Shallow and Mesophotic Reef Communities of the Western Indian Ocean: Implications for Management and Conservation

Kennedy Osuka Edeye

PhD Environmental Science

University of York

Environment and Geography

June 2022

ABSTRACT

Coral ecosystems in the Western Indian Ocean are considered highly threatened and therefore in need of improved knowledge to inform management and conservation policy measures. The reef habitats and fish communities in Pemba Island are under-researched despite experiencing human-related pressures. This study involved application of size-spectra analysis, deployment of marine robots comprising autonomous underwater vehicles (AUVs) and baited remote underwater videos (BRUVS) together with long swims (LS) underwater visual census. Results on size-spectra relationships indicated that highly and well-protected Marine Protected Areas (MPAs) are more productive and support high abundances of small fish. Use of marine robots highlighted the capability of using AUVs to fill the knowledge gap on mesophotic coral ecosystems (MCE), and their potential application for initial survey and subsequent monitoring of MPAs. BRUVS surveys revealed the importance of depth and healthy coral habitats in providing refuge for coral reef predatory fishes from fishing. Identical estimates of species richness, community structure and relative abundance of reef predatory fish species was found between BRUVS and LS. The study suggests: 1) restoration of fish community structure requires addressing fisher needs and supporting effective MPA management to secure ecosystem benefits for coastal communities, 2) presence of MCE composed of corals, algae and fishes on the western margins of Pemba Island, and steeply inclined substrate particularly in mesophotic depths (>30m) that support a highly bio-diverse community, 3) reef fish predator types are discordantly predicted by depth and habitat type, although high abundance and species richness occur in deeper waters and hard and soft coral habitat types, 4) BRUVS and LS are complementary, together providing a complete assessment of reef fish communities. Careful management through effective area and species protection measures, particularly on deeper reefs, are needed to conserve the biologically important area of Pemba Island and prevent further depletion of reef-associated communities.

TABLE OF CONTENTS

LIST OF TABLES

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

LIST OF FIGURES

Chapter 2

Chapter 3

Chapter 4

Chapter 5

LIST OF APPENDICES

Chapter 4

Chapter 5

LIST OF SUPPLIMENTARY MATERIALS

Chapter 2

Chapter 3

Chapter 4

ACKNOWLEDGEMENTS

I would like to thank my respectable supervisors – Dr Bryce Stewart and Dr Colin McClean for their all-important supervision, support and guidance during the journey of my PhD degree. My gratitude extends to my Thesis Advisory Panel members: Dr Melita Samoilys, Dr Philip Platts and Prof Callum Roberts. I am also thankful to my thesis formal review chair Dr Dean Waters and all the staff of the Department of Environment and Geography, University of York. I am deeply grateful to my funders: Sustainable Oceans, Livelihoods, and food Security Through Increased Capacity in Ecosystem research in the Western Indian Ocean (SOLSTICE-WIO) Programme (www.solstice-wio.org), Norwegian agency for development cooperation (Norad), Perivoli Philanthropy and Dev Joory. Additionally, I would like to express my esteemed gratitude to Dr Melita Samoilys and Dr David Obura for their treasured support which was very instrumental in shaping my interest in fishes and coral reefs and critiquing my results. I also thank Dr Brian Bett, Dr Tim Le Bas, Dr John Howe, Dr Saleh Yahya, Dr Ronan Roche, Prof. John Turner, for their mentorship. I would like to thank my friends, colleagues, and research team – Dr Estelle Dumont, Dr Juliane Wihsgott, Colin Abernerthy, Peter Musembi, James Mbugua, Randal Mabwa and Ali Rashid, for a cherished time spent together in the field. My appreciation also goes out to my wife Dr Emily Aradi for all the emotional support, my son Kayden Osuka and daughter Kelsy Osuka for always making me to work harder and smart, my parents Kefa Edeye and Damaris Iminza for prayers and encouragements, and members of Hope Connections Redeemed Church for their encouragement and support all through my study.

DECLARATION

I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as References.

For Chapter 1, I collated data from two published studies in the western and central Indian Ocean and reanalysed the data using a novel approach of size spectra. Consequently, the data collectors, Dr Melita Samoilys, Dr Ronan Roche and Prof John Turner, were made co-authors of the manuscript published in Marine Pollution Bulletin in October 2021. The paper is available at https://doi.org/10.1016/j.marpolbul.2021.113010.

In Chapters 2, 3 and 4, I received fieldwork assistance in the deployment of marine robots (autonomous underwater vehicles and baited remote underwater videos), and data processing support from Dr Brian Bett, Dr Tim Le Bas, Dr John Howe, Colin Abernerthy, Dr Saleh Yahya, Dr David Obura, Dr Melita Samoilys, Peter Musembi, Ali Rashid and James Mbugua, who have been made co-authors based on the type of fieldwork involved and their level of contribution to the study. The second chapter was published in Ocean and Coastal Management in February 2021 and is available at https://doi.org/10.1016/j.ocecoaman.2020.105463. The third chapter was published in Marine Environmental Research in March 2022 and is available at https://doi.org/10.1016/j.marenvres.2022.105587.

Kennedy Osuka Edeye

CHAPTER 1

INTRODUCTION

Coral reefs around the world are facing ongoing degradation from human related pressures, with nearly 14% having been lost since 2009, and another 35% currently considered threatened (Souter et al., 2021). These threats continue to increase, despite these vital ecosystems supporting more than 4,000 fish species of ecological and economic importance, along with livelihoods of millions of people. Those reefs occurring in the Western Indian Ocean (WIO) have recently been assessed as highly threatened, ranging from Vulnerable to Critically Endangered under the International Union for Conservation of Nature (IUCN) Red List of Ecosystems (Obura et al., 2021). This status has predominantly been driven by warming oceans and high fishing pressure. This calls for proactive management measures that will prevent ecosystem-wide collapse through efforts to mitigate climate change and improve the management of fisheries. In addition, it is essential to identify and safeguard reef areas that act as climate and depth refugia (Bongaerts et al., 2010; Beyer et al., 2018), such as mesophotic coral ecosystems. A key component of the ecosystem-based approach that is needed to respond to these threats is to expand the coverage of Marine Protected Areas (MPAs) with analysis suggesting that more than 30% coverage is needed for effective marine biodiversity conservation (O'Leary et al., 2016).

1.1 Benefits of MPAs

MPAs are a widely applied management and conservation measure used to mitigate human associated disturbances, such as fishing, and improve resilience of reefs to climate change (Roberts et al., 2017). Effectively managed MPAs are associated with elevated fish diversity, biomass, and the number of exploited species in adjacent fishing grounds (Russ et al., 2004; Kough et al., 2019). Information from highly protected MPAs, or those in remote locations, has been critical in illuminating the maximum potential abundance and biomass of fishes or ocean systems (McClanahan et al., 2019; McClanahan et al., 2020; MacNeil et al., 2020). In sum, the benefits provided by MPAs do depend on factors such as size, age, level of protection, distance to fish markets, levels of compliance, number of staff and budget capacity (Molloy et al., 2009; Gill et al., 2017; Cinner et al., 2018). Yet, how varying levels of protection impact the relative abundance of different fish sizes and overall fish productivity remains unclear.

In populated areas, addressing human needs is paramount to achieving benefits of MPAs, especially in the WIO region, where population is growing (Obura et al., 2017). Yet, MPAs in the WIO are depth-restricted to shallow waters (<30m) where resource-user conflicts are prevalent and enforcement costs high (Tuda et al., 2014). Involvement of communities in setting up locally managed marine areas with no-take zones are options being adopted to improve management of coral reefs (Rocliffe et al., 2014). More importantly is the investment in protection of deeper reefs that are arguably depth-refugia, through a network of MPAs. This ensures different fish sizes and life history stages are protected (Green et al., 2014) and fish biodiversity and productivity restored and/or maintained of (McClanahan et al., 2007; Lester and Halpern, 2008).

1.2 Shallow and deep-water research

In coral reef environments, there is little marine research of deeper waters (>30 m) compared to shallow waters (0- 30 m) implying that the extent and linkages of shallow and deep habitats is not fully known (Bridge et al., 2012; Wölfl et al., 2019). Yet, information on spatial distribution of such habitats is needed for conservation planning especially in this era of increased impacts on climate change, which are most acute in shallower waters (Pörtner, 2010; Kahng et al., 2019). Habitats in deeper zones are argued to provide refugia from pressures such as fishing and high sea surface temperatures (Bongaerts et al., 2010). Predicting the shift in fish assemblages due to anthropogenic threats, and the corresponding changes in habitat use or colonisation, is therefore critical towards ensuring effective utilisation and management of resources occurring in the various depths.

Like the WIO regional outlook, research of deeper marine habitats of Tanzania is dwarfed by efforts in shallower environments (Groeneveld and Koranteng, 2017). Shallow coral reef surveys date as far back as 1965 and since 1994 both the SCUBA and community-based coral reef monitoring have been conducted along the coastline, notably on reefs in Tanga, Dar es Salaam, Mnazi Bay and the Islands of Pemba, Zanzibar and Mafia (Muhando, 2009). These surveys increased significantly after the 1998 El Niño related coral bleaching event that led to the launch of Coral Reef Degradation in the Indian Ocean (CORDIO) project. The few ship-based deep-water surveys in Tanzania include the RV Dr Fridtjof Nansen acoustic surveys of the whole shelf off Tanzania in 1982/83 (Iversen et al., 1984) and African Coelacanth Ecosystem Programme (ACEP) ship-based expeditions in Zanzibar in 2004, and Tanga in 2007 (Kaehler et al., 2008). The ACEP expeditions utilised Remotely Operated Vehicle (ROV) to locate and film coelacanths and their habitats. In 2010, the Agulhas and Somali Current Large Marine Ecosystems (ASCLME) project conducted inshore habitat mapping in Pemba (ASCLME/SWIOFP, 2012). The results from the bathymetric mapping showed that the shelf was characterised by small ridge-like extrusions while the seafloor from 150 m tended to be flat and smooth (Kaehler et al., 2008).

1.3 Complementarity of survey methods

Combining survey methods helps overcome inherent biases associated with a single method (Cheal et al., 2021). Since reef survey methods are associated with certain biases, combining methods is becoming regarded as the best way to gain a comprehensive picture of reef fish communities. Integration of methods such as underwater visual census (UVC) and baited remote underwater videos (BRUVs) can enable surveys of large defined reef areas and fish communities occurring from the shallow to deeper zones (Colton and Swearer, 2010). This creates an opportunity to compare the in-situ records collected through UVC with the BRUVS video records (Cappo et al., 2004; Cheal et al., 2021). Certainly, combining BRUVS and UVC enables provision of additional details of reef fish communities (Schramm et al., 2020). Therefore, integration of methods provides a complete assessment of reef fish (Cheal et al., 2021).

Until recently predominantly small-scale SCUBA surveys were undertaken to survey coral reefs in shallow areas. New marine robotic technologies and alternate methods have emerged and are allowing for a more complete ecosystem perspective from surveying habitats and species in the shallow to deep areas (Benoist et al., 2019). Marine robotics show great potential to fill knowledge gaps. They are widely applied to study ecosystems such as deeper reefs (Wynn et al., 2014), rare and highly mobile species (MacNeil et al., 2020). The utilities provided by marine robots enable them to provide new insights and understanding of marine ecosystems. For instance, autonomous underwater vehicles (AUVs) have various modules that simultaneously collect multiple data including depth, seafloor properties, photos, and videos of benthic and water column. BRUVs are also increasingly being applied to survey large-sized species due to their ability to survey habitats in a wide variety of depths and attract rare species (Harvey et al., 2012; White et al., 2013).

1.4 Distribution, behaviour, and roles of fishes

Reef fishes play critical roles in community dynamics within coral reef habitats where they regulate reef benthic composition by performing different inter-related functional roles that vary depending on fish size and behaviour (Bellwood *et al.*, 2019). Species can show intra-specific size dependent dietary shifts (e.g., whitemargin unicornfish, *Naso annulatus* shift from a macroalgal diet to planktonic feeding when they reach ~20 cm (Choat *et al.*, 2002)) and interspecific differences in diet (e.g., groupers *Cephalopholis* spp*.* exert top-down control on fish of lower trophic levels (Stewart and Jones, 2001)).

Species also vary based in their functional roles on coral reefs that encompass piscivores, omnivores, corallivores, invertivores, planktivores, detritivores and herbivores (Osuka *et al.*, 2016; Samoilys et al., 2019). These functional roles notably include: a) exerting top-down control on lower trophic groups by piscivores, b) feeding on highly diversified diets by omnivores, c) feeding on coral competitors by invertivores, d) feeding on coral polyps by obligate and facultative corallivores, e) feeding on zooplankton and phytoplankton by planktivores, f) feeding on organic matter and sediment in sediment and coral surface by detritivores, and g) feeding on benthic algae thereby controlling the balance between algae and corals by herbivores. The herbivores show fine-scale variation in functional roles that are further distinguished into large excavators, small excavators, scrapers, browsers, grazers, and grazers-detritivores (after Green and Bellwood, 2009). Since herbivores are critical for enhancing reef resilience through regulating competition between algae and corals, their loss may increase algal dominance and lead to ecological phase shifts (Hughes et al., 2007). Thus, management measures that protect and increase the abundance and biomass of herbivores (Kuempel and Altieri, 2017) are considered critical in counteracting such risks.

Species show association with the reef and can be classified as either resident or transient (Hixon, 2015; Froese and Pauly, 2020). Resident individuals show strong association with the reef structure or seafloor such as groupers, snappers, emperors, sweetlips, and eels. Transient individuals are fast swimming, schooling, and epipelagic species, such as sharks, barracuda, jacks and mackerel. Habitat conditions such as healthy and degraded are expected to be significant predictors of the occurrence, abundance, and diversity of resident predatory species, but sparingly for transient species (Hixon, 2015; Cheal et al., 2021). However, interaction between these predator types with habitat types and their associated depths remains unclear.

1.5 Role of benthic habitats

The cover of hard and soft corals is widely applied indicators of reef health, nutrient, and wave energy conditions (Obura and Grimsditch, 2009). Hard corals comprise the calcified reef building corals while soft corals encompass the non-reef building corals that lack a firm calcium carbonate skeleton. The crustose coralline algae, which refer to calcified encrusting algae, is considered important in fostering coral recruitment as well as fastening the reef framework. The cover of CCA therefore signifies suitability of habitat for coral recruitment. Other forms of algae (e.g., fleshy and turf algae) indicate nutrient and herbivory controls such that higher cover may be driven by higher nutrient loads and/or high fishing pressure on herbivores. Increase in the coverage of fleshy algae can outcompete corals and lead to phase shifts (Hughes et al., 2007). Rubble refers to available loose substratum and indicates suitability for coral recruitment. Its generation is considered a natural process on coral reefs. However, the process can be catalysed by anthropogenic impacts such as physical trampling, ship groundings, dynamite, and blast fishing (Chabanet et al. 2005; Wolfe et al., 2021). Thus, regime shifts from coral dominated to algal/rubble dominated can happen with large scale disturbance from climate change, storms, sedimentation, or damaging fishing gears.

1.6 Motivation for focusing on Pemba Island

The western side of Pemba Island experiences high variability in sea surface temperature, with regular transport or upwelling of deeper cool water to the surface (Mayorga-Adame et al., 2017). This same process is assumed to be a controlling mechanism for providing nutrient rich deep water to the surface and waters close to Pemba Island that help fuel productivity, especially for small pelagic fish (Sekadende et al., 2020). The shallow reefs of Pemba Island show highly variable coral reef conditions with some reefs in healthy states and dominated by hard coral cover, while others are in a degraded state with low coral cover (Grismditch et al., 2009). Fringing reef flats can be found offshore, which drop off rapidly into the deep. Isolating Pemba Island from mainland Tanzania is Pemba Channel, which has a mean and maximum depths of 300 m and 800 m respectively (Semba et al., 2019). As such Pemba Island is classified as a true oceanic island and considered a biologically important area hosting a diversity of ecosystems, demersal and pelagic fishery resources, and threatened species including coelacanths (Archer and Turner, 1993; Richmond 2002; Roberts 2015). The channel is a potential hotspot for pelagic fish that provide nutrition and a source of livelihoods to the local community on both the Pemba Island and mainland Tanzania (Sekadende et al., 2020). However, threats from climate change and fishing, including the effects of historical dynamite fishing (Wells et al., 2009) have almost certainly adversely affected the distribution of fish communities and associated fisheries-based livelihoods (Jacobs et al., 2020, 2021; Wilson et al., 2021).

1.7 Thesis synopsis

In developing this research, I hypothesised that shallow photic reefs (0-30 m) will be connected with mesophotic reef habitats (30-150 m) through depth refuge pathways such that deeper waters host a diverse benthic and fish community, and an abundant predatory fish community. To test this hypothesis and increase understanding of these linkages and climate vulnerability into the future, this thesis collated information on MPAs in the Indian Ocean and applied a variety of survey methods, from marine robots to baited cameras and visual censuses, in the shallow and mesophotic habitats of the Pemba Channel in Tanzania.

The specific objectives of the research were to:

1. Assess the effects of different levels of fishing pressures on reef fish communities in western and central Indian Ocean.
2. Quantify benthic cover of specific biotic (coral, algae and fish) and abiotic (rubble, hard and sand substrate) groups in the Pemba Channel from the surface to a depth of 150 m (photic to mesophotic communities).
3. Investigate the spatial distribution of fishery target taxa by depth and habitat type using a variety of survey methods.
4. Determine best methods to survey and monitor large sized predatory fish communities.

Objective 1 was attained by using existing data collected in the western and central Indian Ocean to assess the effects of different levels of protection and human population density on coral reef fish community structure. Objective 2 was achieved through a series of field-based activities in Pemba Channel to sample the benthic and pelagic species and habitats using autonomous underwater vehicle (AUV) and baited remote underwater videos (BRUVS). Objective 3 was attained through modelling the influence of depth and habitat types on abundance of fish predators in Pemba Island. Objective 4 was achieved through an assessment of the similarity and dissimilarity of BRUVS and a survey method of “long swims”

(150 m x 20 m transects) underwater visual census, in measuring abundance and diversity of large-sized reef associated predators from nine selected fish families.

The study explored four questions:

1. How do different levels of protection influence fish community structure and the overall productivity of the reef systems? Answers to this question are investigated in the second chapter where I utilise existing data collected in the western and central Indian Ocean to assess the effect of different protection regimes using size spectra analysis.
2. What factors drive the presence of seafloor substrates, benthic variables and fish communities from shallow to mesophotic depths in the Pemba Channel and are the patterns similar to those reported elsewhere? This question is explored in the third chapter where I employed AUV in four selected sites off Pemba Island.
3. How are the fish species targeted by fisheries influenced by depth and habitat type off Pemba Island? I explored this in my fourth chapter through modelling the influence of depth and habitat types on abundance of predatory reef fish sampled using BRUVS.
4. Which reef survey method provides more accurate estimates of abundance of large coral reef associated, predatory fish? This question is inspected in the fifth chapter, where I provide an assessment and comparison of BRUVS and long swim underwater visual census method for measuring the abundance and diversity of large reef associated predators from selected fish families.

The results of the study are expected to have implications for marine spatial planning, improving sustainability and addressing threats from climate change. Identification of areas that are acting as refuges from the effects of climate and fishing should in turn lead to them being protected through the designation of MPAs or fishing gear restrictions.

It is worth mentioning that during the course of my doctoral study I contributed to a number of other studies published in the field of coral reef ecology, conservation and management (Table 1). This included contributions in the fields of marine survey technology (Jacobs et al., 2020; Obura et al., 2019, Osuka and Aboud, 2021; Palmer et al., 2021), coral reef fish ecology in the Red Sea and Western Indian Ocean and their vulnerability to collapse (Cowburn et al., 2019; Samoilys et al., 2019a; Obura et al., 2021), management of artisanal fisheries in Kenya and Mozambique (Samoilys et al., 2019b; Alati et al., 2020; Osuka et al., 2021; Wanyonyi et al., 2021), influence of climate change on East Africa's coastal fisheries (Jacobs et al., 2021; Wilson et al., 2021), management and conservation of reef sharks (MacNeil et al., 2020), socio-ecological systems of Mozambique's fisheries (Osuka et al., 2020), implication of COVID-19 on marine protected areas (Phua et al., 2021) and policy pathways of rebuilding coral reefs (Knowlton et al., 2021).

Table 1: List of peer reviewed publications authored/co-authored between 2019 – 2021.

Citation	Journal and Link	Role
Alati et al., 2020	Ocean & Coastal Management https://doi.org/10.1016/j.ocecoaman.2020.105285	Data analysis, review and editing.
Cowburn et al., 2019	Marine Pollution Bulletin https://doi.org/10.1016/j.marpolbul.2019.07.040	Data collection, analysis, review and editing.
Jacobs et al., 2020	Remote Sensing https://doi.org/10.3390/rs12193127	Sourcing secondary fisheries data, review and editing.
Jacobs et al., 2021	Ocean & Coastal Management https://doi.org/10.1016/j.ocecoaman.2021.105627	Sourcing secondary fisheries data, review and editing
Knowlton et al., 2021	International Coral Reef Society and Future Earth https://doi.org/10.53642/NRKY9386.	Review and editing.
MacNeil et al., 2020	Nature https://doi.org/10.1038/s41586-020-2519-y	Data collection in Tanzania and Kenya, review and editing.
Obura et al., 2019	Frontiers in Marine Science https://doi.org/10.3389/fmars.2019.00580	Writing, review and editing.
Obura et al., 2021	Nature Sustainability https://doi.org/10.1038/s41893-021-00817-0	Involved in methodology and conceptual development, including how to use data and inputs, primary analysis, and manuscript writing and editing.
Osuka et al., 2021	African Journal of Marine Science https://doi.org/10.2989/1814232X.2020.1857836	Concept development, data collection, analysis, write-up, review and editing.
Osuka et al., 2020	Sustainability https://doi.org/10.3390/su12093904	Concept development, data collection, analysis, write-up, review and editing.

Osuka & Aboud 2021	Western Indian Ocean Journal of Marine Science 10.4314/wiojms.v20i2.9	Concept development, data collection, analysis, write-up, review and editing.
Palmer et al., 2021	Ocean & Coastal Management https://doi.org/10.1016/j.ocecoaman.2021.105805	Write-up, review and editing.
Phua et al., 2021	Parks https://doi.org/10.2305/IUCN.CH.2021.PARKS-27-SICP.en	Write-up, review and editing.
Samoilys et al., 2019a	Ecology and Evolution https://doi.org/10.1002/ece3.5044	Data collection, analysis, write-up, review and editing.
Samoilys et al., 2019b	Ocean & Coastal Management https://doi.org/10.1016/j.ocecoaman.2019.104924	Data collection, analysis, write-up, review and editing.
Wanyonyi et al., 2021	African Identities https://doi.org/10.1080/14725843.2021.1937050	Data analysis, write-up, review and editing.
Wilson et al., 2021	Ocean & Coastal Management https://doi.org/10.1016/j.ocecoaman.2021.105921	Secondary data collection, write-up, review and editing.

1.8 References

Archer, A. and Turner, D., 1993. Notes on the endemic species and some additional new birds occurring on Pemba Island. Tanzania. *Scopus 16.* 94-98.

Alati, V.M., Olunga, J., Olendo, M., Daudi, L.N., Osuka, K., Odoli, C., Tuda, P. and Nordlund, L.M., 2020. Mollusc shell fisheries in coastal Kenya: Local ecological knowledge reveals overfishing. *Ocean & Coastal Management*, *195*, p.105285.

ASCLME/SWIOFP, 2012. Transboundary Diagnostic Analysis for the western Indian Ocean. Volume 1: Baseline 93pp

Bellwood, D.R., Streit, R.P., Brandl, S.J. and Tebbett, S.B., 2019. The meaning of the term ‘function’in ecology: a coral reef perspective. *Funct. Ecol.* 33 (6), 948–961.

Benoist, N.M., Morris, K.J., Bett, B.J., Durden, J.M., Huvenne, V.A., Le Bas, T.P., Wynn, R.B., Ware, S.J. and Ruhl, H.A., 2019. Monitoring mosaic biotopes in a marine conservation zone by autonomous underwater vehicle. *Conserv. Biol.* 33, 1174–1186.

Beyer, H.L., Kennedy, E.V., Beger, M., Chen, C.A., Cinner, J.E., Darling, E.S., Eakin, C.M., Gates, R.D., Heron, S.F., Knowlton, N. and Obura, D.O., 2018. Risk‐sensitive planning for conserving coral reefs under rapid climate change. *Conservation Letters*, *11*(6), p.e12587.

Bongaerts, P., Ridgway, T., Sampayo, E.M. and Hoegh-Guldberg O. 2010. Assessing the ‘deep reef refugia’ hypothesis: focus on Caribbean reefs. *Coral Reefs* 29: 309–327.

Bridge, T., Beaman, R., Done T. and Webster, J. 2012. Predicting the location and spatial extent of submerged coral reef habitat in the Great Barrier Reef World Heritage Area, Australia. *PLoS ONE* 7(10): e48203.

Cappo M, Speare P, De'ath G (2004) Comparison of baited remote underwater video stations (BRUVS) and prawn (shrimp) trawls for assessments of fish biodiversity in inter-reef areas of the Great Barrier Reef Marine Park. *Journal of Experimental Marine Biology and Ecology*, *302*(2), 123-152.

Chabanet, P., Adjeroud, M., Andréfouët, S., Bozec, Y.M., Ferraris, J., Garcìa-Charton, J.A. and Schrimm, M., 2005. Human-induced physical disturbances and their indicators on coral reef habitats: A multi-scale approach. *Aquatic Living Resources*, *18*(3), pp.215-230.

Choat, J.H., Clements, K.D. and Robbins, W., 2002. The trophic status of herbivorous fishes on coral reefs. *Marine Biology*, *140*(3), pp.613-623.

Cheal, A.J., Emslie, M.J., Currey-Randall, L.M. and Heupel, M.R. 2021. Comparability and complementarity of reef fish measures from underwater visual census (UVC) and baited remote underwater video stations (BRUVS). *Journal of Environmental Management*, *289*, 112375.

Cinner, J.E., Maire, E., Huchery, C., MacNeil, M.A., Graham, N.A., Mora, C., McClanahan, T.R., Barnes, M.L., Kittinger, J.N., Hicks, C.C. and D'agata, S., 2018. Gravity of human impacts mediates coral reef conservation gains. *Proc. Natl. Acad. Sci.* 115 (27), E6116–E6125.

Colton, M.A. and Swearer, S.E., 2010. A comparison of two survey methods: differences between underwater visual census and baited remote underwater video. *Marine Ecology Progress Series*, *400*, pp.19-36.

Cowburn, B., Samoilys, M.A., Osuka, K., Klaus, R., Newman, C., Gudka, M. and Obura, D., 2019. Healthy and diverse coral reefs in Djibouti–A resilient reef system or few anthropogenic threats? *Marine pollution bulletin*, *148*, pp.182-193.

Froese, R. and Pauly, D., 2020. FishBase. World Wide Web electronic publication. www.fishbase.org, (06/2020)

Gill, D.A., Mascia, M.B., Ahmadia, G.N., Glew, L., Lester, S.E., Barnes, M., Craigie, I., Darling, E.S., Free, C.M., Geldmann, J. and Holst, S., 2017. Capacity shortfalls hinder the performance of marine protected areas globally. *Nature*, *543*(7647), 665–669.

Green, A.L., Fernandes, L., Almany, G., Abesamis, R., McLeod, E., Aliño, P.M., White, A.T., Salm, R., Tanzer, J. and Pressey, R.L., 2014. Designing marine reserves for fisheries management, biodiversity conservation, and climate change adaptation. *Coast. Manag.* 42 (2), 143–159.

Green, A.L. and Bellwood, D.R. 2009. *Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience: a practical guide for coral reef managers in the Asia Pacific region* (No. 7). IUCN.

Grimsditch, G.D., Tamelander, J., Mwaura, J., Zavagli, M., Takata, Y. and Gomez, T. 2009. *Coral reef resilience assessment of the Pemba channel conservation area, Tanzania*. Gland, Switzerland: IUCN. 40pp.

Groeneveld, J.C. and Koranteng, K.A., 2017. *RV Dr Fridtjof Nansen in the Western Indian Ocean: Voyages of Marine Research and Capacity Development. 1975-2016*. FAO, Rome, p. 174.

Harvey, E.S., Newman, S.J., McLean, D.L., Cappo, M., Meeuwig, J.J. and Skepper, C.L., 2012. Comparison of the relative efficiencies of stereo-BRUVs and traps for sampling tropical continental shelf demersal fishes. *Fisheries Research*, *125*, pp.108-120.

Hixon, M.A., 2015. Predation: piscivory and the ecology of coral-reef fishes. In: Mora C. (Ed.)

Ecology of fishes on coral reefs. Cambridge University Press Cambridge, UK, pp. 41–53.

Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwskyj, N., Pratchett, M.S., Steneck, R.S. and Willis, B., 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr. Biol.* 17 (4), 360–365.

Iversen, S.A., Myklevoli, S., Lwiza, K. and Yonazi, J. 1984. Tanzanian marine fish resources in the depth region 10−500 m. Investigated by R/V Dr Fridtjof Nansen. Joint Tanzanian/Norwegian seminar to review the marine resources of Tanzania. Mbegani Fisheries Development Centre, Tanzania 6−8 March 1984.

Jacobs, Z.L., Jebri, F., Srokosz, M., Raitsos, D.E., Painter, S.C., Nencioli, F., Osuka, K., Samoilys, M., Sauer, W., Roberts, M., Taylor, S.F., Scott, L., Kizenga, H. and Popova, E., 2020. A major ecosystem shift in coastal East African waters during the 1997/98 Super El Niño as detected using remote sensing data. *Remote Sensing*, *12*(19), p.3127.

Jacobs, Z.L., Yool, A., Jebri, F., Srokosz, M., van Gennip, S., Kelly, S.J., Roberts, M., Sauer, W., Queirós, A.M., Osuka, K.E., Samoilys, M., Becker, A.E. and Popova, E., 2021. Key climate change stressors of marine ecosystems along the path of the East African coastal current. *Ocean & Coastal Management*, *208*, p.105627.

Kaehler, S., Ribbink, A. and Scott. L., 2008. ACEP Final Report 2007/8: Nearshore and offsore studies in the Western Indian Ocean. Final Scientific Cruise Report, African Coelacanth Ecosystem Programme Grahamstown, South Africa. 290pp.

Kahng, S.E., Akkaynak, D., Shlesinger, T., Hochberg, E.J., Wiedenmann, J., Tamir, R. and Tchernov, D., 2019. Light, temperature, photosynthesis, heterotrophy, and the lower depth limits of mesophotic coral ecosystems. *In*: Loya, Y., Puglise, K.A. and Bridge, T.C.L. (Eds.), *Mesophotic Coral Ecosystems*. Springer, Cham, pp. 801–828.

Knowlton, N., Grottoli, A.G., Kleypas, J., Obura, D., Corcoran, E., de Goeij, J.M., Felis, T., Harding, S., Mayfield, A., Miller, M., Osuka, K., Peixoto, R., Randall, C.J., Voolstra, C.R., Wells, S., Wild, C. and Ferse, S., 2021. Rebuilding Coral Reefs: A Decadal Grand Challenge. *International Coral Reef Society and Future Earth Coasts* 56 pp.

Kough, A.S., Belak, C.A., Paris, C.B., Lundy, A., Cronin, H., Gnanalingam, G., Hagedorn, S., Skubel, R., Weiler, A.C. and Stoner, A.W., 2019. Ecological spillover from a marine protected area replenishes an over-exploited population across an island chain. *Conserv. Sci. Pract*. 1 (3), e17

Kuempel, C.D. and Altieri, A.H., 2017. The emergent role of small-bodied herbivores in pre-empting phase shifts on degraded coral reefs. *Sci. Rep.* 7, 39670.

Lester, S.E. and Halpern, B.S., 2008. Biological responses in marine no-take reserves versus partially protected areas. *Mar. Ecol. Prog. Ser.* 367, 49–56.

MacNeil, M. A., Chapman, D. D., Heupel, M., Simpfendorfer, C. A., Heithaus, M., Meekan, M., Harvey, E., et al., 2020. Global status and conservation potential of reef sharks. *Nature*, *583*(7818), 801-806.

McClanahan, T.R., Graham, N.A., Calnan, J.M. and MacNeil, M.A., 2007. Toward pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. *Ecol. App* 17 (4), 1055–1067.

McClanahan, T.R., Schroeder, R.E., Friedlander, A.M., Vigliola, L., Wantiez, L., Caselle, J.E., Graham, N.A., Wilson, S., Edgar, G.J., Stuart-Smith, R.D. and Oddenyo, R.M., 2019. Global baselines and benchmarks for fish biomass: comparing remote reefs and fisheries closures. *Mar. Ecol. Prog. Ser.* 612, 167–192.

McClanahan, T.R., Friedlander, A.M., Graham, N.A., Chabanet, P. and Bruggemann, J.H., 2020. Variability in coral reef fish baseline and benchmark biomass in the central and western Indian Ocean provinces. *Aquat. Conserv. Mar. Freshwat. Ecosyst.*

Mayorga-Adame, C.G., Batchelder, H.P. and Spitz, Y., 2017. Modeling larval connectivity of coral reef organisms in the Kenya-Tanzania region. *Frontiers in Marine Science*, *4*, p.92.

Molloy, P.P., McLean, I.B. and Cote, I.M., 2009. Effects of marine reserve age on fish populations: a global meta-analysis. *J. Appl. Ecol.* 46, 743–751.

