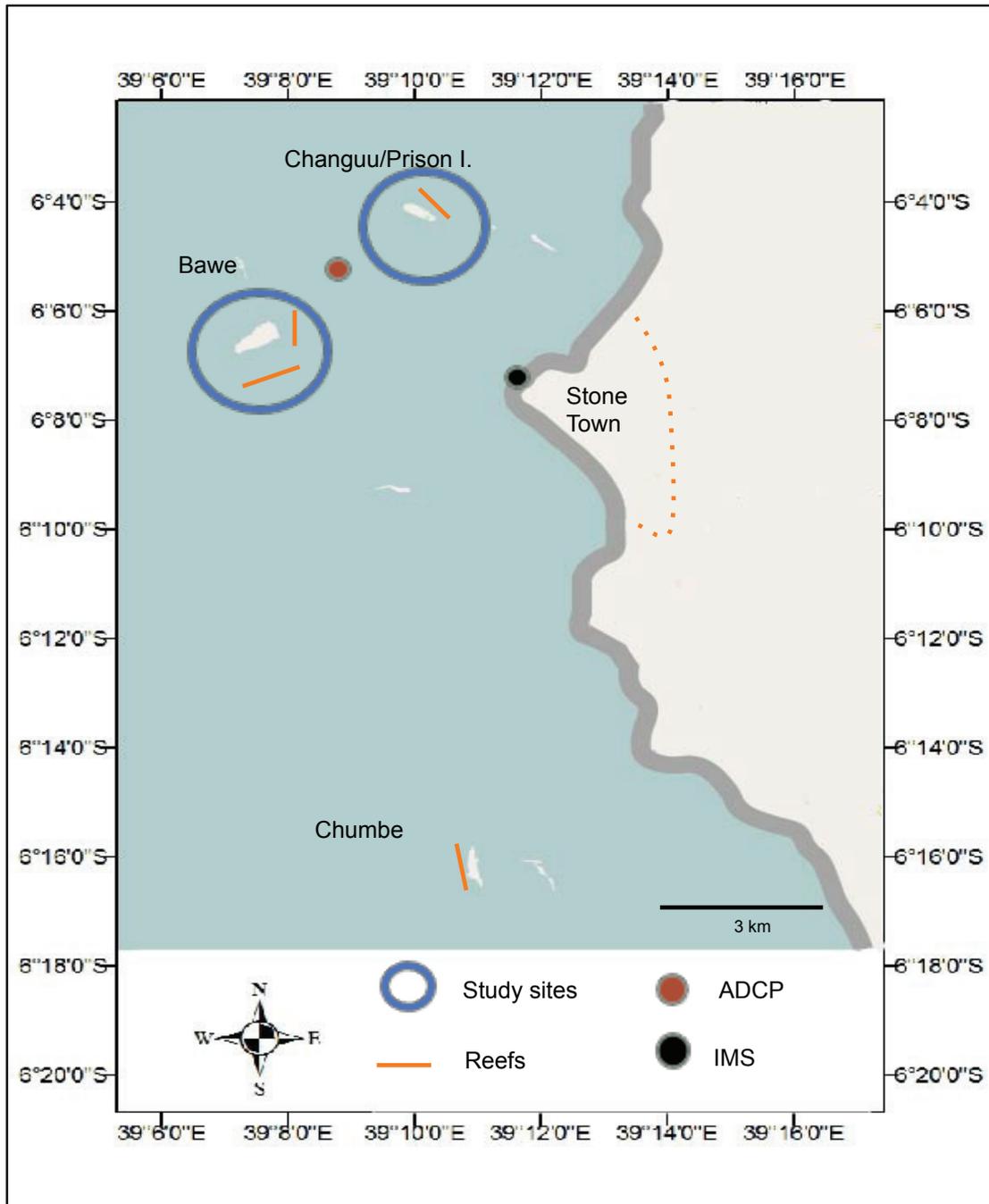


Figure 4-1 - Map of the study site

4.3.2 Sample collection and analysis

Samples were collected during a single field campaign between September and October 2014. Tidal sampling measurements were conducted continuously for 12 hours during diurnal spring tides. Sampling of surface and bottom waters was

conducted every hour, starting and finishing at low tide for Chlorophyll a, organic carbon (OC) and stable isotopes.

Surface and bottom water samples (2 Liters) were collected systematically every hour with a Nisk bottle. Pre-weighted WhatmanTM GF/F glass microfiber filters with a nominal pore diameter of 47 mm were pre-combusted for at least 4 hours at 450°C. In total 96 Liters of water was collected and 48 samples were retrieved, 24 samples at Bawe Reef and 24 samples at Prison Reef. All water samples were filtered on board after collection and all filtered samples were stored dark and cool during field excursion. Chlorophyll a samples were stored at -10°C upon arrival to Institute of Marine Science, Zanzibar (IMS) research station and SPM samples were dried at 40°C to constant weight and stored on individual polystyrol (PS) containers. Chlorophyll a contents of the collected samples were analyzed at the Leibniz Center for Tropical Marine Research (ZMT) with a fluorometer on triplicate by standard trichromatic methods (French 2010), formulas given by Lorenz (1967) and Jeffrey Humphrey (1975) were used for calculations of pigments concentrations. Furthermore, POM freshness was calculated as POC/ CHLa ratio.

For total carbon (TC) and total nitrogen (TN) content, all samples were analyzed making use of a Carlo Erba NA 2100 elemental analyzer by high temperature combustion. For the organic carbon content (OC) we first removed the inorganic carbon by acidification adding 1N hydrochloric acid until the reaction stopped. Subsequent drying at 40°C followed and once the material was dried, OC measurements were conducted similarly to TC and TN analysis. The precision of the measurements was reported as the relative standard deviation of repeated measurements of OAS standard material 1.3 % for OC and 2.2% for TN. The isotopic composition of SPM samples collected were measured from the OC and TN was then

measured with a thermo Finnigan Delta Plus gas isotope ratio mass spectrometer. The units of measure are given in ‰ in reference to the atmospheric nitrogen and PDB standard. The precision of the analysis was extract from repeated measurements of pepton standard, standard deviation ranged from 0.02% and 1.1%.

To characterize the current magnitude, local hydrodynamics and water motion an ADCP (acoustic Doppler current profiler) was deployed for 3 months from January to March, measuring constantly at low frequency. The output data series were averaged, filtered for potential noise and processed using MATLAB software.

To characterize the reef slope and reef framework at Bawe Reef and Prison Reef, we recorded broad banding and backscattering images from the bottom surface. Images were recorded with Compressed High intensity Radiated Pulse (CHIRP) sonar. One HDI dual-frequency sonar transducer was mounted on the lower part of the hull of the boat in order to minimize potential noise produce by the engine. We kept constant speed not exceeding 6 kts and we recorded shallow areas (>35 meters) at high (200Hz) and low (50Hz) frequencies to reveal different levels of detail. To determine the benthic species composition, we applied the line intercept transect method (LIT) (English et al 1997). By convention, six 10 meter transects were randomly placed and independently recorded by SCUBA divers in the reef-slope of each study site at shallow (5 ± 2 meters) and deep (10 ± 2 meters) areas.

4.4 Results

4.4.1 SPM concentrations and composition

SPM concentrations in Prison Reef ranged from 20.0 to 31.7 mgL^{-1} for bottom samples and 18.2 to 36.4 mgL^{-1} for surface samples, with lowest concentrations at low tide in the morning (Figure 4-2). Bawe Reef SPM concentrations showed a bimodal patter (Figure 4-2), which ranged from 19.9 to 35.6 for bottom samples and

19.7 to 37.6 mgL⁻¹ for surface samples. The highest concentrations were recorded during high tide during the afternoon (Figure 4-2). No significant differences were found for the concentration of SPM measured in surface (top water layer) or bottom waters. At Prison Reef mean top and bottom water concentration was 25.6±7.5 mgL⁻¹ and 22.9±3.5 mgL⁻¹, mean values were significantly different (p<0.05). Concentrations in Prison Reef were lower during the early morning and were increasing progressively during the day, reaching maximum concentrations around 9 pm.

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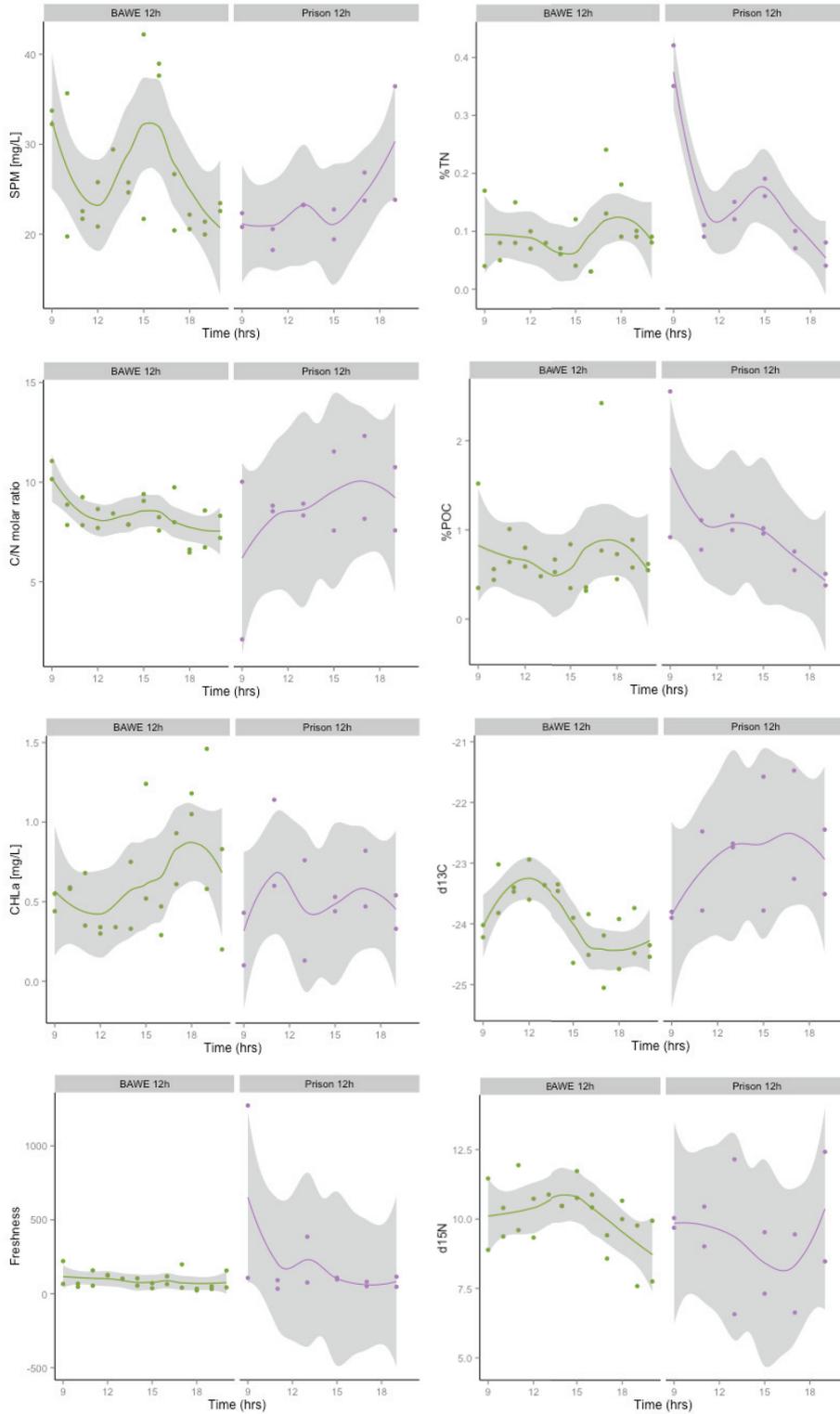


Figure 4-2 – Suspended particulate matter (SPM) concentration and composition analysis of the organic fraction. %TN: Total Nitrogen, C/N: Carbon/Nitrogen molar ratio. %POC: Particulate organic carbon. CHLa: Chlorophyll a content. d13C:

Carbon isotopic ratio. $\delta^{15}\text{N}$: Nitrogen isotopic ratio. Freshness, the POC/CHLa.

The organic carbon (%POC, 0.829 ± 0.3) and total nitrogen (%N, 0.13 ± 0.07) of the POM was higher during low tide in the morning and high tide in the afternoon (Figure 4-2), but no significant differences were found when we compared surface to bottom water contents at Prison Reef. At Bawe Reef, particulate organic carbon (POC) was slightly lower (%POC, 0.71 ± 0.4) and total nitrogen (%TN, 0.09 ± 0.05) at both locations was consistently low. The maximum concentration was measured around 7 pm during mid-low tide, coinciding with the highest chlorophyll a (CHLa) concentrations (CHLa, $0.6\pm 0.3 \text{ ugL}^{-1}$).

4.4.2 Stable isotopes signature

At Prison Reef the top and bottom water composition differed significantly for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. $\delta^{13}\text{C}$ values (MEAN \pm SD) $-22.4\pm 0.7\text{‰}$ and $-23.12\pm 0.5\text{‰}$ for top and bottom samples, respectively. $\delta^{15}\text{N}$ mean values for top and bottom samples were $8.70\pm 2.20\text{‰}$ and $7.10\pm 1.47\text{‰}$, respectively. At Bawe Reef stable isotopic values ranged from $-23.78\pm 0.39\text{‰}$ top samples and $-24.08\pm 0.68\text{‰}$ for bottom samples. $\delta^{15}\text{N}$ values ranged from $10.28\pm 0.9\text{‰}$ to $9.82\pm 1.26\text{‰}$ for top and bottom samples (Figure 4-3). Stable isotopic composition of SPM was also significantly different in both locations with respect to the tidal phase (2-way-ANOVA, $F_{5,29}=4.04$, $p=0.006$). Bawe Reef showed low variability for molar C/N ratio or isotopic values and the tidal cycle did alter SPM composition and concentration in Bawe Reef too. Prison reef SPM concentration was correlated to water energy ($p=0.0042$). There were no significant top and bottom differences for Carbon and Nitrogen elemental ratio (C/N), but the isotopic composition of SPM was significantly different between Prison and Bawe

reefs and for surface and bottom waters in Prison Reef (two-way ANOVA, $p < 0.05$; $F_{1,32} = 21.58$, $p = 5.5 \times 10^{-5}$; $F_{1,32} = 10.81$, $p = 0.002$, respectively).

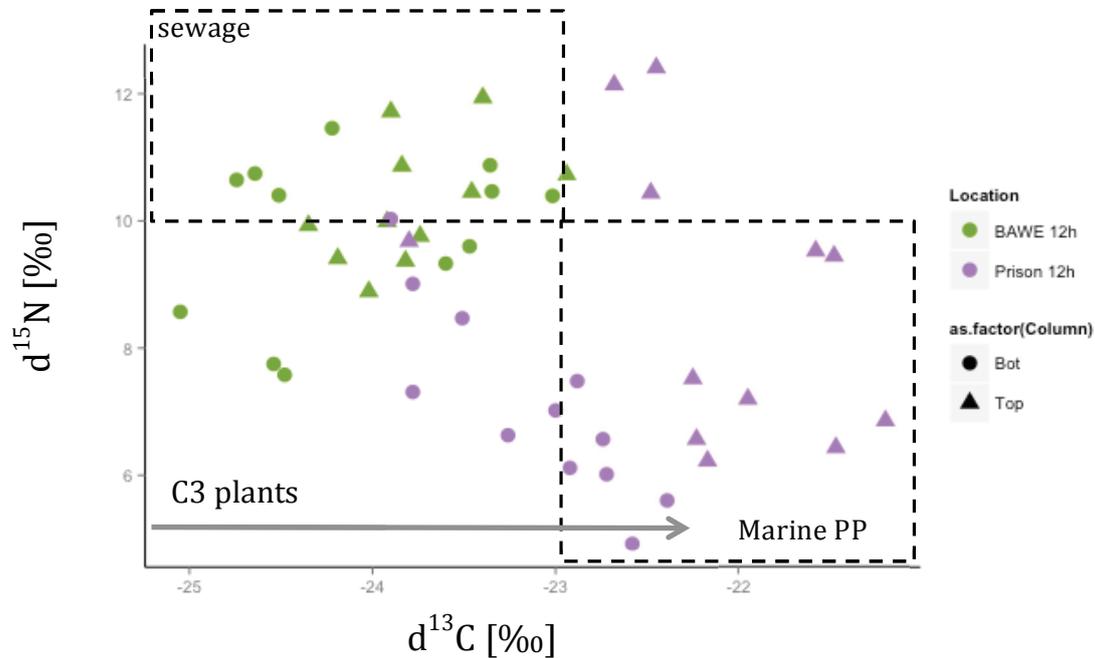


Figure 4-3 - Stable isotopic composition in Prison and Bawe reefs. Squares show the two main sources, of marine primary producers and more enriched nitrogen sewage. Values of the sources are referred to Bristow et al., 2012; Maksymowska et al., 2000.