Muhando, C. A. 2009. Coral reef monitoring in Tanzania: an analysis of the last 20 years. *Western Indian Ocean Journal of Marine Science*, 8(2).

Obura, D., Burgener, V., Owen, S. and Gonzales, A., 2017. Reviving the Western Indian Ocean economy: Actions for a sustainable future. *Gland, Switzerland: WWF International*. (p. 64).

Obura, D. and Grimsditch, G., 2009. *Resilience assessment of coral reefs: assessment protocol for coral reefs, focusing on coral bleaching and thermal stress.* Gland, Switzerland: IUCN. (p. 70).

Obura, D.O., Aeby, G., Amornthammarong, N., Appeltans, W., Bax, N., Bishop, J., Brainard, R.E., Chan, S., Fletcher, P., Gordon, T.A., Gramer, L., Gudka, M., Halas, J., Hendee, J., Hodgson, G., Huang, D., Jankulak, M., Jones, A., Kimura, T., Levy, J., Miloslavich, p., Chou, L.M., Muller-Karger, F., Osuka, K., Samoilys, M., Simpson S.D., Tun, K. and Wongbusarakum, S. 2019. Coral reef monitoring, reef assessment technologies, and ecosystem-based management. *Frontiers in Marine Science*, *6*, p.580.

Obura, D., Gudka, M., Samoilys, M. Osuka, K., Mbugua, J., Keith, A.K., Porter, S. Roche, R, van Hooidonk, R., Ahamada, S., Araman, A., Karisa, J., Komakoma, J., Madi, M., Ravinia, R., Razafindrainibe, H., Yahya, S. Zivane, F. 2021. Vulnerability to collapse of coral reef ecosystems in the Western Indian Ocean. *Nature Sustainabilit*y.

O'Leary, B.C., Winther-Janson, M., Bainbridge, J.M., Aitken, J., Hawkins, J.P. and Roberts, C.M., 2016. Effective coverage targets for ocean protection. *Conservation Letters*, *9*(6), pp.398-404.

Osuka, K., Kawaka, J.A. and Samoilys, M.A., 2021. Evaluating Kenya’s coastal gillnet fishery: trade-offs in recommended mesh-size regulations. *African Journal of Marine Science*, *43*(1), pp.15-29.

Osuka, K., Rosendo, S., Riddell, M., Huet, J., Daide, M., Chauque, E. and Samoilys, M. 2020. Applying a social–ecological systems approach to understanding local marine management trajectories in northern Mozambique. *Sustainability*, *12*(9), 3904.

Osuka, K.E. and Aboud, S.A., 2021. Integrated approach to analyse benthic images from an autonomous underwater vehicle deployed at Pemba Island, Tanzania. *Western Indian Ocean Journal of Marine Science*, *20*(2), pp.109-117.

Palmer, M.R., Shagude, Y.W., Roberts, M.J., Popova, E., Wihsgott, J.U., Aswani, S., Coupland, J., Howe, J.A., Bett, B.J., Osuka, K.E., Abernethy, C., Alexiou, S., Painter, S.C., Kamau, J.N., Nyandwi, N. and Sekadende, B. 2021. Marine robots for coastal ocean research in the Western Indian Ocean. *Ocean & Coastal Management*, *212*, p.105805.

Phua, C., Andradi-Brown, D.A., Mangubhai, S., Ahmadia, G.N., Mahajan, S.L., Larsen, K., Friel, S., eichelt, R., Hockings, M., Gill, D., Veverka, L., Anderson, R., Augustave, L.C., Awaludinnoer, Bervoets, T., Brayne, K., Djohani, R., Kawaka, J., Kyne, F., Ndagala, J., Oates, J., Osuka, K., Prvan, M., Shah, N., Vallarola, F., Wenzel, L., Widodo, H, and Wells, S. 2021. Marine protected and conserved areas in the time of COVID. *Parks 27*

Pörtner, H.O., 2010. Oxygen-and capacity-limitation of thermal tolerance: a matrix for integrating climate-related stressor effects in marine ecosystems. *Journal of Experimental Biology* 213, 881–893.

Richmond, M.D., 2002. A field guide to the seashores of Eastern Africa and the Western Indian Ocean Islands.

Roberts, M.J., 2015. The western Indian Ocean Upwelling research initiative (WIOURI): a flagship IIOE2 project. *Clivar Exchange*, *68*(19), p.3.

Roberts, C.M., O'Leary, B.C., McCauley, D.J., Cury, P.M., Duarte, C.M., Lubchenco, J. and Worm, B., 2017. Marine reserves can mitigate and promote adaptation to climate change. *Proc. Natl. Acad. Sci.* 114 (24), 6167–6175.

Rocliffe, S., Peabody, S., Samoilys, M. and Hawkins, J.P., 2014. Towards a network of locally managed marine areas (LMMAs) in the Western Indian Ocean. *PloS one*, *9*(7), p.e103000.

Russ, G.R., Alcala, A.C., Maypa, A.P., Calumpong, H.P. and White, A.T., 2004. Marine reserve benefits local fisheries. *Ecol. Appl.* 14 (2), 597–606.

Samoilys, M. A., Halford, A. and Osuka, K., 2019a. Disentangling drivers of the abundance of coral reef fishes in the Western Indian Ocean. *Ecology and evolution*, *9*(7), 4149-4167.

Samoilys, M.A., Osuka, K., Mussa, J., Rosendo, S., Riddell, M., Diade, M., Mbugua, J., Kawaka, J., Hill, N. and Koldewey, H., 2019. An integrated assessment of coastal fisheries in Mozambique for conservation planning. *Ocean & Coastal Management*, *182*, p.104924.

Schramm KD, Harvey ES, Goetze JS, Travers MJ, Warnock B, Saunders BJ (2020) A comparison of stereo-BRUV, diver-operated, and remote stereo-video transects for assessing reef fish assemblages. *Journal of Experimental Marine Biology and Ecology*, *524*, 151273.

Semba, M., Lumpkin, R., Kimirei, I., Shaghude, Y. and Nyandwi, N., 2019. Seasonal and spatial variation of surface current in the Pemba Channel, Tanzania. *PloS one*, *14*(1), p.e0210303.

Sekadende, B., Scott, L., Anderson, J., Aswani, S., Francis, J., Jacobs, Z., Jebri, F., Jiddawi, N., Kamukuru, A.T., Kelly, S. and Kizenga, H., 2020. The small pelagic fishery of the Pemba Channel, Tanzania: What we know and what we need to know for management under climate change. *Ocean & Coastal Management*, *197*, p.105322.

Souter, D., Planes, P., Wicquart, J., Logan, M., Obura, D. and Staub, F., 2021. Status of coral reefs of the world: 2020. Introduction. Global Coral Reef Monitoring Network (GCRMN) & International Coral Reef Initiative (ICRI). 11pp

Stewart, B.D. and Jones, G.P. 2001. Associations between the abundance of piscivorous fishes and their prey on coral reefs: implications for prey-fish mortality', *Marine Biology*. Springer, 138(2), pp. 383–397.

Tuda, A.O., Stevens, T.F. and Rodwell, L.D., 2014. Resolving coastal conflicts using marine spatial planning. *Journal of environmental management*, *133*, pp.59-68.

Wanyonyi, I.N., Wamukota, A., Alati, V.M. and Osuka, K., 2021. The influence of 'space' on migrant fisher livelihoods. *African Identities*, pp.1-16.

Wells, S., 2009. Dynamite fishing in northern Tanzania–pervasive, problematic and yet preventable. *Marine Pollution Bulletin*, *58*(1), pp.20-23.

White, J., Simpfendorfer, C.A., Tobin, A.J. and Heupel, M.R., 2013. Application of baited remote underwater video surveys to quantify spatial distribution of elasmobranchs at an ecosystem scale. *Journal of Experimental Marine Biology and Ecology*, *448*, pp.281-288.

Wilson, R.J., Sailley, S.F., Jacobs, Z.L., Kamau, J., Mgeleka, S., Okemwa, G.M., Omukoto, J.O., Osuka, K.E., Samoilys, M., Sauer, W., Silas, M.O., Sululu, J.S. and Roberts, M.J., 2021. Large projected reductions in marine fish biomass for Kenya and Tanzania in the absence of climate mitigation. *Ocean & Coastal Management*, *215*, p.105921.

Wolfe, K., Kenyon, T.M. and Mumby, P.J., 2021. The biology and ecology of coral rubble and implications for the future of coral reefs. *Coral Reefs*, *40*(6), pp.1769-1806.

Wölfl, A.C., Snaith, H., Amirebrahimi, S., Devey, C.W., Dorschel, B., Ferrini, V., Huvenne, V.A., Jakobsson, M., Jencks, J., Johnston, G. and Lamarche, G., 2019. Seafloor mapping–the challenge of a truly global ocean bathymetry. *Frontiers in Marine Science*, *6*, p.283.

Wynn, R.B., Huvenne, V.A.I., Le Bas, T.P., Murton, B.J., Connelly, D.P., Bett, B.J., Ruhl, H.A., Morris, K.J., Peakall, J., Parsons, D.R., Sumner, E.J., Darby, S.E., Dorrell, R.M. and Hunt, J.E., 2014. Autonomous Underwater Vehicles (AUVs): their past, present and future contributions to the advancement of marine geoscience. *Mar. Geol. 352*, 451–468.

CHAPTER 2

PROTECTION OUTCOMES FOR FISH TROPHIC GROUPS ACROSS A RANGE OF MANAGEMENT REGIMES

2.1. Preface

Analysis of size spectra indicators is being increasingly used to assess changes in marine ecosystems from local to regional to global spatial scales (Shin *et al.*, 2005; Petchey and Belgrano, 2010; Polishchuk and Blanchard, 2019). These indicators can help quantify the relative abundance of small and large fish (slope) and overall productivity of the system (intercept) (Shin *et al.*, 2005). Slope is considered as an indicator that quantifies the proportion of small and large fish at a reef such that a more negative slope indicates either high abundance of small sized fish, low abundance of large fish, or both. The intercept is indicative of overall productivity of a system, such that higher values mean higher community biomass (Dickie et al., 1987; Jennings, 2005). In this regard, size spectra indicators have the ability to show the outcome of high exploitation rates and differences in fishing pressure on coral reefs (Dulvy *et al.*, 2004; Wilson *et al.*, 2010). The approach has also been tested in tropical multi-species and multi-gear fisheries that target a wide variety of fish sizes (Bianchi *et al.*, 2000), as well as in grasslands to show the effects of management and protection against human exploitation (Mulder and Elser, 2009). For these reasons, size spectra descriptors are considered robust indicators able to assess differences in the effectiveness of different management regimes.

In this chapter I set out to measure the effect of protection level and human population density of fish communities in the western and central Indian Ocean. This was achieved by combining previously published standardised datasets from multiple countries using size spectra analysis and comparing patterns in the slope and intercept of size-spectra across different levels of protection. The study revealed that the protection level afforded by many marine protected areas is not adequate to support or detect recovery of fishes.

This chapter was written in the style of Marine Pollution Bulletin and was published in October 2021. The paper is available at https://doi.org/10.1016/j.marpolbul.2021.113010.

I declare that the work submitted is my own. The contribution by co-authors was as follows:
Bryce Stewart and Colin McClean: Supervision, review and editing.

Melita A. Samoilys, Ronan C. Roche and John Turner: Provision of secondary data, review and editing.

2.2 References

Bianchi, G., Gislason, H., Graham, K., Hill, L., Jin, X., Koranteng, K., Manickchand-Heileman, S., Paya, I., Sainsbury, K., Sanchez, F. and Zwanenburg, K., 2000. Impact of fishing on size composition and diversity of demersal fish communities. *ICES Journal of marine Science*, *57*(3), pp.558-571.

Dickie, L.M., Kerr, S.R. and Boudreau, P.R., 1987. Size-dependent processes underlying regularities in ecosystem structure. *Ecological monographs*, *57*(3), pp.233-250.

Dulvy, N.K., Polunin, N.V., Mill, A.C. and Graham, N.A., 2004. Size structural change in lightly exploited coral reef fish communities: evidence for weak indirect effects. *Canadian Journal of Fisheries and Aquatic Sciences*, *61*(3), pp.466-475.

Jennings, S. 2005. Aquatic food webs: an ecosystem approach, in Belgrano, A. Belgrano, A., Scharler, U.M., Dunne, J. and Ulanowicz, R.E. (eds). Aquatic Food Webs: An Ecosystem Approach Oxford, UK.: Oxford University Press, pp. 86–97.

Mulder, C. and Elser, J.J., 2009. Soil acidity, ecological stoichiometry and allometric scaling in grassland food webs. Global Change Biology, 15(11), pp.2730-2738.

Petchey, O.L. and Belgrano, A. 2010. Body-size distributions and size-spectra: Universal indicators of ecological status? *Biology Letters*. Royal Society, pp. 434–437.

Polishchuk, L. V, Blanchard, J. L. 2019. Uniting discoveries of abundance-size distributions from soils and seas. *Trends in Ecology & Evolution*, 34(1), pp. 2–5.

Shin, Y.J., Rochet, M.J., Jennings, S., Field, J.G. and Gislason, H., 2005. Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES Journal of marine Science*, *62*(3), pp.384-396.

Wilson, S.K., Fisher, R., Pratchett, M.S., Graham, N.A.J., Dulvy, N.K., Turner, R.A., Cakacaka, A. and Polunin, N.V., 2010. Habitat degradation and fishing effects on the size structure of coral reef fish communities. *Ecological Applications*, *20*(2), pp.442-451.

PROTECTION OUTCOMES FOR FISH TROPHIC GROUPS ACROSS A RANGE OF MANAGEMENT REGIMES

Kennedy E. Osuka[a, b], Bryce D. Stewart[a], Melita A. Samoilys[a,d], Ronan C. Roche[c], John Turner[c] and Colin McClean[a]

Institutional affiliation:

[a] Department of Environment and Geography, University of York (York, UK)

[b] CORDIO East Africa (Mombasa, Kenya)

[c] School of Ocean Sciences, Bangor University (Bangor, UK)

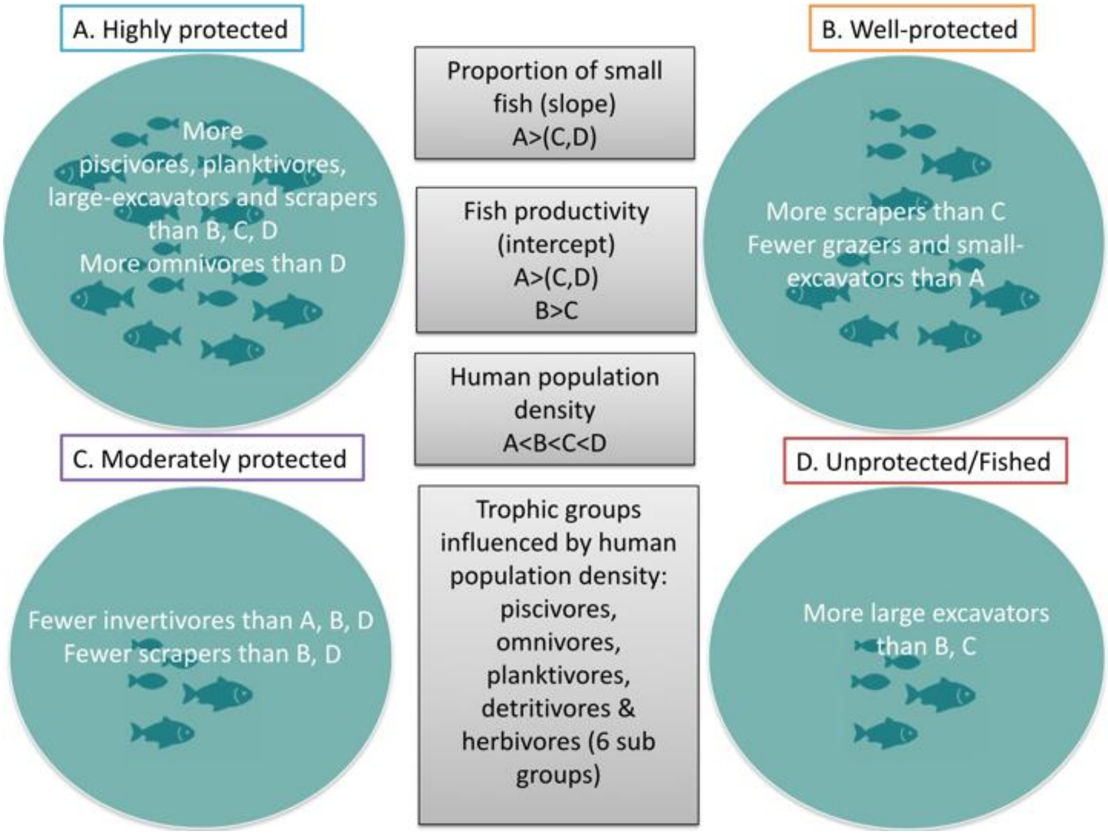
[d] Department of Zoology, University of Oxford (Oxford, UK)

Corresponding author email: koe503@york.ac.uk

Abstract

Understanding how Marine Protected Areas (MPAs) improve conservation outcomes across anthropogenic pressures can improve the benefits derived from them. Effects of protection for coral reefs in the western and central Indian Ocean were assessed using size-spectra analysis of fish and the relationships of trophic group biomass with human population density. Length-spectra relationships quantifying the relative abundance of small and large fish (slope) and overall productivity of the system (intercept) showed inconsistent patterns with MPA protection. The results suggest that both the slopes and intercepts were significantly higher in highly and well-protected MPAs. This indicates that effective MPAs are more productive and support higher abundances of smaller fish, relative to moderately protected MPAs. Trophic group biomass spanning piscivores and herbivores, decreased with increasing human density implying restoration of fish functional structure is needed. This would require addressing fisher needs and supporting effective MPA management to secure ecosystem benefits for coastal communities.

Graphical abstract



Keywords: Marine Protected Areas, size-spectra, fish biomass, fishing effects, compliance.

1. Introduction

Reef fishes play critical roles in community dynamics within coral reef habitats where they regulate reef benthic composition by performing different inter-related functional roles. These roles support coral reef ecosystem functions (Pratchett et al., 2011), and importantly, can alter depending on fish size (Bellwood et al., 2019). In the presence of continuing over-exploitation through fishing and habitat degradation through climate change (Hoegh-Guldberg et al., 2018; Reynolds et al., 2005), protection of functionally important fish species is an increasingly prevalent aspect of reef conservation efforts.

Fish assemblages are fundamentally influenced by the resources and shelter provided by coral reefs (Richardson et al., 2018). These bottom-up control mechanisms mean that healthy coral habitats support high fish abundance including juveniles of large-bodied species (Graham et al., 2007), which recruit to become fishable stocks over time. Similarly, high fish productivity is expected where the ecosystem is in better condition, which can be achieved through high levels of protection. Conversely, fishing has a top-down control on reef fishes and continuous harvesting reduces fish size, abundance and biomass (Zgliczynski and Sandin, 2017; Robinson et al., 2020). High fishing pressure lowers abundance of large-bodied fishes and increases the relative abundance of small-bodied fishes (Graham et al., 2007), causing significant impacts on the size structure of reef fish assemblages (McClanahan et al., 2011). The identification of factors such as reef productivity that influence the size structure of reef fish populations could allow for fisheries management initiatives, which identify specific reef zones for protection (Ojea et al., 2017).

No-take zones in Marine Protected Areas (MPAs) are a widely applied management and conservation measure used to mitigate human associated disturbances, such as fishing, and improve resilience of reefs to climate change (Mellin et al., 2016; Roberts et al., 2017). MPAs can increase fish diversity, biomass, and the number of exploited species in adjacent fishing grounds (Russ et al., 2004; Kough et al., 2019). A network of MPAs ensures different fish sizes and life history stages are protected (Green et al., 2014) and this is critical in the recovery and maintenance of fish biodiversity and productivity, which refers to the rate of generation of biomass in an aquatic system (Halpern, 2003; Lester and Halpern, 2008; McClanahan et al., 2007).

Assessing the effectiveness of MPAs in achieving desired objectives requires information from highly protected MPAs, or those in remote locations. This is essential for determining the maximum potential abundance and biomass of fishes or ocean systems (McClanahan et al., 2019; McClanahan et al., 2020; MacNeil et al., 2020). It is now established that the benefits of protected areas depend on their size, age, level of protection, distance to fish markets, levels of compliance, number of staff and budget capacity (Molloy et al., 2009; Gill et al., 2017; Cinner et al., 2018). Yet, it remains unclear how varying levels of protection impact the relative abundance of different fish sizes and overall fish productivity.

Examining the size-spectra of fishes can inform the decision-making process when comparing areas in different geographical locations or management levels (Graham et al., 2007; Polishchuk and Blanchard, 2019). Size-spectra descriptors of slope and intercept are considered robust indicators, able to show fish population structure at different spatial scales (Petchey and Belgrano, 2010; Zgliczynski and Sandin, 2017). These indicators quantify the relative abundance of small and large fish (slope) and the overall productivity of the system (intercept) (Shin et al., 2005). Slope becomes steeper (more negative) when small fish are more abundant than large fish, while intercepts become greater where fish community productivity is high. Due to these properties, size-spectra analysis is a useful tool in evaluating the ecosystem effects of fishing and guiding the management of tropical multi-species and multi-gear fisheries (Graham et al., 2005; Shin et al., 2005; Guiet et al., 2016; Zgliczynski and Sandin, 2017).

Here we use fish density and size data collected from a consistent reef morphology (ocean exposed fringing coral reefs: Andréfoüet et al., 2009, Samoilys et al., 2019) in the western and central Indian Ocean, to compare size spectra indicators and biomass of trophic groups across a range of management regimes. Trophic groups were selected to represent a wide range of functional roles on coral reefs (Osuka et al., 2018; Parravicini et al., 2020). The study tested the hypotheses that the abundance of both small and large fish is higher in protected areas than unprotected areas and that local human population density influences this protection outcome.

2. Methods

2.1 Study area

Reefs in the Western Indian Ocean (WIO) exhibit a range of geomorphologies, which have been categorised as: ocean-exposed fringing reefs, coastal barrier reef complexes, inner seas patch reef complexes, inner seas exposed fringing reefs, lagoon exposed fringing reef, and bank barrier or bank lagoon reefs (Andréfoüet et al., 2009; Samoilys et al., 2019). Reef geomorphology strongly influences coral reef fish communities and biomass (Taylor et al., 2015; Samoilys et al., 2019). Therefore, this study only focused on fish assemblages within the consistent geomorphology of ocean-exposed fringing reefs (Figure 1). Fish data were collated from two published studies based on surveys carried out between 2009 and 2015 in the western and central Indian Ocean (Table 1), which rapidly assessed sites that were selected haphazardly to maximize a range of protection levels occurring in the Indian Ocean. A site refers to a reef surveyed on two dives, where fish were counted in two or three replicate transects, with each transect measuring 50 m × 5 m (250 m^2). Data from WIO were sourced from Samoilys et al. (2019). This included data from 24 sites across four countries: Tanzania – seven sites, Mozambique - seven, Comoros – six, and Madagascar – four (Figure 1). An additional dataset was collected from eight sites in the Chagos Archipelago (Samoilys et al., 2018; Figure 1). These sites were grouped into four protection levels based on the existence and effectiveness of management rules as determined from IUCN protected area categories (IUCN, 2004), consultations with managers, personal knowledge and literature: highly protected, well-protected, moderately protected and unprotected (fished) (Table 1). Highly protected sites came from the Chagos Archipelago (IUCN category I - strict nature reserve). Well-protected included sites from Mafia Marine National Park (IUCN category VI - protected area with sustainable use of natural resources), Metundo and Vamizi Islands (no assigned IUCN category but considered as effective in-situ conservation areas, due to high awareness and adherence to informal management practices). Moderately protected sites from Mnazi Bay Ruvuma Estuary Marine Park (IUCN category VI) and Mnemba Island Marine Conservation Area (IUCN category VI) (Supporting information Table S1). Fished sites were drawn from Comoros and Ambodivahibe and Loky in Madagascar. Data on human population counts and reef area (km^2) in 2015 and within a radius of 20 km of site geographic coordinates, were derived from the Marine Socio-Environmental Covariates dataset (Yeager et al., 2017). Human population counts at each site were divided by reef area and log transformed to calculate local population density. Highly protected areas had zero human population values yielding a minimal population category. This was followed by well-protected, moderate protection and fished areas that were categorised as lightly, moderately, and heavily populated, respectively (Table 1). Highly protected areas were located in remote areas with very low human population and also showed relatively high compliance with no-take zone (NTZ) management rules (Sheppard et al., 2012), therefore the reef system was considered as a remote highly protected area.

2.2. Fish surveys

Fish surveys were conducted based on methods detailed in Samoilys et al. (2019). The surveys involved estimating fish species densities and total lengths (TL) in 5 cm size classes from 6 cm, by an experienced diver (M.A.S) with over 20 years' experience of conducting Underwater Visual Census (UVC) surveys.

A total of 155 fish species from 11 families (Acanthuridae, Balistidae, Caesionidae, Chaetodontidae, Haemulidae, Lethrinidae, Lutjanidae, Pomacanthidae, Serranidae, Scarinae (Labridae) and Siganidae) were surveyed. The families and species were chosen because they are good indicators of disturbance effects across all trophic levels (Samoilys and Randriamanantsoa, 2011). The biomass of each species was calculated based on length–weight relationships presented in Samoilys et al. (2018). Species were assigned to the following trophic groups: piscivores, omnivores, corallivores, invertivores, planktivores, detritivores and herbivores (Osuka et al., 2018; Samoilys et al., 2019; Parravicini et al., 2020). The herbivores included six sub-groups composed of: large excavators, small excavators, scrapers, browsers, grazers and grazers-detritivores (Bellwood et al., 2019).

2.3. Data analysis

Multivariate dimensional scaling (MDS) analyses based on Bray-Curtis similarity index were performed on log (x + 1) transformed fish density and biomass data with an assumption that the influence of protection outweighed site differences. This was after performing MDS based on location and a combined factor of location and protection (Supplementary material Figure S1a–d). A permutation-based hypothesis testing analysis of similarities (ANOSIM) was used to compare fish density and biomass across the four protection levels (Clarke and Gorley, 2006).

Size-spectra analysis was performed for each site based on fish densities in each of the 19 size classes ranging from 11 to 105 cm. This involved determining the slope and intercept of a linear regression of log transformed midpoint of size classes and $\log_{10}(x + 1)$ transformed count data. Prior to analysis, the midpoint lengths were centred across the size range at a site, thereby removing the correlation between slope and intercept (Daan et al., 2005). The mean slopes and intercepts of protection levels were compared using One-way ANOVA (Zar, 1999). Tukey's post-hoc tests were then performed to determine significant pairwise protection differences.

Reef area is an important variable controlling fish productivity (Williams et al., 2015), therefore biomass data were divided by reef area derived from the Marine Socio-Environmental Covariates dataset (Yeager et al., 2017) before comparing protection levels. Differences in fish trophic group biomass among protection levels were tested using a One-way Kruskal-Wallis test after failing both normality and homogeneity of variance tests using Shapiro-Wilk and Levene tests respectively, even after log-transformations (Zar, 1999). Mann-Whitney post-hoc tests were then performed to determine significant pairwise differences. Differences in the human population densities were only compared between three protection levels (well-protected, moderately protected and fished areas) using one-way ANOVA followed by Tukey post-hoc tests after passing normality and homogeneity tests. Highly protected areas showed no variance in human population density. The relationship between trophic groups, and human population density was then assessed using generalised additive models (GAMs) using the *mgcv* package in R (www.r-project.org). Contribution of the predictors to the model was assessed from GAMs effective degrees of freedom (edf), which represents the complexity of the smoothing term. An edf of 1 represents a straight line or a linear effect while an edf of ≥2 describes a non-linear effect. To validate the influence of human population on the biomass of trophic groups, effect of spatial autocorrelation was checked using Moran's I test (Supplementary material Table S2). Where spatial autocorrelation was detected, generalised least squares regression models were fitted using five different types of spatial correlation structures (exponential, gaussian, spherical, linear, and rational quadratic). Akaike information criterion (AIC) model selection method was thereafter applied to select the best model in comparison to a model without spatial autocorrelation structure.

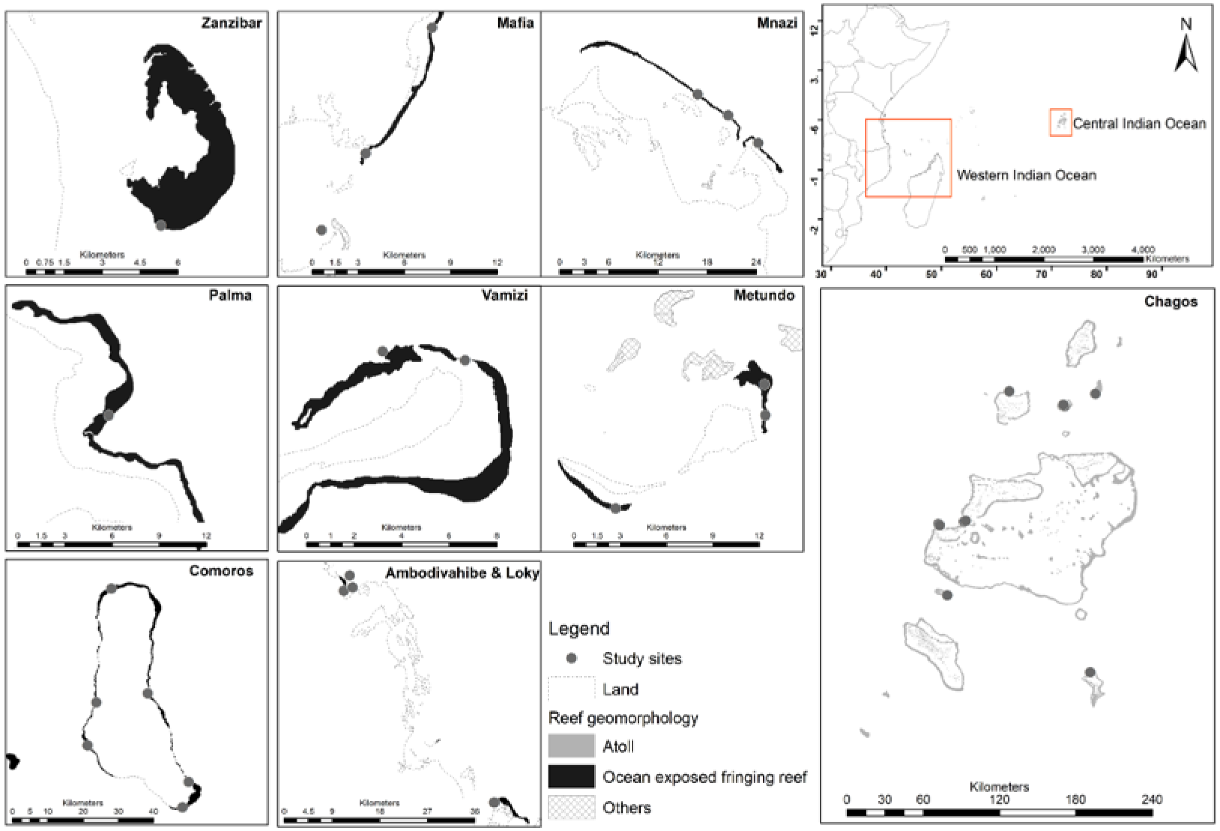


Figure 1: Map of the survey sites from the western Indian Ocean (WIO) and central Indian Ocean (CIO). WIO survey sites comprised reefs sampled in Tanzania (Zanzibar, Mafia and Mnazi), Mozambique (Palma, Vamizi and Metundo), Comoros and Madagascar (Ambodivahibe and Loky). CIO survey sites were sampled from the Chagos Archipelago.

Table 1: Details of fish survey sites in ocean exposed fringing reefs and atolls with their depths, reef type, protection index and local human population density derived from the Marine Socio-Environmental Covariates data set (Yeager et al., 2017). Protection levels are defined as: high protection - a gazetted no-take marine protected area (MPA) in remote location with strict enforcement; well-protected - a gazetted MPA or a tourism zone with informal rules and good enforcement; moderate protection- a gazetted MPA established though effectiveness weak due to poor enforcement; Fished – reef with no management in place at all. (Data sources: Samoilys et al., 2018; Samoilys et al., 2019).

Protection level	**Location (sites)**	**Max – Min depth (m)**	**Reef type**	**Local human population density ($\log_{10}$ persons per km^2 of reef)**	
				Mean (±SE)	**Population category**
High protection	Chagos (8)	3 - 23	Forereef and terrace	0.00 (0.00)	Minimal
Well protected	Mozambique (4), Tanzania (3)	3 - 22	Forereef and deep terrace	1.58 (0.21)	Lightly populated
Moderate protection	Tanzania (4)	5 - 22	Forereef and deep terrace	2.62 (0.10)	Moderately populated
Fished	Madagascar (4), Comoros (6), Mozambique (3)	3 - 20	Forereef	2.98 (0.17)	Heavily populated

3. Results

3.1 Fish community structure

MDS plot of fish community biomass and density showed that sites separated out largely in relation to the four protection levels (Figure 2). However, a few of the fished sites particularly in Mozambique overlapped in multivariate space with well and moderately protected sites. ANOSIM results revealed a clearer protection pattern in fish biomass (R = 0.435; p<0.001) than in fish density (R = 0.315; p<0.001). All protection levels showed significant differences in fish biomass; but with fish density, only highly protected areas differed significantly from well-protected, moderately protected and fished areas (Table 2).