4.4.3 Hydrodynamics

The hydrodynamic regime in the western part of Unguja Island is driven by two main currents (north and south current), strengthened by the seasonal trade winds. North and south current components are driven by strong semi-diurnal meso to macrotidal range (3-4 meters). Generally, the flood period will move the water southwards and the ebb period northwards. The infilling with fresh oceanic water might wash both of our

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study sites (Figure 4-4). The magnitude of the ebb and flood strength is not symmetrical, but the southern component commands the net water motion (Figure 4-4). Overall, the water energy is higher during spring tides, with a maximum onset speed of 20 cm s^{-1} . Maximum velocities occur during ebb to flood tide and it lasts for ~2 to 4 hours after low tide. Overall 30% of the day the water energy would reach the threshold of 10 to 15 cm s^{-1} and 62% of the day the velocity ranges from 5 cm^{-1} to 10 cm^{-1} . The duration of slack water (zero velocity to 5 cm s^{-1}) is relatively long, approx. 8% of the day, which should enable settlement of suspended particles.

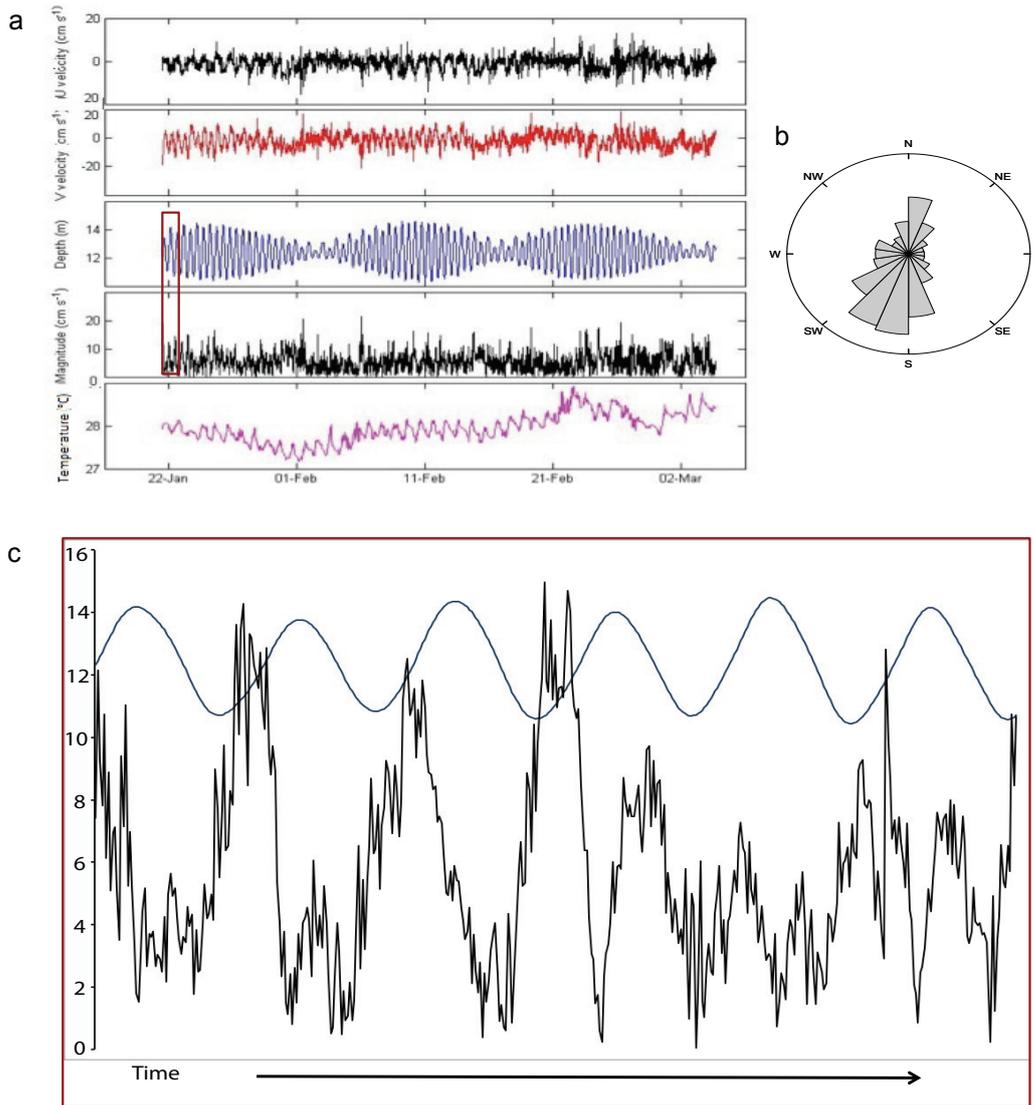


Figure 4-4 –a) ADCP measurements; u, v velocity, water depth, current magnitude, water temperature. b) Rose-chart showing the main directions of the described water bodies. c) Detail of the relation between water depth (m) (dark blue sinusoidal wave) and water net velocity (cms⁻¹) (black lines).

4.4.4 Reef morphology

The fore reef slope of Bawe Reef is well developed and gently deepening to approx. 30 meters (Figure 4-5). However, live photosynthetic scleractinian corals were found at maximum depths of 16 ± 2 meters. Ahermatypic coral assemblages colonize the

deeper fore reef areas (>30 meters). Prison Reef showed a steep fore reef slope and photosynthetic scleractinian corals baseline occurs at shallower depths (10±2 meters). Bawe Reef community composition is dominated by massive and submassive species, but large colonies of *Turbinaria* sp. were found at 5±2 meters water depth. Such species are completely absent in Prison Reef, where shallow zones are dominated by *Porites rus*, *Galaxea* spp. and small colonies (<30 cm) of *Montipora* sp. *Acropora* spp. was only found in the 5-meter range at Bawe Reef. At Prison reef, deeper reef areas (10±2 meters) we cover by large colonies (>1 meter diameter) of *Physogyra* and *Plerogyra*. The deeper sections of Bawe reef slope were cover by massive corals, such as *Platygyra*, however scarce occurrence of *Physogyra* was also recorded at Bawe Reef.

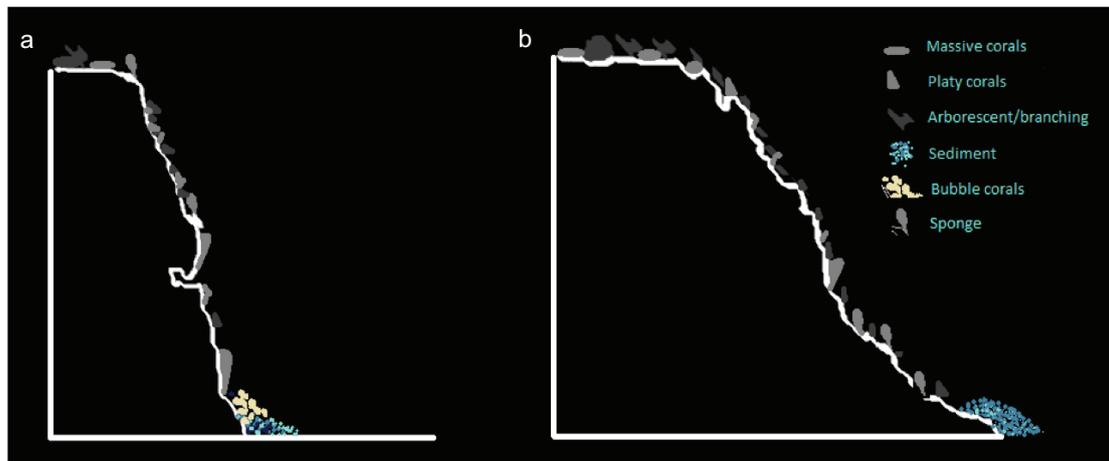


Figure 4-5 – Two conceptual reef slope profiles at a) Prison Reef profile controlled by sedimentation and b) Bawe Reef, turbidity-dominated reef development.

4.5 Discussion:

4.5.1. SPM composition

The organic fraction of the SPM at both study sites differed slightly. At Prison Reef, we have found enriched $\delta^{13}\text{C}$, when compared to the organic carbon found at Bawe Reef, where the isotopic signal is more depleted. Baker et al., (2010), interpreted the isotopic fractionation, discrimination against heavy carbon isotopes, controlled not only by light availability, but also by its intensity. Higher C / N molar ratios, characterizes autotrophic carbon sources, whereas, low molar ratios would relate the carbon source to heterotrophic organisms. Other authors discussed that low molar fractions are indicative of polluted organic matter. Rogers, 1999, reports low C / N molar ratios ~ 8 on sewage water samples, while high values ~ 16 , were reported on pristine control sites. Several studies have described primary producers, such as macroalgae or seagrass (17.5; Briand et al. 2015).

Few studies report direct isotopic C and N measurements taken from water column samples. Rogers, 1999, reports crude values of a pollution effluent whose isotopic value of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was -23.5‰ and 1.8 to 2.5‰ , respectively. Certainly $\delta^{15}\text{N}$ signal in polluted effluents may vary depending on wastewater treatment received (Baker et al., 2010). Nitrate in non-treated effluents may have an isotopic signature $>10\text{‰}$ (Katz, 2004). Other sources indicate that $\delta^{15}\text{N}$ fractionation is usually much higher than $\delta^{13}\text{C}$, as $\delta^{15}\text{N}$ can increase up to 3‰ at each trophic level (Bristow et al., 1992; Keough et al., 1996). The isotopic $\delta^{15}\text{N}$ signature, ranges from 4.97 to 12.41‰ at Prison Reef and 7.58 to 11.94‰ at Bawe Reef. Usually, $\delta^{15}\text{N}$ values during upwelling range between 4 to 7‰ , while the nitrogen fixed by diazotrops is highly depleted -1 to 0‰ (Karl et al., 2002). In general the values on our study area are significantly different between surface (top) and bottom samples at Prison Reef, but

not at Bawe Reef. Prison Reef bottom POM values show more depleted $\delta^{13}\text{C}$ values. This suggests that more degraded particles stay in bottom layers, indicating either sedimentation of surface particles or resuspension of bottom sediments. The geographic location and orientation of Prison Reef (Figure 4-1) would interfere with the main current component, flowing southwards. The occurrence of major reef formations perpendicular to the water flow will reduce water flow velocity drastically. Therefore, during the high current velocity peaks (first 3 hours after low tide) we observed more depleted $\delta^{13}\text{C}$ values at Prison Reef. This indicates, that depleted OM stored in bottom sediments is being re-worked during higher energy conditions as $\delta^{13}\text{C}$ values increase throughout the day at Prison Reef.

4.5.2 Physical controls

The constant resuspension of the finer sediment fractions (>45 μm) on the lower reef slope zone may have significant effect on benthic organisms. First, the light attenuates exponentially with depth. Optimal coral development occurs down to 30 to 40% of subsurface irradiance (SI) and no significant reef accretion is found below 10% SI (Achtuv and Dubinsky 1990). In areas with a visibility of 2 meters and less, only 10% of the SI reach the first 8 meters depth and only 5% reach 10 meters depth (Chuang 1977). Secondly, the settlements of fine particles create a sediment film covering the coral tissue, that not only blocks the irradiance necessary to photosynthesize, but it activates a costly metabolic response (*e.g.* secreting mucus) causing coral stress. 65% of the energy produced during a whole day, will be used on such a metabolic response, so that if the stressor persists, the coral will finally starve (Erfteimeijer et al., 2012).

Corals have a range of strategies to remove sediments from its surface, one effective strategy that does not depend on water movements is the use of globular polyps to form a slippery surface, in which the sediment does not adhere (Erftemeijer et al., 2012). At Prison Reef, corals that inhabit the deeper reef slope zones (approx. 10 meters depth) are bubble corals (with globular polyps) such as, *Physogyra* (Figure 4-5). The reef slope of Prison Reef is also characterized by small platy-like colonies (>40 cm) of *Montipora* sp. at the mid depths of the reef slope zone (Figure 4-5). The tabular or platy forms are one of the most susceptible morphotypes to sedimentation, but in turn the most effective ones assimilating light (Erftemeijer et al., 2012). So large colonies of platy corals could not withstand high sedimentation rates, but rather small corals that offer less depositional surface. High water flows promote the clean off particles on coral tissue (Course et al., 2012). However, Prison Reef shallow unconsolidated bottoms (10±2 meters) will allow the resuspension of sediment. Yet, high current speeds (0.2 cm s⁻¹) will not facilitate the cleaning of the polyps but rather resuspension and sedimentation of the fine sediment fraction.

At Bawe Reef we find high abundance of *Turbinaria* sp. at the 5-meter range. We find a number of massive corals on deeper areas. *Turbinaria* sp. is one of the corals most resistant to sedimentation, as the inclination of its "leaves" favor the slip of the sediment to the basal coral area, whereas its platy shape increases the light harvest (Todd, 2008). Erftemeijer et al., (2012) reported a meta-analysis of morphologies more resistant to sedimentation and turbidity. The analysis included 89 coral species (only about 10% of all known corals). The results established that foliaceous (particularly *Turbinaria* sp.) and massive corals tolerate better high turbidity levels, which is consistent with coral morphologies found in our study site.

4.6 Conclusion

We conclude by highlighting the fact that tides dominate the transport and sedimentation of the fine sediment fraction in our study sites. The turbidity values at both locations were not significantly different, thus that indication of sedimentation patterns in the lower reef zones of Prison Reef, will inhibit reef formation on deeper reef zones, which induce steep-reef slope formations. However, at Bawe Reef no distinction between top and bottom waters suggest higher water velocities mixing and transporting away fine particles.

We identified two main SPM sources: Relative enriched $\delta^{13}\text{C}$ values and higher C / N molar ratio indicates that the main carbon source in Prison Reef is marine primary producers (PP). Enriched $\delta^{15}\text{N}$ values at top and bottom waters in Bawe Reef suggest that enriched allochthonous Nitrogen is being uptaken by PP. At Bawe Reef, $\delta^{15}\text{N}$ low variability and values consistently over 10‰ points sewage as the primary SPM source. This implies that local anthropogenic pressures threatens Bawe Reef and potentially Prison Reef as we also see enriched $\delta^{15}\text{N}$ on surface waters. However, Chlorophyll values are still in the upper oligotrophic range and there is no sign of benthic macroalgal blooms. We also propose that due to short residual times of the water bodies, untreated sewage discharge nitrogen not accessible for most marine biota. The gradual disintegration and decay of such particles occurs partially on the reefs, but the strong tidal currents transport some extent of the suspended particles offshore.