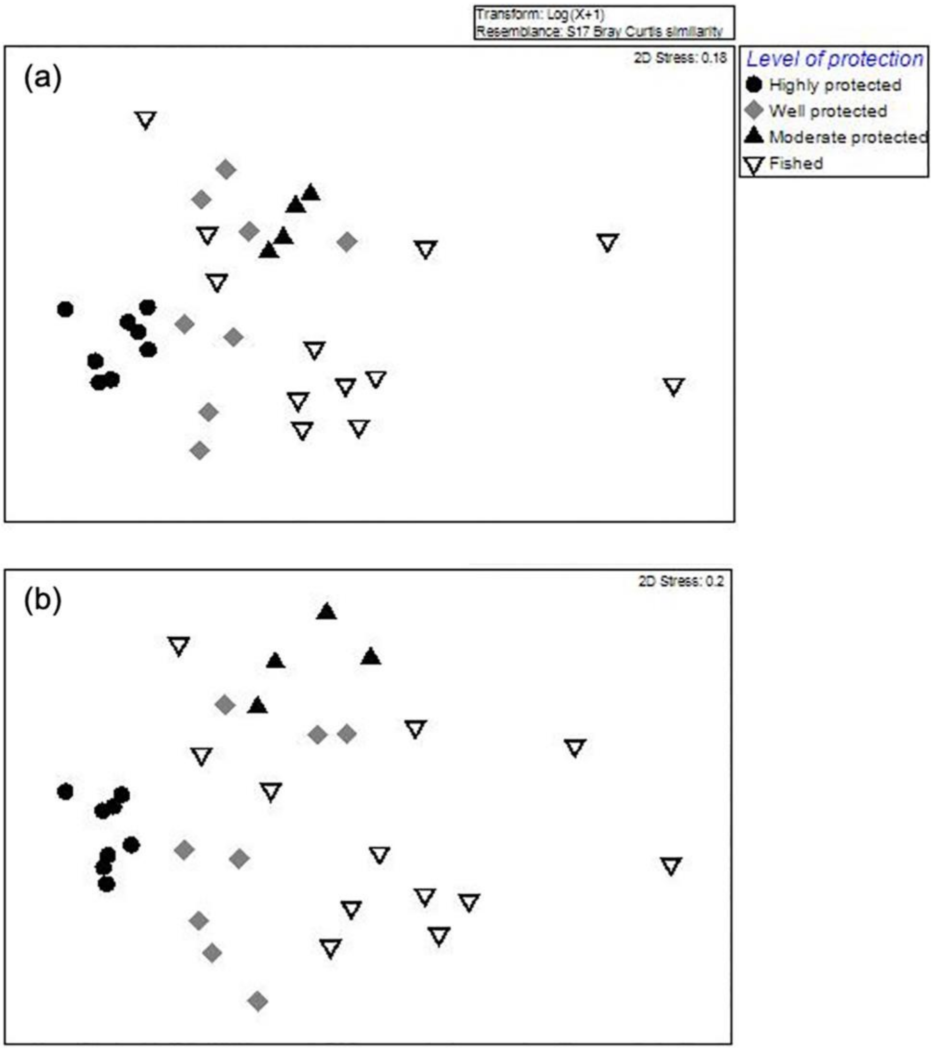


Figure 2: Multidimensional scaling plots based on Bray-Curtis similarity statistic on fish species: a) density and b) biomass between four protection levels from five countries in western and central Indian Ocean.

Table 2: Results from ANOSIM tests showing global and pairwise tests on fish density and biomass between protection levels. Bolded p-values indicate significant comparisons.

	Density		Biomass	
	R value	P value	R value	P value
Global test	0.315	**0.001**	0.435	**0.001**
Pairwise tests				
High protection, Well-protected	0.568	**0.002**	0.575	**0.001**
High protection, Moderate protection	0.998	**0.002**	1.000	**0.002**
High protection, Fished	0.403	**0.001**	0.527	**0.002**
Well-protected, Moderate protection	0.165	0.121	0.331	**0.030**
Well-protected, Fished	0.120	0.089	0.241	**0.011**
Moderate protection, Fished	0.002	0.473	0.251	**0.050**

3.2 Size-spectra and protection

The mean slope differed considerably across protection levels (Figure 3; ANOVA $F_{3, 28} = 9.87$, $p < 0.001$). Post-hoc Tukey's tests showed that slopes in the highly protected areas were similar to well-protected areas but significantly more negative than moderately protected and fished areas (Table 3a). The means of intercepts also varied considerably across protection levels (Figure 3; ANOVA $F_{3, 28} = 12.00$, $p < 0.001$). Post-hoc Tukey's tests showed overall productivity in the highly protected areas was greater than moderately protected and fished areas while well-protected areas showed greater intercepts than fished areas (Table 3b).

3.3 Influence of protection on fish biomass

The median biomass of trophic groups showed significant differences across the four levels of protection except for detritivores, browsers and grazer detritivores (Table 4). Mann-Whitney post-hoc tests showed that in all trophic groups except invertivores, the highest biomass, more than 2.6-fold, was seen in highly protected areas compared to all other protected or fished areas (Figure 4). Scrapers, invertivores and large excavators had higher biomass in fished areas than moderately protected or well-protected areas (Figure 4). The biomass of piscivores, omnivores, planktivores, small excavators and grazers was similar across well-protected, moderately protected and fished areas, while scrapers showed higher biomass in well-protected areas compared to moderately protected areas (Figure 4).

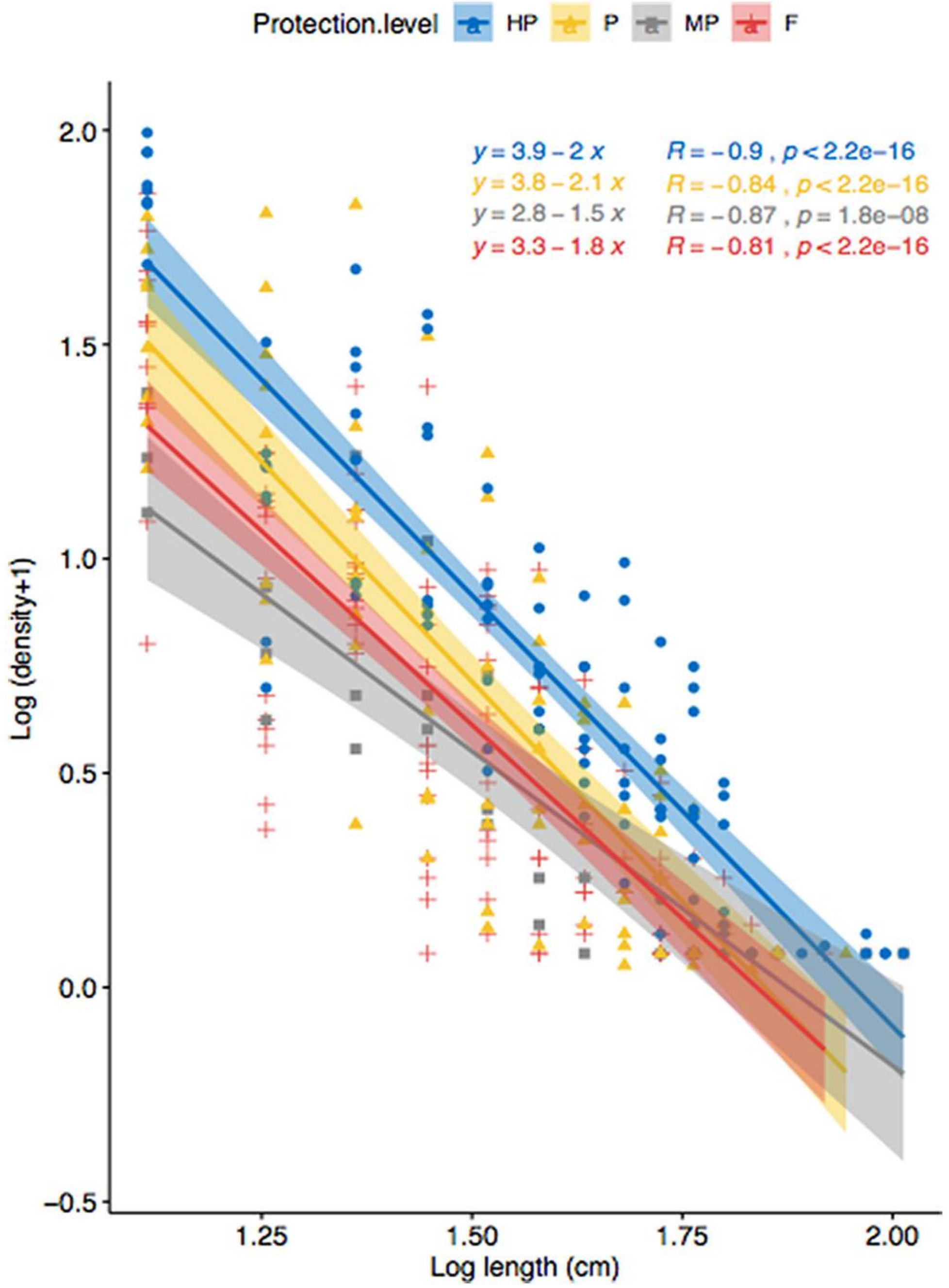


Figure 3: Relationships between fish length and density for four protection levels in western and central Indian Ocean. HP = high protection, P = well-protected, MP = moderate protection and F = fished. Shaded area around the line is 95% confidence interval.

Table 3: Tukey post-hoc pairwise test results with F values (unshaded) and p-values(shaded) for size spectra slopes and size intercepts. Significant comparisons are bold.

(a) Slope	Fished	Moderate-protection	Well-protected	High protection
Fished		0.8763	0.104	**0.001**
Moderate-protection	1.060		0.377	**0.007**
Well-protected	3.369	2.309		0.234
High protection	6.116	5.057	2.747	

(b) Intercept	Fished	Moderate-protection	Well-protected	High protection
Fished		0.997	**0.010**	**0.001**
Moderate-protection	0.300		0.153	**0.001**
Well-protected	3.385	3.085		0.125
High protection	6.625	6.324	3.239	

3.4 Influence of local human population on fish biomass

Comparisons of local human population density excluding zero data from remote highly protected areas, revealed significant differences across protection levels (ANOVA $F_{2, 21} = 5.61$, p = 0.011). A pairwise Tukey's test showed that only well-protected areas were located in areas with low human density (1.58 ± 0.21(se) $\log_{10}$ persons per km^2 of reef) compared to fished areas (2.98 ± 0.17(se) $\log_{10}$ persons per km^2 of reef).

A significant nonlinear relationship signified by an edf ≥2 was evident in nine trophic groups notably: piscivores, omnivores, planktivores, detritivores, large excavators, small excavators, scrapers, grazers and grazer-detritivores (Table 5). Overall, biomass decreased with increasing human density except for detritivores, grazers and grazer-detritivores (Figure 5). Detritivores and grazers showed high biomass in both minimal and heavily populated areas and low biomass in moderately populated areas (Figure 5). Grazer-detritivores showed no apparent pattern although elevated biomass was observed in moderately populated areas. Relationships within the other four trophic groups were not significant. Models without spatial autocorrelation effects showed significant decrease in biomass with increasing human population density for piscivores, planktivore, large- and small excavators (Table 6).

Table 4: Tabulated medians and interquartile range (IR) and one-way Kruskal-Wallis tests on trophic group biomass compared between four protection levels.

Variable	High protection		Well protected		Moderate protection		Fished		Kruskal-Wallis	
	Median	IR	Median	IR	Median	IR	Median	IR	H-value	p-value
a) Trophic group biomass (kg/ha) per reef area(km^2)										
Piscivores	6.63	3.45, 11.0	0.40	0.17, 1.19	0.36	0.25, 0.43	0.47	0.21, 1.12	15.44	**<0.001**
Omnivores	12.52	2.61, 37.3	1.66	0.05, 4.86	2.07	0.76, 5.02	1.02	0.30, 3.35	7.96	**0.047**
Invertivores	0.50	0.23, 0.70	0.32	0.10, 0.60	0.00	0.00, 0.00	0.42	0.24, 0.75	10.89	**0.012**
Planktivores	10.03	4.79, 15.91	1.13	0.11, 2.26	0.26	0.06, 0.28	0.45	0.21, 1.3	19.12	**<0.001**
Detritivores	0.56	0.36, 1.02	0.14	0.07, 0.27	0.12	0.02, 0.19	0.30	0.17, 1.32	1.42	0.231
Large excavators	3.16	1.94, 6.36	0.00	0.00, 0.24	0.00	0.00, 0.16	0.42	0.16, 1.20	19.76	**<0.001**
Small excavators	1.99	0.36, 2.8	0.22	0.09, 0.62	0.29	0.07, 0.42	0.55	0, 0.84	8.36	**0.039**
Scrapers	2.60	0.88, 6.08	0.58	0.27, 1.07	0.13	0.06, 0.29	0.74	0.56, 1.76	12.52	**0.006**
Browsers	0.67	0.11, 1.65	1.14	0.12, 2.03	0.29	0.14, 0.55	0.52	0.15, 1.00	2.33	0.506
Grazers	1.12	0.47, 2.23	0.21	0.11, 0.28	0.27	0.21, 0.29	0.43	0.17, 1.47	9.86	**0.020**
Grazer detritivores	0.35	0.06, 0.56	0.03	0.00, 0.29	0.00	0.00, 0.37	0.31	0.13, 0.8	6.74	0.080

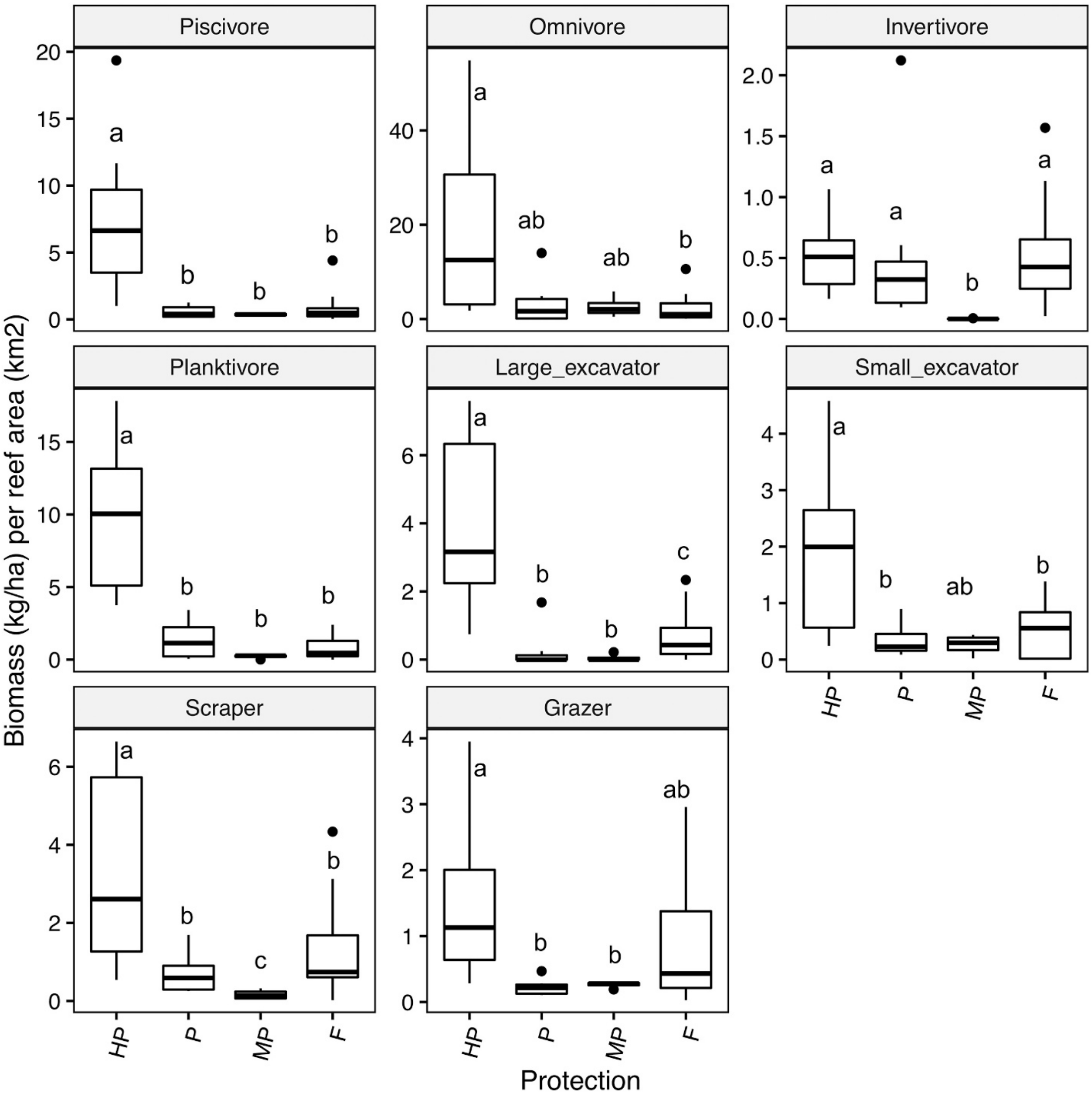


Figure 4: Median biomass of trophic groups that showed significant differences across protection levels from western and central Indian Ocean. The lowercase letters above each box show Mann-Whitney posthoc test with unique letters indicating significant differences and duplicated letters showing no statistical significance. HP = high protection, P = well-protected, MP = moderate protection and F = fished.

Table 5: Generalised additive model results for the biomass (kg per ha per per km^2 of reef) of 11 trophic groups showing effective degrees of freedom (edf), deviance explained by the model for their relationships with human population from five locations in western and central Indian Ocean. Bolded p-values indicate significant relationships.

Trophic group	edf	p-value	Deviance explained (%)
Piscivores	2.8	**<0.001**	50.7
Omnivores	2.3	**0.016**	31.8
Invertivores	1.8	0.209	14.0
Planktivores	2.9	**<0.001**	67.2
Detritivores	4.7	**<0.001**	73.5
Large excavators	2.9	**<0.001**	56.0
Small excavators	2.0	**0.003**	37.0
Scrapers	2.3	**0.014**	33.2
Browsers	1.0	0.642	0.7
Grazers	3.6	**<0.001**	54.7
Grazer-detritivores	7.0	**0.047**	48.5

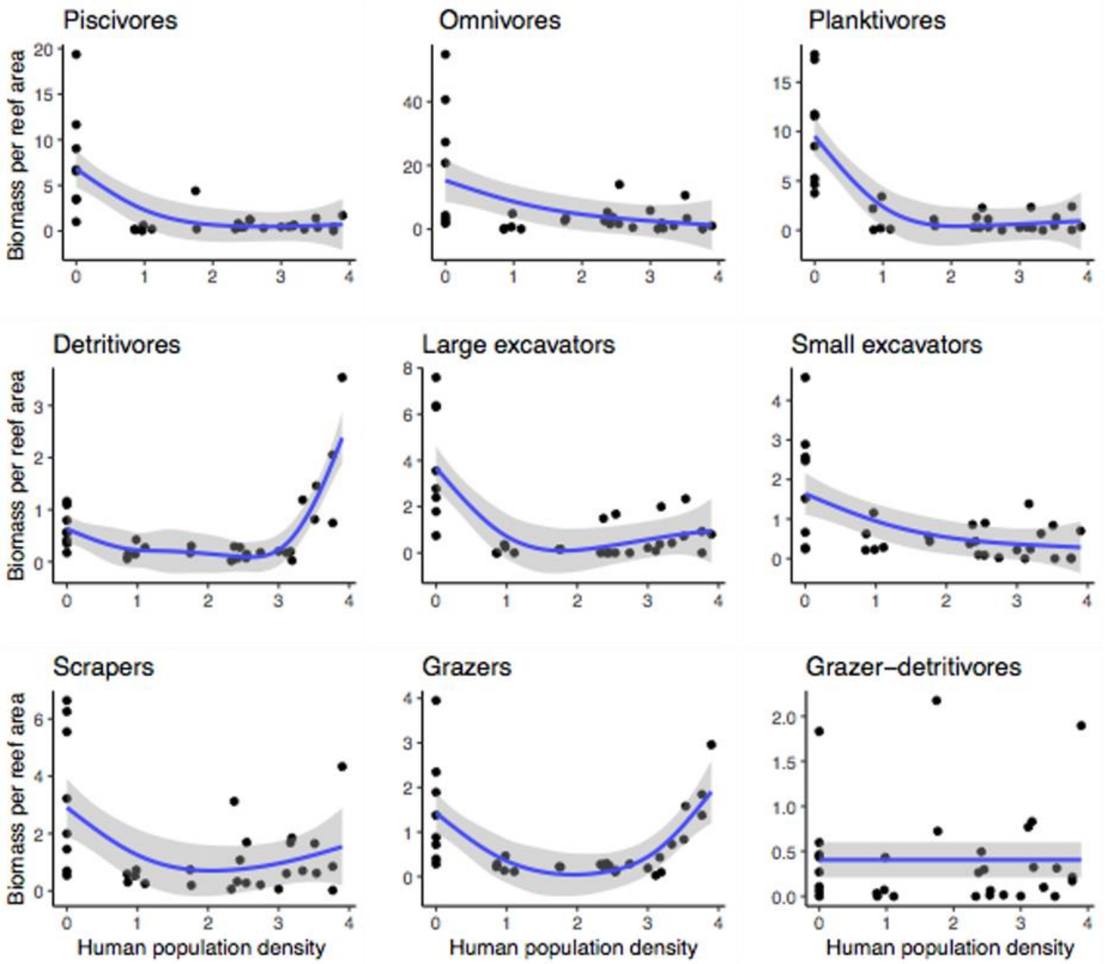


Figure 5: Relationship using generalised additive model (GAM) smoothing method between local human population density (log persons per km^2) and biomass (kg/ha) per reef area (km^2) of nine fish trophic groups sampled from western and central Indian Ocean.

Table 6: Coefficients of the best generalised least squares models showing the relationship between human population and biomass of 11 trophic groups from five locations in western and central Indian Ocean. Models were selected from different types of spatial autocorrelation structures (exponential, gaussian, spherical, linear, and rational quadratic) using the Akaike Information Criterion (AIC) model selection process. Significant relationships are in bold.

Trophic group	Autocorrelation structure	Coefficient	Estimate	se	t-value	p-value
Piscivores	Gaussian	Intercept	5.763	1.484	3.882	**0.001**
		Human population	-1.748	0.653	-2.679	**0.012**
Omnivores	Spherical	Intercept	11.795	4.765	2.475	**0.019**
		Human population	-2.861	2.167	-1.320	0.197
Invertivores		Intercept	0.356	0.143	2.495	**0.018**
		Human population	0.059	0.061	0.956	0.347
Planktivores	Gaussian	Intercept	7.671	1.734	4.425	**0.000**
		Human population	-2.480	0.787	-3.152	**0.004**
Detritivores	Gaussian	Intercept	0.381	0.246	1.545	0.133
		Human population	0.156	0.108	1.438	0.161
Large excavators	Spherical	Intercept	2.402	0.898	2.675	**0.012**
		Human population	-0.540	0.362	-1.492	**0.046**
Small excavators		Intercept	1.521	0.265	5.745	**0.000**
		Human population	-0.386	0.114	-3.390	**0.002**
Browsers		Intercept	1.060	0.349	3.038	0.005
		Human population	-0.071	0.150	-0.470	0.642
Scrapers	Rational quadratic	Intercept	2.377	0.670	3.549	0.001
		Human population	-0.420	0.300	-1.403	0.171
Grazers	Exponential	Intercept	0.850	0.386	2.203	**0.035**
		Human population	-0.082	0.174	-0.473	0.640
Grazer detritivores		Intercept	0.392	0.173	2.272	**0.030**
		Human population	0.007	0.074	0.096	0.924

4. Discussion

This study revealed three key findings. Firstly, size spectra analysis showed fish community size structure on coral reefs in the western and central Indian Ocean varied according to protection level. However, similar fish community size structure was found between highly protected and well-protected areas. Secondly, effects of protection on fish trophic groups differed but were highest between remote highly protected areas and other protection levels. Moderately protected areas showed no apparent benefits in biomass for any of the trophic groups. Thirdly, the biomass of nine trophic group showed significant non-linear relationships with human population density. However, clearer linear biomass reductions with increasing human population were only evident in four trophic groups spanning piscivores to herbivores. This indicates protected and fished areas in close proximity to high human population densities are likely to have low biomass of key trophic groups, particularly piscivores, plankivores, large- and small excavators (Cinner et al., 2013; Robinson et al., 2017). These results illustrate the value of remote highly protected areas (Graham et al., 2013; Samoilys et al., 2018; Cinner et al., 2020) in illuminating the effects of protection of coral reefs in the WIO region.

4.1 Implications of size-spectra indicators

A high proportion of small fish was found in highly protected areas, inconsistent with expected size spectra slopes of minimally populated areas. This potentially reflects removal of meso-predators by top-predators or previous fishing effects leading to prey release (Stallings, 2009; Sandin et al., 2010). Indeed, a previous study in the Chagos Archipelago noted fewer large-sized *Epinephelus* spp. groupers in 2014, which was attributed to lag effects of a previous handline fishery that closed in 2010 (Samoilys et al., 2018). Given a four-year period may not be adequate to allow recovery, this could explain why high and well protected sites showed similar results. While relatively larger fish occurred in highly protected areas compared to moderately protected and fished areas, their influence on shallowing the size-spectra slopes was overwhelmed by the exceptionally high abundance of small fish. This suggests that processes other than exploitation, may be driving fish abundance and increasing the proportions of small fish.

Steeper size-spectra slopes reflect fewer large-sized individuals, more small fish, or a combination of both (Wilson et al., 2010). In this study, steeper size-spectra slopes were seen in highly and well-protected areas and were due to relatively high densities of small fish, which occurs when the majority of small fish that would usually be composed of juveniles of larger fish species are protected (Russ et al., 2018). While the size spectra result in this study represented the community level processes, it is possible that the proportion of large individuals acting as parental stocks in highly and well-protected areas is sufficient to support and maintain a high abundance of small fish. This could indicate that processes such as recruitment rates, are propelling fish abundance (Russ et al., 2018) thereby increasing the densities of small fish. Accordingly, the shallower slopes in moderately protected and fished areas could suggest lower rates of juvenile recruitment, which is a concern for sustainability of the fish populations in these areas (Graham et al., 2007; Russ et al., 2018). Therefore, implementation of well-enforced MPAs will be critical in enhancing recruitment and supporting the long-term viability of reef fish populations in the WIO region.

Greater fish productivity overall also occurred in highly and well-protected areas. This can be linked to several key factors in these areas: high compliance to management rules, remoteness, low human population densities and reef condition. Fishing removes target species, changing community size structure and overall fish biomass (Zgliczynski and Sandin, 2017). High exploitation rates are expected in densely populated areas such as those next to moderately protected sites in Tanzania, and fished sites in Madagascar and Comoros, posing a management challenge, particularly where the use of destructive and indiscriminate fishing methods and poaching occurs (Mwaipopo, 2008). Interestingly, some fished sites in Mozambique grouped with sites under well- and moderately protected regimes suggesting their potential to support high fish productivity possibly due to use of low-technology and sustainable artisanal fishing gears (Osuka et al., 2020).

Collectively, the size-spectra results suggest that fisheries may not influence the slope as expected but could reduce overall productivity. This could either be because the fisheries target all fish and not only larger fish, or the fisheries have impacted ecosystem condition and productivity by removing key species or using destructive methods.

4.2 Influence of protection on trophic groups

Moderately protected areas showed low biomass within a wide range of trophic groups, which is a conservation concern for the MPAs in the WIO. Indeed, moderately protected areas exhibited no significant benefits to any fish trophic groups. This is important and alarming, as it indicates that the lack of effective management regulations in well-protected areas can drastically reduce the biomass to levels equivalent or lower than those found in fished areas. Since larger fish in moderately protected areas are generally fished out first (McClanahan and Mangi, 2000), overall fish productivity is also expected to reduce.

Highly protected areas were effective in sustaining high biomass of piscivores, which can exert top-down control on fish of lower trophic levels. Similarly, highly protected areas had higher biomass of omnivores than fished areas. The lack of apparent differences in the biomass of two key fishery target trophic groups (piscivores and omnivores) between well-protected, moderately protected and fished areas suggest that these groups may require highly protected MPAs to thrive (Edgar et al., 2014; MacNeil et al., 2020).

The biomass of planktivorous fish was also particularly high in highly protected areas compared to other protection levels within the WIO. Planktivorous fish rely on allochthonous planktonic food materials including pelagic zooplankton, and are more abundant in exposed reef areas, where suspended food levels are high (McLachlan and Defeo, 2017). The high biomass in highly protected areas in this study may have been driven by the high abundance of pelagic zooplankton resulting from upwelling along the Seychelles-Chagos ridge (Sheppard et al., 2012). Significant inter-atoll differences in planktivores have been reported in these areas (Samoilys et al., 2018) and such localised processes coupled with fishing effects are important in understanding the dynamics in abundance of planktivorous fishes.

The overall biomass of herbivorous fish was consistently low in moderately protected areas. In particular, scrapers were more than four-fold lower in moderately protected than well-protected areas. Since herbivores are critical for enhancing reef resilience through regulating competition between algae and corals, their loss in moderately protected areas may increase algal dominance and associated ecological phase shifts and reef-scale productivity (Hughes et al., 2007). Such a risk can be counteracted through management measures that protect and increase the abundance and biomass of small-bodied herbivores (Kuempel and Altieri, 2017).

4.3 Influence of human population on trophic groups

Local human population densities appear to be a key driver of the coral reef fish biomass patterns found in the WIO. Fisheries target trophic groups such as piscivores and omnivores are sensitive to fishing pressure, and where human population density is high, their biomass can reduce significantly, leading to cascading impacts on ecosystem functioning and triggering loss of functional roles (Zgliczynski and Sandin, 2017). The ultimate outcome of a reduction in biomass of piscivores can be changes in food web interactions that result in prey release (Sandin et al., 2010). Equally, in populated areas, planktivorous fishes experience increased fishing pressure (McClure et al., 2021) and would need protection to maintain a high biomass especially when ecological drivers such as upwelling shift or fail (Jacobs et al., 2020).

Within herbivorous fishes, large- and small excavators showed a significant decrease in biomass with increasing human population density. This demonstrates susceptibility of herbivores to fishing, though in heavily populated areas, various sub-trophic groups particularly detritivores, scrapers and grazers can show increased biomass per reef area. The different patterns reflect the importance of both physical (such as reef type and reef area) and human (such as fishing pressure and market demand) factors (Cinner et al., 2013; Heenan et al 2016; McClure et al., 2021) in shaping herbivorous fish biomass. The high biomass of detritivores in heavily populated areas points to a reef system in an altered ecosystem condition having a high cover of rubble and organic matter in sediment and reef surface (Tebbett et al., 2017). Taken together, our findings suggest that maintenance and in turn restoration of key trophic groups requires high levels of protection while ensuring fishers livelihood needs are met (Cinner et al., 2013; MacNeil et al., 2020). This can be challenging as many locations become more populated therefore calling for effective multiple-use zones that could balance protection goals and human uses.

4.4 Role of MPAs and No-take zones

Small-sized fish may be responsible for fuelling reef trophodynamics and maintaining high community biomass (Brandl et al., 2019). A high biomass of small-sized trophic groups, notably planktivores, small-excavators, grazers and scrapers occurred in remote highly protected areas, indicating the benefits of well-enforced MPAs in protecting small fish. These benefits were also visible in well-protected areas where human population density was relatively low. Moderately protected areas were less effective in supporting high biomass of most invertivores, large excavators and scrapers. Invertivores feed on coral competitors such as soft corals and invertebrates (Kramer et al., 2015), while large excavators and scrapers play considerable roles in bioerosion and removal of algae, sediment and other material from reef substrate. Therefore, the low biomass of invertivores and herbivorous fishes in moderately protected areas is a concern for reef resilience (Jouffray et al., 2015) given feeding on coral competitors can prevent the substrate from being overgrown by macroalgae thus allowing coral recruits to settle. The low biomass in moderately protected areas is similar to a study in Kenya that found Reserve MPAs (where fishing using traditional gears is allowed) were inadequate for maintaining or restoring reef fishes compared with no-take Park MPAs (Samoilys et al., 2017). Indeed, moderately protected areas in Mnazi Bay have experienced dynamite fishing in the past (Mwaipopo, 2008), which caused coral reef destruction and overexploitation of fishes (Wells, 2009). Thus, recovery of parental fish stocks from such historic pressures is likely to take several years.

Overall, our results highlight the ever greater need to invest in MPAs and strengthen and support management regimes, particularly for the moderately protected MPAs, and within areas of high human population density. As more MPAs are expected to be established to meet the Convention of Biodiversity (CBDs) 30% by 2030 targets (CBD, 2021), our findings suggest that biodiversity conservation targets are more likely not to be met unless an expansion of MPAs in populated areas, is accompanied by changes in human behaviour reducing impacts on marine resources. Ensuring high levels of protection and effective MPA networks in the WIO region can help realise the benefits observed in highly protected areas. Coral reefs occurring in well-protected and in lightly populated locations in the WIO are associated with high fish biomass of key trophic groups, which in turn support coastal fishing communities (Chirico et al., 2017; Ban et al., 2019). Increasing community support for MPAs through measures that encourage compliance to management rules and addressing fish demand aspects related to high fishing pressure can help improve effectiveness of MPAs and also restore the functional roles played by different trophic groups. This will increase the resilience of coral reef fish communities and contribute towards sustainable livelihood security.