Finally we propose that in turbid reef settings two main processes control reef slope development and reef growth; sedimentation and turbidity. Both processes should be described and assess separately and not assumed to happen simultaneously, as previously described in the literature. Steep reef slope profiles are characteristic of

CHAPTER 4

reefs controlled by sedimentation processes, showing dominant vertical growth component and limited lateral progradation due to limited accommodation space. In addition, reef development does not exceed 10 ± 2 meters depth. The light diffracted by suspended particles and subsequent shading effect promotes a more gentle, but shallow reef slope profiles not exceeding 16 ± 2 meters depth as SI attenuates rapidly through the water column. Therefore, turbidity-dominated reefs, accretion, progradation and reef slope development on deeper sectors is limited, but still feasible.

5. Seagrass community-level controls over organic carbon storage are constrained by geophysical attributes within meadows of Zanzibar, Tanzania

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Running head: Seagrass traits and carbon storage

Keywords: Plant traits, organic carbon storage, seagrass

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5.1 Abstract

The aim of this work was to explore the feasibility of using seagrass functional traits to predict differences in sediment carbon storage. At 19 *a priori* selected sites within highly diverse seagrass meadows of Zanzibar, Tanzania, species cover was estimated along with three community traits hypothesized to influence sediment carbon storage (amount of above and belowground biomass, seagrass tissue nitrogen content, and shoot density). We identified five distinct seagrass communities that had notable variations in key plant traits but these differences did not translate into differences in sediment organic carbon (OC) storage. Across all communities, sediment OC was very low (ranging from 0.15% to 0.75%) and there were no differences in OC storage among communities, which was considerably lower ($33.9 \pm 7.7 \text{ Mg C ha}^{-1}$) than the global average ($194.2 \pm 20.2 \text{ Mg C ha}^{-1}$) reported for other seagrass ecosystems. In spite of high seagrass diversity and clear zonation among plant communities, sediments in all communities were shallow (ranging from 19 to 78 cm) and composed of medium-coarse grained carbonate sand on top of carbonate rock. We hypothesize that the geophysical conditions, including energetic flow regime and relatively coarse carbonate parent material, led to a low-deposition, sediment-limited environment not conducive to OC stabilization. This may outweigh any variation in the quantity or quality of plant inputs, ultimately leading to low OC storage within all seagrass communities. This highlights the complexity of OC cycling in seagrass ecosystems and cautions against the use of plant traits as a proxy for OC storage across all seagrass ecosystems.

5.2 Introduction

Seagrasses influence key ecological functions within coastal ecosystems through their productivity and by trapping sediment, altering hydrodynamics, and modifying biogeochemical processes in the water column and sediment (Duarte and Chiscano 1999; Marba et al. 2006). Through their effects on ecosystem processes seagrasses provide numerous ecosystem services including sediment stabilization, coastline protection, nutrient cycling, pathogen reduction, support of fisheries, and enhancement of biodiversity (la Torre Castro and Rönnbäck 2004; Duffy 2006; Orth et al. 2006; Lamb et al. 2017). In the last decade, seagrasses have been recognized as potentially important ‘blue’ carbon (organic carbon sequestered by vegetated coastal ecosystems) sinks, adding climate regulation to their list of well-established ecosystem services (Nellemann et al. 2009).

A surge in research efforts has revealed the wide range (up to 18-fold) of sediment organic carbon (OC) storage within seagrass sediments, demonstrating the complexity of the carbon cycle within these ecosystems (Nellemann et al. 2009; Duarte et al. 2010; Fourqurean et al. 2012a; Lavery et al. 2013; Duarte et al. 2013; Macreadie et al. 2014; Campbell et al. 2014; Serrano et al. 2014; 2015; Miyajima et al. 2015; Phang et al. 2015; Armitage and Fourqurean 2016; Röhr et al. 2016; Serrano et al. 2016; Samper-Villarreal et al. 2016; Schile et al. 2016; Jankowska et al. 2016; Dahl et al. 2016). The variability in OC storage occurs across multiple spatial scales, ranging from within-meadow variation (Serrano et al. 2014), to regional (Lavery et al. 2013; Miyajima et al. 2015) and global-scale variation (Fourqurean et al. 2012a). This presents a formidable obstacle for reliably valuing this ecosystem service because a baseline of the OC stock is required before conservation or restoration can be

incentivized under a blue-carbon framework (Costanza et al. 1997; Barbier et al. 2011; Herr et al. 2012; Macreadie et al. 2014).

A potential solution is to utilize easy-to-measure functional traits that can be linked to ecosystem functions underlying the service of carbon storage (Grime 2001; Kremen 2005; de Chazal et al. 2008; de Bello et al. 2010). Plant functional traits have been shown to be valuable tools for assessing and managing ecosystem services (Díaz et al. 2007; de Bello et al. 2010). An important trade-off of plant traits linked to OC cycling, known as the ‘fast-slow plant economic spectrum’, consists of a suite of coordinated characteristics that either promote fast carbon acquisition and decomposition, or promote the conservation of resources within well-protected tissues with inherently slower decomposition rates (Reich et al. 1997; Grime 2001; Díaz et al. 2004; Wright et al. 2004; Freschet et al. 2012; Conti and Díaz 2012). Acquisition traits such as high specific leaf area, high nutrient content, low tissue longevity and density are consistently associated with high carbon inputs via photosynthesis and high carbon losses through decomposition (Herms and Mattson 1992; Grime et al. 1997; Díaz et al. 2004; Wright et al. 2004; Cornwell et al. 2008; Reich 2014). Conservative traits include the opposite of the above characteristics and promote slow-growing, long-lived biomass with low carbon losses via decomposition. At the ecosystem level, acquisition traits promote high carbon fluxes, while conservation traits are conducive for high carbon stocks (Wardle et al. 2004; De Deyn et al. 2008; Díaz et al. 2009; Conti and Díaz 2012).

Several seagrass traits have been proposed to be important determinates of organic carbon sequestration and storage within seagrass sediments (Duarte et al. 2011). Canopy characteristics, such as high leaf density and complexity, have been shown to enhance OC burial within the sediment by filtering and trapping particles from the

water column and promoting sediment deposition and retention (Duarte and Chiscano 1999, Gacia et al. 1999, Gacia and Duarte 2001, Hendriks et al. 2008, Duarte et al. 2005, Peterson et al. 2004). Seagrass tissue stoichiometry has been correlated with decomposition rates and carbon preservation within seagrass sediments, with tissues containing relatively higher nitrogen and phosphorus content decomposing faster (Enriquez et al. 1993; Duarte et al. 2010). Seagrass biomass has been correlated to OC storage (Armitage and Fourqurean 2016; Serrano et al. 2016). Belowground production of seagrass roots and rhizomes places OC directly into sediments, which can be stabilized on mineral surfaces, within aggregates, or if microbial activity is suppressed due to lack of oxygen (Duarte et al. 2010; Belshe et al. 2017). In addition, the binding of the sediment by the root-rhizome system (Christianen et al. 2013) and the high lignin content of belowground tissues (Klap et al. 2000), promote OC storage. And larger plants disproportionately contribute to OC accumulation by shedding more biomass per unit ground area (Garnier et al. 2004; Lavorel and Grigulis 2011). Seagrass interspecies variation in these traits place them within the continuum of the ‘fast-slow’ ecological spectrum, with small-bodied, ephemeral species, such as *Halophila spp.*, *Halodule spp.*, and *Zostera spp.* on the ‘fast’ acquisition end, and large-bodied, persistent species, such as *Enhalus spp.*, *Thalassia spp.* and *Posidonia spp.*, on the ‘slow’ conservation end (Orth et al. 2006).

The objective of this study was to explore the utility of seagrass community traits for identifying where high sediment OC stocks occur within diverse meadows of Tropical Indo-Pacific. We measured three plant community traits (above- and belowground biomass, tissue nitrogen content, and shoot density) within five seagrass communities and hypothesized that communities with either high shoot density, low tissue nitrogen

content, or a high proportion of belowground biomass would store more OC within their sediments.

5.3 Materials

5.3.1 Description of study sites

This study was conducted within the largest and most diverse bioregion of seagrasses, the Tropical Indo-Pacific, specifically in coastal waters of Unguja Island (-6.15809°S, 39.19181°E) of Zanzibar, Tanzania. The climate is warm and moist, with temperatures between 27 and 35°C, with an annual rainfall of 1600 mm that is strongly influenced by two opposing monsoon seasons driven by the southeast monsoonal circulation of the central Western Indian Ocean (McClanahan 1988; Mahongo and Shaghude 2014). The regional hydrodynamics are complex and primarily influenced by ebb-flood tidal phases but are also influenced by the East African Coastal Current (EACC) and monsoon winds (Shaghude et al. 2002; Mahongo and Shaghude 2014; Zavala-Garay et al. 2015). The tidal cycles are semi-diurnal ranging from mesotidal during neap tide (~1 meter amplitude) to macrotidal (from 3 to 4 meters in amplitude) during spring tide (Shaghude et al. 2002; Zavala-Garay et al. 2015). Strong tidal currents can reach velocities that range from 0.25 to 2 m/s (Shaghude et al. 2002).

Sample sites were established within three seagrass meadows (M1, M2, M3) in open coastal waters adjacent to islands 1-5 km west of the main city, Zanzibar Town (Figure 5-1). During October 2013, physical properties (temperature, pH, dissolved oxygen and conductivity) of the water column were measured using a WTW 3430 multi-parameter probe (Weilheim, Germany). Light levels at the surface (I_0) and bottom (I_d) of the water column were measured with Li-1400 (Li-Cor Biosciences, Lincoln, Nebraska, USA). Light attenuation (k) at a given depth (d) was calculated

using the following equation: $k = \ln(I_d/I_0)/-d$. Landscape sediment characteristics were assessed within four biogeographic zones (reef flat, fore reef, tidal channel and seagrass meadow). The upper 5-10 cm of sediment was collected using a *Van Veen* sampler (3 mm plate, 250 cm²) at 27 locations following the bathymetric gradient and covering the four biogeographic areas. Sedimentary samples were rinsed with clean freshwater in order to remove soluble components and dried at 40°C for at least 48h. Two subsamples (of each set) were sieved in a stack-shaker sieve for 10 min. We applied the Udden-Wentworth scale (Wentworth 1922) as following: gravel (>2000 µm), coarse sand (1000-2000 µm), medium sand (500-1000 µm), medium-fine sand (250-500 µm), fine sand (125-250 µm), very fine sand (63-125 µm) and silt (<63 µm). Each individual fraction was calculated as weight percentage of the total bulk sediment. We used the logarithmic Folk and Ward (1957) method to convert the measurements into phi scale, and the physical description of sediments was based on the granulometric output and appearance of the bulk sediment after Folk (1954). Summary statistics for each zone were estimated from log-transformed data using the G2Sd R package (Fournier et al. 2014). Surface sediments (top 2-3 cm) were also collected within different seagrass species assemblages to assess differences in local sediment characteristics, compared to landscape sediment properties. A representative sediment sample of each community (see below for information on seagrass communities) was photographed at high-resolution over a 5-mm grid and qualitatively compared based on appearance and texture (Folk 1954).

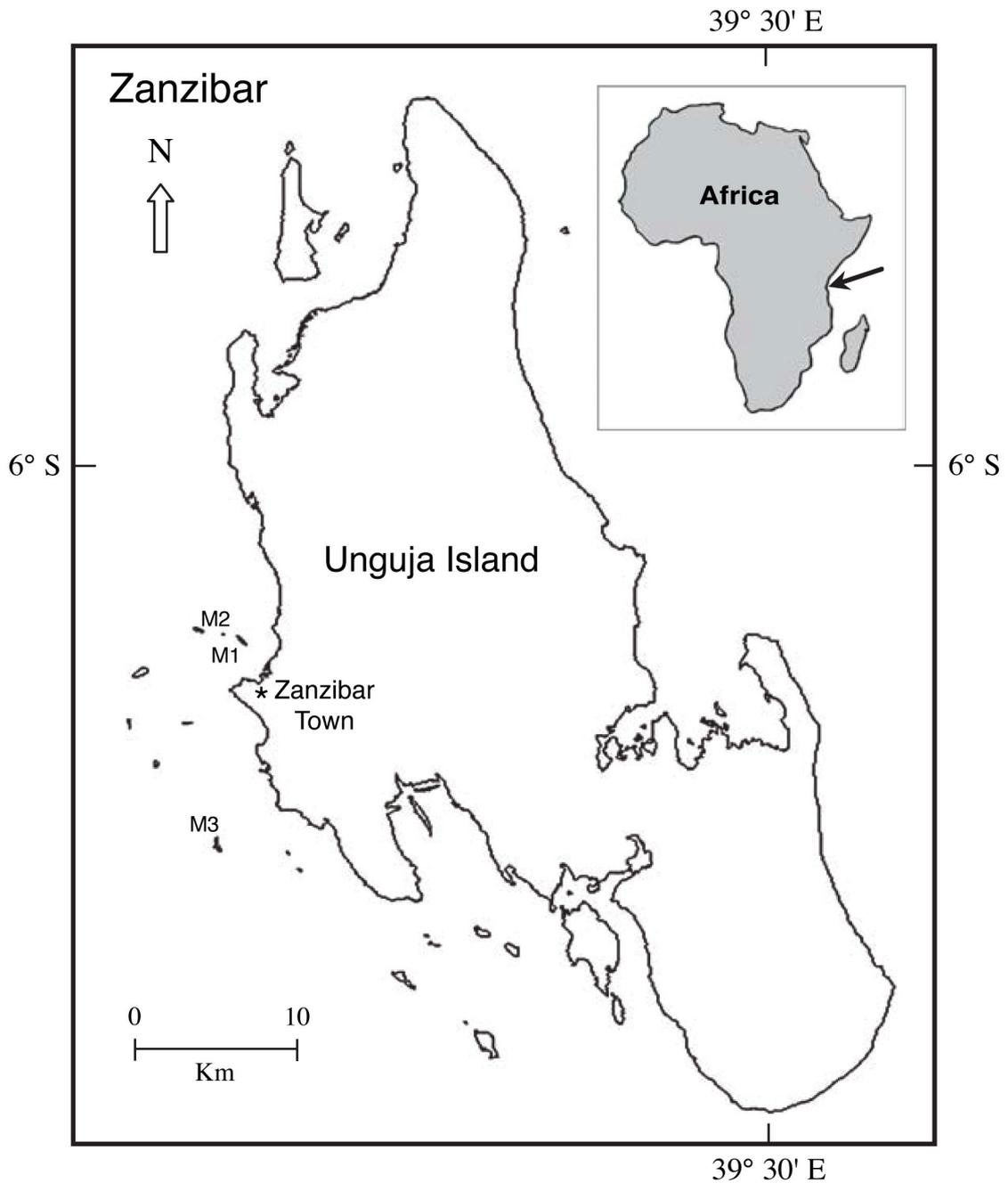


Figure 5-1 - Study sites were located within three meadows (M1, M2, M3) in open coastal waters adjacent to islands 1-5 km west of the main city, Zanzibar Town, Unguja Island (-6.15809°S, 39.19181°E) of Zanzibar, Tanzania.

5.3.2 Community data and analysis

In October of 2013, seagrass species composition was quantified at 19 *a priori* selected sites within three seagrass meadows, and eight seagrass species were identified: *Thalassodendron ciliatum*, *Cymodocea serrulata*, *Cymodocea rotundata*, *Thalassia hemprichii*, *Syringodium isoetifolium*, *Halodule univervis*, *Holophila ovalis*, and *Halophila stipulacea*. Sites were selected to capture the zonation of species assemblages found across the extent of each meadow. At each site, six 0.25 m² quadrats were haphazardly tossed and seagrass cover was visually estimated and assigned values based on a modified Braun-Blanquet scale (Mueller-Dombois and Ellenberg 2012).

Multivariate analyses were used to describe and categorize the patterns in seagrass species assemblages found at the 19 sample sites. First, Braun-Blanquet cover categories were converted to the midpoint of the cover range (Wilkum and Shanholtzer 1978), square root transformed to down weight the influence of abundant species, and relativized to the total abundance of each site. A Bray-Curtis similarity index was then calculated based on the similarity of species composition and cover among sites (Bray and Curtis 1957). Then, based on this similarity matrix, both nonmetric multidimensional scaling (NMDS) and hierarchical cluster analysis (average linkage) were performed to group sites by similarity in seagrass species composition and cover (Kent and Coker 1992; Braak 1995; Legendre and Legendre 1998). These categorizations were used to identify the seagrass species assemblages (communities) present in the sampled meadows. The vegan package (version 2.2-0; (Oksanen et al. 2014)) in R (R Core Development Team 2014) was used for all multivariate analysis.

5.3.3 Trait data and analysis

To quantify traits of each seagrass community, three biomass cores and five seagrass plants of each species present, were collected at each site. Core samples were taken with a 13-cm diameter PVC core and used to quantify shoot density and above and below ground biomass. Plant material from the cores was washed free of sediment in the field, stored in plastic bags, and frozen for subsequent analysis. After thawing in the lab, seagrasses were sorted by species and short shoot density (number m^{-2}) was calculated. Green leaves (above-ground biomass) and living root, rhizome, and short-shoots (below-ground biomass) were separated and dried at 60°C until a constant weight was reached, then weighed to obtain above and below ground biomass (g DW m^{-2}) for each species. Species weights were then summed for core-level estimates of above and below ground biomass.

Differences in short-shoot density among the seagrass communities was determined using a generalized linear model, specifically a negative binomial (link=log) because the data were counts and found to be over dispersed (Zuur et al. 2009). Communities were considered to be different when there was no overlap in 95% confidence intervals of model estimates. Models were fit using the MASS package (version 7.3-35; Venables and Ripley 2002)) in R. Differences in above and below ground biomass among communities were determined using an ANOVA with post-hoc Tukey HSD at $p \leq 0.05$ significance level.

Seagrass tissue collected at each site was used to quantify the % nitrogen (N) of leaf and rhizome tissue of each species. A section of rhizome and the second-ranked leaf of each of the five shoots was taken, cleaned of epiphytes, and dried at 60°C for 48 hours. Tissue samples were then homogenized and measured on an elemental analyzer (Euro EX 3000; EuroVector) to determine the % N of each species at each

site. The % N of each community was then estimated by calculating the mean and standard deviation of the % N weighted by the abundance of each species present within the community. Communities were considered different when there was no overlap between 95% confidence intervals (weighted mean \pm 1.96*weighted SD).

5.3.4 Deep sediment cores and carbon analysis

To determine if carbon storage within sediments varied among different seagrass communities and if this variation could be explained by specific traits, sediment cores were taken within the seagrass communities (determined from the multivariate analysis) at the same sites during October of 2014. Three sediment cores were taken with a hand-driven corer on SCUBA, within each of the identified seagrass communities and outside of seagrass meadows on bare sediment. In the lab, cores were sectioned into 3 cm slices. From each slice, a subset of 15 ml of sediment was taken and oven dried (60°C) for bulk density determination. Dried sediments were homogenized in a ball mill and % organic carbon (OC) was determined, after acidification to remove carbonates, on an elemental analyzer (Euro EX 3000; EuroVector). The OC content (CC) of each 3-cm slice was calculated from measured % OC and the dry bulk density (DBD) of the slice:

$$CC_{slice} = z_{slice} \times DBD_{slice} \times OC_{slice} / 100$$

where z_{slice} is the slice thickness (cm), and the % OC content of the slice is multiplied by 100 to convert % to grams OC per dry weight. The amount of carbon stored in each core was calculated by summing the OC content in each depth increment (slice). Because the total core length varied among sites (from 19 to 78 cm) total core carbon storage was estimated in two ways. First, estimates of storage in the top 25 cm of sediment were calculated because at this depth there were nearly full data sets in all cores. Second, to make estimates comparable to other studies, storage in the top meter

of sediment was estimated by gap filling missing data down to one meter using a negative exponential model with the drc package (version 3.0-1; Ritz et al. 2015)). All graphics were produced with the ggplot package (version 1.0.0; Wickham 2009)) in R (R Core Development Team 2016).

5.4 Results

5.4.1 Seagrass meadow environment

Physical properties of the water column were similar among meadows, with pH ranging from 8.19 to 8.31 ($F_{2,35}=9.01$, $p=0.06$), dissolved oxygen ranging from 6.5 to 8.8 mg/L ($F_{2,35}=2.53$, $p=0.09$), conductivity ranging from 53.7 to 54.1 S/m ($F_{2,35}=0.18$, $p=0.84$). Water temperature ranged from a mean of 26.4°C in M1, to 26.3°C in M2 and 27.1°C in M3. In general water clarity was high and light attenuation (Kd) through the water column was similar among meadows (mean Kd=0.35, $F_{2,29}=1.45$, $p=0.25$). Sediments across the landscape were composed of coarse to medium sized carbonate sands, that were poorly sorted but actively reworked, suggesting energetic hydrodynamic conditions. The texture was consistently classified as gravelly sand; however, the mean grain size was slightly smaller within seagrass meadows (1953 μm) when compared to the reef flat (2818 μm), fore reef (2352 μm) or sediments found on deeper areas of the channel (2546 μm ; Supplementary Table 1). There were no major (compositional or granometrical) differences among the four bioregions, with all classified as poorly-sorted, gravelly sand. At the local scale, there were no large qualitative visual differences among surface sediments beneath the different seagrass communities, and all were consistent with the sediment characterization of the region (Supplementary Figure 5-1).

5.4.2 Seagrass community composition

Five distinct seagrass species assemblages were identified using a combination of nMDS and hierarchical clustering (Figure 5-2 a & b). Because both methods produced similar results, we felt confident that these five groupings represented an inherent structure in the similarity of seagrass species composition and cover found at the 19 sites within the three meadows. For simplicity, we refer to the five distinct assemblages as communities A, B, C, D and E. The first two communities, A and B are monospecific, composed 100% of *Cymodocea serrulata* (CS) and *Thalassodendron ciliatum* (TC), respectively (Figure 5-2 c). Although a single species does not fit the strict definition of a community, we use the terminology for congruity throughout the manuscript. Community C was comprised mostly of small-bodied, fast-growing species 67% *Halodule uninervis* (HU), 19% *Cymodocea rotundata* (CR), 8% *Halophila ovalis* (HO), 1% *Halophila stipulacea* (HS), but also contained a small percentage (5%) of *Thalassia hemprichii* (TH). Community D was dominated by TH (91%) with a lesser occurrence of CR (8%) and TC (1%). Community E had the highest evenness of all communities with 46% TH, 26% CS, 22% *Syringodium isoetifolium* (SI), 5% HU, and 1% TC.

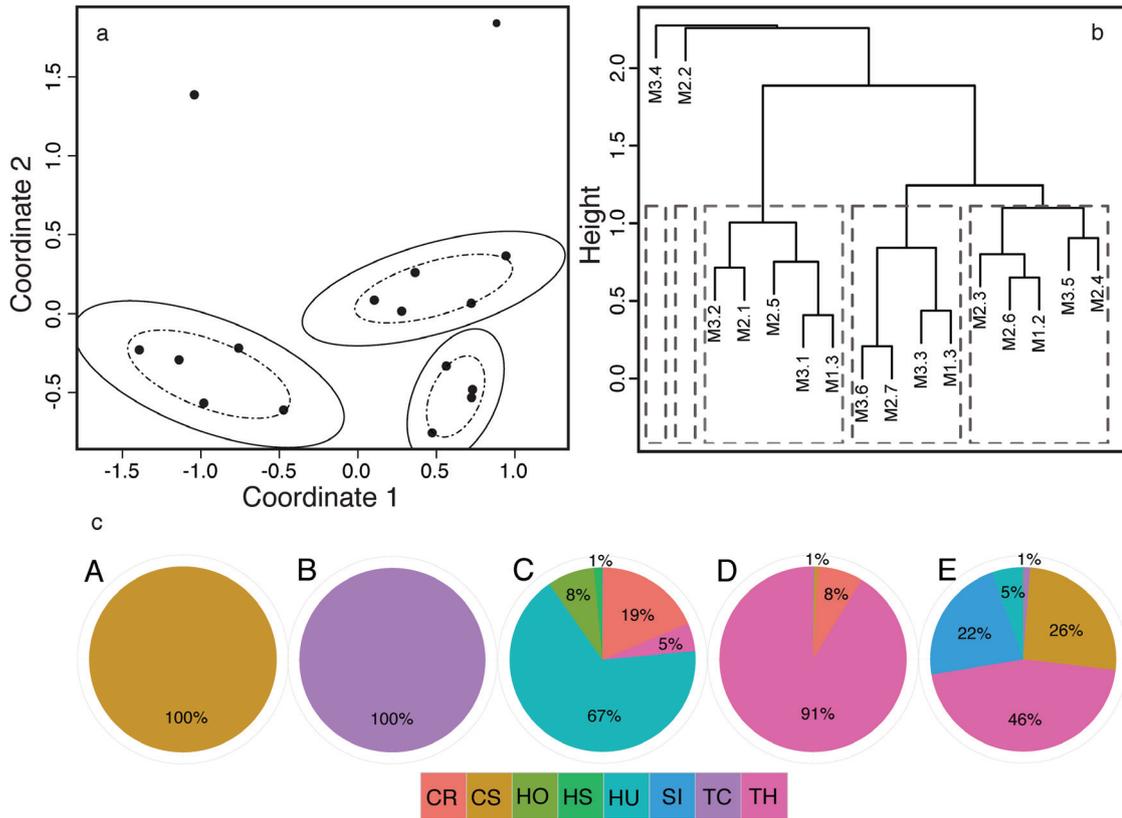


Figure 5-2 - Seagrass communities Seagrass communities were determined by grouping the 19 sites based their similarity in seagrass species composition and cover. Two different methods were utilized. First, a) NMDS ordination plot was used to group sites (●) into a community if they fell within the dashed and solid ellipses representing the 66% and 95% confidence intervals of groupings. Note that within two communities there was 100% overlap in site similarities, so multiple sites are overlain and confidence ellipses were not plotted. Second, b) hierarchical cluster analysis (average linkage) grouped the same 19 sites from the three meadows (M1, M2, M3) and converged on the same five communities. Again, because of the high similarity (100%) of sites within the first two grouping, only one site name is plotted even though multiple sites were grouped into these communities. c) Pie charts of each community (A-E)

show the mean percent cover and species composition, with colors representing the different species: CR: *Cymodocea rotundata*, CS: *Cymodocea serrulata*, HO: *Holophila ovalis*, HS: *Halophila stipulacea*, HU: *Halodule univervis*, SI: *Syringodium isoetifolium*, TC: *Thalassodendron ciliatum*, TH: *Thalassia hemprichii*.

5.4.2 Community traits

There was a significant difference in both above (AG; $F_{4,43}=28.82$, $p<0.0001$) and belowground (BG; $F_{4,43}=16.41$, $p<0.0001$) biomass among seagrass communities (Figure 5-3). This difference was driven by a significantly higher amount of aboveground (AG: 863 ± 609 g DWm⁻²) and belowground (BG: 682 ± 380 g DWm⁻²) biomass in community B. This community, dominated by *Thalassodendron ciliatum* (TC), contained AG and BG biomass up to 1472 g DWm⁻² and 1062 g DWm⁻², respectively. The remaining four communities had similar AG and BG biomass, on average ranging from (AG) 50 to 131 g DWm⁻² and (BG) 261 to 470 g DWm⁻² (Figure 5-3).

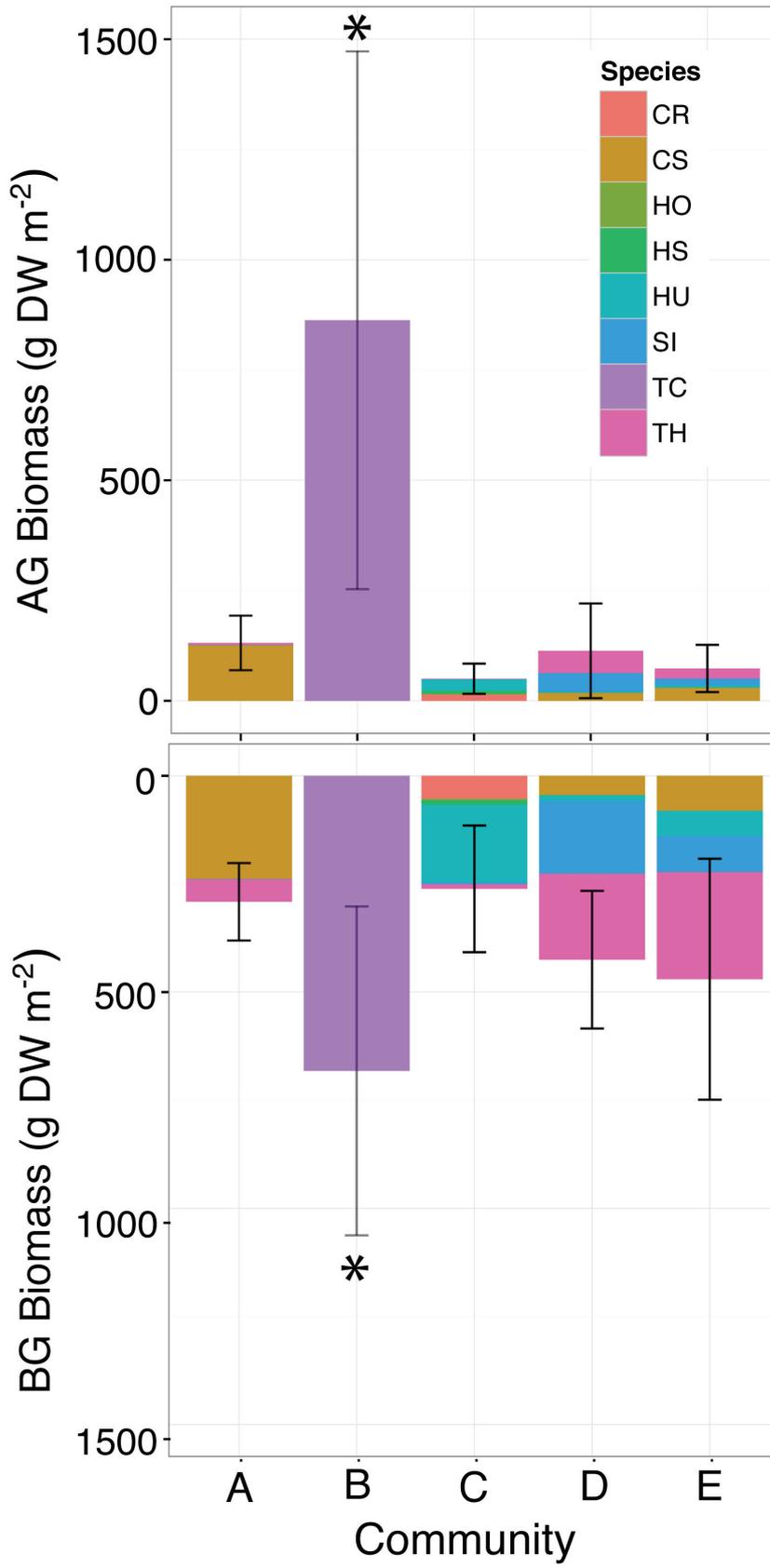


Figure 5-3 - Seagrass above- (AG) and belowground (BG) biomass (g DW m⁻²) for each community (A-E), with the mean contribution of each species to the cumulative mean of the community indicated by different colors. Whiskers represent the standard deviation and statistical difference at the significance level $p \leq 0.05$ indicated by the asterisk (*). List of the seagrass species: CR: *Cymodocea rotundata*, CS: *Cymodocea serrulata*, HO: *Holophila ovalis*, HS: *Halophila stipulacea*, HU: *Halodule univervis*, SI: *Syringodium isoetifolium*, TC: *Thalassodendron ciliatum*, TH: *Thalassia hemprichii*.