Acknowledgements

We are grateful to different grants to CORDIO East Africa and Bangor University that funded the field surveys including the Marine Science for Management Programme of the Western Indian Ocean Marine Science Association (WIOMSA: MASMA/OR/2008/05), Conservation International (CI) in Madagascar, the European Union’s Biodiversity Management Programme in Mozambique (DCI-ENV/2013/323-897) and DEFRA Darwin Initiative grant 19-027 in Chagos Archipelago. KEO was funded by CORDIO East Africa through grants from the SOLSTICE-WIO project and Norwegian agency for development cooperation (Norad), Perivoli Foundation and Dev Joory. We are grateful to Callum Roberts for his critical review of an early draft.

References

Andréfoüet, S., Chagnaud, N. and Kranenburg, C.J., 2009. Atlas of Western Indian Ocean Coral Reefs. Centre IRD de Noum´ea, New-Caledonia.

Ban, N.C., Gurney, G.G., Marshall, N.A., Whitney, C.K., Mills, M., Gelcich, S., Bennett, N. J., Meehan, M.C., Butler, C., Ban, S. and Tran, T.C., 2019. Well-being outcomes of marine protected areas. *Nat. Sustain*. 2 (6), 524–532. https://doi.org/10.1038/ s41893-019-0306-2.

Bellwood, D.R., Streit, R.P., Brandl, S.J. and Tebbett, S.B., 2019. The meaning of the term 'function'in ecology: a coral reef perspective. *Funct. Ecol.* 33 (6), 948–961. https:// doi.org/10.1111/1365-2435.13265.

Brandl, S.J., Tornabene, L., Goatley, C.H., Casey, J.M., Morais, R.A., Côté, I.M., Baldwin, C.C., Parravicini, V., Schiettekatte, N.M. and Bellwood, D.R., 2019. Demographic dynamics of the smallest marine vertebrates fuel coral reef ecosystem functioning. *Science*, *364*(6446), pp.1189-1192. https://doi.org/10.1126/science.aav3384.

Chirico, A.A., McClanahan, T.R. and Eklöf, J.S., 2017. Community-and government-managed marine protected areas increase fish size, biomass and potential value. *PloS one* 12 (8), e0182342. https://doi.org/10.1371/journal.pone.0182342.

Cinner, J.E., Graham, N.A., Huchery, C. and MacNeil, M.A., 2013. Global effects of local human population density and distance to markets on the condition of coral reef fisheries. *Conserv. Biol*. 27 (3), 453–458. https://doi.org/10.1111/j.1523- 1739.2012.01933.x.

Cinner, J.E., Maire, E., Huchery, C., MacNeil, M.A., Graham, N.A., Mora, C., McClanahan, T.R., Barnes, M.L., Kittinger, J.N., Hicks, C.C. and D'agata, S., 2018. Gravity of human impacts mediates coral reef conservation gains. *Proc. Natl. Acad. Sci.* 115 (27), E6116–E6125. https://doi.org/ 10.1073/pnas.1708001115.

Cinner, J.E., Zamborain-Mason, J., Gurney, G.G., Graham, N.A., MacNeil, M.A., Hoey, A.S., Mora, C., Villéger, S., Maire, E., McClanahan, T.R. and Maina, J.M., 2020. Meeting fisheries, ecosystem function, and biodiversity goals in a human-dominated world. *Science* 368 (6488), 307–311.

Clarke, K.R. and Gorley, R.N., 2006. User manual/tutorial. *Primer-E Ltd.,* Plymouth Marine Laboratory, 93

Convention on Biological Diversity, 2021. In: First Draft of the Post-2020 Global Biodiversity Framework CBD/WG2020/3/3, p. 12.

Daan, N., Gislason, H., G. Pope, J. C. and Rice, J., 2005. Changes in the North Sea fish community: evidence of indirect effects of fishing? *ICES J. Mar. Sci.* 62 (2), 177–188. https://doi.org/10.1016/j.icesjms.2004.08.020.

Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T., Berkhout, J. and Buxton, C.D., 2014. Global conservation outcomes depend on marine protected areas with five key features. *Nature* 506 (7487), 216–220. https://doi.org/10.1038/ nature13022.

Gill, D.A., Mascia, M.B., Ahmadia, G.N., Glew, L., Lester, S.E., Barnes, M., Craigie, I., Darling, E.S., Free, C.M., Geldmann, J. and Holst, S., 2017. Capacity shortfalls hinder the performance of marine protected areas globally. *Nature*, *543*(7647), 665–669. https://doi.org/10.1038/nature21708.

Graham, N.A.J., Dulvy, N.K., Jennings, S. and Polunin, N.V.C., 2005. Size-spectra as indicators of the effects of fishing on coral reef fish assemblages. *Coral Reefs* 24 (1), 118–124. https://doi.org/10.1007/s00338-004-0466-y.

Graham, N.A., Wilson, S.K., Jennings, S., Polunin, N.V., Robinson, J.A.N., Bijoux, J.P. and Daw, T.M., 2007. Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. *Conserv. Biol.* 21 (5), 1291–1300. https://doi.org/ 10.1111/j.1523-1739.2007.00754.x.

Graham, N.A., Pratchett, M.S., McClanahan, T.R. and Wilson, S.K., 2013. The status of coral reef fish assemblages in the Chagos Archipelago, with implications for protected area management and climate change. *In*: Sheppard, C.R.C. (Ed.), Coral reefs of the United Kingdom overseas territories. Springer, Dordrecht, pp. 253–270.

Green, A.L., Fernandes, L., Almany, G., Abesamis, R., McLeod, E., Aliño, P.M., White, A.T., Salm, R., Tanzer, J. and Pressey, R.L., 2014. Designing marine reserves for fisheries management, biodiversity conservation, and climate change adaptation. *Coast. Manag.* 42 (2), 143–159. https://doi.org/10.1080/08920753.2014.877763.

Guiet, J., Poggiale, J.C. and Maury, O., 2016. Modelling the community size-spectrum: recent developments and new directions. *Ecol. Model.* 337, 4–14. https://doi.org/ 10.1016/j.ecolmodel.2016.05.015.

Halpern, B.S., 2003. The impact of marine reserves: do reserves work and does reserve size matter? *Ecol. Appl.* 13 (sp1), 117–137.

Heenan, A., Hoey, A.S., Williams, G.J. and Williams, I.D., 2016. Natural bounds on herbivorous coral reef fishes. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1843), p.20161716.

Hoegh-Guldberg, O., Kennedy, E.V., Beyer, H.L., McClennen, C. and Possingham, H.P., 2018. Securing a long-term future for coral reefs. *Trends Ecol. Evol.* 33 (12), 936–944. https://doi.org/10.1016/j.tree.2018.09.006.

Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwskyj, N., Pratchett, M.S., Steneck, R.S. and Willis, B., 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr. Biol.* 17 (4), 360–365.

IUCN, 2004. IUCN Eastern African Regional Programme, Nairobi.

Jacobs, Z.L., Jebri, F., Srokosz, M., Raitsos, D.E., Painter, S.C., Nencioli, F., Osuka, K., Samoilys, M., Sauer, W., Roberts, M., Taylor, S.F., Scott, L., Kizenga, H. and Popova, E., 2020. A major ecosystem shift in coastal East African waters during the 1997/98 Super El Niño as detected using remote sensing data. *Remote Sensing*, *12*(19), p.3127. https://doi.org/10.3390/ rs12193127.

Jouffray, J.B., Nystr¨om, M., Norstr¨om, A.V., Williams, I.D., Wedding, L.M., Kittinger, J. N. and Williams, G.J., 2015. Identifying multiple coral reef regimes and their drivers across the Hawaiian archipelago. *Philos.Trans.R.Soc.B Biol.Sci*. 370 (1659), 20130268. https://doi.org/10.1098/rstb.2013.0268.

Kough, A.S., Belak, C.A., Paris, C.B., Lundy, A., Cronin, H., Gnanalingam, G., Hagedorn, S., Skubel, R., Weiler, A.C. and Stoner, A.W., 2019. Ecological spillover from a marine protected area replenishes an over-exploited population across an island chain. *Conserv. Sci. Pract*. 1 (3), e17 https://doi.org/10.1111/csp2.17.

Kramer, M.J., Bellwood, O., Fulton, C.J. and Bellwood, D.R., 2015. Refining the invertivore: diversity and specialisation in fish predation on coral reef crustaceans. *Mar. Biol.* 162 (9), 1779–1786. https://doi.org/10.1007/s00227-015-2710-0.

Kuempel, C.D. and Altieri, A.H., 2017. The emergent role of small-bodied herbivores in pre-empting phase shifts on degraded coral reefs. *Sci. Rep.* 7, 39670.

Lester, S.E. and Halpern, B.S., 2008. Biological responses in marine no-take reserves versus partially protected areas. *Mar. Ecol. Prog. Ser.* 367, 49–56. https://doi.org/10.3354/ meps07599.

MacNeil, M.A., Chapman, D.D., Heupel, M., Simpfendorfer, C.A., Heithaus, M., Meekan, M., Harvey, E., Goetze, J., Kiszka, J., Bond, M.E. and Currey-Randall, L.M., 2020. Global status and conservation potential of reef sharks. *Nature*, *583*(7818), pp.801-806. https://doi.org/10.1038/s41586-020-2519-y.

McClanahan, T.R. and Mangi, S., 2000. Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. *Ecol. Appl.* 10 (6), 1792–1805. https://doi.org/ 10.1890/1051-0761(2000)010[1792:SOEFFA]2.0.CO;2.

McClanahan, T.R., Graham, N.A., Calnan, J.M. and MacNeil, M.A., 2007. Toward pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. *Ecol. App* 17 (4), 1055–1067.

McClanahan, T.R., Graham, N.A., MacNeil, M.A., Muthiga, N.A., Cinner, J.E., Bruggemann, J.H. and Wilson, S.K., 2011. Critical thresholds and tangible targets for ecosystem-based management of coral reef fisheries. *Proc. Natl. Acad. Sci.* 108 (41), 17230–17233. https://doi.org/10.1073/pnas.1106861108.

McClanahan, T.R., Schroeder, R.E., Friedlander, A.M., Vigliola, L., Wantiez, L., Caselle, J.E., Graham, N.A., Wilson, S., Edgar, G.J., Stuart-Smith, R.D. and Oddenyo, R.M., 2019. Global baselines and benchmarks for fish biomass: comparing remote reefs and fisheries closures. *Mar. Ecol. Prog. Ser.* 612, 167–192. https://doi.org/10.3354/meps12874.

McClanahan, T.R., Friedlander, A.M., Graham, N.A., Chabanet, P. and Bruggemann, J.H., 2020. Variability in coral reef fish baseline and benchmark biomass in the central and western Indian Ocean provinces. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* https://doi.org/10.1002/aqc.3448.

McClure, E.C., Hoey, A.S., Sievers, K.T., Abesamis, R.A. and Russ, G.R., 2021. Relative influence of environmental factors and fishing on coral reef fish assemblages. Conserv. Biol. 35 (3), 976–990. https://doi.org/10.1111/cobi.13636.

McLachlan, A. and Defeo, O., 2017. The ecology of sandy shores. UK, Academic Press, London, p. 572.

Mellin, C., MacNeil, A.M., Cheal, A.J., Emslie, M.J. and Caley, J.M., 2016. Marine protected areas increase resilience among coral reef communities. *Ecol. Lett.* 19 (6), 629–637. https://doi.org/10.1111/ele.12598.

Molloy, P.P., McLean, I.B. and Cote, I.M., 2009. Effects of marine reserve age on fish populations: a global meta analysis. *J. Appl. Ecol.* 46, 743–751. https://doi.org/ 10.1111/j.1365-2664.2009.01662.x.

Mwaipopo, N.R., 2008. International Collective in Support of Fishworkers, Dar es Salaam, Tanzania.

Ojea, E., Pearlman, I., Gaines, S.D. and Lester, S.E., 2017. Fisheries regulatory regimes and resilience to climate change. *Ambio* 46 (4), 399–412. https://doi.org/10.1007/s13280-016-0850-1.

Osuka, K., Kochzius, M., Vanreusel, A., Obura, D. and Samoilys, M., 2018. Linkage between fish functional groups and coral reef benthic habitat composition in the Western Indian Ocean. *J. Mar. Biol. Assoc. UK*. 98 (2), 387–400. https://doi.org/10.1017/S0025315416001399.

Osuka, K., Rosendo, S., Riddell, M., Huet, J., Daide, M., Chauque, E. and Samoilys, M., 2020. Applying a social-ecological systems approach to understanding local marine management trajectories in Northern Mozambique. *Sustainability* 12 (9), 3904.

Parravicini, V., Casey, J.M., Schiettekatte, N.M., Brandl, S.J., Pozas-Schacre, C., Carlot, J., Edgar, G.J., Graham, N.A., Harmelin-Vivien, M., Kulbicki, M. and Strona, G., 2020. Global gut content data synthesis and phylogeny delineate reef fish trophic guilds. *bioRxiv*. https://doi.org/10.1101/2020.03.04.977116.

Petchey, O.L. and Belgrano, A., 2010. Body-size distributions and size-spectra: universal indicators of ecological status? *Biol. Lett.* https://doi.org/10.1098/rsbl.2010.0240.

Polishchuk, L.V. and Blanchard, J.L., 2019. Uniting discoveries of abundance-size distributions from soils and seas. *Trends Ecol. Evol.* 34 (1), 2–5. https://doi.org/10.1016/j.tree.2018.10.007.

Pratchett, M.S., Hoey, A.S., Wilson, S.K., Messmer, V. and Graham, N.A., 2011. Changes in biodiversity and functioning of reef fish assemblages following coral bleaching and coral loss. *Diversity* 3 (3), 424–452. https://doi.org/10.3390/d3030424.

Reynolds, J.D., Dulvy, N.K., Goodwin, N. B and Hutchings, J.A., 2005. Biology of extinction risk in marine fishes. *Proc. Royal Soc. B* 272 (1579), 2337–2344.

Richardson, L.E., Graham, N.A., Pratchett, M.S., Eurich, J.G. and Hoey, A.S., 2018. Mass coral bleaching causes biotic homogenization of reef fish assemblages. *Glob. Chang. Biol.* 24 (7), 3117–3129. https://doi.org/10.1111/gcb.14119.

Roberts, C.M., O'Leary, B.C., McCauley, D.J., Cury, P.M., Duarte, C.M., Lubchenco, J. and Worm, B., 2017. Marine reserves can mitigate and promote adaptation to climate change. *Proc. Natl. Acad. Sci.* 114 (24), 6167–6175. https://doi.org/10.1073/pnas.1701262114.

Robinson, J.P., Williams, I.D., Edwards, A.M., McPherson, J., Yeager, L., Vigliola, L. and Baum, J.K., 2017. Fishing degrades size structure of coral reef fish communities. *Glob. Chang. Biol.* 23 (3), 1009–1022. https://doi.org/10.1111/gcb.13482.

Robinson, J.P., McDevitt-Irwin, J.M., Dajka, J.C., Hadj-Hammou, J., Howlett, S., Graba-Landry, A., Hoey, A.S., Nash, K.L., Wilson, S.K. and Graham, N.A., 2020. Habitat and fishing control grazing potential on coral reefs. *Funct. Ecol.* 34 (1), 240–251. https://doi.org/10.1111/1365- 2435.13457.

Russ, G.R., Alcala, A.C., Maypa, A.P., Calumpong, H.P. and White, A.T., 2004. Marine reserve benefits local fisheries. *Ecol. Appl.* 14 (2), 597–606. https://doi.org/10.1890/03-5076.

Russ, G.R., Payne, C.S., Bergseth, B.J., Rizzari, J.R., Abesamis, R.A. and Alcala, A.C., 2018. Decadal-scale response of detritivorous surgeonfishes (family Acanthuridae) to no-take marine reserve protection and changes in benthic habitat. *J. Fish Biol.* 93 (5), 887–900. https://doi.org/10.1111/jfb.13809.

Samoilys, M. and Randriamanantsoa, B., 2011. Reef fishes of northeast Madagascar. In: Obura, D., Carlo, G. Di and Rabearisoa, A. (Eds.), A Rapid Marine Biodiversity Assessment of the coral reefs of northeast Madagascar. RAP Bull Biol Assessment, 61. Conservation International, Arlington, VA, pp. 29–39.

Samoilys, M.A., Osuka, K., Maina, G.W., Obura, D.O., 2017. Artisanal fisheries on Kenya's coral reefs: decadal trends reveal management needs. *Fish. Res.* 186, 177–191. https://doi.org/10.1016/j.fishres.2016.07.025.

Samoilys, M., Roche, R., Koldewey, H. and Turner, J., 2018. Patterns in reef fish assemblages: insights from the Chagos archipelago. *PloS one* 13 (1), e0191448. https://doi.org/10.1371/journal.pone.0191448.

Samoilys, M.A., Halford, A. and Osuka, K., 2019. Disentangling drivers of the abundance of coral reef fishes in the Western Indian Ocean. *Ecol. Evol*. 9 (7), 4149–4167. https:// doi.org/10.1002/ece3.5044.

Sandin, S.A., Walsh, S.M. and Jackson, J.B., 2010. Prey release, trophic cascades, and phase shifts in tropical nearshore marine ecosystems. In: Terborgh, J., Estes, J.A. (Eds.), Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature. Island Press, Washington, DC, pp. 71–90.

Sheppard, C.R., Ateweberhan, M., Bowen, B.W., Carr, P., Chen, C.A., Clubbe, C. and Gaither, M.R., 2012. Reefs and islands of the Chagos Archipelago, Indian Ocean: why it is the world's largest no-take marine protected area. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* 22 (2), 232–261. https://doi.org/10.1002/aqc.1248.

Shin, Y.J., Rochet, M.J., Jennings, S., Field, J.G. and Gislason, H., 2005. Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES J. Mar. Sci.* 62 (3), 384–396. https://doi.org/10.1016/j.icesjms.2005.01.004.

Stallings, C.D., 2009. Predator identity and recruitment of coral-reef fishes: indirect effects of fishing. *Mar. Ecol.-Prog. Ser.* 383, 251–259. https://doi.org/10.3354/ meps08004.

Taylor, B.M., Lindfield, S.J. and Choat, J.H., 2015. Hierarchical and scale-dependent effects of fishing pressure and environment on the structure and size distribution of parrotfish communities. *Ecography* 38 (5), 520–530. https://doi.org/10.1111/ ecog.01093.

Tebbett, S.B., Goatley, C.H. and Bellwood, D.R., 2017. Clarifying functional roles: algal removal by the surgeonfishes *Ctenochaetus striatus* and *Acanthurus nigrofuscus. Coral Reefs* 36 (3), 803–813. https://doi.org/10.1007/s00338-017-1571-z.

Wells, S., 2009. Dynamite fishing in northern Tanzania–pervasive, problematic and yet preventable. *Mar. Pollut. Bull.* 58 (1), 20–23. https://doi.org/10.1016/j. marpolbul.2008.09.019.

Williams, I.D., Baum, J.K., Heenan, A., Hanson, K.M., Nadon, M.O. and Brainard, R.E., 2015. Human, oceanographic and habitat drivers of central and western Pacific coral reef fish assemblages. *PLoS One* 10 (4), e0120516. https://doi.org/10.1371/journal. pone.0120516.

Wilson, S.K., Fisher, R., Pratchett, M.S., Graham, N.A.J., Dulvy, N.K., Turner, R.A., Cakacaka, A. and Polunin, N.V., 2010. Habitat degradation and fishing effects on the size structure of coral reef fish communities. *Ecol. Appl.* 20 (2), 442–451. https://doi. org/10.1890/08-2205.1.

Yeager, L.A., Marchand, P., Gill, D.A., Baum, J.K. and McPherson, J.M., 2017. Marine socio-environmental covariates: queryable global layers of environmental and anthropogenic variables for marine ecosystem studies. *Ecology* 98 (7), 1976. https:// doi.org/10.1002/ecy.1884.

Zar, J.H., 1999. Biostatistical Analysis, 4th ed. Prentice-Hall Inc., New Jersey.

Zgliczynski, B.J. and Sandin, S.A., 2017. Size-structural shifts reveal intensity of exploitation in coral reef fisheries. *Ecol. Indic.* 73, 411–421. https://doi.org/10.1016/j. ecolind.2016.09.045.

CHAPTER 3

CHARACTERISTICS OF SHALLOW AND MESOPHOTIC ENVIRONMENTS OF THE PEMBA CHANNEL, TANZANIA: IMPLICATIONS FOR MANAGEMENT AND CONSERVATION

3.1 Preface

There has been little research in many deeper marine habitats due to the challenges associated with the high ship-based costs, logistics and low-capacity (Wölfl et al., 2019). In particular, Mesophotic Coral Ecosystems (MCEs) in the Western Indian Ocean (WIO) are some of the most understudied marine ecosystems of the world (Laverick et al., 2018; Pyle and Copus, 2019). As such the conservation importance of MCEs and their linkages with shallow biotopes remain unclear.

In this chapter I describe and model substrates types and benthic communities in the shallow to mesophotic depths (5-150 m) using bathymetric, backscatter and photographic data collected by autonomous underwater vehicle (AUV) deployed at four selected sites of interest on the south west of Pemba Channel.

This chapter was written in the style of Ocean and Coastal Management and was published in February 2021. The paper is available at https://doi.org/10.1016/j.ocecoaman.2020.105463.

I declare that the work submitted is my own. The contribution by co-authors was as follows:

Bryce Stewart and Colin McClean: Supervision, review and editing.

John Howe, Colin Abernerthy, Brian J. Bett, Tim Le Bas and Saleh Yahya: Directed the AUV and technical operations, deployment and retrieval of the AUV support, support with processing of backscatter and bathymetry datasets

David Obura and Melita Samoilys: Funding, review and editing

3.2 References

Laverick, J.H., Piango, S., Andradi-Brown, D.A., Exton, D.A., Bongaerts, P., Bridge, T.C., Lesser, M.P., Pyle, R.L., Slattery, M., Wagner, D. and Rogers, A.D., 2018. To what extent do mesophotic coral ecosystems and shallow reefs share species of conservation interest? A systematic review. *Environmental Evidence*, *7*(1), pp.1-13.

Pyle, R.L. and Copus, J.M., 2019. Mesophotic coral ecosystems: introduction and overview. *In:* Loya, Y., Puglise, K.A., Bridge, T.C.L. (Eds.), Mesophotic Coral Ecosystems. Springer, Cham, pp. 3–27.

Wölfl, A.C., Snaith, H., Amirebrahimi, S., Devey, C.W., Dorschel, B., Ferrini, V., Huvenne, V.A., Jakobsson, M., Jencks, J., Johnston, G. and Lamarche, G., 2019. Seafloor mapping–the challenge of a truly global ocean bathymetry. *Frontiers in Marine Science*, *6*, p.283.

CHARACTERISTICS OF SHALLOW AND MESOPHOTIC ENVIRONMENTS OF THE PEMBA CHANNEL, TANZANIA: IMPLICATIONS FOR MANAGEMENT AND CONSERVATION

Kennedy E. Osuka[1, 2, *]; Colin McClean[2], Bryce Stewart[2], Brian J. Bett[3], Tim Le Bas[3], John Howe[4], Colin Abernerthy[4], Saleh Yahya[5], David Obura[1] and Melita Samoilys[1]

Affiliations

[1.] Coastal Oceans Research and Development – Indian Ocean (CORDIO East Africa). 9 Kibaki Flats P.O. Box 10135-80101, Mombasa, Kenya

[2.] Department of Environment and Geography, University of York, Heslington, York, YO10 5NG, United Kingdom

[3.] National Oceanography Centre, Southampton, SO14 3ZH, United Kingdom

[4.] Scottish Association for Marine Science, Dunbeg, Oban, PA37 1QA, United Kingdom

[5.] Institute of Marine Sciences, Zanzibar, Tanzania

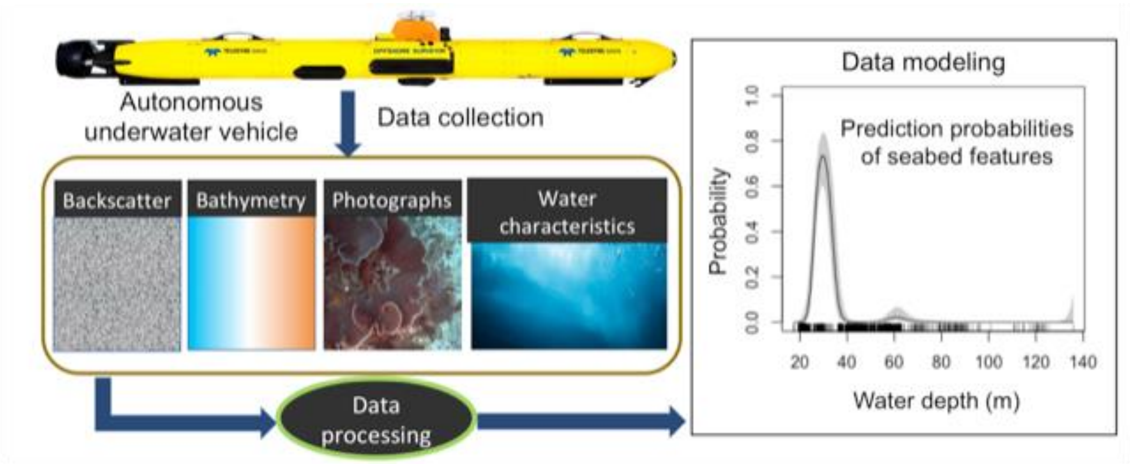
* Corresponding author.

E-mail address: koe503@york.ac.uk (K.E. Osuka).

Abstract

Information on the spatial distribution of habitats and vulnerable species is important for conservation planning. In particular, detailed knowledge on connectivity of marine ecosystems in relation to depth and seafloor characteristics is crucial for any proposed conservation and management actions. Yet, the bulk of the seafloor remains under-sampled, unstudied and unmapped, thereby limiting our understanding of connections between shallow and deep-water communities. Recent studies on mesophotic coral ecosystems (MCEs) have highlighted the Western Indian Ocean as a particularly understudied marine region. Here we utilise an autonomous underwater vehicle (AUV) to collect in-situ temperature, oxygen concentration, bathymetry, acoustic backscatter and photographic data on benthic communities from shallow (<30 m) and mesophotic (30–150 m) depths at selected sites in the Greater Pemba Channel, Tanzania. Further, we use generalised additive models (GAMs) to determine useful predictors of substratum (hard and sand) and benthic community type (coral, turf algae, fleshy algae, fish). Our results revealed the presence of a complex seafloor characterised by pockmarks, steep slopes, submarine walls, and large boulders. Photographs confirmed the *presence of MCE composed of corals, algae and fishes on the eastern margins of the Pemba Channel. The GAMs on the presence and absence of benthic community explained 35%–91% of the deviance in fish and fleshy algae assemblages, respectively. Key predictors of the distribution of hard substrata and the coral reef communities were depth, showing the upper boundary of MCEs present at 30–40 m, and seafloor slope that showed more occurrences on steep slopes. The upper 100 m of water column had stable temperatures (25–26 °C) and oxygen concentrations (220–235 µmol/l). We noted the presence of submarine walls, steeply inclined bedrock, which appeared to support a highly bio-diverse community that may be worthy of particular conservation measures. Our results also highlight the capability of using marine robotics, particularly autonomous vehicles, to fill the knowledge gap for areas not readily accessible by divers or with surface vessels, and their potential application for the initial survey and subsequent monitoring of Marine Protected Areas*.

Graphical abstract



Keywords: Autonomous underwater vehicle; Mesophotic coral ecosystems; Bathymetry; Acoustic backscatter; Western Indian Ocean

1 Introduction

Coral reef ecosystems are characterised by a light dependent biotic community comprising corals, sponges, and algae, with associated fish species that are distributed from shallow (0–30 m) to mesophotic (30–150 m) depths. In the latter depth range they are typically referred to as Mesophotic Coral Ecosystems (MCEs) (Laverick et al., 2018; Pyle and Copus, 2019). MCEs are considered distinct from their shallow counterparts due to a decrease in light attenuation and temperature with increasing depth, resulting in a vertical zonation of community structure (Kahng et al., 2019). As such, MCEs can provide, to a variety of species, a refuge against high temperature (Kahng et al., 2019), which has significant impacts on shallow coral reef systems by causing massive coral bleaching and mortality, as evidenced in different Western Indian Ocean (WIO) locations (Obura et al., 2017; Gudka et al., 2019). MCEs are also important for the maintenance of biodiversity and, in some places, the provision of fisheries resources, or as a refuge from high fishing pressure in shallow waters (Tyler et al., 2009; Bongaerts et al., 2010; Pinheiro et al., 2016). As such, understanding distribution of organisms and habitat use is critical towards ensuring effective sustainable management of marine areas.

Nearly 10% of the global ocean floor is mapped (Wölfl et al., 2019). This is especially the case in the WIO region where water column and seafloor characteristics are under-sampled (Groeneveld et al., 2017). In particular, MCEs in the WIO are amongst the most understudied marine ecosystems of the world (Laverick et al., 2018; Pyle and Copus, 2019). This contrasts with the shallow coral ecosystems that in general have been adequately surveyed. The dichotomy in sampling effort stems from logistical and capacity challenges associated with accessing these ecosystems. Shallow coral ecosystems are easily accessible by SCUBA divers and have benefited from long-term monitoring programmes, particularly those set up after the 1998 El Niño event (Souter et al., 2000; Muhando, 2009). Data acquisition in deep areas is associated with high ship-based costs related to time and human resources (Wölfl et al., 2019), and a lack or limited access to technology. For instance, since the 1970s, there have been less than ten ship-based deep-sea surveys in Tanzania (Kaehler et al., 2008; Groeneveld and Koranteng 2017; Gates et al., 2021). In part, these surveys involved the deployment of remotely operated vehicles aimed at locating and filming coelacanths (*Latimeria chalumnae*) and their habitats. Nevertheless, information on the existence and spatial distribution of MCEs is underreported or non-existent, limiting any efforts in conservation planning especially in this era of increasing ocean temperatures (Bridge et al., 2012; Hoegh-Guldberg et al., 2018).

The potential importance of the WIO's mesophotic depths is indicated by the high fish biomass (1100 kg/ha) recorded on ocean-exposed fringing reefs that occur at the boundary between shallow and upper mesophotic depths (Samoilys et al., 2019; Osuka et al., 2021). However, given the limited number of surveys in the WIO, the extent and overall linkages between shallow and mesophotic systems remains unknown.

Unmanned, autonomous vehicles offer an alternative option for reducing the high operational costs and logistical challenges associated with surveying deeper waters (Wynn et al., 2014; Benoist et al., 2019). They can provide an improved mission safety and can undertake distant operations beyond the detection ranges of human observers (Verfuss et al., 2019). Water column vehicles, such as autonomous underwater vehicles (AUVs), have the ability to: survey greater depths (some being full ocean depth capable; see e.g., Durden et al., 2020), provide high spatial resolution data (0.1–0.5 m) on seabed properties and simultaneously collect data on water column properties, bathymetry, acoustic backscatter, and benthic habitats and species (Wynn et al., 2014; Huvenne et al., 2018). For these reasons, application of unmanned vehicles has increased rapidly in recent years and is now widely applied in remote seabed mapping and oceanography studies (Simon-Lledó et al., 2019), and the monitoring of Marine Protected Areas (MPAs) and wildlife (Verfuss et al., 2019; Benoist et al., 2019; Zelada Leon et al., 2020).

Seafloor and water column characteristics can help to predict the occurrence of biotic communities such as those composed of coral and algae (Sterne et al., 2019; Pörtner 2010). Abiotic predictors, such as water depth, seabed slope, rugosity, and aspect, influence the distribution of benthic communities and habitats (Wilson et al., 2007). Water depth has distinctive, and occasionally contrasting, associations with benthic communities. For example, scleractinian zooxanthellate corals are anticipated to reduce in abundance with increasing water depth (Stefanoudis et al., 2019). However, at greater depths (e.g., >30 m), the coral community (e.g., octocorals and antipatharians) can show a positive relationship with depth (Schmahl et al., 2008; Stefanoudis et al., 2019). Benthic communities also show well-established relationships with seafloor slope, rugosity, and plan curvature (Wedding and Friedlander, 2008). Slope is defined as steepness of seafloor surface and is useful in calculating slope of slope i.e., the rate of change in steepness, while rugosity describes the ruggedness of seafloor surface. Plan curvature refers to how sloping surfaces are shaped, whether concave, convex or linear, this influences the convergence and divergence of flow (Sterne et al., 2019).

Aspect denotes the direction a surface faces and can determine the direction of water flow over the seafloor as well as influence both the distribution of substratum types and benthic communities (Sterne et al., 2019). Thus, particular benthic community and substratum may occur where prevailing currents are low or high. Water column temperature and oxygen concentrations frequently show distinct relationships with water depth (Kahng et al., 2019). Both water temperature and oxygen concentration have significant physiological impacts on the organisms present (Pörtner, 2010), such that both absolute values and variability in these parameters can be critical in determining distribution and survival of organisms.

For the present study, we deployed a comparatively low-logistics autonomous underwater vehicle (AUV) (Hiller et al., 2012) at multiple sites in the Pemba Channel to collect baseline information on water column characteristics (temperature and oxygen), marine habitats and benthic communities from 5 to 150 m depths. Our aim was to increase the understanding of the distribution of habitats and benthic communities, and hence inform about their vulnerability and long-term sustainability. We hypothesised that substrata and benthic communities in the Greater Pemba Channel are structured according to water column and seafloor characteristics. These characteristics have either linear or non-linear effects on the availability of key substrata and broad taxa groups. We identify main substrata and benthic communities from AUV photographs and use bathymetry and acoustic backscatter data to model their distribution based on a set of predictive factors (water depth, acoustic backscatter, slope, slope of slope, plan curvature, rugosity and aspect). We further delineate the probable boundary of shallow and MCEs in the Pemba Channel.