The density of seagrass short shoots differed among seagrass communities (no overlap in 95% confidence intervals of model estimates), with community C having significantly higher shoot density than all other communities (Figure 5-4). This community is dominated by small-bodied fast-growing seagrass species. The estimated mean shoot density of community C was 4178 shoots m⁻² based on the negative binomial model, while the estimated means of the remaining communities

were all similar and ranged from 885 to 1390 shoots m^{-2} .

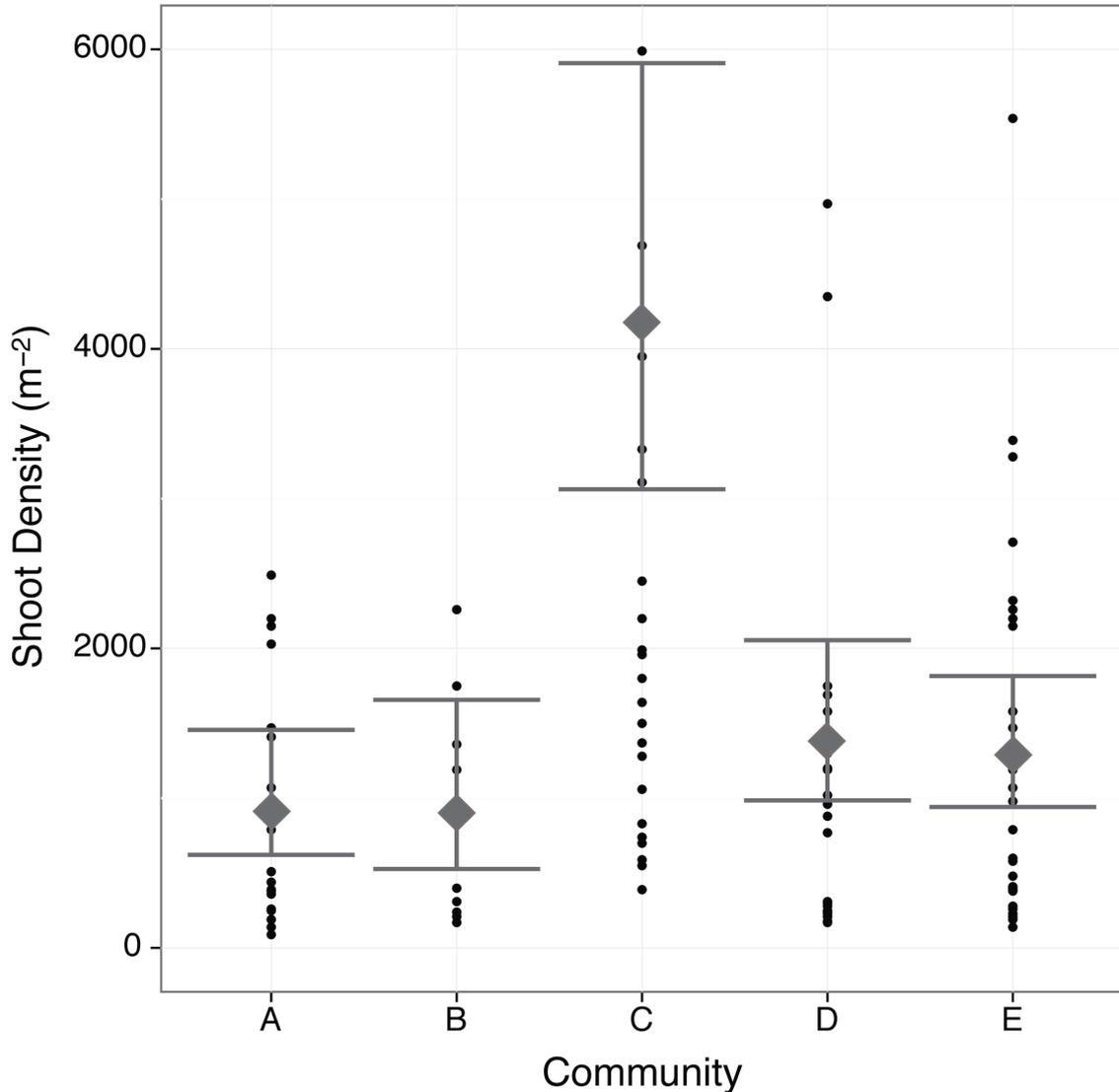


Figure 5-4 - Estimated mean (◆) and 95% confidence intervals of seagrass shoot density (shoots/m²) within each seagrass community (A-E).

The nitrogen content within seagrass leaves varied among seagrass communities, with community D having the highest % nitrogen (2.42 ± 0.28 %), which was significantly higher than communities A (1.40 ± 0.09 %) and B (1.54 ± 0.05 %; Figure 5-5). Differences were considered significant when there was no overlap in 95% confidence intervals. Communities C (1.82 ± 0.25 %) and E (1.76 ± 0.12 %) had

intermediate leaf nitrogen concentrations. The higher level of leaf nitrogen in community D was driven by the high relative abundance of *Thalassia hemprichii*, which contained the highest leaf nitrogen (2.46%) of any seagrass species. Leaf stoichiometry (C:N ratio) was on average within the range of 22-24, for all communities except community D (mean C:N = 17.7), indicating the potential for higher microbial carbon-use efficiency with litter from community D. On the contrary, the nitrogen content within the rhizome did not vary among communities, with the weighted mean % nitrogen in all communities ranging from 0.42% to 0.67% (Figure 5-5) and rhizome C:N ratios ranging from 78 to 97.

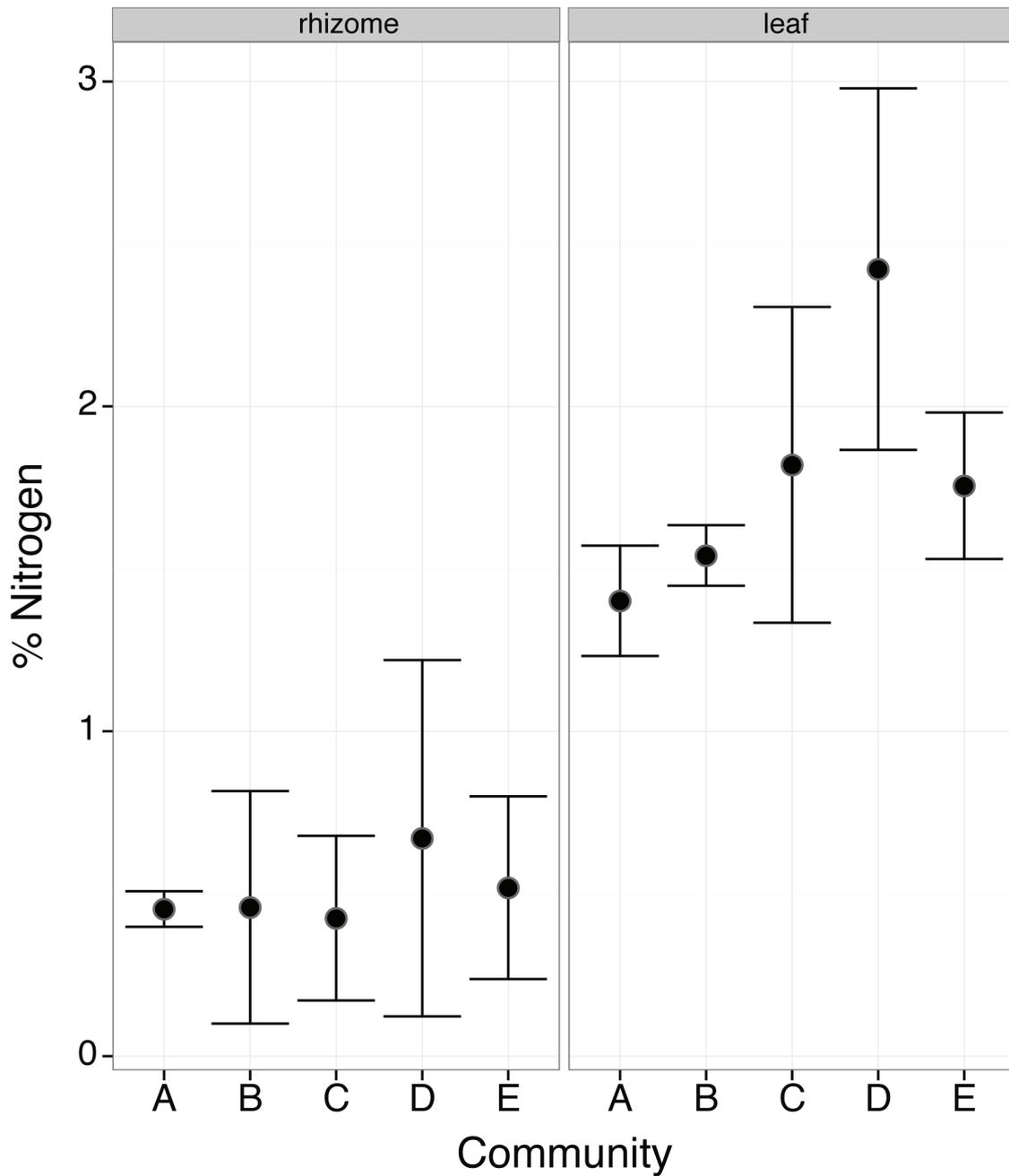


Figure 5-5 - Percent nitrogen (N) in rhizome (left) and leaf (right) tissues from seagrass species assemblages of each community. Circles (●) denote the mean and whiskers the 95% confidence intervals of the % N weighted by the abundance of each species present within the community (weighted mean \pm 1.96*weighted standard deviation).

5.4.3 Sediment carbon

The depth that cores penetrated into the sediment varied from 19 to 78 cm and was dictated by the limited sediment accumulation on top of carbonate rock. The percentage of OC within the sediment was low within all communities (A-E), varying from a maximum of 0.75% in surface sediments to a minimum of 0.15% down core (Figure 5-6). There were no differences in % OC among seagrass communities (A-E; $F_{4,226}=0.84$, $p=0.5$) but there was significantly higher % OC in communities with seagrass (A-E) compared to bare sediment (F, $F_{1,281}=46.5$, $p=0.001$). Generally, all cores exhibited the typical trend of decreasing % OC with depth into the sediment, except two cores taken outside of seagrass meadows (F: bare sediment; Figure 5-6). This indicates that the bare areas may have been colonized by seagrass in the past, contributing to an increase in carbon storage within deeper layers of the sediment. Thus, it must be noted that in order to associate present seagrass communities with long term carbon storage in sediments, we assumed there were no historic differences in communities during past carbon deposition.

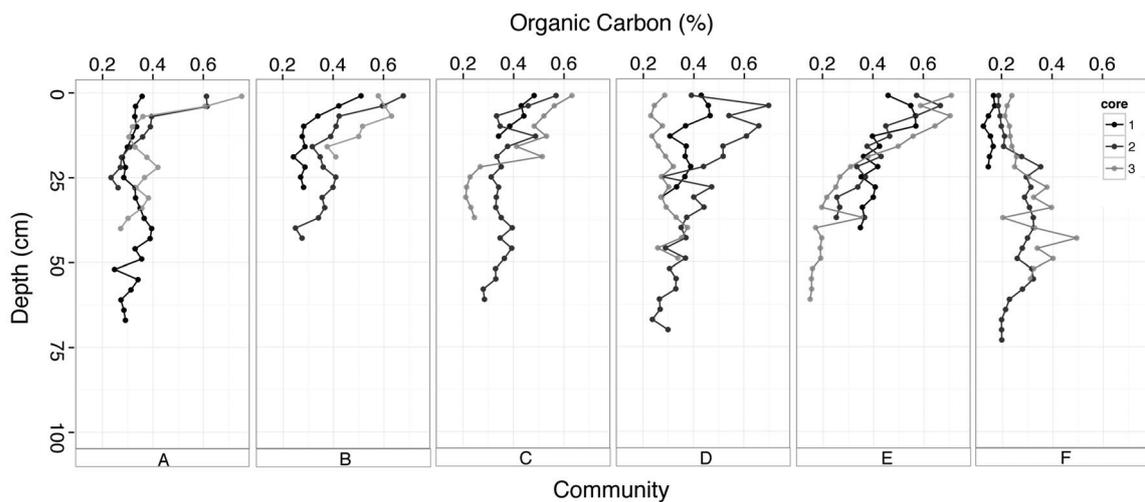


Figure 5-6 - Percent organic carbon at different depths (cm) down each sediment core taken within the five seagrass communities (A-E) and bare sediment (F).

OC storage within the top 25 cm of sediment did not differ among seagrass communities (A-E, $F_{4,14}=0.82$, $p=0.54$) and was low, on average 14.1 ± 2.2 Mg C ha⁻¹, but was significantly higher than adjacent bare sediment (7.5 ± 2.1 Mg C ha⁻¹, $F_{5,13}=4.99$, $p=0.009$; Figure 5-7). Similarly, OC storage down to 1 meter did not differ among seagrass communities (A-E, $F_{4,11}=0.24$, $p=0.9$) and was on average 33.9 ± 7.7 Mg C ha⁻¹, but with the gap filled data there was no longer a significant difference in OC storage between seagrass communities and bare sediment (19.3 ± 8.2 Mg C ha⁻¹, $F_{5,13}=1.663$, $p=0.213$). Additionally, there were no difference in OC storage in the top 25 cm of sediment among the three seagrass meadows ($F_{2,13}=0.94$, $p=0.4$) indicating that spatial variation among the meadows was not masking trends among communities.

5.5 Discussion

In three seagrass meadows off the coast of Zanzibar Town, Tanzania, we identified five distinct seagrass communities, and within these communities there were notable differences in key plant traits shown in other ecosystems to influence ecological processes linked to OC sequestration and storage (Aerts and Chapin 2000; Chapin 2003; Díaz et al. 2004). Community B had significantly higher AG and BG biomass, while community C composed of small-bodied seagrass species had higher shoot density. Both communities A and B had significantly lower % leaf nitrogen than community D, and their entire range of nitrogen content fell below the global threshold (1.82%) indicating nutrient limitation in seagrasses (Duarte 1990). Leaf stoichiometry (C:N ratio) for communities A (24.2) and B (24.5) were at the upper limit of the threshold (20-25) indicating the potential for nitrogen limitation and low microbial carbon-use efficiency during litter decomposition, both of which can lead to

higher sediment OC sequestration (Berg and McLaugherty 2003; Hessen et al. 2004). In addition, weighed mean % nitrogen of belowground tissues (rhizome) were low in all communities. We hypothesized that community B (dominated by *Thalassodendron ciliatum*), which exhibited traits of high AG and BG biomass and low tissue nutrient content, would store more OC within the sediment. However, these traits did not translate into differences in sediment OC storage among seagrass communities. Across all communities and depths, percent sediment OC was low (ranging from 0.15% to 0.75%) and there were no differences among seagrass communities in OC storage in the top 25 cm ($14.1 \pm 2.2 \text{ Mg C ha}^{-1}$) or the top 1 m ($33.9 \pm 7.7 \text{ Mg C ha}^{-1}$) of sediment (Figure 5-7). This magnitude of sediment OC storage is comparatively lower than the global average ($194.2 \pm 20.2 \text{ Mg C ha}^{-1}$ in the top meter) for seagrass ecosystems (Fourqurean et al. 2012a), and considerably lower to what has been reported for *Posidonia oceanica* (105 to 829 Mg C ha^{-1}), *Thalassia testudinum* (124 to 210 Mg C ha^{-1}) and *Amphibolis antarctica* (115 to 335 Mg C ha^{-1}) meadows (Mateo et al. 1997; Fourqurean et al. 2012b; Serrano et al. 2012; 2014). All four of these seagrass species (*P. oceanica*, *T. testudinum*, *A. antarctica* and *T. ciliatum*) are late-successional, slow-growing species with traits that place them on the ‘slow’ conservation-side of the plant economic spectrum associated with higher ecosystem OC storage (Díaz et al. 2004; Wright et al. 2004; Orth et al. 2006; Reich 2014). The breakdown of the relationship among plant traits and OC storage in our study indicates that other factors must be interacting to control OC deposition and stabilization within the sediment.

To try to disentangle why seagrass traits at the sites sampled here were not useful for predicating OC storage, we place this study into the state-factor framework (Jenny 1941) adapted for subaqueous sediments (Demas and Rabenhorst 2001; Trumbore

2009; Torn et al. 2009; Belshe et al. 2017). In this model, a soil property such as OC storage is described by the function:

$$\text{Soil property} = f(\text{C}, \text{O}, \text{B}, \text{F}, \text{P}, \text{T})$$

where C=climate, O=organism, B=bathymetry, F=flow regime, P=parent material, T=time. Here we explored the effects of different vegetation (organism), within meadows where other state factors were similar, but we did not find differences in the sediment property of OC storage. Three state factors stand out (parent material, flow regime and climate) that in specific combination we speculate can override the effect of seagrass traits on sediment OC storage. Climate and geographic location interplay to determine the six seagrass bioregions (Short et al. 2007), which dictates the pool of seagrass species, with their associated traits, available to make up a meadow. Flow regime in combination with parent material determine sediment characteristics, such as minerology and grain size, which can be important determinates for the occurrence of particular seagrass species (Koch 2001) and the stabilization of OC carbon (Burdige 2007; Trumbore 2009; Torn et al. 2009; Belshe et al. 2017). Flow regime also regulates the hydrodynamic energy of the system, which in turn determines the degree of deposition versus export of materials (Gillis et al. 2014), and effects the dispersal and distribution of seagrasses (Fonseca and Kenworthy 1987). Although seagrasses are capable of establishing and growing in a wide range of current regimes (Fonseca and Kenworthy 1987; Madsen et al. 2001; Koch 2001), the hydrodynamic environment affects, in part, the level and frequency of disturbance (from sediment loading to meadow erosion), which influences the species composition and status of the meadow (Fonseca and Kenworthy 1987).

Our sample sites are located in the Tropical Indo-pacific seagrass bioregion on an uplifted Pleistocene carbonate platform (Kent et al. 1971; Short et al. 2007). Water

flow in the area is energetic and tidal-dominated with moderate to high current velocities, ranging from 0.25 to 2 ms⁻¹ (Shaghude et al. 2002). The sediments are biogenic, with the major constituents being benthic foraminifera, molluscs (pelecypods and gastropods) and coral, with negligible terrigenous inputs (G.R. Narayan unpubl.; Shaghude et al. 2002). The seagrasses are growing within a shallow sediment layer (ranging from 19 to 78 cm) on top of solid carbonate rock, which determined the maximum depth of our sediment cores (Figure 5-6). The limited sediment available under the seagrass meadows and the small amount of fine sediments (~1% <63 size fraction) suggest an overall low-depositional environment (Supplementary Table 1, G.R. Narayan unpubl.) or that the sediment source is a limiting factor. Some of the shallowest sediments were found under *T. ciliatum* stands, which uncommon to other seagrasses are known to survive on rocky substrate in highly energetic hydrodynamic environments (Gullström et al. 2002; Bandeira 2002), and still maintain dense meadows with high biomass. The combined attributes of the energetic flow regime, carbonate parent material, and the large species pool of the tropical Indo-pacific, lead to diverse meadows with species containing a wide-spectrum of plant traits residing within a relatively coarse, sediment-limited environment. This combination of biological and physical properties did not support a high accumulation and retention of OC within the sediment at our study sites.

The geophysical constraint of sediment limitation has been attributed to low OC storage in seagrass meadows of the Arabian Gulf, where similar to this study, OC storage was low (0.7 to 13.2 Mg C ha⁻¹), and not correlated with seagrass biomass (Campbell et al. 2014). Likewise, seagrass meadows in Florida Bay are located on a carbonate platform with a gradient of sediment accumulation from northeast (low) to southwest (high) within the Bay (Fourqurean and Robblee 1999), which mirrors the

pattern of OC storage and seagrass biomass (Hall et al. 1999; Hackney and Durako 2004; Armitage and Fourqurean 2016). The potential effect of geophysical conditions on OC storage at our sites on the western coast of Unguja Island, Zanzibar, is revealed when compared to meadows located in the south and east coast of the island. Within meadows at these locations, sediment OC storage is two to three times higher than what was measured in our sites, and is positively correlated to seagrass biomass at the landscape scale, with the largest stocks located in sediments beneath large, persistent species (M. Gullstrom pers. comm.). Because most seagrass species occur at all locations, the contrast in OC storage among sites is likely influenced by differences in the depositional environment and/or sediment. The biogenic carbonate sediments that occur on the western side (where our sites occur) differ greatly from the eastern and southern coasts of the Island (Shaghude et al. 2001). The western carbonate sediments are composed of reefal foraminifera, mollusk, echinoderm and coral components, whereas the eastern and southern sediments are composed primarily of the calcareous green algae *Halimeda* (Shaghude et al. 2001), which form algal mounds, allowing for greater deposition of finer particles (carbonate mud) and deeper sediment accumulation (Muzuka et al. 2005; Kangwe et al. 2012).

In other seagrass ecosystems, the relative importance of plant characteristics versus geophysical attributes as indicators for OC storage has been shown to be location or species specific (Armitage and Fourqurean 2016; Röhr et al. 2016; Serrano et al. 2016; Samper-Villarreal et al. 2016; Alongi et al. 2016; Dahl et al. 2016). As a general trend, in high-depositional environments with relatively high allochthonous OC inputs (where small-bodied, ephemeral species often occur), the abundance of fine grain sediments has been correlated with high OC stocks (van Katwijk et al. 2011; Röhr et al. 2016; Serrano et al. 2016; Dahl et al. 2016). This correlation holds

for small-bodied seagrass species at 20 sites across three bioregions (Temperate Southern Ocean, Tropical Indo-Pacific, and Mediterranean; Serrano et al. 2016)). At adjacent estuarine sites in Thailand with a high contribution of terrestrial inputs and fine sediment, a relatively smaller-bodied seagrass (*Cymodocea serrulata*: 120 Mg C ha⁻¹) had higher OC storage than the large-bodied, persistent seagrass (*Enhalus acoroides*: 86 Mg C ha⁻¹), indicating a modulation of plant trait effects by geophysical properties of the site (Miyajima et al. 2015). A similar association between high OC storage and fine sediment was demonstrated across a range of conditions in the Temperate North Atlantic for the small-bodied species, *Zostera marina* (Dahl et al. 2016). However, at sites with relatively coarser sediment, characteristics of *Z. marina* (biomass, density, and cover) became better predictors for OC storage (Dahl et al. 2016). This shift in explanatory power from fine sediments to plant traits was also seen for large-bodied, persistent species (*Posidonia spp.* and *Amphibolis spp.*) inhabiting coarser sediments in more exposed sites (Serrano et al. 2016). Sites with the largest stores of OC recorded for seagrass are not correlated with fine sediment content and occur within dense meadows of the long-lived species *P. oceanica*, which form and persist in stable environments without high sediment loading (Peirano and Bianchi 1995; Serrano et al. 2016). This again indicates that the relative importance of plant traits for determining OC storage is in part dependent on the geophysical environment.

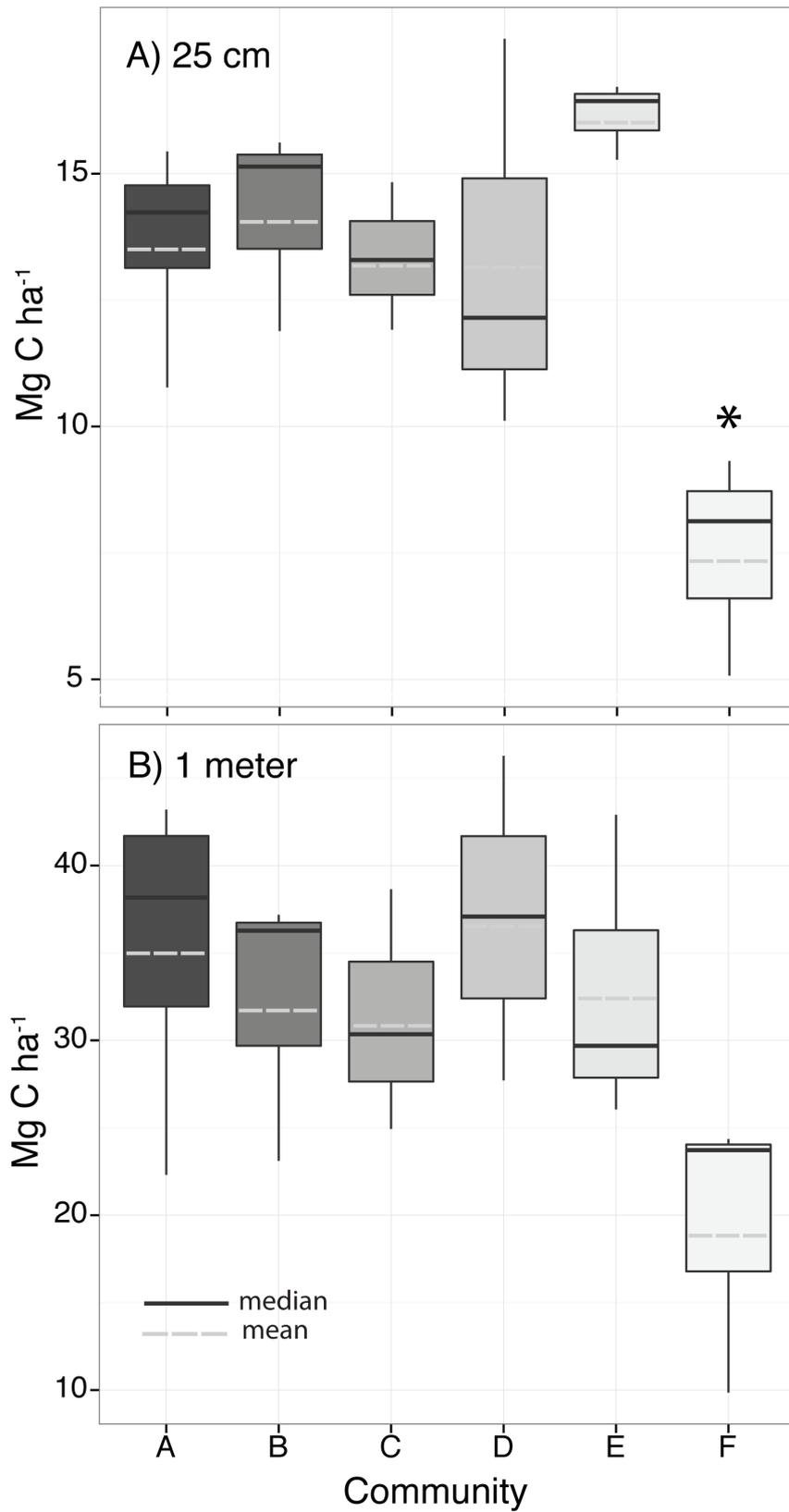


Figure 5-7 - Organic carbon storage of A) the top 25 cm of the sediment and B) the top meter of sediment within the five seagrass communities (A-

E) and bare sediment (F). Box and whiskers denote the 25th and 75th, and the 5th and 95th quartiles, respectively, with the solid line denoting the median and dashed line denoting the mean. Statistical difference at the significance level $p \leq 0.05$ indicated by the asterisk (*).

Based on the results presented here, in combination with the findings outlined above, we hypothesize that the effect of sediment on OC storage is non-linear and dominates at the extremes of the sedimentation spectrum. In high-depositional areas with an abundance of fine sediment, OC storage can be high even in meadows composed of species with “fast” traits. In moderate depositional areas, the importance of plant traits increase and meadows with “slow” traits will store more OC. Once the flow-regime becomes energetic enough to create sediment limitation, properties of the sediment again outweigh plant traits to limit OC storage even under meadows with traits conducive to OC storage. Of course, this hypothesis needs to be rigorously tested but this modulation of trait effects by geophysical properties provides hints that different OC stabilization mechanisms are potentially operating under the various combination of state factors (Burdige 2007; Belshe et al. 2017; Miyajima et al. 2017).

This study, placed into the context of the growing body of evidence of the large variation in OC storage in seagrass ecosystems (Lavery et al. 2013; Serrano et al. 2014; 2015; Miyajima et al. 2015; Röhr et al. 2016; Serrano et al. 2016; Samper-Villarreal et al. 2016; Dahl et al. 2016), illustrates the complexity of controls and mechanisms that govern OC storage in seagrass sediments. Care must be taken to not narrow our understanding of OC dynamics when searching for broad unifying predictors of OC storage across all seagrass ecosystems. Misidentifying why OC is

stabilized within seagrass sediments will hinder our ability to correctly predict the magnitude and rate of OC emissions with the degradation and loss of seagrass ecosystems (Waycott et al. 2009).

5.6 Conclusions

In this study, we were unable to link variations in plant traits to differences in sediment OC stocks within diverse seagrass meadows off the coast of Zanzibar Town, Tanzania. The geophysical constraints of the environment outweighed any effects of trait differences on OC stabilization and resulted in low OC storage across all seagrass communities. In spite of being constrained within the particular environment (combination of state factors), seagrasses still managed to store twice as much OC as bare sediment (0). In addition, seagrass density and biomass was high in most communities; therefore, the production not stored within sediment beneath the meadows was either exported to support secondary production (la Torre Castro et al. 2014) or sequestered within marine sediments elsewhere (Duarte and Krause-Jensen 2017). This highlights the importance of seagrass habitats for OC cycling in coastal marine ecosystems; however, further research is needed to identify under which geophysical conditions seagrass traits can be linked to the ecosystem function of OC storage.

6. Final remarks and outlook

The calcium carbonate production budget measured in Zanzibar indicates an extremely high production when compared globally to other reefs where the same methodology was applied (Chapter 2). High coral cover (>50%), and medium- low Shannon biodiversity and Margalef richness values (1.23 ± 0.52 and 1.52 ± 0.75 respectively) in adjacent reefs to Stone Town to medium-high values in CHICOP (1.82 ± 0.21 and 2.53 ± 0.47 , respectively), suggest an overall medium-good to very good reef condition, despite high SPM levels.

Several factors strongly favor the production of carbonates in these reefs. For example, the EACC warm current (Narayan unpubl.) flows through the Zanzibar channel by tidal currents, effectively renews the fringing reefs with oligotrophic waters up to two times a day. On the other hand, we have observed a high roughness or structural complexity linked to very high (> 50%) coral coverage. Hard hermatypic corals were the dominant benthic taxa, and no significant occurrence of macroalgae was reported in our study sites. However, the large abundance of sea urchins control effectively the overgrow of algae (Liddell and Ohlhorst, 1986; Aburto-Oropeza et al., 2015) by grazing on the reef framework (Coyer et al., 1993). Urchins will impede that macroalgal compete with hard corals for space, allowing ultimately high hard coral cover. In other nearshore reefs, similar high coral coverage was reported (Mallela et al., 2004; Morgan et al., 2016b) and was mainly control by light availability and reduced accommodation space. Limited accommodation space will trigger ecological spatial competition also in most degraded study sites (Chapter 2).