2. Materials and methods

2.1. Study area

Pemba Island is part of the Zanzibar Archipelago, and is located about 50 km from mainland Tanzania. It is isolated from the mainland Tanzania by a deep-water channel and is classified as a true oceanic island (Archer and Turner, 1993). It is also surrounded by fringing reefs that cover an area of 222 km^2, representing ca. 9% of Tanzania's coral reefs (Klaus, 2014; Levin et al., 2018). The shallow reefs of Pemba Island show a broad range of reef conditions, with some reefs in healthy states and dominated by hard coral cover, while others are in a degraded state with low coral cover (Grimsditch et al., 2009). The western side of the island contains 60% of the islands' fringing reefs, which drop off rapidly into the deep water of the Pemba Channel.

Previous surveys have estimated that the coral cover averages 23% and ranges from 3% to 86%, with the highest coral cover and greatest diversity, 42 coral genera, occurring at Misali Island on the western fringe of the Pemba Archipelago (Grimsditch et al., 2009).

Sites were selected based variously on a preliminary towed side-scan survey, previous research of the shallow coral reef ecosystem (Grimsditch et al., 2009), information from key local knowledge on management and fishing pressure, and the prevailing sea state. The AUV was deployed at three sites located in the south west of Pemba Island (West Misali, South Misali, and Mkoani) and one site in the northwest sector of Unguja Island (Tumbatu Shoal) (Figure 1). The Pemba Island sites are all located within the Pemba Channel Conservation Area (PECCA) while Tumbatu Shoal is not subject to any form of management, although it neighbours the Tumbatu Island Marine Conservation Area (TUMCA).

2.2 Methods

A Teledyne Gavia Offshore Surveyor AUV '*Freya*' was used to survey seafloor and water column properties in depths between 5 and 150 m. The AUV was a modular vehicle consisting of camera, geoswath, control and command centre, and science bay (Table 1). It collected data on bathymetry, backscatter and benthic communities following methods described in Howe et al. (2019). Bathymetry provided information on water depth, backscatter indicated sediment grain-size and seafloor roughness, while benthic community was assessed from photographs captured by the AUV.

The AUV was variously operated in three primary modes: (a) for seafloor mapping, the vehicle was programmed to survey from 10 m above the seafloor for ca. 2-hours, giving a 30 m swath width and a resolution of 0.1 m; (b) for detailed seabed photography, the vehicle was programmed to survey from 2 m above the seafloor for ca. 1-hour; (c) for an oceanographic survey, the vehicle was programmed to profile the water column between 5 and 150 m (Table 2). The surveys were conducted over three days in July 2019, covering a total distance of 75 km, with a total underwater duration of 13 h. All operations were carried out from the RV Angra Pequena. During AUV missions, a SonTek [YSI] CastAway-CTD was used to collect additional water column conductivity, temperature, and depth (CTD) profiles (Supplementary Material Table S1). These measurements, together with the AUV's on-board sound velocity probe, were used to calculate the speed of sound in water. Progress of the AUV missions was closely checked using Ultra-Short Base line pinger, which received signals up to 2 km away from the surface vessel.

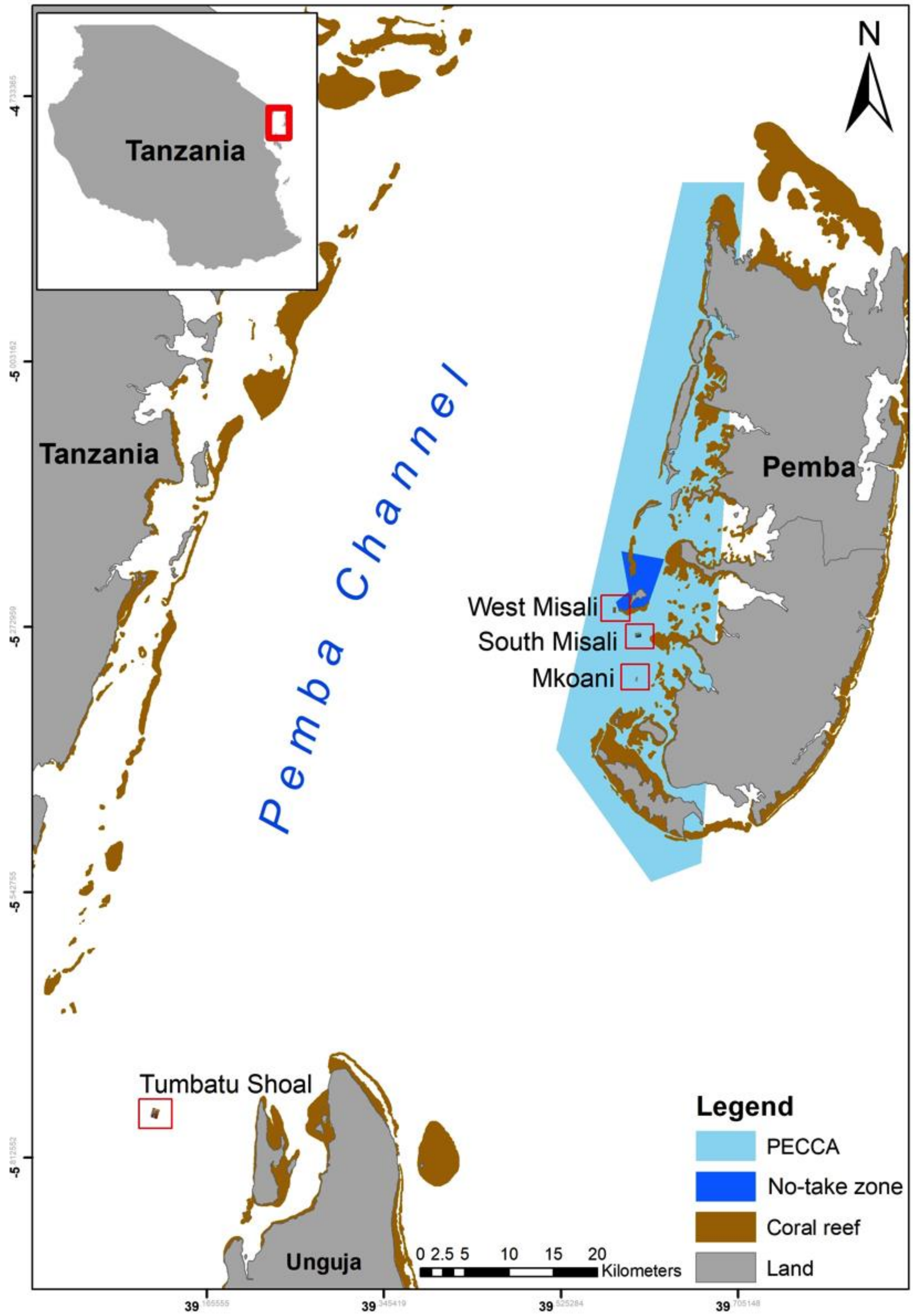


Figure 1: Greater Pemba Channel area, showing where the autonomous underwater vehicle (AUV) was deployed: West Misali, South Misali, Mkoani, and Tumbatu Shoal. PECCA: Pemba Channel Conservation Area, a Marine Protected Area.

Table 1: Autonomous underwater vehicle configuration characteristics.

Module	Function	Data type
Nosecone (camera)	Camera (FLIR [Point Grey] Grasshopper, Sony ICX285 CCD sensor) with a strobe, providing seabed images.	.jpg
GeoSwath Plus Sonar	500 kHz interferometric sonar (Kongsberg GeoAcoustics), providing bathymetric and acoustic backscatter data.	.rdf
Control and Command Centre	Provide commands and storage of data.	KML, KMZ, Log
Science Bay	Conductivity (salinity), temperature, and depth (CTD; Seabird SBE-49) sensors, and dissolved oxygen sensor (Aanderaa oxygen optode 4831) to provide oceanographic data.	.raw

Table 2: Autonomous underwater vehicle missions in the Greater Pemba Channel.

Site	Mission Number	Total distance (km)	Duration (hours)	Vehicle altitude (m)	Depth range (m)
Mkoani	2	8.6	1.4	10	13.1 – 25.1
	3	10	2.7	Variable	5.0 – 150.0
	4	4.2	0.7	2	11.0 – 25.0
West Misali	5	9.9	1.7	10	21.1 – 150.0
	7	4.6	0.8	2	20.6 – 51.3
South Misali	6	10.0	1.6	10	18.5 – 24.9
Tumbatu Shoal	10	27.3	4.2	10	35.5 – 66.2

Missions 8 and 9 were aborted due to bad weather.

2.3 Data analysis

2.3.1 Bathymetry and acoustic backscatter

Tidal and sound velocity corrections were undertaken to process the raw bathymetry and backscatter data (Howe et al., 2019). Tidal corrections involved applying a synthetic 'zero-tide' in order to reduce survey depths to a common datum (lowest astronomical tide), while sound velocity correction was done by removing sound artefacts using in-situ sound velocity measurements to correct for water column density, salinity, and temperature.

The GeoAcoustic data (bathymetry and side-scan sonar) were filtered and cleaned using the learning algorithm in GeoAcoustics GS4 software (www.kongsberg.com) and Sonarwiz (www.chesapeaketech.com). This produced flagged *.rdf* files that were imported into Caris HIPS and SIPS v.11 (www.teledynecaris.com). The data were then further cleaned using Side Scan editor and Swath sub-editors, and a Combined Uncertainty Bathymetric Estimator (CUBE) surface produced which had a resolution of 0.5 m (bathymetry) and 0.1–0.5 m (acoustic backscatter), dependent on data density and quality.

These surfaces were exported as geo-corrected rasters into ArcMap v.10 (Environmental Systems Research Institute). The focal statistic function was applied to ensure acoustic backscatter and bathymetry raster layers matched the AUV's image spatial footprint of 54 m^2. The focal statistic tool used the median operation to compute an output raster of backscatter and bathymetry layers in a 9 x 9 neighbourhood window. These data were used to calculate several bathymetric derivatives: slope, slope of slope, plan curvature, and aspect. Additionally, an extension Remote Sensing Object Based Image Analysis (RSOBIA) was applied to calculate ruggedness (Le Bas, 2016).

2.3.2 Image processing

Images from each AUV mission were geo-referenced by extracting their latitude and longitude information using open-source BR ExIF software (www.br-software.com). Correction of illumination and colour representation was performed followed by identification of key substratum and benthic community characteristics in every 20th image recorded by the AUV. This represented an inter-image distance of ca. 20 m between photos.

Species-level identification of benthic community routinely requires high-resolution imagery, which depends on the height of the camera. For this reason, benthic organisms photographed during the AUV's seafloor mapping survey, were identified and placed in broad taxa groups: corals, fleshy algae, turf algae and fish. Corals were composed of habitat-forming taxa of Scleractinia (hard coral), Octocorallia (octocorals/soft corals) and Antipatharia (black corals) (Stefanoudis et al., 2018). Other invertebrates such as molluscs and crustaceans were observed but were not analysed further. Turf algae encompassed filamentous algae, while fleshy algae were macro algae (Littler and Littler, 2011; Stefanoudis et al., 2018). Fish were defined as vertebrate organisms either cartilaginous or bony species identified from fish manuals (Lieske and Myers 2002).

A primary substratum type was identified based on majority area of the image (≥50 %) following definitions given in Benoist et al. (2019): “hard”, “coarse”, and “sand”. A secondary substratum was recorded when it covered ≥10 % of the seafloor. Combination of primary and secondary substratum yielded mixed substrata (Supplementary material Table S2). The image geo-reference data were used to attribute corresponding data on acoustic backscatter, bathymetry, slope, slope of slope, plan curvature, aspect and ruggedness.

2.3.3 Temperature and oxygen profile

To simplify the presentation and interpretation of data, and to acknowledge sensor (time) lag during vehicle ascend and descend, temperature and oxygen data were binned at 10 m depth intervals and summarised as box plots.

2.3.4 Modelling

Presence and absence data on substrata and key benthic community types were derived from seabed images from the seafloor-mapping missions conducted at West Misali (n = 377) and South Misali (n = 458), and Tumbatu Shoal (n = 792). The photographs from Mkoani were excluded from modelling because of high turbidity at the site that limited taxa identification. Generalised additive models (GAMs) were fitted on presence and absence data using the *mgcv* package in R (Woods, 2012, www.r-project.org). Substrata and benthic community types were predicted using acoustic backscatter, bathymetry, slope, slope of slope, plan curvature, aspect, and ruggedness. Site based GAM analyses were first performed to determine key seafloor predictors (Supplementary Material Figures S1-5) The site data were thereafter pooled, and the dataset partitioned into training (70%) and testing (30%) data (Platts et al., 2008). Slope of slope and ruggedness were removed from the GAM analyses as they showed substantial correlations ($r > 0.5$) with slope and plan curvature respectively. GAM assessments were run using the restricted maximum likelihood criterion (Wood, 2011), to predict the probabilities of presence of hard and sand substratum, corals, turf algae, fleshy algae, and fish. Contribution of the predictors to the GAM model was assessed from effective degrees of freedom (edf), which represents the complexity of the smoothing term. An edf of 1 represented a straight line or a linear effect while an edf of ≥2 described a non-linear effect with quadratic or wiggly curves. The accuracy of GAMs was assessed firstly by calculating area under the receiver operating curve (AUC ROC), and secondly by determining the number of times presence was categorised into either present or absent using a threshold probability value (Deleo, 1993). AUC ROC refers to the probability that the model correctly predicts a randomly chosen positive observation and a randomly chosen negative observation. A threshold probability value was determined for each independent variable by iteratively searching for the optimal cut-off probability. Application of thresholds is recommended where the data contains more absences than presences (Sigler et al., 2015; Hosmer and Lemeshow, 2004) in order to balance the number of false positives and false negatives.

3. Results

3.1 Site bathymetry and acoustic backscatter

The AUV was deployed at sites showing varying gradients of water depths and benthic communities as detailed below.

3.1.1 West Misali

The AUV surveys at West Misali extended from shallow to mesophotic water depths and mapped the reef transition from 20 to 150 m, including the terraced margins (Figure 2a). The water depths increased westwards with two rock walls of slopes >70° evident from the reef crest at ca. 40–50 m and 90–110 m. The walls formed staircase structures that were separated by a gentle west-oriented slope (ca. 20°) with sparse corals and large boulders (>1 m) (Figure 2a). The shallow areas <25 m was dominated by healthy hard corals as evidenced from the high acoustic backscatter (Figure 2a; Supplementary material Figure S2) and photographs (Figure 3b). Beyond 25 m depth the seafloor showed decreasing availability of hard substrata and increasing sandy substrata (Supplementary material Figure S1). The sandy substrata occurred on platforms with low slopes (<30°) and low backscatter signals. Deeper areas (>100 m) were characterised by the presence of octocorals (Figure 3 f, h, i). Fish occurred from shallow to lower mesophotic depths. However, due to differences in the capture angle and resolution of the photographs, it was not always possible to identify fish to the lowest taxonomic unit. Nevertheless, of note was the observation of soldier fish (Holocentridae) found at 117 m (Figure 3g).

3.1.2 South Misali

The AUV survey at south Misali was conducted in an east-west lawnmower pattern and in depths ranging from 18 to 25 m (Figure 2b). Sand mixed with hard substrata characterised the seafloor, which had a low slope of <10° (Supplementary material Figure S3). The relief was generally featureless except for one depression. Fleshy and turf algae were the dominant benthic community type (Figure 3c).

3.1.3 Mkoani

The AUV surveys at Mkoani covered water depths from 13 to 25 m with acoustic backscatter data showing mixed sediments and a diversity of submarine landform features in a north-south orientation (Figure 2c). The seafloor features included coral heads, rubble and depressions or pockmarks exclusively occurring in sandy substrata. The coral heads occurred in the north and in shallow waters of <15 m and were characterised by a darker acoustic backscatter resulting from a high reflectance signal. Mixed substrata, composed of patchy corals, sand and rubble, showed moderate backscatter and occurred on the seafloor south of the coral heads. Numerous seafloor pockmarks were noted during a preliminary towed side-scan survey in water depths of ca. 20 m. The AUV surveyed more than 30 pockmarks that occurred in the south and in water depths of 18–21 m. The rims of the pockmarks had a moderate lighter backscatter in comparison to the centre of the depression that had darker backscatter. Photographs revealed pockmarks varied in diameter from 5 to 10 m and in depth from 3 to 5 m (Figure 3a).

3.1.4 Tumbatu Shoal

The AUV surveys were conducted in a northeast orientation and in upper mesophotic water depths ranging from 36 to 66 m (Figure 2d). The site had a relatively low slope of <40°, with the seafloor either of sand or sand mixed with hard substrata (Supplementary material Figure S4). These were noticeable in acoustic backscatter as indicated by darker and lighter backscatter signals for hard and sand substrata respectively (Figure 2d). Pockmark features were conspicuous in water depths >40 m. Availability of hard substrata decreased with increasing depth and decreasing slope (Supplementary material Figure S4). Patchy corals were found on the western margin in depths <45 m and where seafloor surface was concavely shaped and extended from south to north (Supplementary material Figure S5). School of surgeonfish (Acanthuridae) and snappers (Lutjanidae) were photographed at upper mesophotic depths at 31 m and 42 m respectively (Figure 3d–e).

3.2 Temperature and oxygen profiles

The water column temperature increased from <18 °C in lower mesophotic depths (150 m) to 26 °C in surface waters (<10 m) (Figure 4). The greatest change in temperature occurred below 100 m. Oxygen concentrations increased from 180 µmol/l at 150 m to 220 µmol/l in surface waters.

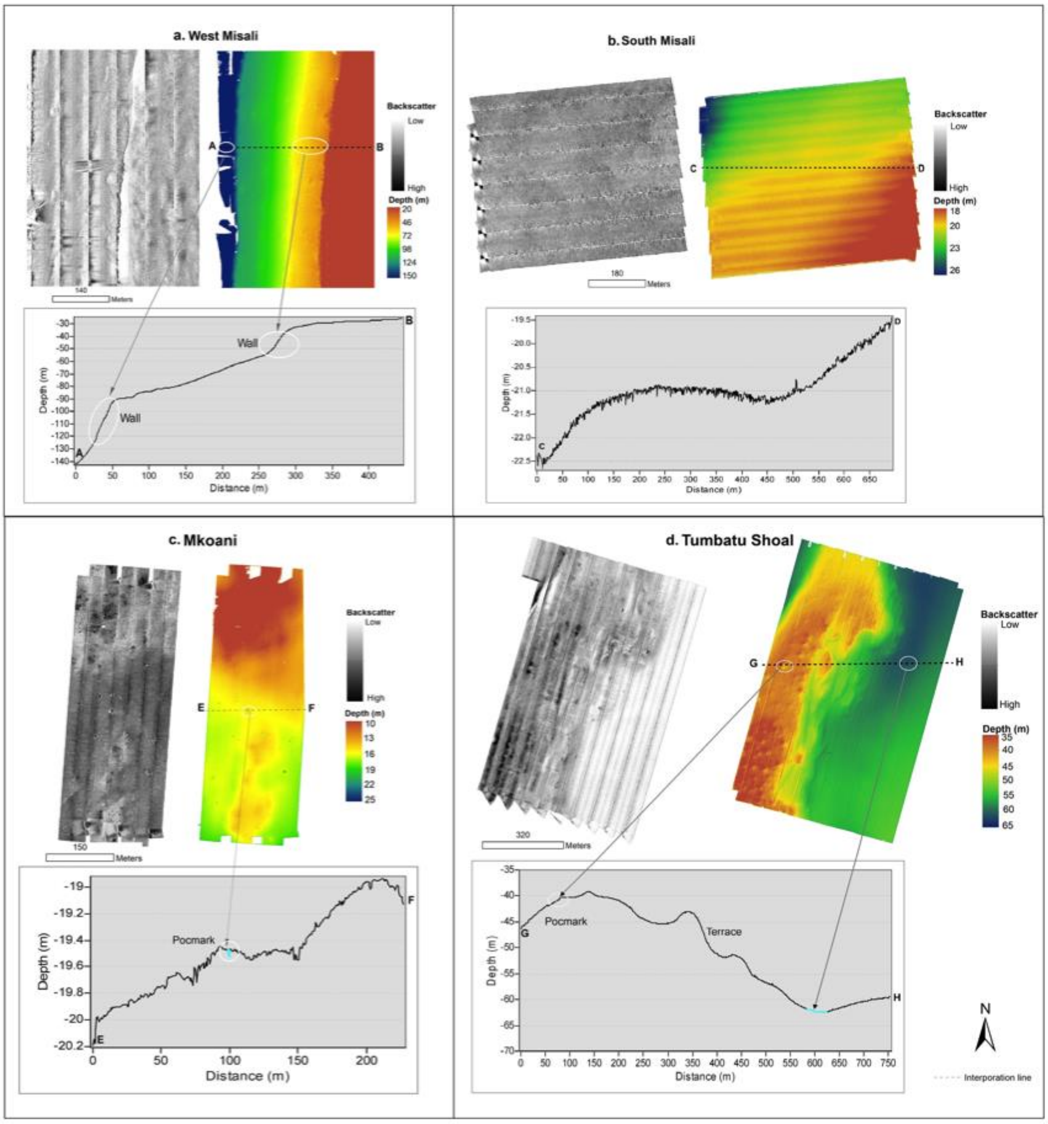


Figure 2: Seafloor survey detail of the four Greater Pemba Channel sites. Each panel illustrates (i) acoustic backscatter (greyscale), (ii) bathymetry (colour scale), and (iii) example bathymetric profile (line plot). Refer to Figure 1 for a, b, c and d. Artefact due to AUV roll error was noted in South Misali.

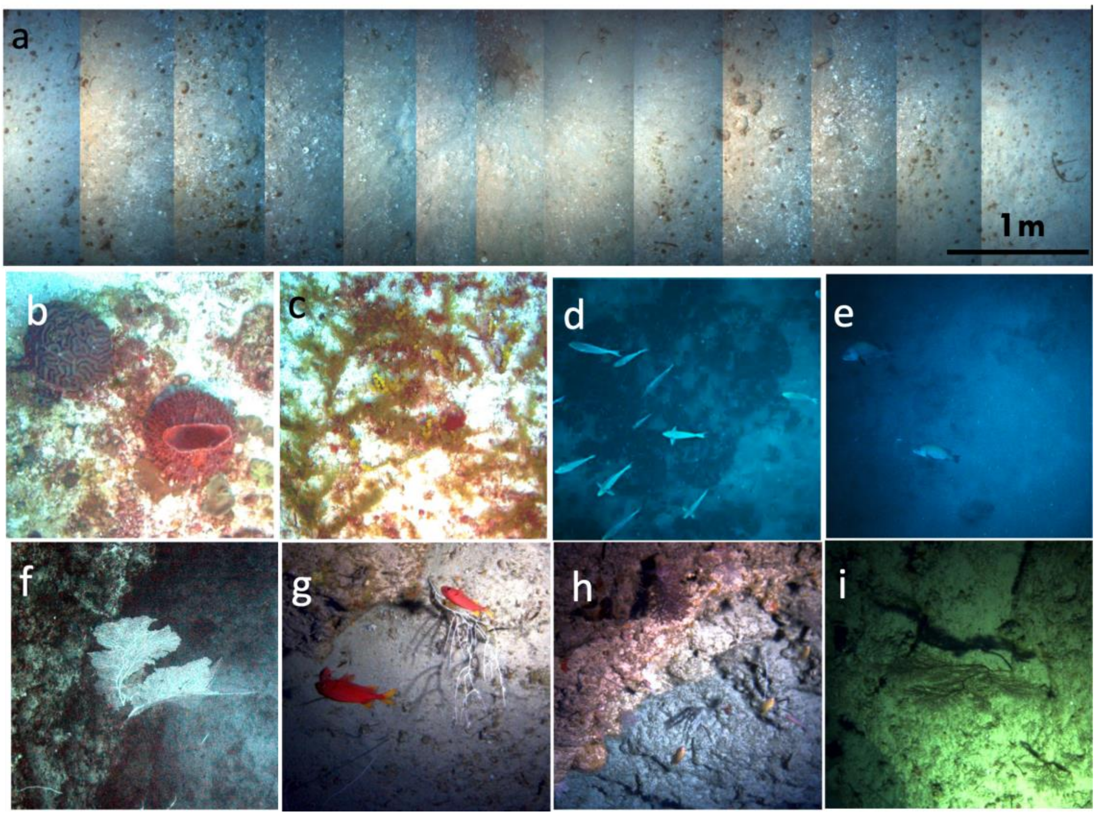


Figure 3: Example images of substrata and benthic community types from shallow and mesophotic environments in the Greater Pemba Channel, as captured from ca. 2 m altitude (a, b, f-i) and ca. 10 m altitude (c-e). a) by autonomous underwater vehicle. a) Mosaicked images of pockmark, 22 m water depth, Mkoani. b) Healthy hard coral and sponge, 15 m, West Misali. c) Turf and fleshy algae, 23 m, South Misali. d) Hard coral and surgeonfish (Acanthuridae), 35 m, Tumbatu Shoal, e) Snapper (Lutjanidae) on mixed sand hard substrata, 42 m, Tumbatu Shoal. f) Octocorals, 39 m, West Misali. g) Soldier fish (Holocentridae), 117 m, West Misali. h) Hard substrata with octocorals and small fish, 117 m, West Misali. i) Octocorals 118 m, West Misali.

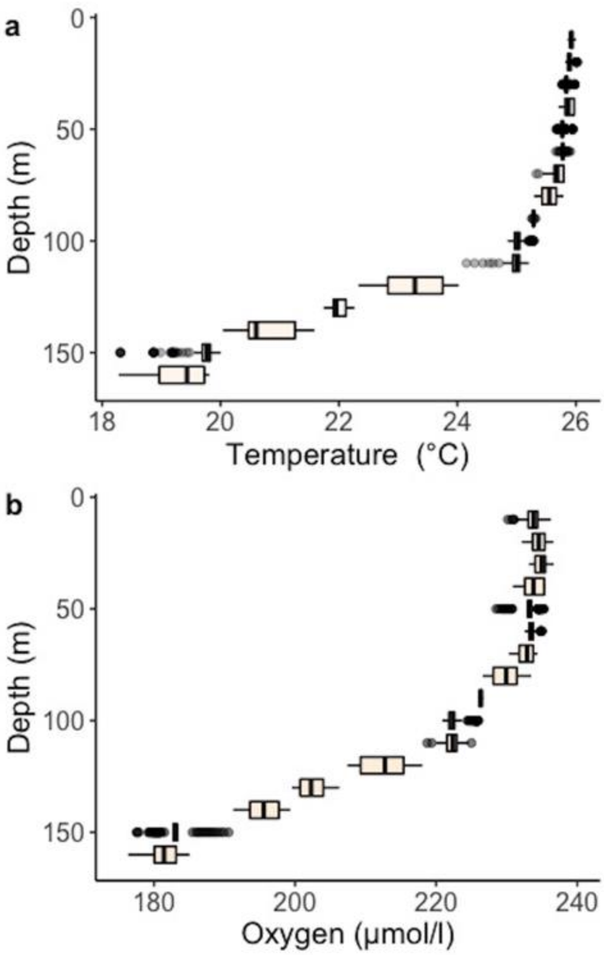


Figure 4: Summary boxplots of water temperature (°C) and oxygen concentrations (μmol/l) in the water column in Mkoani in the Greater Pemba Channel.

3.3 Prediction of substrata and benthic community

The AUC ROC of training and test data indicated good (>0.80) model results that ranged from 0.85 for fish to 0.99 for fleshy algae (Table 3). GAMs on the two primary substrata explained 64% and 60% of the deviance for hard and sand substrata respectively (Table 3). The significant explanatory variables were depth and slope. Presence-absence of hard substrata was correctly predicted 95% and 91% of the times on training and test data respectively, based on threshold probabilities of 0.07. In reference to effective degrees of freedom (edf), depth had a non-linear effect (edf = 8.1) on presence of hard substrata with greater probabilities occurring in shallow areas (20–30 m; Figure 5). As expected, the presence of hard substrata was increasingly probable on steeper slopes (30°–70°) and walls (>70°). Opposing patterns, with respect to depth and slope were found for sand substrata.

The GAMs on presence-absence of coral, turf algae, fleshy algae and fish explained 35–91% of the deviance (Table 3). The significant predictors were acoustic backscatter (coral, turf algae), depth (coral, fleshy algae, turf algae), slope (coral, fleshy algae, turf algae, fish), and aspect (fleshy algae). Curvature did not show any significant contribution to the models. The greatest model accuracy was predicted for fleshy algae at 98% and 91% of the times on training and test data respectively, based on threshold probabilities of 0.04 (Table 3). The model accuracy for corals was 80% on training data and 73% on test data based on threshold of 0.15. Higher probabilities of occurrence of corals were found where acoustic backscatter was high. Depth had a non-linear effect (edf = 7.7) on the presence of corals with greater probabilities (>0.5) at depths between shallow (25 m) and upper mesophotic (55 m) (Figure 5). Presence of coral was greater on steep slopes (30°–70°) particularly found at 30 m, and walls (>70°) occurring in ca. 40–50 m depths, compared to low slopes. Depth, backscatter and slope had a non-linear effect (edf >2) on presence of turf algae (Table 3). High probabilities of >0.5 occurred at around 30 and 80 m water depth and on steep slopes. Marginally higher probabilities of presence of turf algae were found where acoustic backscatter was mid-range (Figure 5).

Depth and slope affected the presence of fleshy algae, with greater probabilities in shallow areas (ca. 20 m) and low slopes (<30°) respectively (Figure 5). Aspect had significant but minimal influence on the presence of fleshy algae, with greater probabilities at south facing areas.

Presence of fish increased rapidly from a seafloor slope of 25°–45° where maximum probability was evident, and then declined more gradually on steep slopes of 70° to similar probabilities to those at 20–25° (Figure 5). Other predictors showed non-significant contribution to the model.

Table 3: Generalised additive model results for substrata (hard and sand) and benthic community types (coral, turf algae, fleshy algae, fish) showing significant predictors ($p < 0.05$), effective degrees of freedom (edf), deviance explained by the model, area under the receiver operating curve (AUC ROC), threshold probability used to test model accuracy, and total percentage occurrence correctly predicted.

Substratum or community type	Significant predictors (edf)	Deviance explained (%)	AUC ROC		Threshold	Correct predictions (%)	
			Training	Test		Training	Test
Hard substratum	Depth (8.1), Slope (3.2)	63.8	0.97	0.95	0.07	95	91
Sand substratum	Depth (8.2), Slope (3.6)	60.0	0.96	0.92	0.06	95	93
Coral	Backscatter (1.0), Depth (7.7), Slope (1.0)	38.6	0.88	0.91	0.15	80	73
Turf algae	Backscatter (3.0), Depth (8.2), Slope (3.6)	38.1	0.90	0.87	0.07	87	88
Fleshy algae	Depth (5.2), Slope (4.7), Aspect (1.0)	90.5	0.99	0.99	0.04	98	91
Fish	Slope (4.6)	35.2	0.93	0.85	0.09	99	96

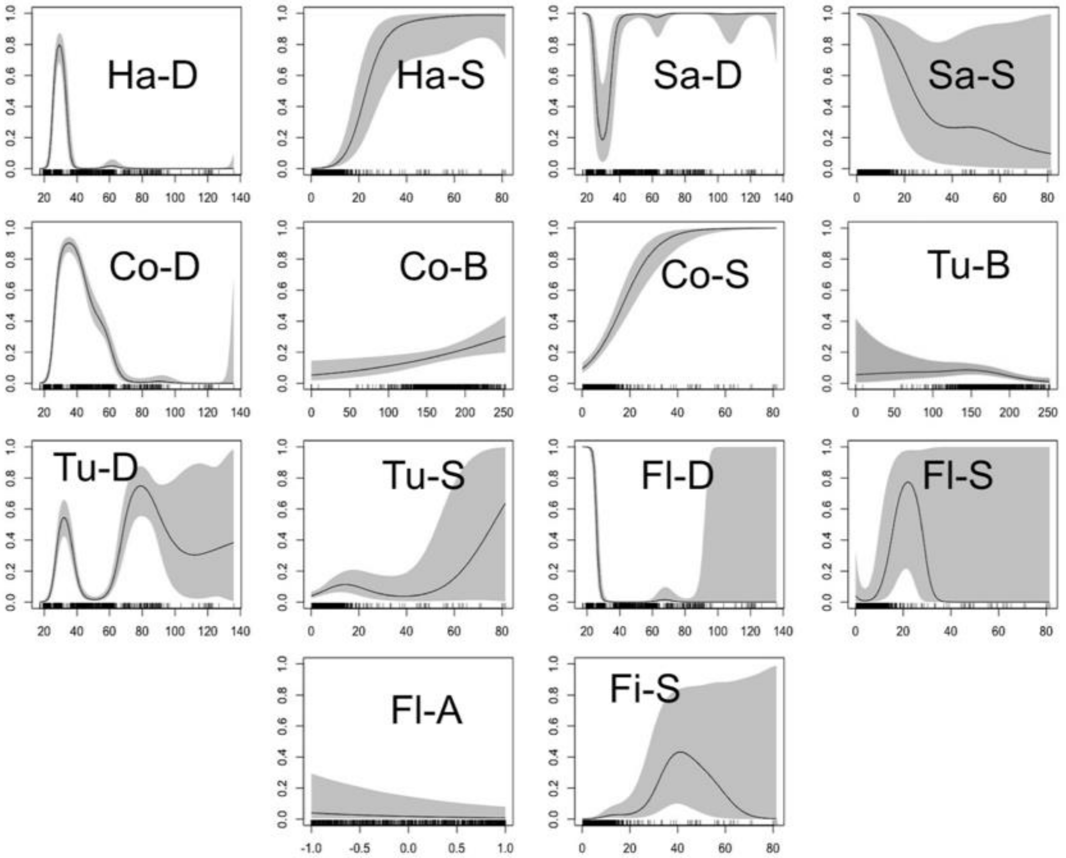


Figure 5: Generalised additive model plots for substrata (Ha, hard; Sa, sand) and benthic community types (Co, coral; Tu, turf algae; Fl, fleshy algae; Fi, fish), for significant predictor variables (B, acoustic backscatter; D, depth (m); S, slope (°); A, aspect (cosine transform)), shaded areas represent 95% confidence intervals. Plots are identified by Yy-X letter coding where Yy codes the dependant variable and X the independent variable.