Photosynthetic hermatypic carbonate build-ups in our study sites were bathymetrically constrained to 16 ± 2 meters. Chuang (1977) found only 10% of the surface light irradiance reached down 8 meters, whereas only the 0.35% reached down 16 ± 2 meters depth. In accordance, turbidity tends to be one of the major environmental constraints in our location. This is supported by the spatial distribution of ahermatypic sand-dwelling corals, which inhabit deeper reef areas (Chapter 3). To better constrain uncertainties on how light attenuation controls carbonate production and benthic spatial distribution, new algorithms to retrieve (historical) turbidity from remote-sensed data could be applied in the shallow carbonate platform of Zanzibar. To test on a higher geographical scale ($>50\text{km}$) whether or not turbidity controls carbonate production all around the Island.

Corals have the ability to respond (actively or passively) to sediment stress. They can actively reject sediment at a high energetic cost through polyp inflation, ciliary and tentacular action or mucus production (Erftemeijer et al., 2012). The high nitrogen composition of coral mucus is usually associated with an increased nutrient concentration in coral reefs. Some other mechanisms include intraspecific morphological variation and mobility of free-living corals (Chapter 3). Although mobility on unconsolidated substrates is a very effective strategy to avoid burial, the great complexity and high specialization of the coral larvae settlement required for the establishment of this interspecific symbiosis, minimize the actual success of the strategy. In total 3 species of different families (4 with the symbiotic algae zooxanthellae) are involved in the *Heterocyathus aequicostatus* and *Heteropsammia cochlea* symbiosis (Chapter 3).

It remains to be clarified, what kind of gastropod species or in this case, which shell morphology and size range facilitate the settlement of coral larvae and, more general, whether several species can facilitate coral settlement. Other questions remain open, such as establishing which symbiotic relationship takes place first. Does the commensalistic tubeworm-gastropod relationship occurs first or does the tubeworm inhabit the gastropod shell and thereafter the coral larvae settles? Or does once the coral larvae settlement and encrustation of the gastropod shell takes place, the tubeworm find the favorable conditions? In any case in view of the results shown in Chapter 3, the space within the coral framework is optimized by the tubeworm, suggesting that the coral is forced to grow quickly during early stages to ensure this complex relationship.

Despite high turbidity and high sediment load ($18.2 - 37.6 \text{ mg L}^{-1}$), conditions that impose stress in symbiotic reef organisms (Anthony, 2000), nutrient levels were still in the range of oligotrophic waters (Narayan unpubl.). Risk and Edinger (2011) stated “the inextricable linking of sediment input and nutrient increase, that has made the field such a difficult area of research”. This is usually the case because the increase of sediment load is usually linked to urban development, remobilization of sediments or to the influence of nutrient-rich river discharges (Fabricius et al., 2013; Junjie et al., 2014; Pollock et al., 2014). However, this is not necessarily the case for particles with a large organic fraction, since thanks to the complex ecological interlinks that exist in coral reefs habitats, larger amounts of OM can be utilized by pelagic and benthic consumers. In addition, the inexistence of terrigenous influence and/or river input in our area of study, offers the perfect environmental setting to study the undisturbed dynamics of suspended particles and the potential effect they have on reef-building

organisms (Chapter 4) and further understand the resultant geomorphological mechanisms acting over larger time-scales (e.g. sediment transport and net CaCO_3 export).

Coral reefs are extremely complex on spatial and temporal levels (Nyström and Folke, 2001). The importance of spatial connectivity in shallow marine ecosystems is increasingly becoming relevant in marine research (Adam et al., 2011; Andréfouët et al., 2002; Mumby, 2006; Munday et al., 2009). Coral reefs as bio-engineers, adapt and modify the physical environment, for instance, by exporting carbonate sands, which are used by other marine organisms and ecosystems. For example, most seagrass species depend and contribute to CaCO_3 production (Mazarrasa et al., 2015). In addition, seagrass has the ability to trap and stabilize unconsolidated sediments rich in organic carbon (Chapter 5), reducing sediment load ultimately. Indeed, global estimations of the carbonate stock on seagrasses is still not available. As in Chapter 5 was highlighted, seagrass beds on the western coast of Zanzibar, does not show there a linkage between community traits and organic carbon storage. Although, this linkage probably exist in other locations of the Zanzibar Island, which show different oceanographic and geophysical settings. Another probable cause other than the threshold proposed in Chapter 5 is that the organic carbon trapped within seagrass is potentially utilized by invertebrates and filter feeders dwelling within seagrass beds, which in turn converts particular organic carbon (POC) into inorganic carbon by means aragonite or calcite. Likewise, calcifying organisms that occupy a certain volume underground, provide seagrass beds with an underlay three-dimensional structure or roughness. However, to date most work on carbon pools has focused on POC stocks (Fourqurean et al., 2012; Lavery et al., 2013). Further application of a

CHAPTER 6

modified Reef budget (see supplementary material) could explore the potential of seagrass beds to produce CaCO_3 , which would allow us to learn more about carbon stocks in seagrass meadows.

6.1 Final conclusions:

In this study, we linked reef condition to distance to highly populated areas of Stone Town. Coral reefs on Zanzibar conservation area CHICOP shows a very healthy state, whereas coral reefs adjacent to Stone Town (Chapwani and Prison Reef) are more degraded in comparison to CHICOP. Nonetheless, reef health measured with proxies such as biodiversity, reef structure, and coral cover scored consistently high on all locations, when compared globally. We also concluded that high structural complexity could be estimated on reefs showing intermediate disturbances, where the reef framework is highly breakable and susceptible to collapse. Overall, those proxies indicated that local human pressures affected negatively carbonate production, but more research is needed in order to disentangle specific effect of local pressures on calcium carbonate production.

Zanzibar budgetary state is export dominated, as the CaCO_3 produced is mostly exported to other associated ecosystems (e.g. seagrass). Therefore, major sedimentary formations (sandbanks, sandbars, beaches) are located far from the reef perimeter. In addition, low OC storage within seagrass meadows also indicates limited sedimentation (of the organic fraction) on Zanzibar reef environments, despite high sediment loads ($>20\text{mgL}^{-1}$). Such unique environmental conditions favored the adaptation of solitary, sediment-dwelling corals by building a complex partnership with a sipunculid. Once the coral-sipunculan symbiosis is established, the sipunculid wins protection to predators and the coral wins mobility, which is a very effective strategy to avoid burial and to withstand high sedimentation. However, the high level of complexity and therefore high vulnerability of those corals to changes and/or

disturbances limit the effectiveness of this symbiosis, as three organisms are involved in the success of such strategy.

We identified two main SPM sources: marine POM and sewage SPM. The tidal currents are highly relevant in this area because they retain or disperse untreated wastewater ($>10 \delta^{15}\text{N}$) towards the reefs and Open Ocean. We see that the principal local anthropogenic stressor that affects calcifiers health and distribution is sewage disposal, which favors high turbidity ($>20 \text{ mgL}^{-1}$). Nonetheless, sewage carbon and nitrogen is not directly accessible for most marine biota, the gradual disintegration and decay of such particles occur partially on the reefs, but some extent is transported away by tidal-currents. We concluded that tidal patterns, washes out sediments deposited on coral polyps twice per day, by means, the high frequency but mid-low duration of stress, enables high carbonate production and reef formation on western Zanzibar reefs.

Two conceptual models on reef progradation and reef slope development on turbid reefs settings are proposed depending on the principal controlling mechanism: 1) steep and shallow reef slope profiles are characteristic of reefs controlled by sedimentation processes, showing dominant vertical growth and limited lateral accretion patterns due to reduced accommodation space. Lateral accretion or progradation occurs by the breakdown and physical splitting of the reef flank with the posterior colonization of viable fragments by coral nubbins. 2) Turbidity-dominated reefs show a gentler and slightly deeper reef slope. Calcium carbonate production and reef progradation are limited by light availability reaching deeper sectors of the reef slope.

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ANNEX 1 –SUPPLEMENT MATERIAL CHAPTER 2

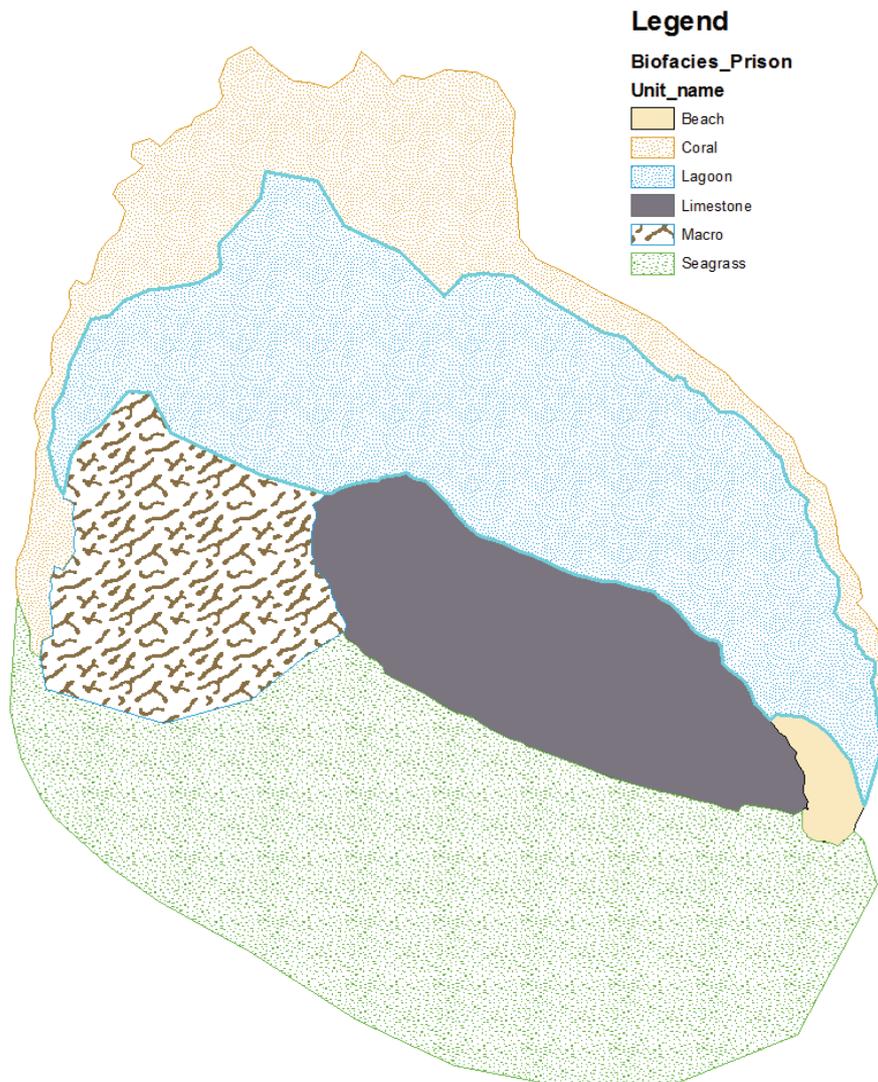
Table 1.S1 - Rank abundance raw data from the different taxon's encounter in our study sites.

Locations		Bawe			Prison			Chumbe			Chapwani		
Taxon	Abbreviation	Morphological strategy	Abundance	Proportion									
<i>Porites rus</i>	Syna	Submassive/Platy/Branding	81	47.4	69	40.8	9	5.2	34	50.7			
<i>Porites porites</i>	Pobr	Branching	15	8.8	9	5.3	2	1.1	1	1.5			
<i>Galaxea</i> spp	Gala	Submassive	11	6.4	19	11.2	9	5.2	3	4.5			
<i>Pocillopora</i> spp	Poci	Branching	11	6.4	6	3.6	6	3.4	4	6.0			
<i>Acropora</i> spp	Acro	Branching	10	5.8	11	6.5	55	31.6	6	9.0			
<i>Porites lobata/lutea</i>	Poma	Massive	10	5.8	7	4.1	30	17.2	8	11.9			
<i>Seriatopora</i> sp	Seri	Branching	5	2.9	6	3.6	10	5.7	3	4.5			
<i>Fungia</i> spp	Fung	Massive	4	2.3	10	5.9	4	2.3	3	4.5			
<i>Turbinaria</i>	Turb	Platy	4	2.3	0	0	1	0.6	0	0.0			
<i>Lobopyllia</i> spp	Lobo	Massive	3	1.8	1	0.6	1	0.6	0	0.0			
<i>Millepora</i>	Mill	Branching	3	1.8	0	0	5	2.9	3	4.5			
<i>Pachyseris</i>	Pachy	Platy	3	1.8	2	1.2	7	4	0	0.0			
<i>Physogyra</i>	Physo	Massive	2	1.2	5	3	3	1.7	1	1.5			
<i>Psammacora</i>	Psam	Submassive	2	1.2	4	2.4	0	0	0	0.0			

<i>Favites</i>	Favit	1	0.6	0	0	0	0	0	0.0
<i>Gardinoseris</i>	Gard	1	0.6	1	0.6	3	1.7	0	0.0
<i>Goniastrea</i>	Gonia	1	0.6	0	0	0	0	0	0.0
<i>Goniopora</i>	Gonio	1	0.6	1	0.6	6	3.4	0	0.0
<i>Montipora</i>	Monti	1	0.6	2	1.2	2	1.1	0	0.0
<i>Plerogyra</i>	Plero	1	0.6	0	0	0	0	0	0.0
<i>Siderastrea</i>	Side	1	0.6	3	1.8	0	0	0	0.0
<i>Halomitra</i>	Halo	0	0	0	0	1	0.6	0	0.0
Hard coral branching (Unclassified (<i>Acropora</i> spp))	HCB	0	0	0	0	5	2.9	0	0.0
<i>Acanthastrea</i>	Acan	0	0	1	0.6	1	0.6	0	0.0
<i>Coscinarea</i>	Cosc	0	0	1	0.6	1	0.6	0	0.0
<i>Echinopora</i>	Echpo	0	0	4	2.3	2	1.2	0	0.0
<i>Euphyllia</i>	Euph	0	0	0	0	2	1.2	0	0.0
<i>Favia</i>	Favia	0	0	6	3.4	0	0	0	0.0
<i>Herpolitha</i>	Herp	0	0	1	0.6	1	0.6	0	0.0
<i>Merulina</i>	Meru	0	0	0	0	1	0.6	0	0.0
<i>Montastrea</i>	Monta	0	0	0	0	2	1.2	0	0.0
<i>Oulophyllia</i>	Oulo	0	0	0	0	1	0.6	0	0.0
<i>Pavona</i>	Pavo	0	0	1	0.6	0	0	1	1.5
<i>Platygyra</i>	Platy	0	0	0	0	1	0.6	0	0.0
<i>Pleiastrea</i>	Plei	0	0	0	0	1	0.6	0	0.0

ANNEX 2 SUPPLEMENT MATERIAL CHAPTER 4

Detail map of Prison Reef and Bawe Reef bioregions



Legend

Biofacies_Bawe

<all other values>

Unit_name

Beachrock

Dense Coral

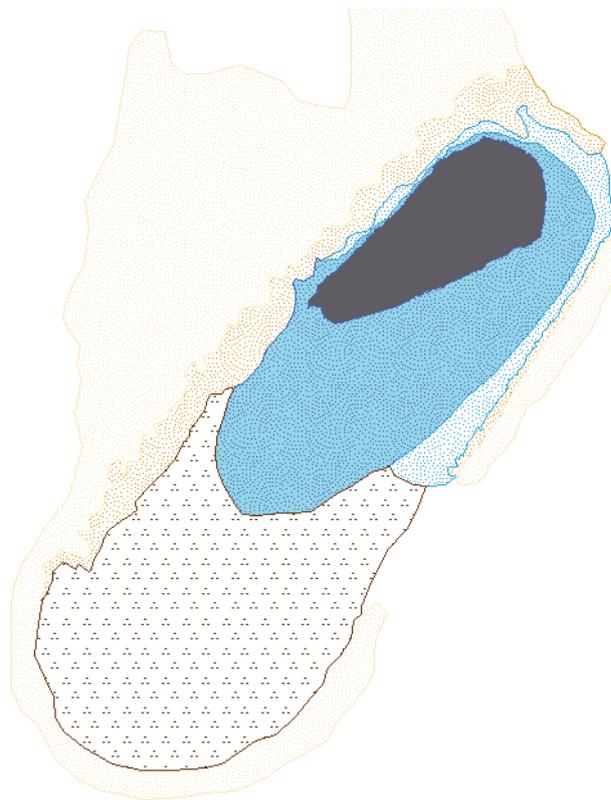
Dense CoralCopy

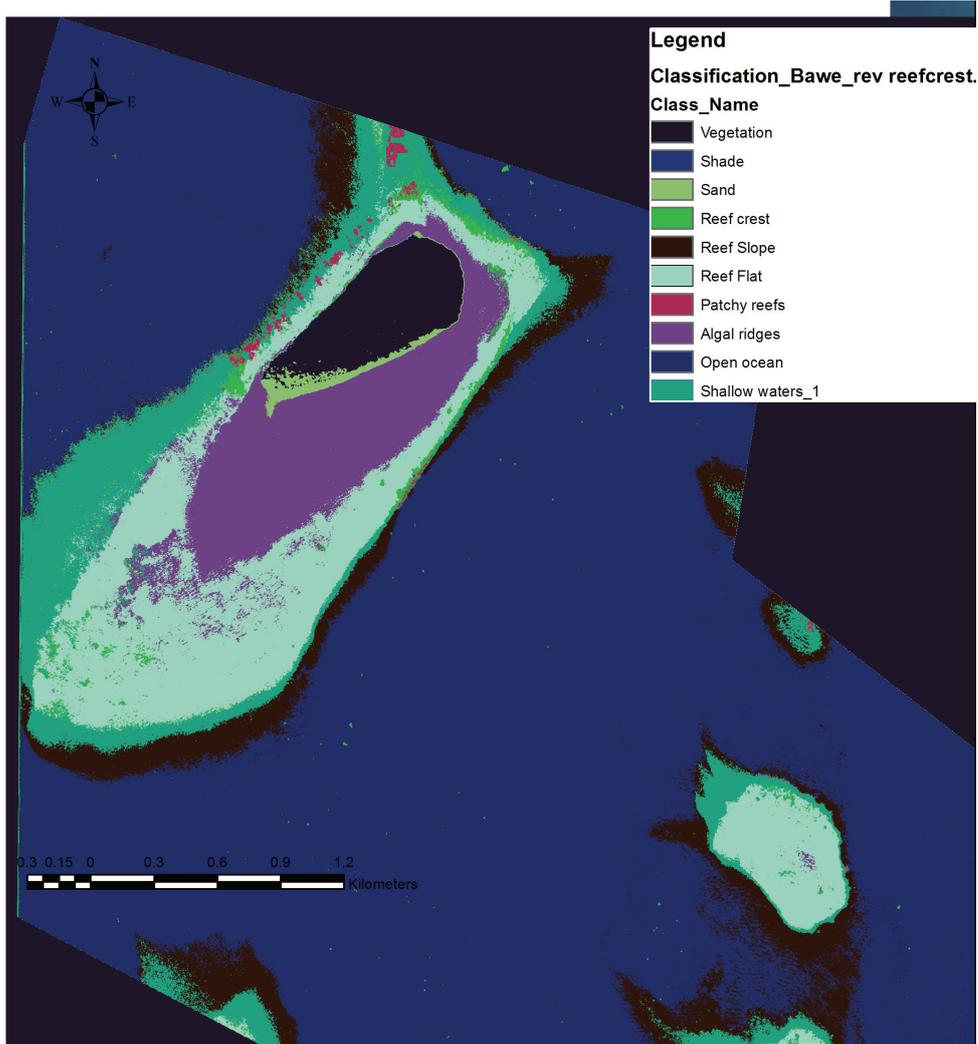
Intertidal zone

Lagoon

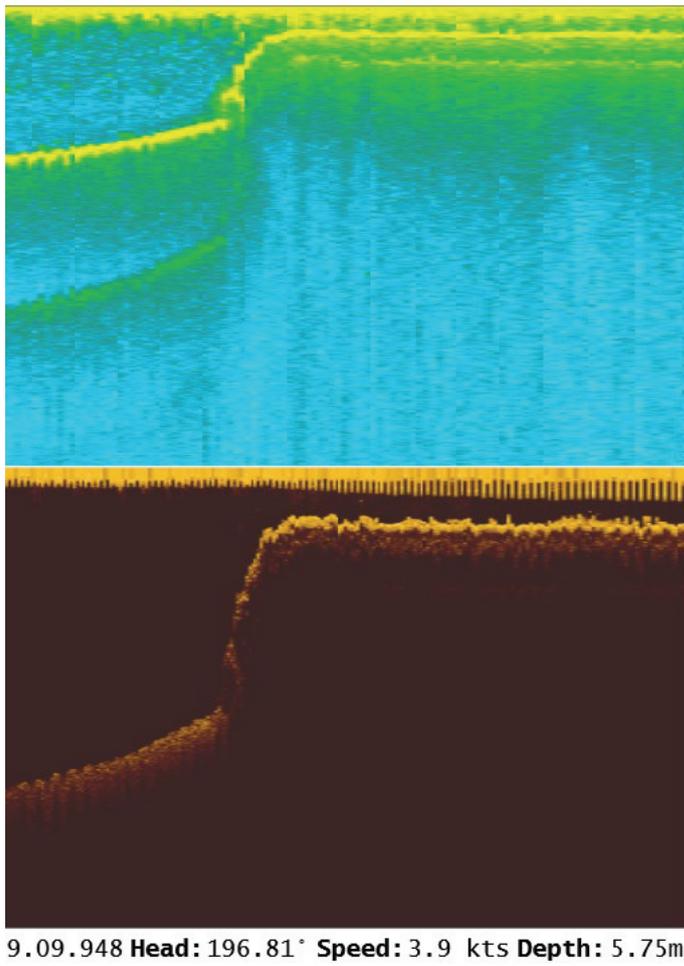
Limestone

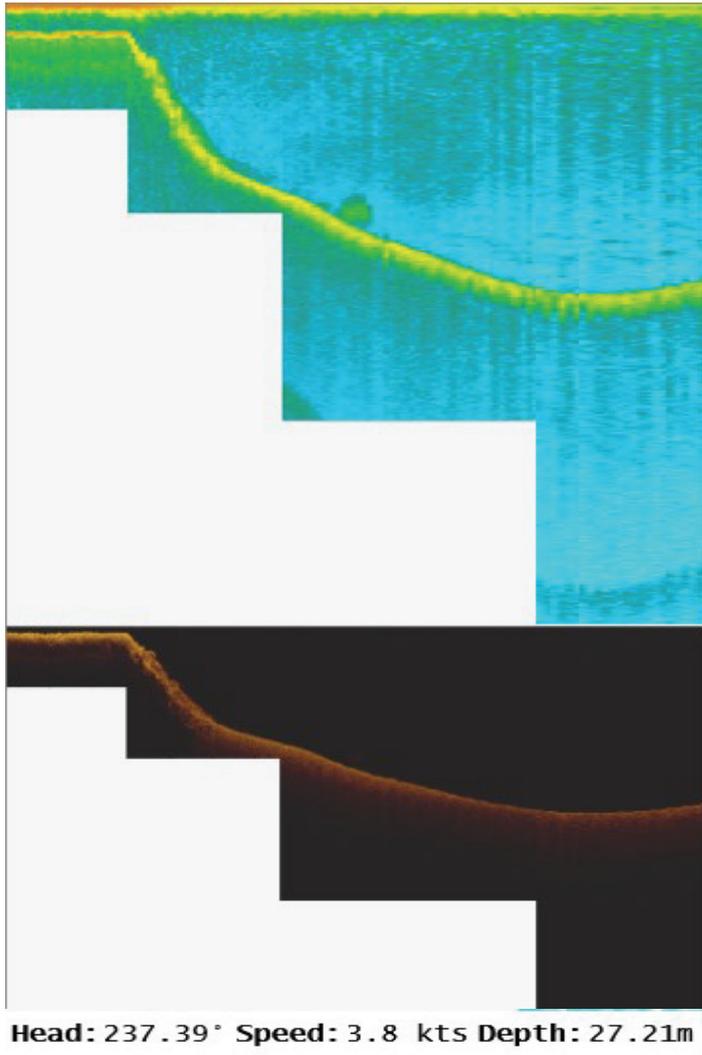
Open Coral





Reef profiles at Prison Reef and Bawe Reef (Raw backscattering imagery).





ANNEX 3 –SUPPLEMENT MATERIAL CHAPTER 5

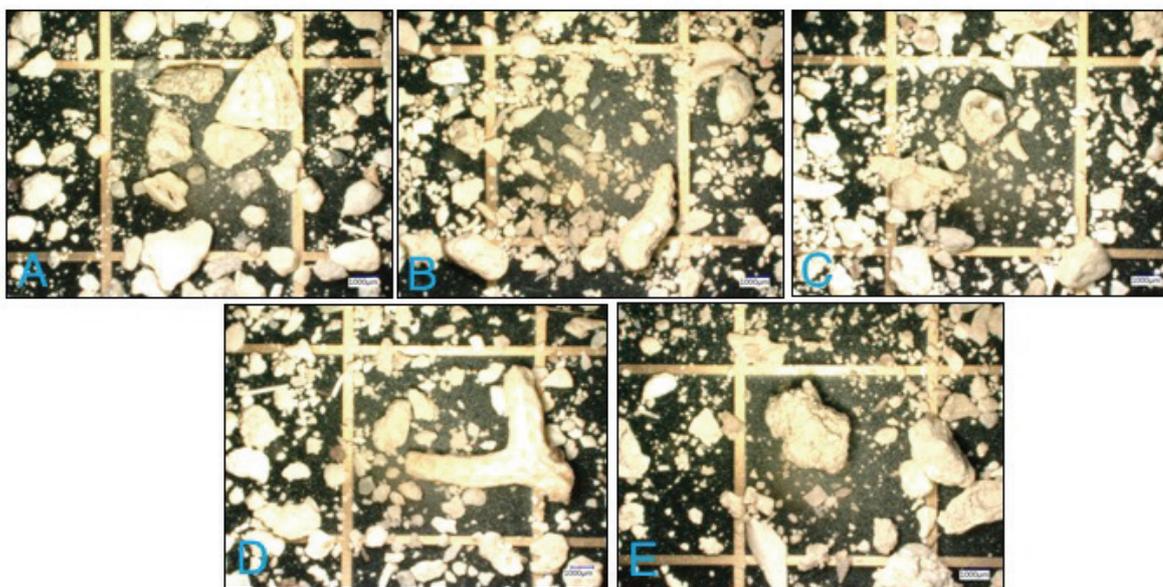
Landscape sediment characteristics were assessed within four biogeographic zones (reef flat, fore reef, tidal channel and seagrass meadow) in the coastal waters adjacent to Zanzibar Town, Tanzania. The upper 5-10 cm of sediment was collected using a *Van Veen* sampler (3 mm plate, 250 cm²) at 27 locations following the bathymetric gradient and covering the four biogeographic areas. Sedimentary samples were rinsed with clean freshwater in order to remove soluble components and dried at 40°C for at least 48h. Two subsamples (of each set) were sieved in a stack-shaker sieve for 10 min. We applied the Udden-Wentworth scale (Wentworth 1922) as following: gravel (>2000 µm), coarse sand (1000-2000 µm), medium sand (500-1000 µm), medium-fine sand (250-500 µm), fine sand (125-250 µm), very fine sand (63-125 µm) and silt (<63 µm). Each individual fraction was calculated as weight percentage of the total bulk sediment. We used the logarithmic Folk and Ward (1957) method to convert the measurements into phi scale, and the physical description of sediments was based on the granulometric output and appearance of the bulk sediment after Folk (1954). Summary statistics for each zone were estimated from log-transformed data using the G2Sd R package (Fournier et al. 2014).

Supplementary Table 1. Landscape sediment characteristics of the four biogeographic zones.

Zone	Reef Flat	Fore Reef	Tidal Channel	Seagrass
Mean grain size (µm)	2818	2352	2546	1953
Mean grain size (phi)	0.539	0.631	0.432	0.656
SD grain size (phi)	1.105	1.129	1.347	1.252
Skewness	-0.379	-0.295	-0.107	-0.052
Kurtosis	1.137	1.025	0.987	0.965
Sorting	Poorly Sorted	Poorly Sorted	Poorly Sorted	Poorly Sorted
Texture	Gravelly Sand	Gravelly Sand	Gravelly Sand	Gravelly Sand
% Gravel	15.4	13.6	16.8	14.8
% Sand	84.1	85.6	82.1	84.4
% Mud (>63 µm)	0.5	0.8	1.1	0.7

The texture of the four biogeographic zones was consistently classified as gravelly sand; however, the mean grain size was slightly smaller within seagrass meadows (1953 μm) when compared to the reef flat (2818 μm), fore reef (2352 μm) or sediments found on deeper areas of the channel (2546 μm). There were no major (compositional or granometrical) differences among the four bioregions, with all classified as poorly-sorted, gravelly sand. All regions contained approximately 15% gravel, 84% sand and 1% mud (Supplementary Table 1).

To qualitatively assess local sediment characteristics of the 5 seagrass communities, high-resolution images were taken of a representative sample of surface sediments (top 2-3 cm) from each community (Supplementary Figure 1) and qualitatively compared based on appearance and texture (Folk 1954). We found no large qualitative visual differences among surface sediments beneath the different seagrass communities, and all were consistent with the sediment characterization of the region (poorly-sorted, gravelly sand).



Supplementary Figure 1: Images of representative sediments from each seagrass community (A-E), laid over a 5-mm grid.

ANNEX 4 –SUPPLEMENT MATERIAL CHAPTER 6

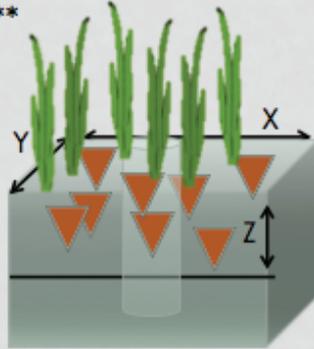
Carbonate production rate in Seagrass= $R_z * ((X_i/100)*((D_i*G_i*10,000)/1000)$

X_i =mean percentage cover

D_i =density org g*cm³

G_i =growth of the Species cm/year
Productivity**

R_z =rugosity



X_i = place 5 quadrats (1x1m) each transect

D_i = weight&measure org

G_i = literature.

R_z = rugosity

$$R_z = \sum R_i \quad ;$$

$$R_i = V_i / V_t \quad ;$$

$$R_i = \frac{4 \Pi a b h}{3(\Pi R^2 h)}$$

$$S_{\text{Quadrat}} (i) = \iint h_i(x, y) dx dy.$$

Hegoak ebaki banizkio

Nerea izango zen,

Ez zuen aldegingo.

Hegoak ebaki banizkio

Nerea izango zen,

Ez zuen aldegingo.

Bainan, honela

Ez zen gehiago txoria izango

Bainan, honela

Ez zen gehiago txoria izango

Eta nik...

Txoria nuen maite.

Eta nik...Txoria nuen maite.

- Mikel Laboa -