4. Discussion

4.1 General observations

This study presents a first attempt to document mesophotic coral ecosystems (MCEs) in the understudied Western Indian Ocean (WIO) using an autonomous underwater vehicle (AUV), which collected in-situ data on bathymetry (water depth), acoustic backscatter (substratum) and benthic community types (seabed images) from selected sites in the Greater Pemba Channel. The bathymetry and acoustic backscatter data showed the presence of a complex seafloor variously characterised by pockmarks, steep slopes, ‘staircase walls’, and large boulders. These landscape features may have been formed through geological processes and over time have become ecologically important in sustaining the coral reef ecosystems in the Greater Pemba Channel (Sherman et al., 2019). Additionally, the AUV photographs confirmed presence of MCE composed of corals, algal and fish communities on the continental margins of Pemba and Unguja islands. Corals and fleshy algae were typically present in the shallow (<30 m) and upper mesophotic depths (30–45 m), while turf algae and fish occurred at different depths from shallow to lower mesophotic depths (60–150 m). The modelled occurrence of substrata and benthic community showed peak probabilities for hard substrata, corals, turf algae and fleshy algae to occur at ca. 30–40 m. This indicates that the boundary between shallow and mesophotic coral ecosystems in the Greater Pemba Channel was located at ca. 30–40 m, which concurs with other studies around the world (Bridge et al., 2012; Laverick et al., 2018; Pyle and Copus, 2019). Given the complexity of the seafloor environments encountered, and the study being constrained to only four sites, two of which were less than 25 m in depth, there will certainly be other features of MCE such as species distribution of corals, fleshy algae, sponges, and fish that warrant further study. This study serves to highlight the potential distribution of broad taxa groups of the MCE in the Greater Pemba Channel and provides an interpretation based on available data.

Of particular note was the occurrence of pockmarks that were widespread in 20–40 m water depths. The origin of these pockmarks remains unknown, although previous observations of pockmarks on other continental shelves describe their origin as being bio-erosional, methane gas, or other fluid, escape related (Sumida et al., 2004; Audsley et al., 2019). Surveys using baited remote underwater videos (BRUVs) deployed in Mkoani recorded a high abundance of sea urchins around these pockmarks (Osuka, unpubl. data). Apparent aggregations of sea urchins have previously been noted in association with fluid escape structures in the Gulf of Cadiz (Cunha et al., 2002) and with large hydrocarbon-related pockmarks offshore of Angola (Hughes and Bett, 2007). Therefore, the pockmarks that we surveyed in Mkoani and Tumbatu Shoal sites may be of fluid-escape origin rather than bio-erosional. Further studies are needed to establish their distribution more completely and ascertain their particular origins.

4.2. Modelling efforts

Modelling using generalised additive models gave relatively high prediction accuracies but low threshold levels, suggesting threshold probabilities were trading off sensitivity and specificity to result in high area under the curve (AUC ROC) values. Of note were the large proportion of absences in some taxa, such as fleshy algae and fish, which could have led to low thresholds

(Sigler et al., 2015). Absences can result from low image resolution in greater water depths, further hindering full quantitative assessment of benthic community types (Armstrong et al., 2019). Indeed, this reduction in image resolution prompted this study to use broad morphotype groups, rather than more specific taxonomic groups, which are likely to mask the specific habitat requirements of individual species associated with the group. For instance, low numbers of fish were observed in the randomly selected AUV photographs, despite the complexity of seafloor in Misali and Tumbatu Shoal. The low abundance of fish in AUV photographs suggests that the vehicle may be scaring away fish causing biased and unreliable estimates (Hagen et al., 1999). This may also be exacerbated by the low sampling effort in mesophotic depths, which were halted by rough southeast monsoon winds of up to 30 knots that peaked during the survey, even leading to cancellation of two missions (Table 2). The variables selected and scales at which the data were collected thus limit generalisability of our results. However, even with four sites, the models provide some satisfactory performance for predicting the presence of substrata and benthic community types from shallow to mesophotic depths.

4.3. Distribution of habitats and communities

4.3.1. Hard and sand substrata

Hard substrata were widespread in shallow and upper mesophotic depths, while sand dominated the lower mesophotic depths. Hard substrata in tropical marine environments provide an important attachment platform for organisms, especially those in mesophotic depths, to colonise and grow (Sherman et al., 2019). They can support more than twice the number of species compared to mixed or sandy substrata (Ruiz et al., 2009). The high level of diversity on hard substrata relates to their ability to provide stable basal structures and high topographical complexity, which are both essential for the successful larval development of sessile and sub-adult mobile species. The hard substrata in the upper mesophotic depths may therefore be key to the presence of MCEs found in the Greater Pemba Channel.

Hard substrata were predominantly found on steep slopes and walls rather than flat or low slopes. The most biodiverse MCEs in Hawaii have been linked with either hard substrata with discontinuous features such as limestone outcrops and ledges, or walls with complex structures (Pyle and Copus, 2019; Sherman et al., 2019). The MCEs in the Greater Pemba Channel may therefore sustain a highly biodiverse community. Indeed, walls are widespread along the western side of Pemba Island, stretch from north to south, interspersed by several reef passes (Grimsditch et al., 2009). These walls were formed through geological processes involving tectonic movements (Baker and McConnell, 1970; Sherman et al., 2019), and over time strong physical erosion from the north flowing East African Coastal Current (EACC) has had a pronounced effect on their complexity (Klaus, 2014). The EACC is also particularly important in increasing and maintaining connectivity between coral reef ecosystems (Obura 2012; Gamoyo et al., 2019; Sekadende et al., 2020). The current coupled with a changing seasonal monsoon winds, and the proximity of the walls to the shoreline (ca. 2 km) implies the water column is well mixed. The stable temperature and oxygen concentrations recorded in the upper 100 m of the water column in the Greater Pemba Channel (Figure 4) also provide some evidence of a well-mixed water column, which may help promote the survival of fish and benthic communities in the area. The walls of the Pemba Channel may therefore be of particular conservation interest, suggesting the need for a careful management against anthropogenic pressures such as fishing.

4.3.2. Coral, fleshy and turf algae

Water depth was a significant predictor of the presence of coral, fleshy, and turf algae. Vertical zonation of community structure is influenced by light and temperature and both are key factors restricting the distribution of MCEs (Kahng et al., 2010, 2019). Light provides energy to photosynthesising communities such as scleractinian zooxanthellate corals and algae, while water temperature is essential in setting the thermal tolerance for physiological processes. The mid-water AUV surveys revealed stable temperature in the upper 100 m of water column, providing some indication that light was a limiting abiotic factor (Kirk 2011; Kahng et al., 2019). Very low light levels experienced in deep walls can limit occurrence of corals, particularly Scleractinia zooxanthellate. Therefore, changes in temperature and light intensity with depth are not only associated with changes in the occurrence of coral and algal community types, but also taxon composition (Pyle and Copus, 2019). Similar changes in species composition are expected for algal and sponge community types. To establish this will require high-resolution photography across the entire mesophotic depth, which can be achieved by flying the AUV close to the seafloor at ca. 2 m. However, drawing on studies from Bermuda (Stefanoudis et al., 2019), a turnover in coral taxa can be expected in the Greater Pemba Channel for instance, scleractinians (hard corals) can occur in the shallow water depths (15–30 m), and overlap at the upper MCE boundary (30–40) with octocorals. The octocorals can extend to 60 m below which the anthiparians (black corals) become more abundant. Algae will occur in all water depths although the turnover in taxa groups will reflect the decrease in temperature and primary productivity.

Occurrence of corals was higher on steep slopes or walls than low slopes, consistent with findings from the Caribbean (Sherman et al., 2010) but different from results from the Great Barrier Reef MCEs (Bridge et al., 2011a, 2011b), which showed corals were concentrated and most diverse on the flatter surfaces of submerged reefs at depths <60 m. Occurrence of MCEs in the Caribbean were influenced by the downslope sediment transport and water clarity, such that steeper slopes easily shed off accumulated sediments while low relief slopes accumulate sediments, which can suppress coral recruitment and growth (Sherman et al., 2010). Erosional rates coupled with sediment retention are therefore important factors influencing the occurrence and distribution of MCEs in the Greater Pemba Channel. Fleshy algae were highly restricted to the shallow reef depth transition (ca. 20 m), low slopes and south facing seafloor. While an increase in the coverage of shallow fleshy algae can outcompete corals and lead to phase shifts (Hughes et al., 2007), the presence of mesophotic fleshy algae is regarded an important refugium habitat for other organism providing protection against environmental stress (Spalding et al., 2019). Fleshy algae are versatile marine plants able to grow in depths greater than 200 m and on both hard and soft substrata. It is therefore likely that the presence of fleshy algae is more widespread than found in this study. Our findings also contrast with reports from American Samoa, where fleshy algae were more pronounced in the upper mesophotic water depth from 50 to 70 m (Bare et al., 2010). That depth range, however, was similar to the peak depths for turf algae, which this study found to be in the shallow (30 m) and upper mesophotic depths (80 m). Turf algae were also associated with seafloor areas having mid-range acoustic backscatter and slopes, suggesting their preference or ability to grow on mixed hard and sandy substrata that are characterised by varying slopes (Spalding et al., 2019). In contrast to fleshy algae, turf algae showed non-significant predictions with aspect suggesting they are not constrained by current. These findings underscore the ability of algae to change with increasing depth as well as colonise different forms of substrata.

4.3.3. Fish

Fish were more abundant in areas with steep slopes rather than on platforms or flat seafloor. High fish abundance on steep slopes and walls is expected (Jankowski et al., 2015) because of their exposure to currents and waves, which are also essential in maintaining high levels of suspended food resources (McLachlan and Defeo, 2017). The presence of suspended food drives the abundance of fish, especially planktivores and omnivores (Pinheiro et al., 2016; Goodbody-Gringley et al., 2019), which subsequently serve as prey for higher trophic level predatory species (Stewart and Jones, 2001). These trophic groups are more likely to be abundant in lower mesophotic depths than shallow and upper mesophotic depths where a high abundance of herbivorous fish is expected (Jankowski et al., 2015; Medeiros et al., 2010). Thus, it was surprising for water depth to be a non-significant predictor of fish occurrence in the present study. Furthermore, due to threats of overfishing and destructive fishing practices in the Pemba Island area (Grimsditch et al., 2009), we expected fish to be more abundant in greater depths, including walls where rapid changes in water depth would help in escaping from fishing pressure. Moreover, local fishing gears are less adapted to deep environments (Tyler et al., 2009; Samoilys et al., 2011). In Bermuda, fish population metrics (abundance, biomass and species richness) were found to increase with water depth, supporting the deep reef refugia hypothesis – where more fish move to deeper areas to escape from high fishing pressure (Pinheiro et al., 2016; Stefanoudis et al., 2019). Such fish movements affect the overall productivity of shallow areas and can have negative impacts on the livelihoods that dependent on them. Taken at face value, our results might suggest that fish abundance was low. However, based on the findings of similar studies (Bongaerts et al., 2010; Pinheiro et al., 2016), a more probable explanation is the limited ability of the AUV to photograph fish at mesophotic depths and in regions of steep slopes and crevices. As fish communities are partitioned according to abiotic factors (Jankowski et al., 2015), Pemba's Channel fish communities are likely to be dissimilar at different water depths and over different seabed slopes. This, together with the distribution of shallow species on steep slopes, requires further research. Nevertheless, the modelling results for fish occurrence contribute to a better understanding of the importance of walls in offering natural protection from fishing and, therefore, their consideration as important in conservation planning.

4.4. Conservation and management

There are few conservation efforts directed towards deep environments such as MCE, yet they sustain distinct biodiversity and are probably acting as refugia for shallow reefs (Pyle and Copus, 2019; Turner et al., 2019). Conservation efforts for MCEs in Pemba Island area would require targeted detailed monitoring surveys across the mesophotic depth range to assess the effectiveness of any management measures. At present, the logistical challenges in gathering such data and the high costs associated with monitoring MCEs may be the greatest bottleneck

(Wölfl et al., 2019). Despite these challenges, the development and investment in low-cost marine robotics, such as low-logistics AUVs like the Gavia vehicle used in the present study, clearly offers opportunities to reduce monitoring costs to within the budget range of most management agencies. These costs are expected to be comparatively low in the Pemba Island case as a result of the proximity of the MCEs to the shore, particularly those found on walls. Another important consideration is to encourage the involvement of local communities in the management of MCE. A first step towards this realisation will require building awareness of the existence of MCEs and their importance as depth refugia (Tyler et al., 2009; Turner et al., 2019). As such, awareness raising through stakeholder engagement should also involve discussions regarding the conservation of mesophotic depths and walls. A second potential step would involve the amendment of fisheries and conservation policies to include MCEs in the management plans for various forms of conservation areas, notably Marine Protected Areas (MPAs) and Locally Managed Marine Areas (LMMAs) (Turner et al., 2019). A potential intermediate option for studying the Western Indian Ocean's MCEs could involve using divers equipped with closed-circuit rebreathers (Pyle, 2019). Other tools such as mid-water remote camera systems may also be considered when surveying fish communities. Application of multiple techniques will enable accurate measurement of fish community composition (Goodbody-Gringley et al., 2019). Whether achieved through marine robotics or technical diving teams, the initial costs for acquiring the technology and the training of technical personnel would need support.

AUVs will likely play two important roles in conservation and marine management operations: (i) initial baseline data acquisition, and (ii) routine monitoring programmes. They may have particular value in conducting initial surveys and collecting baseline data in areas that are not easily accessible and/or where staff may otherwise be limited (Wynn et al., 2014; Huvenne et al., 2018; Wölfl et al., 2019). Their use might therefore be encouraged in regions such as the WIO, where survey and monitoring costs appear to be the biggest challenge. The multiple data streams that can be derived from AUV operations, as demonstrated in the present study, can be used to inform managers on location and status of MCEs and other features and species of conservation interest. Such AUV-derived data may also be of particular value in informing and planning more targeted vessel-based surveys where unexpected or high interest features are detected. AUVs also have clear value in the repeat or routine monitoring of habitats and species of interest (see e.g., Benoist et al., 2019; Zelada Leon et al., 2020). Other possible monitoring applications may include studies of topographical complexity, invasive species, and fish diversity (Ferrari et al., 2016; Ling et al., 2016; James et al., 2017). Such operations can be likely be launched from locally available platforms and make use of low-logistics AUVs to enable cost-effective implementations of marine robotics in the future.

5. Conclusions

Application of a low-logistics AUV showed great potential for mapping the photic and mesophotic coral ecosystems of the Greater Pemba Channel. This was due to their ability to follow a pre-designed track, map deep areas down to 500 m and beyond, and to collect high-resolution data of both the water column and the seabed. Therefore, AUVs should certainly be considered for the collection of baseline and routine monitoring data, not least for tackling under-researched ecosystems such as the MCEs of the WIO. This study has indicated that wall areas are potential hotspots of MCE biodiversity, such that they and should be considered as priority areas for management and conservation.

Acknowledgements

This work contributes to, and was funded by, the Sustainable Oceans, Livelihoods, and food Security Through Increased Capacity in Ecosystem research in the Western Indian Ocean (SOLSTICE-WIO) Programme (www.solstice-wio.org), a collaborative project funded through the UK Global Challenges Research Fund (GCRF) under NERC grant NE/P021050/1. KEO acknowledges additional support from Norwegian agency for development cooperation (Norad), Perivoli Philanthropy and Dev Joory for funding this work as part of his PhD research. We are grateful to Phil Platts, James Mbugua, Estelle Dumont and Juliane Wihsgott for their assistance in data mining and analysis.

References

Archer, A. and Turner, D., 1993. Notes on the endemic species and some additional new birds occurring on Pemba Island. Tanzania. *Scopus* 16, 94–98.

Armstrong, R.A., Pizarro, O. and Roman, C. 2019. Underwater robotic technology for imaging mesophotic coral ecosystems. *In:* Loya, Y., Puglise, K.A. and Bridge, T.C.L. (Eds.), *Mesophotic Coral Ecosystems*. Springer, Cham, pp. 973–988.

Audsley, A., Bradwell, T., Howe, J.A. and Baxter, J.M. 2019. Distribution and classification of pockmarks on the seabed around western Scotland. *J. Maps* 15, 807–817. https:// doi.org/10.1080/17445647.2019.1676320.

Baker, B.H. and McConnell, R.B., 1970. The structural pattern of the Afro-Arabian rift system in relation to plate tectonics. *Phil. Trans. Roy. Soc. Lond*. 267, 383–391. https ://www.jstor.org/stable/73628.

Bare, A.Y., Grimshaw, K.L., Rooney, J.J., Sabater, M.G., Fenner, D. and Carroll, B., 2010. Mesophotic communities of the insular shelf at Tutuila, American Samoa. *Coral Reefs* 29, 369–377. https://doi.org/10.1007/s00338-010-0600-y.

Benoist, N.M., Morris, K.J., Bett, B.J., Durden, J.M., Huvenne, V.A., Le Bas, T.P., Wynn, R.B., Ware, S.J. and Ruhl, H.A., 2019. Monitoring mosaic biotopes in a marine conservation zone by autonomous underwater vehicle. *Conserv. Biol.* 33, 1174–1186. https://doi.org/10.1111/cobi.13312.

Bongaerts, P., Ridgway, T., Sampayo, E.M. and Hoegh-Guldberg, O., 2010. Assessing the 'deep reef refugia' hypothesis: focus on Caribbean reefs. *Coral Reefs* 29, 309–327. https://doi.org/10.1007/s00338-009-0581-x.

Bridge, T., Done, T., Beaman, R., Friedman, A., Williams, S., Pizarro, O. and Webster, J., 2011a. Topography, substratum and benthic macrofaunal relationships on a tropical mesophotic shelf margin, central Great Barrier Reef, Australia. *Coral Reefs* 30, 143–153. https://doi.org/10.1007/s00338-010-0677-3.

Bridge, T.C.L., Done, T.J., Friedman, A., Beaman, R.J., Williams, S.B., Pizarro, O. and Webster, J.M., 2011b. Variability in mesophotic coral reef communities along the Great Barrier Reef, Australia. *Mar. Ecol. Prog. Ser*. 428, 63–75. https://doi.org/ 10.3354/meps09046.

Bridge, T., Beaman, R., Done, T. and Webster, J., 2012. Predicting the location and spatial extent of submerged coral reef habitat in the Great Barrier Reef world heritage area, Australia. *PLoS One* 7, e48203. https://doi.org/10.1371/journal.pone.0048203.

Cunha, M.R., Subida, M.D., Vandendriessche, S., Lima, I. and Ravara, A., 2002. TTR 11 Scientific Party, Macrofaunal communities associated to the carbonate chimneys from the Gulf of Ca'diz. Preliminary results from the video imagery and dredge sampling obtained during the TTR-11 Cruise. In: *Final Proceedings of the International Conference on Fluid Escape Structures and Tectonics at Continental Margins and Ocean Ridges*. Aveiro, Portugal, pp. 77–78.

Deleo, J., 1993. Receiver operating characteristic laboratory (ROCLAB): software for developing decision strategies that account for uncertainty. In: Proceedings 2nd International Symposium on Uncertainty Modelling and Analysis, pp. 318–325.

Durden, J.M., Bett, B.J. and Ruhl, H.A., 2020. Subtle variation in abyssal terrain induces significant change in benthic megafaunal abundance, diversity, and community structure. *Prog. Oceanogr*. 186, 102395. https://doi.org/10.1016/j.pocean.2020.102395.

Ferrari, R., Bryson, M., Bridge, T., Hustache, J., Williams, S.B., Byrne, M. and Figueira, W., 2016. Quantifying the response of structural complexity and community composition to environmental change in marine communities. *Global Change Biol*. 22, 1965–1975. https://doi.org/10.1111/gcb.13197.

Gamoyo, M., Obura, D. and Reason, C.J., 2019. Estimating connectivity through larval dispersal in the Western Indian Ocean. J. Geophys. Res. Biogeosci. 124, 2446–2459. https://doi.org/10.1029/2019JG005128.

Gates, A.R., Durden, J.M., Richmond, M.D., Muhando, C.A., Khamis, Z.A. and Jones, D.O.B., 2021. Ecological considerations for marine spatial management in deep-water Tanzania. *Ocean Coast Manag*. 210, p.105703

Goodbody-Gringley, G., Noyes, T. and Smith, S.R., 2019. In: Loya, Y., Puglise, K.A., Bridge, T.C.L. (Eds.), *Mesophotic Coral Ecosystems*. Springer, Cham, pp. 31–45. Bermuda.

Grimsditch, G.D., Tamelander, J., Mwaura, J., Zavagli, M., Takata, Y. and Gomez, T. 2009. *Coral reef resilience assessment of the Pemba channel conservation area, Tanzania*. Gland, Switzerland: IUCN. 40pp.

Groeneveld, J.C. and Koranteng, K.A., 2017. *RV Dr Fridtjof Nansen in the Western Indian Ocean: Voyages of Marine Research and Capacity Development. 1975-2016*. FAO, Rome, p. 174.

Groeneveld, J., Koranteng, K., Francis, J. and Bianchi, G., 2017. The Nansen programme in the western Indian ocean–a synthesis of results. In: Groeneveld, J. and Koranteng, K.A. (Eds.), *The RV Dr Fridtjof Nansen in the Western Indian Ocean: Voyages of Marine Research and Capacity Development. 1975-2016*. FAO, Rome, pp. 143–159.

Gudka, M., Obura, D., Mbugua, J., Ahamada, S., Kloiber, U. and Holter, T., 2019. Participatory reporting of the 2016 bleaching event in the Western Indian Ocean. Coral Reefs 39, 1–11. https://doi.org/10.1007/s00338-019-01851-3.

Hagen, P.E., Storkersen, N.J. and Vestgard, K., 1999. HUGIN-use of UUV technology in marine applications. Oceans '99. MTS/IEEE. In: Riding the Crest into the 21st Century. Conference and Exhibition. Conference Proceedings (IEEE Cat. No.99CH37008). https://doi.org/10.1109/OCEANS.1999.805003.

Hiller, T., Steingrimsson, A. and Melvin, R., 2012. Expanding the Small AUV Mission Envelope; Longer, Deeper & More Accurate. In: 2012 IEEE/OES Autonomous Underwater Vehicles (AUV). IEEE, pp. 1–4. https://doi.org/10.1109/AUV.201 2.6380725.

Hoegh-Guldberg, O., Kennedy, E.V., Beyer, H.L., McClennen, C. and Possingham, H.P., 2018. Securing a long-term future for coral reefs. *Trends Ecol. Evol*. 33 (12), 936–944. https://doi.org/10.1016/j.tree.2018.09.006.

Hosmer, D.W. and Lemeshow, S., 2004. Applied Logistic Regression, (2nd ed.) John Wiley & Sons, Hoboken.

Howe, J.A., Husum, K., Inall, M.E., Coogan, J., Luckman, A., Arosio, R., Abernethy, C. and Verchili, D., 2019. Autonomous underwater vehicle (AUV) observations of recent tidewater glacier retreat, western Svalbard. *Mar. Geol*. 417, 106009 https://doi.org/ 10.1016/j.margeo.2019.106009.

Hughes, J.A. and Bett, B.J., 2007. Angola Block 18WAD and Block 31 pre-operational environmental survey, October 2005: analysis of seabed images taken using WASP (Wide-Angle Seabed Photography) National Oceanography Centre Research and Consultancy Report No 29. National Oceanography Centre, Southampton, 40pp.

Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwskyj, N., Pratchett, M.S., Steneck, R.S. and Willis, B., 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr. Biol.* 17, 360–365. https://doi.org/ 10.1016/j.cub.2006.12.049.

Huvenne, V.A., Robert, K., Marsh, L., Iacono, C.L., Le Bas, T. and Wynn, R.B., 2018. Rovs and Auvs. In: Micallef, A., Krastel, S. and Savini, A. (Eds.), Submarine Geomorphology. Springer, Cham, pp. 93–108.

James, L.C., Marzloff, M.P., Barrett, N., Friedman, A., Johnson, C.R., 2017. Changes in deep reef benthic community composition across a latitudinal and environmental gradient in temperate Eastern Australia. *Mar. Ecol. Prog. Ser.* 565, 35–52. https:// doi.org/10.3354/meps11989.

Jankowski, M.W., Gardiner, N.R. and Jones, G.P., 2015. Depth and reef profile: effects on the distribution and abundance of coral reef fishes. *Environ. Biol. Fish.* 98, 1373–1386. https://doi.org/10.1007/s10641-014-0365-1.

Kaehler, S., Ribbink, A. and Scott, L., 2008. ACEP final report 2007/8: nearshore and offsore studies in the western Indian ocean. In: Final Scientific Cruise Report, African Coelacanth Ecosystem Programme Grahamstown, South Africa, p. 290.

Kahng, S.E., García-Sais, J.R., Spalding, H.L., Brokovich, E., Wagner, D., Weil, E., Hinderstein, L. and Toonen, R.J., 2010. Community ecology of mesophotic coral reef ecosystems. *Coral Reefs* 29, 255–275. https://doi.org/10.1007/s00338-010-0593-6.

Kahng, S.E., Akkaynak, D., Shlesinger, T., Hochberg, E.J., Wiedenmann, J., Tamir, R. and Tchernov, D., 2019. Light, temperature, photosynthesis, heterotrophy, and the lower depth limits of mesophotic coral ecosystems. *In:* Loya, Y., Puglise, K.A. and Bridge, T.C. L. (Eds.), *Mesophotic Coral Ecosystems*. Springer, Cham, pp. 801–828.

Kirk, J.T.O., 2011. Light and Photosynthesis in Aquatic Ecosystems. Cambridge University Press, New York.

Klaus, R., 2014. Coral Reef Atlas and Outlook -South Western Indian Ocean Islands (Report to the Indian Ocean Commission. ISLANDS Project).

Laverick, J.H., Piango, S., Andradi-Brown, D.A., Exton, D.A., Bongaerts, P., Bridge, T.C., Lesser, M.P., Pyle, R.L., Slattery, M., Wagner, D. and Rogers, A.D., 2018. To what extent do mesophotic coral ecosystems and shallow reefs share species of conservation interest? A systematic review. *Environ. Evid*. 7 (15) https://doi.org/10.1186/ s13750-018-0127-1.

Le Bas, T., 2016. RSOBIA—a new OBIA toolbar and toolbox in ArcMap 10.x for segmentation and classification. *Photogramm. Eng. Rem. Sens.* 70, 1081–1091. https://doi.org/10.3990/2.448.

Levin, N., Beger, M., Maina, J., McClanahan, T. and Kark, S., 2018. Evaluating the potential for transboundary management of marine biodiversity in the Western Indian Ocean. *Australas. J. Environ. Manag. 25*, 62–85. https://doi.org/10.1080/ 14486563.2017.1417167.

Lieske, E. and Myers, R., 2002. Coral Reef Fishes: Indo-Pacific and Caribbean. Princeton University Press, Princeton.

Ling, S.D., Mahon, I., Marzloff, M.P., Pizarro, O., Johnson, C.R. and Williams, S.B., 2016. Stereo-imaging AUV detects trends in sea urchin abundance on deep overgrazed reefs. *Limnol Oceanogr. Methods 14*, 293–304. https://doi.org/10.1002/ lom3.10089.

Littler, M.M. and Littler, D.S., 2011. Algae. In: Hopley, D. (Ed.), *Encyclopedia of Modern Coral Reefs*. Encyclopedia of Earth Sciences Series. Springer, Dordrecht.

McLachlan, A. and Defeo, O., 2017. Surf-zone Zooplankton and Nekton. The Ecology of Sandy Shores. Academic Press, London.

Medeiros, P.R., Grempel, R.G., Souza, A.T., Ilarri, M.I. and Rosa, R.S., 2010. Non-random reef use by fishes at two dominant zones in a tropical, algal dominated coastal reef. *Environ. Biol. Fish. 87*, 237–246. https://doi.org/10.1007/s10641-010-9593-1.

Muhando, C.A., 2009. Coral reef monitoring in Tanzania: an analysis of the last 20 years. *West. Indian Ocean J. Mar. Sci. 8,* 203–214. https://doi.org/10.4314/wiojms. v8i2.56981.

Obura, D., 2012. The diversity and biogeography of Western Indian Ocean reef-building corals. *PloS One 7*, e45013. https://doi.org/10.1371/journal.pone.0045013.

Obura, D., Gudka, M., Rabi, F.A., Gian, S.B., Bijoux, J., Freed, S., Maharavo, J., Mwaura, J., Porter, S., Sola, E. and Wickel, J., 2017. *Coral Reef Status Report for the Western Indian Ocean (2017).* Global Coral Reef Monitoring Network (GCRMN)/ International Coral Reef Initiative (ICRI): Indian Ocean Commission. 144pp.

Osuka, K.E., Stewart, B.D., Samoilys, M.A., Roche, R.C., Turner, J. and McClean, C., 2021. Protection outcomes for fish trophic groups across a range of management regimes. *Mar. Pollut. Bull.*, *173*, p.113010.

Pinheiro, H.T., Goodbody-Gringley, G., Jessup, M.E., Shepherd, B., Chequer, A.D. and Rocha, L.A., 2016. Upper and lower mesophotic coral reef fish communities evaluated by underwater visual censuses in two Caribbean locations. *Coral Reefs 35*, 139–151. https://doi.org/10.1007/s00338-015-1381-0.

Platts, P.J., McClean, C.J., Lovett, J.C. and Marchant, R., 2008. Predicting tree distributions in an East African biodiversity hotspot: model selection, data bias and envelope uncertainty. *Ecol. Model. 218*, 121–134. https://doi.org/10.1016/j. ecolmodel.2008.06.028.

Portner, H.O., 2010. Oxygen-and capacity-limitation of thermal tolerance: a matrix for integrating climate-related stressor effects in marine ecosystems. *J. Exp. Biol. 213*, 881–893. https://doi.org/10.1242/jeb.037523.

Pyle, R.L., 2019. Advanced technical diving. In: Loya, Y., Puglise, K.A. and Bridge, T.C.L. (Eds.), *Mesophotic Coral Ecosystems*. Springer, Cham, pp. 959–972.

Pyle, R.L. and Copus, J.M., 2019. Mesophotic coral ecosystems: introduction and overview. In: Loya, Y., Puglise, K.A. and Bridge, T.C.L. (Eds.), *Mesophotic Coral Ecosystems*. Springer, Cham, pp. 3–27.

Ruiz, G.M., Freestone, A.L., Fofonoff, P.W. and Simkanin, C., 2009. Habitat distribution and heterogeneity in marine invasion dynamics: the importance of hard substrate and artificial structure. In: Wahl, M. (Ed.), *Marine Hard Bottom Communities*. Springer-Verlag, Berlin, pp. 321–332.

Samoilys, M.A., Maina, G.W. and Osuka, K., 2011. Artisanal Fishing Gears of the Kenyan Coast. CORDIO/USAID, Mombasa.

Samoilys, M.A., Halford, A. and Osuka, K., 2019. Disentangling drivers of the abundance of coral reef fishes in the Western Indian Ocean. *Ecol. Evol. 9,* 4149–4167. https://doi. org/10.1002/ece3.5044.

Schmahl, G.P., Hickerson, E.L. and Precht, W.F., 2008. Biology and ecology of coral reefs and coral communities in the flower garden banks region, northwestern Gulf of Mexico. In: Riegl, B.M. and Dodge, R.E. (Eds.), Coral Reefs of the USA. Springer, Dordrecht, pp. 221–261.

Sekadende, B., Scott, L., Anderson, J., Aswani, S., Francis, J., Jacobs, Z., Jebri, F., Jiddawi, N., Kamukuru, A.T., Kelly, S. and Kizenga, H., 2020. The small pelagic fishery of the Pemba Channel, Tanzania: What we know and what we need to know for management under climate change. *Ocean & Coast.l Manag.*, *197,* p.105322. https://doi.org/10.1016/j.ocecoaman.2020.105322.

Sherman, C., Nemeth, M., Ruíz, H., Bejarano, I., Appeldoorn, R., Pag ́an, F., Sch ̈arer, M. and Weil, E., 2010. Geomorphology and benthic cover of mesophotic coral ecosystems of the upper insular slope of southwest Puerto Rico. Coral Reefs 29, 347–360. https:// doi.org/10.1007/s00338-010-0607-4.

Sherman, C.E., Locker, S.D., Webster, J.M. and Weinstein, D.K., 2019. Geology and geomorphology. In: Loya, Y., Puglise, K.A., Bridge, T.C.L. (Eds.), *Mesophotic Coral Ecosystems.* Springer, Cham, pp. 849–878.

Sigler, M.F., Rooper, C.N., Hoff, G.R., Stone, R.P., McConnaughey, R.A. and Wilderbuer, T. K., 2015. Faunal features of submarine canyons on the eastern Bering Sea slope. *Mar. Ecol. Prog. Ser.* 526, 21–40. https://doi.org/10.3354/meps11201.

Simon-Lled ́o, E., Bett, B.J., Huvenne, V.A., Schoening, T., Benoist, N.M., Jeffreys, R.M., Durden, J.M. and Jones, D.O., 2019. Megafaunal variation in the abyssal landscape of the clarion clipperton zone. *Prog. Oceanogr. 170*, 119–133. https://doi.org/ 10.1016/j.pocean.2018.11.003.

Souter, D., Obura, D. and Lindén, O., 2000. Coral Reef Degradation in the Indian Ocean. Status Report 2000. CORDIO. SAREC Marine Science Program. Sweden, Stockholm.

Spalding, H.L., Amado-Filho, G.M., Bahia, R.G., Ballantine, D.L., Fredericq, S., Leichter, J.J., Nelson, W.A., Slattery, M. and Tsuda, R.T., 2019. Macroalgae. In: Loya, Y., Pu uglise, K.A., Bridge, T.C.L. (Eds.), *Mesophotic Coral Ecosystems*. Springer, Cham, pp. 507–536.

Stefanoudis, P.V., Smith, S.R., Schneider, C.W., Wagner, D., Goodbody-Gringley, G., Xavier, J., Rivers, M., Woodall, L. and Rogers, A., 2018. Deep Reef Benthos of Bermuda: Field Identification Guide. Nekton, Oxford.

Stefanoudis, P.V., Rivers, M., Smith, S.R., Schneider, C.W., Wagner, D., Ford, H., Rogers, A.D. and Woodall, L.C., 2019. Low connectivity between shallow, mesophotic and rariphotic zone benthos. *Roy. Soc. Open Sci. 6*, 190958 https://doi.org/ 10.1098/rsos.190958.

Sterne, T.K., Retchless, D., Allee, R. and Highfield, W., 2019. Predictive modelling of mesophotic habitats in the north-western Gulf of Mexico. *Aquat. Conserv. 30*, 846–859. https://doi.org/10.1002/aqc.3281.

Stewart, B.D. and Jones, G.P., 2001. Associations between the abundance of piscivorous fishes and their prey on coral reefs: implications for prey-fish mortality. *Mar. Biol*. 138, 383–397.

Sumida, P.Y.G., Yoshinagaa, M.Y., Madureira, L.A.S.P. and Hovland, M., 2004. Seabed pockmarks associated with deepwater corals off SE Brazilian continental slope, Santos Basin. *Mar. Geol. 207*, 159–167. https://doi.org/10.1016/j. margeo.2004.03.006.

Turner, J.A., Andradi-Brown, D.A., Gori, A., Bongaerts, P., Burdett, H.L., Ferrier- Pagès, C., Voolstra, C.R., Weinstein, D.K., Bridge, T.C., Costantini, F. and Gress, E., 2019. Key questions for research and conservation of mesophotic coral ecosystems and temperate mesophotic ecosystems. In: Loya, Y., Puglise, K.A. and Bridge, T.C.L. (Eds.), *Mesophotic Coral Ecosystems*. Springer, Cham, pp. 989–1003.

Tyler, E.H., Speight, M.R., Henderson, P. and Manica, A., 2009. Evidence for a depth refuge effect in artisanal coral reef fisheries. *Biol. Conserv. 142*, 652–667. https://doi.org/ 10.1016/j.biocon.2008.11.017.

Verfuss, U.K., Aniceto, A.S., Harris, D.V., Gillespie, D., Fielding, S., Jiḿenez, G., Johnston, P., Sinclair, R.R., Sivertsen, A., Solbø, S.A. and Storvold, R., 2019. A review of unmanned vehicles for the detection and monitoring of marine fauna. *Mar. Pollut. Bull. 140*, 17–29. https://doi.org/10.1016/j.marpolbul.2019.01.009.

Wedding, L.M. and Friedlander, A.M., 2008. Determining the influence of seascape structure on coral reef fishes in Hawaii using a geospatial approach. *Mar. Geodes. 31*, 246–266. https://doi.org/10.1080/01490410802466504.

Wilson, M.F.J., O'Connell, B., Brown, C., Guinan, J.C. and Grehan, A.J., 2007. Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. *Mar. Geodes. 30*, 3–35. https://doi.org/10.1080/ 01490410701295962.

Wolfl, A.C., Snaith, H., Amirebrahimi, S., Devey, C.W., Dorschel, B., Ferrini, V., Huvenne, V.A., Jakobsson, M., Jencks, J., Johnston, G. and Lamarche, G., 2019. Seafloor mapping – the challenge of a truly global ocean bathymetry. *Front. Mar. Sci. 6* (283) https://doi.org/10.3389/fmars.2019.00283.

Wood, S.N., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semi-parametric generalized linear models. *J. Roy. Stat. Soc. B 73*, 3–36. https://doi.org/10.1111/j.1467-9868.2010.00749.x.

Woods, S., 2012. GAMs with GCV/AIC/REML Smoothness Estimation and GAMMs by PQL. R Package Version 1.7–9. Available at. http://cran.rproject.org/web/packages/mgcv/index.html.

Wynn, R.B., Huvenne, V.A.I., Le Bas, T.P., Murton, B.J., Connelly, D.P., Bett, B.J., Ruhl, H.A., Morris, K.J., Peakall, J., Parsons, D.R., Sumner, E.J., Darby, S.E., Dorrell, R.M. and Hunt, J.E., 2014. Autonomous Underwater Vehicles (AUVs): their past, present and future contributions to the advancement of marine geoscience. *Mar. Geol. 352*, 451–468. https://doi.org/10.1016/j.margeo.2014.03.012.

Zelada Leon, A., Huvenne, V.A., Benoist, N., Ferguson, M., Bett, B.J. and Wynn, R.B., 2020. Assessing the repeatability of automated seafloor classification algorithms, with application in Marine Protected Area Monitoring. *Rem. Sens. 12*, 1572. https://doi.org/10.3390/rs12101572.

CHAPTER 4

BAITED REMOTE UNDERWATER VIDEOS REVEAL A POTENTIAL DEPTH REFUGE FOR PREDATORY REEF FISH OFF PEMBA ISLAND, TANZANIA

4.1 Preface

Many coral reefs, such as those around Pemba Island, Tanzania, face significant threats from local fishing including the effects of historic dynamite fishing (Grimsditch et al., 2009). The deep channel off Pemba Island is considered a potential hotspot for large reef predators (Tyler et al., 2009). Yet, the effects of such local anthropogenic stressors on distribution of fish communities in this area, including how predatory reef fishes are influenced by depth and habitat type, is little known.

In this chapter I utilise baited underwater remote videos (BRUVS) to survey predatory reef fish over a range of habitats and depths off Pemba Island to test a potential depth refuge effect in the area and recommend conservation measures to protect predatory reef fish populations.

This chapter has been written in the style of Marine Environmental Research and was submitted on 4th October 2021 and published in March 2022 *and is available at https://doi.org/10.1016/j.marenvres.2022.105587*.

I declare that the work submitted is my own. The contribution by co-authors was as follows:
Bryce Stewart, Melita Samoilys and Colin McClean: Supervision, review and editing.
Peter Musembi, Saleh Yahya, Ali Rashid and James Mbugua: Assistance in the field

4.2 References

Grimsditch, G.D., Tamelander, J., Mwaura, J., Zavagli, M., Takata, Y. and Gomez, T. 2009. *Coral reef resilience assessment of the Pemba channel conservation area, Tanzania*. Gland, Switzerland: IUCN. 40pp.

Tyler, E.H., Speight, M.R., Henderson, P. and Manica, A., 2009. Evidence for a depth refuge effect in artisanal coral reef fisheries. *Biological Conservation*, *142*(3), pp.652-667

BAITED REMOTE UNDERWATER VIDEOS REVEAL A POTENTIAL DEPTH REFUGE FOR PREDATORY REEF FISH OFF PEMBA ISLAND, TANZANIA

Kennedy E. Osuka[1,2], Bryce Stewart[1], Melita Samoilys[2], Colin McClean[1], Peter Musembi[2], Saleh Yahya[3], Ali Rashid[4] and James Mbugua[2]

Affiliations

[1.] Department of Environment and Geography, University of York, Heslington, York, YO10 5NG, United Kingdom

[2.] Coastal Oceans Research and Development – Indian Ocean (CORDIO East Africa). 9 Kibaki Flats P.O. Box 10135-80101, Mombasa, Kenya

[3.] Institute of Marine Sciences, University of Dar es Salaam, Zanzibar, Tanzania

[4.] Department of Fisheries Development, Zanzibar-Tanzania

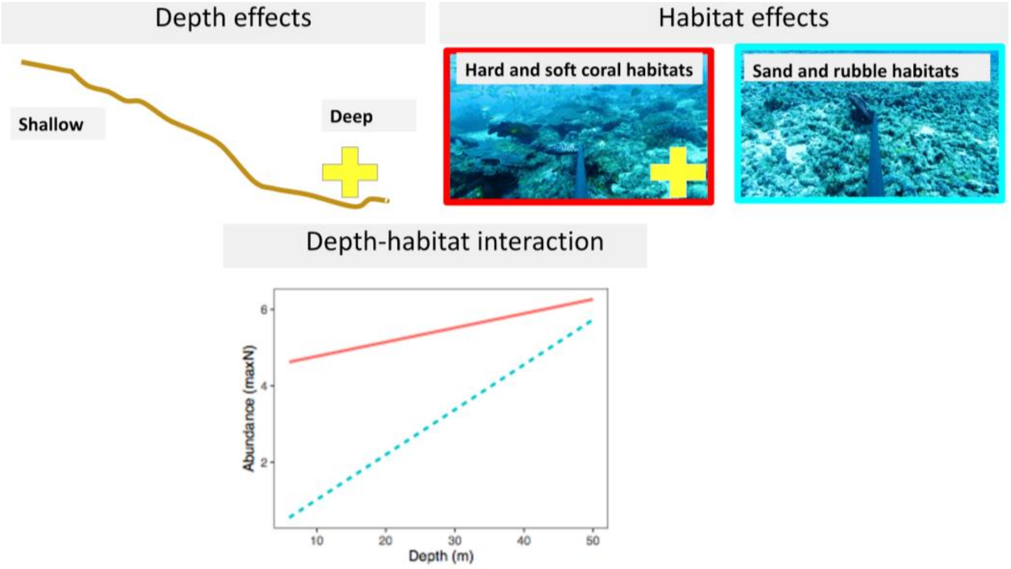
* Corresponding author.

E-mail address: koe503@york.ac.uk (K.E. Osuka).

Abstract

Coral reefs across the world face significant threats from fishing and climate change, which tends to be most acute in shallower waters. This is the case off Pemba Island, Tanzania, yet the effects of these anthropogenic stressors on the distribution and abundance of economically and ecologically important predatory reef fish, including how they vary with depth and habitat type, is poorly understood. Thus, we deployed 79 baited remote underwater videos (BRUVs) in variable water depths and habitats off Pemba Island, and modelled the effects of depth and habitat on abundance of predatory reef fish. Predatory reef fish types/taxa were significantly predicted by depth and habitat types. Habitats in relatively deeper waters and dominated by hard and soft corals hosted high species richness and abundance of predatory reef fish types/taxa compared to mixed sandy and rubble habitats. The findings add to the growing evidence that deep waters around coral reefs are acting as 'refuge' for fish predators. Thus, careful management, through effective area and species protection measures, are needed to prevent further depletion of predatory reef-associated populations and conservation of this biologically important area.

Graphical abstract



Keywords: Coral reefs, depth refugia, habitat effects, predation, movement behaviour, fisheries, conservation

1. Introduction

Coral reef predatory fishes - fish that feed on other fish or marine animals - have profound economic and ecological importance (Moberg and Folke, 1999; Hammerschlag *et al.*, 2019). They are an important source of animal protein and contribute significantly to the livelihoods of more than 20 million people living in close proximity to the eastern African coast (Bell *et al.*, 2016). Their large body size makes them a desirable but relatively easy target, but the late maturation and longevity of many species makes them more susceptible to overfishing (de Mitcheson *et al.*, 2020). Fishing pressure on large reef predators has increased significantly in recent decades, causing major declines in many areas around the world (Worm *et al.*, 2013). Overfishing of predatory fish populations can have severe ecological impacts as it often destabilizes food webs leading to community-wide impacts (Bascompte et al., 2005; Worm *et al.*, 2013; Hussey *et al.*, 2014; Sandin and Zgliczynski, 2015). Reef predators structure reef fish communities by directly exerting top-down control of prey organisms (Stewart and Jones, 2001; Baum and Worm, 2009), and indirectly by influencing the behaviour of prey assemblages while searching for food (Hixon, 2015; Rasher et al., 2017) or when resting and mating as part of their life history (Green *et al.*, 2015). The role of predatory fishes is therefore multi-faceted, extending from the oceans to the coastal communities.

Predatory fish show preferences for particular habitat types such as forereef ledges (Papastamatiou *et al.*, 2009), outer atolls and shelf areas (Cappo et al., 2007; Skinner *et al.*, 2020) that are associated with abrupt changes in depth. Such habitats are characterised by a wide depth range that can provide reef predator populations with a refuge from local fishing gears (Tyler *et al.*, 2009). Thus, the abundance, biomass and diversity of predators often increases from shallower lagoon reefs to deeper seaward reefs (Jennings et al., 1996; Pinheiro *et al.*, 2016). Fishing pressure, which is usually highest in shallow coral reef areas, can amplify this pattern. Similarly, outer deep reef habitats or contiguous to deep and nutrient rich waters often host a high abundance of schooling planktivorous species, an important food item that draws highly mobile predators into such areas (Wyatt *et al.*, 2013; Frisch *et al.*, 2014). Interaction between different predator types (e.g., schooling transient and resident predators) with habitat types and their associated depths remains unclear (Hixon, 2015). Increasing water depth is anticipated to have positive and negative relationships with abundance of fish predators and fishing pressure, respectively (Tyler *et al.*, 2009; Pinheiro *et al.*, 2016; Stefanoudis *et al.*, 2019). Noteworthy, shallower areas are more vulnerable to climate-induced coral bleaching (Graham et al., 2013; Obura et al., 2017), which can lead to coral mortality and loss of structural complexity. This in turn can cause declines in the prey that predatory reef fish generally consume (Hempson et al., 2017). Recovery of such reefs after bleaching is generally greatest where reefs are structurally complex and in deeper waters (Graham et al., 2015). However, the cover of live coral also declines below a certain depth, due to light limitation (Osuka et al, 2021). Therefore, the depth distribution of predatory reef fish will be governed by the combined influences of fishing disturbance, habitat structure and food availability, and how they interact with one another.

One area that is thought to support high numbers of predatory coral reef fish, but that is also under pressure from fishing, is the Pemba Channel off the coast of Tanzania. The western margins of Pemba Island neighbours a deep channel that averages 300 m and reaches a maximum of 800 m, making the Island a true oceanic Island (Semba et al., 2019). The shallow (<20 m) marine areas of Pemba Island have highly variable coral reef conditions, with some in healthy states with a high cover of hard coral, while others are in degraded states with low hard coral cover (Grimsditch et al., 2009). Reefs with low coral cover have been linked to destructive fishing activities particularly dynamite fishing (Grimsditch *et al.*, 2009; Wells *et al.*, 2010; Slade and Kalangahe, 2015). The mesophotic reef areas (30-150 m) are characterised by ledges, and oceanic steep outer reef slopes forming “staircase” walls in some locations (Osuka *et al.*, 2021). These seafloor features, together with a deep channel and the remoteness of the island, makes Pemba Island a potential hotspot for large reef predators. Yet, little is understood of the influence of depth and habitat on fish predators in this area.

The Pemba Island fishery is mainly artisanal involving the use of traditional gears (e.g., gillnets, hook and line) and introduced gears (e.g., small purse seines) to target coral reef-associated fish (Rehren et al., 2020). Evidence of overfishing has been reported at several sites. Indeed, a study conducted a decade ago in waters <21 m recorded no sharks, implying high rates of overfishing (Grimsditch *et al.*, 2009). Similarly, other large predatory taxa like groupers and snappers were either rare or of small size. In recent times, surveys on apex predators in Tanzanian waters (western margins of Pemba Channel) suggest that shark populations are “functionally extinct” (MacNeil *et al.*, 2020). Further, biomass projections of commercial species including large reef-associated predators in the Tanzanian Exclusive Economic Zone predict declines of up to 56-69% under increased fishing and climate change scenarios by the end of the 21st Century (Wilson et al., 2021). The decline in large reef-associated predator stocks is considered a key driver motivating fishers’ migration to other distant fishing grounds as far as Mozambique and Kenya, where depletion of fish stocks has been reported in the host fishing grounds (Wanyonyi *et al.*, 2016).

Sampling of coral reef fish communities in areas that are inaccessible or challenging for SCUBA divers was traditionally done with traps or nets (Collin, 1990; Bacheler et al., 2017). However, an increasingly popular method is the use of baited remote underwater videos (BRUVs). BRUVs are considered a non-invasive and non-destructive technique, which has been applied to assess occurrences of larger and more mobile species (Harvey *et al.*, 2012; White *et al.*, 2013). The method has been widely applied over extensive geographic areas, depth ranges and habitats (Harvey *et al.*, 2013; MacNeil *et al.*, 2020). Surveys with BRUVs ensure fish are not disturbed by divers, species are likely attracted from far areas by the bait, and a permanent record is produced. Use of BRUVS enhances species ID and allows more detailed analysis of the surrounding habitats and more importantly can be deployed much deeper than SCUBA (Harvey *et al.*, 2012).

Coral reef communities show clear spatial patterns that vary across a range of fine-scale local habitat conditions (Karisa et al., 2020). The outer reefs of Pemba Island have been little surveyed to date, likely due to logistical challenges associated with sampling deeper reefs with standard SCUBA underwater visual censuses. Indeed, previous ecological fish surveys conducted around Pemba Island were restricted to depths <21m and conducted either on SCUBA (e.g., Daniels et al., 2003; Grimsditch et al., 2009) or snorkel (e.g., Jones et al., 2019). The results from these studies lacked consensus on the diversity of reef predators. Therefore, we considered that BRUVs would be ideal for providing a more complete picture of the predatory reef fish community in this area.

This study aimed to examine key environmental characteristics that may be driving the abundance, distribution and diversity of predatory reef fish and to recommend conservation measures to protect these populations around Pemba Island. We hypothesized that predatory reef fish would be more confined to deeper than shallower reefs and would show significant relationships with healthy habitats dominated by hard corals. Further, habitat conditions such as healthy and degraded were expected to be stronger predictors of the occurrence, abundance and diversity of resident predatory species (i.e., those showing strong association with the reef structure), rather than transient species (i.e., schooling and epipelagic species).

2. Materials and methods

2.1 Study site

The survey was conducted on the outer reefs of the western margins of Pemba Island (Figure 1). Reefs selected for sampling corresponded in part with previous surveys conducted in the Greater Pemba Channel within the Pemba Community Conservation Area (PECCA) using SCUBA (Grimsditch *et al.*, 2009; Gudka et al., *in prep*) and autonomous underwater vehicles - AUV (Osuka *et al.*, 2021). Sites were chosen to be representative of different reef habitats and on the basis of depth (5-47 m) using a real-time depth echo sounder (Figure 1). Stations were largely fore reefs on the western margins of Pemba Island spanning from reefs in the north to the south (Figure 1). The BRUV stations occurring in continuous reef and separated to the next set of stations by a reef pass were pooled together to form a ’sector’. This resulted in three sectors conveniently named as north, central and south. The north and central sectors were separated by a deep channel called the Fundo Gap (Figure 1). Similarly, the central and south sectors were separated by a channel north of Misali Island (Figure 1). The survey was conducted over a five-day period during daytime hours in November 2019 during the northeast monsoon period.

Each sampling involved deployment of a mono-BRUV unit consisting of a video GoPro Hero4 camera Silver fixed on a stainless-steel frame, which was attached to a 1.65 m conduit pipe in the field of view of the camera (Appendix 1). A green meshed bait bag was mounted on the pipe and filled with bait of ca. 1 kg composed of oily fish from the families Scombridae and Carangidae. The bait was cut into small pieces, which were filled into the bait bags. The BRUV unit was tied with a rope to the top of the frame to facilitate deployment and a buoy on the other end to enable detection and retrieval.

Each BRUV system was calibrated following the Standard Operating Procedure described in Langlois et al. (2018). The first BRUV unit was deployed close to pre-set Global Positioning System (GPS) coordinates while subsequent deployments were done ca. 500 m away but along the reef. This distance was selected to minimize the chances of the same fish individuals being documented on neighbouring BRUV deployments. If there was insufficient reef in an area to allow this spacing, re-sampling was done at an interval of ca. 250 m but on a different day. The deployment points were geo-referenced using a handheld GPS. The time of deployment, depth, visibility, cloud cover, tidal state, currents and GPS readings were recorded during the deployment. Each BRUV unit was retrieved after at least 1-hour of recording.

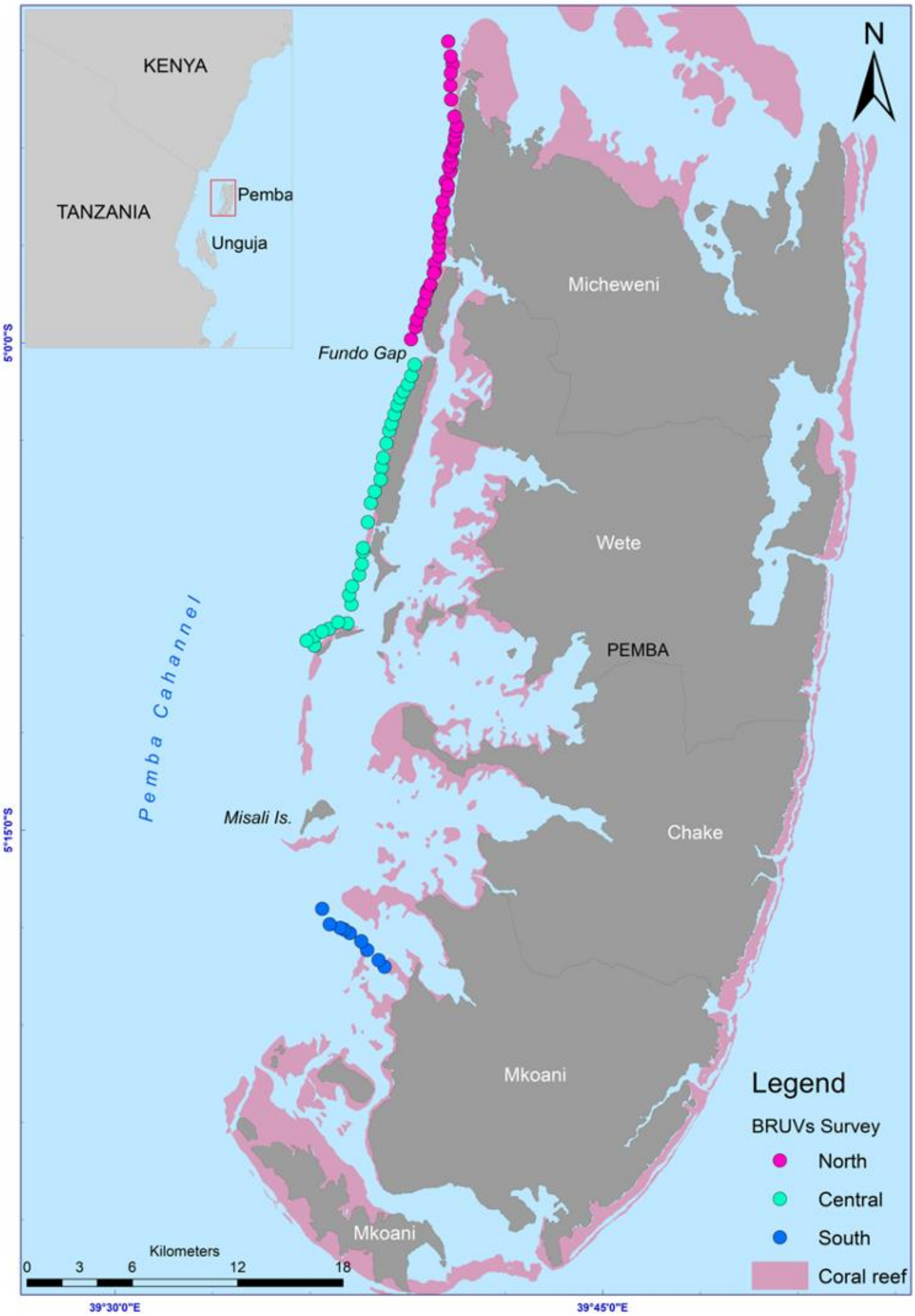


Figure 1: Map showing location of 79 baited remote underwater videos (BRUVS) stations in Pemba Island deployed in three sectors: north, central and south.

2.2 Video footage processing

After the BRUV unit was retrieved, visibility, field of view, profile and percentage cover of habitat/substrate types (hard coral, soft coral, sea fans, halimeda, sponges, fleshy and turf algae, rubble and sand) was visually estimated for each video recording. Fish species identification from the video footage focused solely on predatory fish from 14 families at normal play speed. These were: Aulostomidae (trumpetfish), Carangidae (jacks), Carcharhinidae (sharks), Congridae (conger eels), Dasyatidae (whiptail stingrays), Haemulidae (sweetlips), Fistulariidae (cornetfish), Lethrinidae (emperors), Lutjanidae (snappers), Muraenidae (moray eels), Myliobatidae (eagle rays), Scombridae (mackerel), Epinephelidae (groupers), and Sphyraerinidae (barracuda) (Appendix 2). Wherever video footage of individuals was unclear the genus or family was used. Two researchers (KEO, PM) reviewed species identification to ensure accuracy. Species identification was done using Lieske and Myers, (1994) and Taquet and Diringer, (2012) and confirmed using Eschmeyer's Catalog of Fishes (Fricke et al., 2021). Species observed were classified according to their association with the reef as either resident or transient (Hixon, 2015; Froese and Pauly, 2020). Resident predators were species showing strong association with the reef structure or seafloor such as groupers, snappers, emperors, sweetlips and eels. Transient predators were fast swimming, schooling and epipelagic species, such as sharks, barracuda, jacks and mackerel (Appendix 2). The conservation status of each species was derived from the International Union for Conservation of Nature (IUCN) Red List website (IUCN, 2021).

2.3 Data analysis

The maximum number of individuals (MaxN) of each species of predatory reef fish observed at one time from each video with a recording time of 1-hour was quantified. These data were used to derive a summary of the number of individuals and species per reef sector, and a rarefaction curve based on the cumulative number of BRUV deployments (Hammer et al., 2001).

Nonmetric multidimensional scaling (nMDS) based on Bray–Curtis similarity (Clarke and Warwick 2001), was performed on square root transformed MaxN data (Supplementary material Figure S1) to graphically assess patterns in abundance of reef predators across the three geographic sectors. A one-way SIMPER analysis was used to identify species that contributed the most towards dissimilarity of the sectors.

Principal components analysis (PCA) was applied to benthic variables to determine key variables contributing greatest to the variation. The loading of the first component was used to differentiate BRUVs stations into two major habitat types: hard coral and soft coral *versus* sand and rubble. An ordinary least squares regression of the first component loadings and depth was thereafter conducted to determine the relationship of habitat variables with depth.

Three predictor variables of fish abundance: sector, habitat and depths were modelled (Table 1) using zero-inflated Poisson (ZIP) model. Generalised linear model (GLM) and zero-inflated Poisson (ZIP) model outputs were first compared using Vuong non-nested hypothesis test-statistic (Vuong, 1989; Long and Long, 1997). The test showed ZIP was better than the standard Poisson model. Therefore, ZIP was fitted to MaxN data on pooled predators, resident predators, transient predators, species richness, fish family and species. The ZIP model had two parts: a Poisson regression model to model fish count (MaxN) using predictor variables of Depth and Habitat; and the logit model for predicting the probability of excess zeros in random variables of Sector. The logit model provided the basis for uncovering the excessive absence of reef predators in a sector, as an indication of overfishing. To help with the interpretation of the results we assessed the interaction effects between depth and habitat type using GLM.

Table 1: Predictors used in the analysis of predatory fish taxa

Predictor	Abbreviation	Data type	Description
Habitat	Hab	Categorical	Two major habitat-types identified from PCA i.e., Sand and Rubble (SA_RU) and Hard coral and Soft coral (HC_SC).
Sector	Sec	Categorical	Three sectors separated by reef passes i.e., North, Central and South
Depth	Dep	Continuous	Station depth in metres

3. Results

3.1 Predatory reef fish abundance and taxonomic richness

A total of 5,767 individuals from 71 species and 14 families were recorded, with 83% of the species occurring in depths > 20 m (Appendix 2). Overall, a majority (89%) of the species sampled were in the Least Concern category under the IUCN Red List of species. Only two species (< 3% of the total), the sky emperor *Lethrinus mahsena* and honeycomb stingray *Himantura uarnak*, were classified as Endangered. Vulnerable species accounted for 4% and included the silvertip shark *Carcharhinus albimarginatus,* spotted eagle ray *Aetobatus ocellatus,* brown-marbled grouper *Epinephelus fuscoguttatus*, while only one Near Threatened species, the narrow-barred Spanish mackerel *Scomberomorus commerson* was observed. Two species assessed as Data Deficient were also recorded – Indian mackerel *Rastrelliger kanagurta* and Kuhl's maskray *Neotrygon kuhlii.*

The species rarefaction curve of the cumulative number of BRUV deployments showed that the curve was flattening suggesting that the predatory reef fish community had been relatively well sampled overall (Figure 2). However, the southern sector was least sampled yielding fewer species compared to the northern and central sectors. The total number of species encountered in the northern and central sectors were 54 and 42 species, respectively, compared to six in the southern sector.

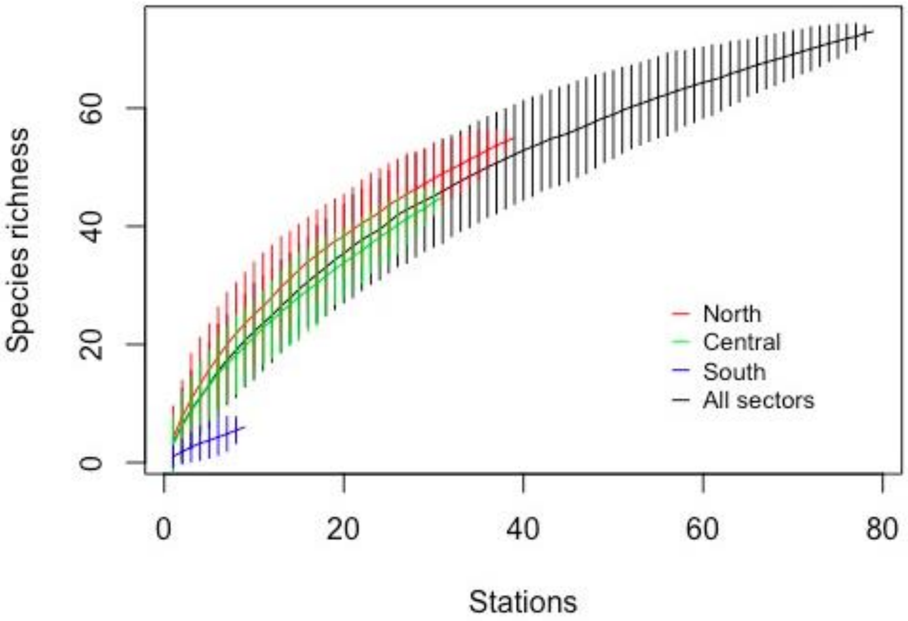


Figure 2: Species rarefaction curve with their 95% confidence interval separated by sectors: North - red, Central - green, South - blue and all sectors - black.

The mean fish abundance (MaxN) showed least differences across the sectors, although relatively higher values were found in the northern (8.87 ± 1.49 (se)) and central (9.90 ± 2.98 (se)) sectors compared to the southern sector (5.11 ± 3.30 (se)). Proportion of zero counts for species encountered during the survey across three sectors showed predators were more encountered in the north than the central and the south (Figure 3). Resident predators were more encountered in the north and central sectors while transient predators occurred more in the north sector (Figure 3).

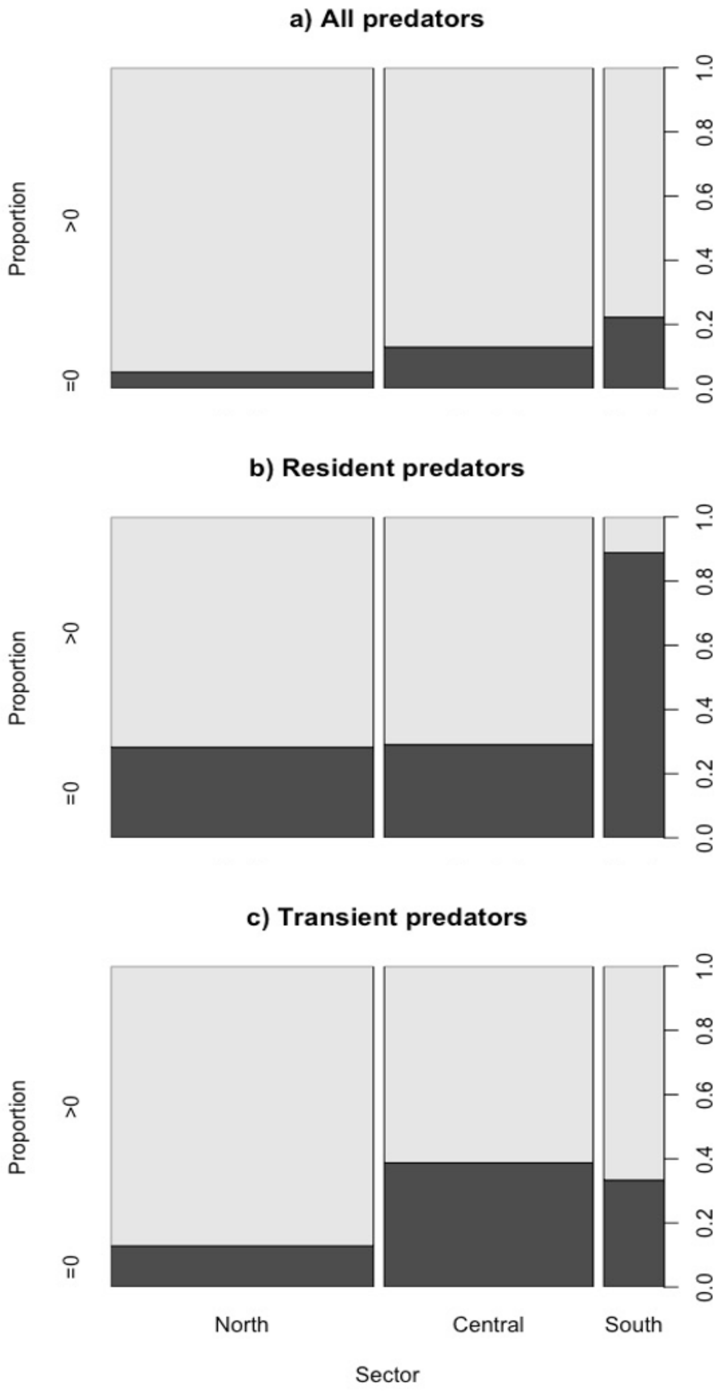


Figure 3: Proportion of zero counts (dark shadings) across three sectors for all predators (a), resident predators (b), and transient predators (c). The widths of the bars show the number of BRUVS per sector North n = 39, Central n = 31 and South n = 9.

3.2 Predator community structure

SIMPER analysis revealed that dissimilarity in predatory reef fish between the sectors was generally high (> 90%). The greatest dissimilarity was between North and South (Average dissimilarity = 96.2%) driven by snubnose pompano *Trachinotus blochii,* small-toothed jobfish *Aphareus furca,* green jobfish *Aprion virescens* and Chinese trumpetfish *Aulostomous chinensis* (Table 2).

Table 2: Results of one-way SIMPER analyses of species contributing more than 5% of the dissimilarity in abundance (%) in the three sectors of Pemba Island – North, Central and South. Species are classified according to their association with the reef as either resident (R) or transient (T).

Species	Average abundance		Average dissimilarity	Contribution (%)
Average dissimilarity = 93.2	North	Central		
Aprion virescens (T)	1.3	0.1	8.6	9.3
Aulostomous chinensis (T)	0.6	0.5	6.7	7.2
Lethrinus olivaceus (R)	0.3	0.8	6.3	6.8
Aphareus furca (T)	0.8	0.4	5.9	6.4
Cephalopholis argus (R)	0.2	0.7	5.0	5.4
Average dissimilarity = 94.5	South	Central		
Aphareus furca (T)	1.1	0.4	14.5	15.3
Trachinotus blochii (T)	3.3	0.0	13.3	14.1
Aulostomous chinensis (T)	0.1	0.5	6.4	6.8
Cephalopholis argus (R)	0.0	0.7	6.2	6.6
Lethrinus olivaceus (R)	0.0	0.8	5.8	6.1
Average dissimilarity = 96.2	North	South		
Trachinotus blochii (T)	0.0	3.3	12.5	13.0
Aphareus furca (T)	0.8	1.1	12.3	12.8
Aprion virescens (T)	1.3	0.0	10.4	10.8
Aulostomous chinensis (T)	0.6	0.1	7.4	7.7

3.3 Description of benthic structure

On the face value, the cover of benthic variables showed minimal differences between the north and central sectors, but together they differed from the southern sector that had high cover of sand (52%) and fleshy algae (20%) (Supplementary material Figure S2). Hard and soft coral cover averaged around 19% and 9% respectively in the north and central sectors. Overall, sand was dominant in all sectors, reaching 21% and 30% in central and northern sectors respectively. The cover of rubble was 15% in the north, 10% in the central and 4% in the south sectors.

The first component (PC1) of the PCA explained 51.53% of variation in habitat composition (Figure 4), showing positive correlation with the cover of sand (r = 0.82) and rubble (r = 0.13), and negative correlations with the cover of hard corals (r = -0.48) and soft corals (r = -0.27). The second PCA explained an additional 19.12% and was positively correlated to sand (0.41) and hard coral (0.39) and negatively correlated to rubble (-0.81). Linear regression of PC1 loadings and depth showed sites with high cover of sand and rubble to be in deeper areas compared to those with high cover of hard corals and soft corals in shallower depth ($R^2 = 0.13$; $p<0.001$; Figure 5)

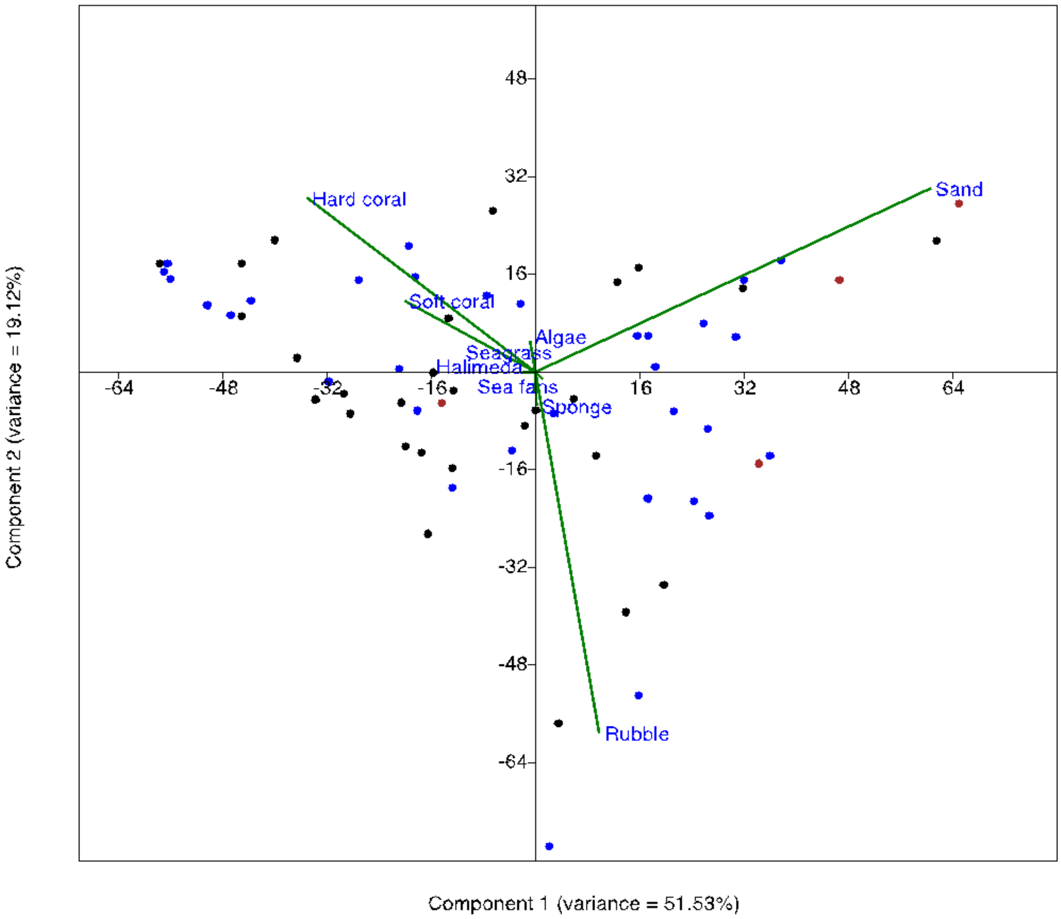


Figure 4: Principal component analysis plot showing the loadings of stations on the first and second principal components and bi-plots of the benthic variables. North, central and south sectors represented by blue, black and red dots.

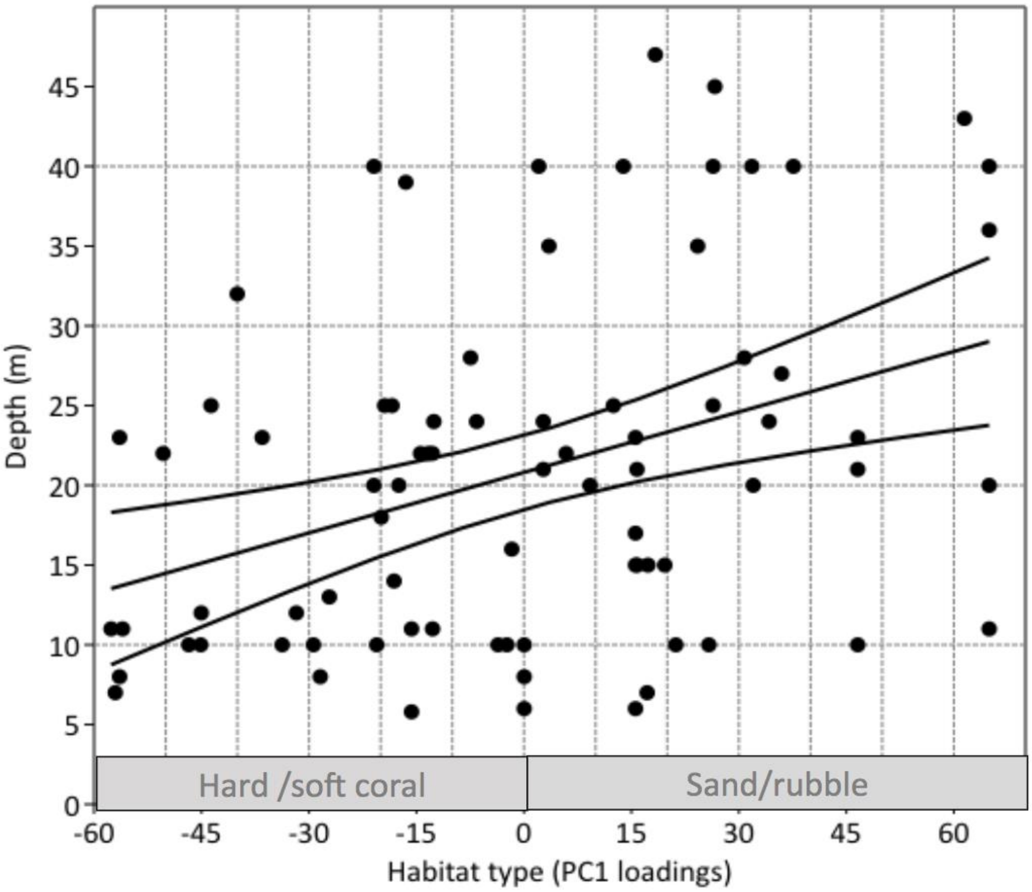


Figure 5: Relationship between first principal component (PC1) habitat loadings and depth. Sites with negative loadings were correlated with high cover of hard and soft coral while those with positive loadings were correlated with sand and rubble cover.

3.4 Influence of depth and habitat types

Species richness and the abundance of all predators (cumulative MaxN) and resident predators were significantly ($p<0.05$) influenced by depth and habitat type, with higher counts in deeper than in shallower areas as well as in coral habitats than in sandy and rubble habitats (Supplementary material Table S1). The zero-inflation model showed resident predators had significantly excess zeros in the south than the central sector, while transient predators had significantly excess zeros in the central than north sector (Table 3). GLM results showed significant interaction between habitat type and depth for all predators, resident and transient predators (Figure 6). In sandy and rubble habitats, every increase in depth was associated with an increase in abundance ranging from 0.7-12 individuals for all predators, resident and transient predators.

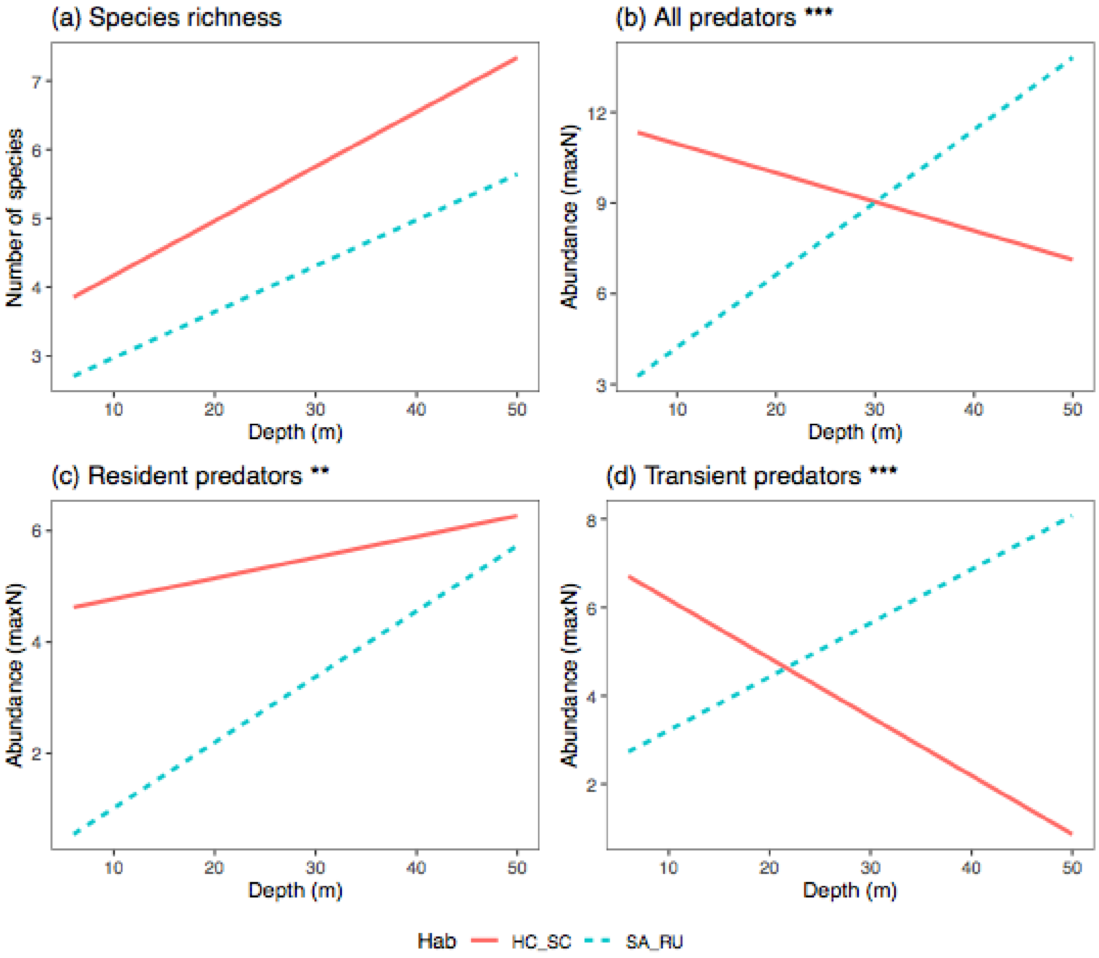


Figure 6: Simple-slope plots of the interaction between depth and habitat type (Hab) in predicting four aggregate abundance metrics. Habitat is represented by Hard coral and Soft coral (HC_SC) and Sand and Rubble (SA_RU). All trend lines indicate significant relationships and asterisks indicate significant interaction with '***' = <0.001, '**' = <0.01, '* = <0.05.

Table 3: Estimated coefficients of zero-inflation model (ZIP) and their standard errors (S.E.) for resident and transient predators and three species. Significant codes: '***' = <0.001, '**' = <0.01, '* = <0.05. Sec = sector. Reference group for Sec was the Central sector.

	Estimate	Coefficients	S.E
a) Resident predators	Intercept*	-0.92	0.40
	Sec_North	-0.07	0.55
	Sec_South**	2.98	2.63
b) Transient predators	Intercept	-0.46	0.37
	Sec_North*	-1.47	0.61
	Sec_South	-0.24	0.80
c) Species			
Lethrinus harak	Intercept**	2.80	1.05
	Sec_North**	-3.19	1.22
	Sec_South	15.17	5797.15
L. rubrioperculatus	Intercept*	1.47	0.80
	Sec_North*	-0.43	0.95
	Sec_South	15.89	2183.26
Aprion virescens	Intercept***	2.07	0.62
	Sec_North**	-2.08	0.73
	Sec_South	16.33	3994.54

The predictor variables showed significant influence on four families (Figure 7; Supplementary material Table S2). The abundance of Haemulidae and Lethrinidae showed significant positive relationships with increasing depth, while only Aulostomidae displayed significant negative relationships. Other families particularly Carcharhinidae, Dasyatidae, Fistulariidae, Muraenidae, Myliobatidae, Epinephelidae and Sphyraerinidae exhibited non-significant relationships. Abundance of Lutjanidae was greater in hard and soft coral habitats compared to sandy and rubble habitats. A contrast observation was found for Carangidae showing higher abundance in sandy and rubble than hard and soft coral habitats.

The GLM with interaction effects showed significant interaction between habitat type and depth for Lethrinidae, Lutjanidae, Haemulidae, Fistulariidae and Scombridae (Figure 7). Every increase in depth within hard coral and soft coral habitats was associated with an increase in abundance of 1.0, 7.1 and 10.8 individuals for Lethrinidae, Haemulidae and Fistulariidae correspondingly. In sandy and rubble habitats, every increase in depth was associated with an increase in abundance of 1.5 and 1.7 individuals for Lutjanidae and Scombridae respectively.

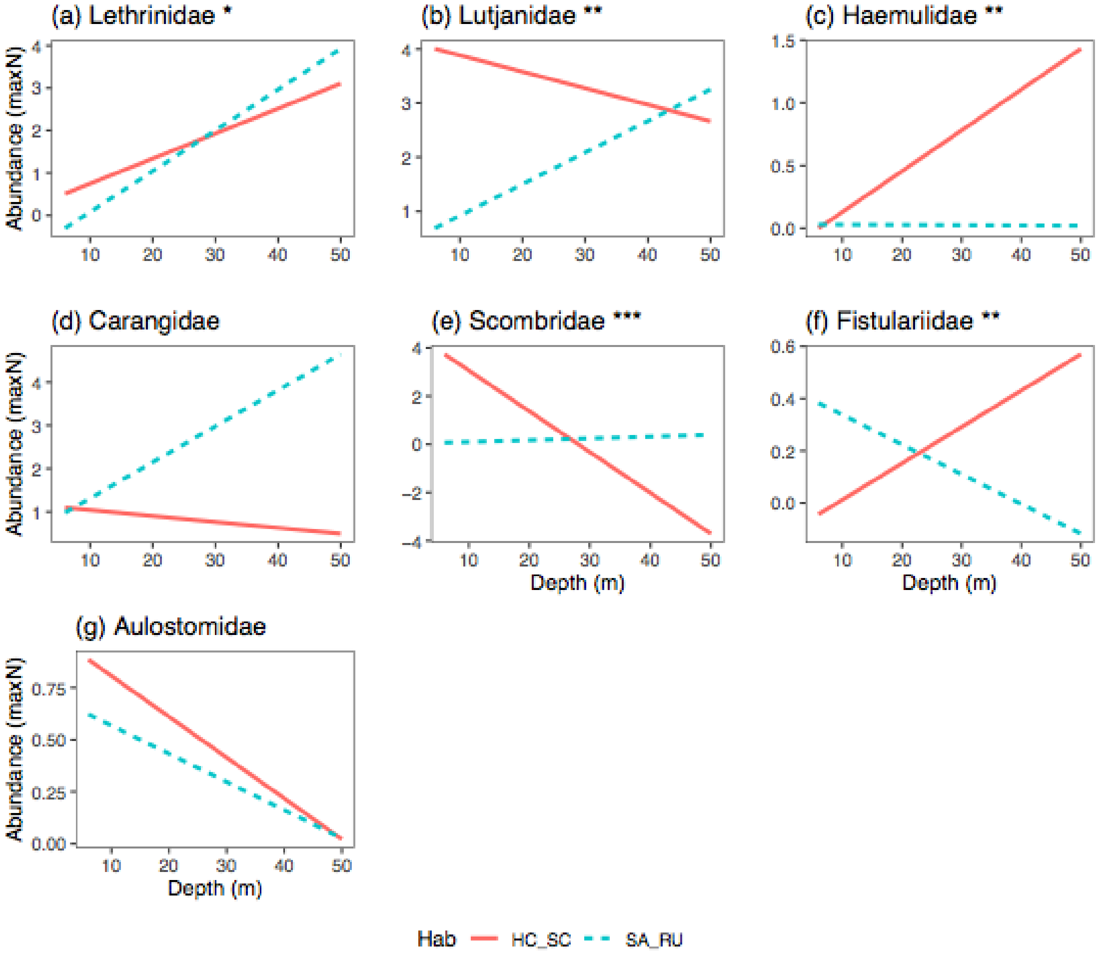


Figure 7: Simple-slope plots of the interaction between depth and habitat type (Hab) in predicting abundance of three resident predator fish families (a-c) and four transient predator fish families (d-g). Habitat is represented by hard coral and soft coral (HC_SC) and sand and rubble (SA_RU). All trend lines indicate significant relationships and asterisks indicate significant interaction with '***' = <0.001, '**' = <0.01, '* = <0.05.

The abundance of *Trachinotus blochii* and spotcheek emperor *Lethrinus rubrioperculatus* increased with increasing depth, while for *Aulostomous chinensis,* bluefin trevally *Caranx melampygus* and Indian mackerel *Rastrelliger kanagurta* it decreased with depth (Figure 8; Supplementary material Table S3). The abundance of thumbprint emperor *Lethrinus harak* and *Aprion virescens* was higher in hard and soft coral habitats compared to sandy and rubble habitats. This was different for *Aphareus furca* and *Rastrelliger kanagurta,* which had greater abundance in sandy and rubble habitats than hard and soft coral habitats. The zero inflated models showed that excess zeros occurred in central than northern sectors for three species: *Lethrinus harak, Lethrinus rubrioperculatus* and *Aprion virescens* (Table 5b). GLM results showed significant interaction between habitat type and depth for *Lethrinus olivaceus* (Figure 8), with every increase in depth within hard coral and soft coral habitats being associated with an increase in abundance of 6.7 individuals.

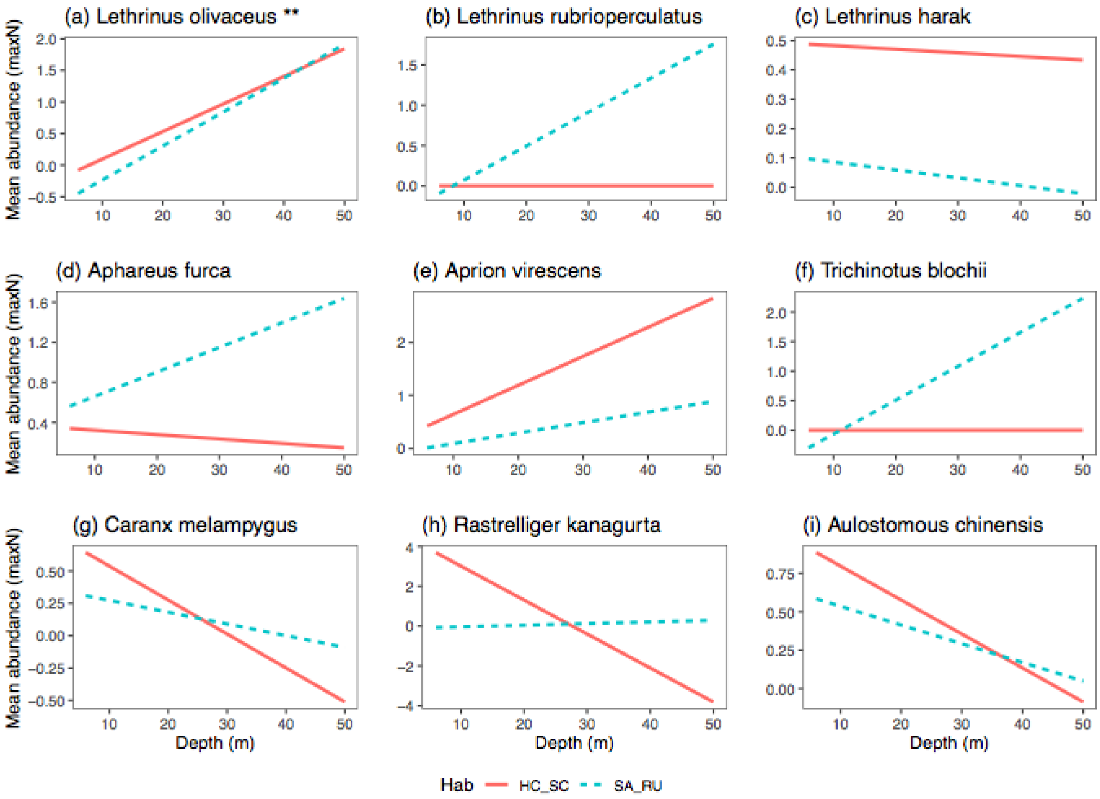


Figure 8: Simple-slope plots of the interaction between depth and habitat type (Hab) in predicting fish abundance of three resident predator species (a-c) and six transient predator species. Habitat is represented by hard coral and soft coral (HC_SC) and sand and rubble (SA_RU). All trend lines indicate significant relationships and asterisks indicate significant interaction with '***' = <0.001, '**' = <0.01, '* = <0.05.

4. Discussion

4.1 General observations and novelty of the study

Predatory reef fish have excessively been targeted around the world and latest studies show that many of these species are increasingly becoming absent in regions such as the western

Indian Ocean (WIO) (de Mitcheson *et al.*, 2020; MacNeil *et al.*, 2020). The present study, one of the first reef surveys to sample the west coast of Pemba Island, showed 83% of the 71 predator species encountered were present in depths greater than 20 m. This indicates a potential depth refuge for certain predatory reef fish (Tyler, et al., 2009; Bongaerts et al., 2010). This study therefore provides both a valuable baseline for the study area, and findings that are likely to be of wider interest to coastal communities and managers in coral reef areas around the world.

4.2 Habitat and depth influence

Habitat and depth have a profound influence on predator abundance, although these factors often interact (Pinheiro *et al.*, 2016; Skinner *et al.*, 2020). In our study, the abundance of all reef-associated predators in the shallow areas was high in the hard and soft coral habitats, but in relatively deeper areas of up to 47m, high levels of abundance were seen in the sandy and rubble habitats. This strongly implies that shallow coral reefs areas in a healthy state, or recovering from historical impacts, play an important role in hosting predatory fishes. However, the high fishing pressure that is prevalent in shallow areas around Pemba (Grimsditch et al., 2009), appears to be leading to a shift in the distribution of predatory fishes into the deep areas where sandy habitats dominate.

4.3 Transient and resident predators - habitat and depth associations

The abundance of predatory reef types with different movement behaviours (transient *versus* resident) was influenced by habitat types and depth in a non-random manner (Hixon, 2015; Filous *et al.*, 2017; Paxton *et al.*, 2020). Resident predators presented strong positive relationships with hard and soft coral habitat and increasing depth. This habitat association was expected since resident predators show high degrees of site fidelity and are usually confined to 'home' reefs', which offer both shelter and food resources (Stewart and Jones, 2001; Dance et al., 2011). Contrastingly, transient predators are highly mobile epipelagic species that generally show the weakest relationships with coral habitat types, except when the abundance of target prey species is above certain thresholds or the habitat is structurally complex with an extensive vertical relief (Paxton *et al.*, 2020). Interestingly, the depth effect was observed in all habitat types for resident predators but only in sandy and rubble habitats for transient predators. This suggests that both coral and mixed sandy and rubble habitats in relatively deeper waters provide a refuge to a range of fish targeted by fisheries (Tyler, et al., 2009; Bongaerts et al., 2010), which in turn attract transient predators utilising them as a food source. Certainly, predatory reef fish are attracted to areas of high prey fish density that tend to occur in areas of live coral and high structural complexity (Stewart and Jones 2001; Chong-Seng et al., 2012). Therefore, the influence of habitat and depth on the abundance of reef fish was clearer in resident predators but more complex for transient predators.

Despite the above differences, management efforts geared towards promoting the attainment and maintenance of thresholds of prey densities (McClanahan et al., 2011; Hill et al., 2020) should benefit both resident and transient predators. To ensure the sustainability of predatory reef fish in areas like Pemba Island, where human population is growing (NBS 2018) and fishing effort is increasing (Jacquet and Zeller, 2007; Rehren et al., 2020), it will be important to manage both the fisheries and protect the habitats that their prey fish rely upon.

4.4 Species driving the pattern

We found three to six key species within the resident and transient predator types were the most responsible for the patterns in the habitat and depth relationships. Within the resident predators, significant interaction between habitat and depth was only apparent in longface emperor, *Lethrinus olivaceus,* highlighting increased abundance in deeper areas but more so for those individuals occurring in sandy and rubble habitats. A positive depth effect was evident in spotcheek emperor, *Lethrinus rubrioperculatus,* while coral habitat effects were detected in thumbprint emperor, *Lethrinus harak*. In general, emperors are linked to sandy habitats where they feed by hunting less mobile prey (Kulbicki et al., 2005). Spotcheek emperors prefer outer reef slopes in waters greater than 10 m (Sommer et al., 1996; Fricke et al., 2011) thus it was not surprising that their abundance increased with increasing depth. Similar studies in the Maldives have shown coral habitats to host more thumbprint emperors (Skinner *et al.*, 2020). The species move either in small schools or solitary and can traverse different habitats including shallow sandy and hard coral habitats (Carpenter and Allen, 1989). We therefore postulate that emperor species respond to habitat and depth effects in varying ways.

We observed habitat and depth effects with no interaction effects within the transient predators. Green jobfish, *Aprion virescens,* showed significant association with hard coral and soft coral in contrast to small-toothed jobfish *Aphareus furca*, which were more affiliated to sandy and rubble habitats. The opposing patterns in these closely related species is likely related to their biology and movement patterns. The adults of green job fish inhabit seaward reefs, while those of small-toothed jobfish prefer inshore coral and sandy habitats (Anderson and Allen, 2001). Positive depth effects were evident in snubnose pompano, *Trachinotus blochii,* while negative relationships with depth were found for Chinese trumpetfish, *Aulostomous chinensis,* and schooling species of bluefin trevally, *Caranx melampygus,* and Indian mackerel, *Rastrelliger kanagurta*. These associations are coherent with ontogenetic shifts and feeding behaviour that involve various depths and habitat types (Green *et al.*, 2015; Nash *et al.*, 2015). For example, the juveniles of snubnose pompano occur in shallow sandy habitats and later move to adjacent relatively deeper coral reef habitats as they grow (Fischer et al., 1990). This suggests the individuals surveyed in sandy habitats were all sub-adults. Chinese trumpetfish utilise multiple habitat types such as seagrass lagoons, coral and rocky reefs in the shallow areas and caves reaching 200 m in the deep areas (Bowen *et al.*, 2001; McGratten and Pollom, 2015). The species is also not fished which makes it ubiquitous in shallow water depths. Bluefin trevally and Indian mackerel are mobile predators and often hunt in shallow waters (Sancho, 2000), where their food items are generally most abundant, and they may exhibit high residency in such depths (Filous *et al.*, 2017). Taken together, these findings indicate that schooling transient predator species are least dependent on healthy coral habitat types and therefore, less likely to be affected by changes in habitat conditions.

4.5 Family patterns

Resident fish families like Haemulidae and Lethrinidae increased in abundance with increasing depth, particularly in hard and soft coral habitats. This finding may be explained by the idea that during the day, coral heads on the reef offer shelter to these nocturnal species and where present in waters >20m they provide further refuge from fishing pressure. For example, at night haemulids forage on diets composed of small fish, invertebrates and dead animals in seagrass beds but during the day shift to coral associated habitats to escape predation from meso-predators (Burkepile and Hay, 2008). A contrasting result was found for lutjanids that have been observed to regularly take baits during daytime fishing operations (Bacheler et al., 2021). While Lutjanidae also rest during the day in reef ledges and feed during the night (Nagelkerken et al., 2000), it is possible that the pattern observed was due to the bait plume from our BRUVs (Harvey et al., 2012; Espinoza et al., 2014) attracting them during the day and especially in the open sandy and rubble habitats.

A non-significant influence of habitat type and depth was found on resident predators of the subfamily Epinephelinae. This could reflect high abundance or diversity within this group, which can influence the ability to detect relationships (Gerrodette, 1987). Nonetheless, the non-significant results are in contrast to a previous study in the Maldives that showed deep outer reefs had greater abundance of Epinephelinae than shallow lagoonal reefs (Skinner *et al.*, 2020). However, the depth preferences of different species within the Epinephelinae (Froese and Pauly, 2020), could be masking the relationships with depth.

Among the transient predators, there was evidence of habitat effects for the family Carangidae and interaction effects for Scombridae and Fistularidae. Fish belonging to the families Carangidae and Scombridae generally move in schools, often at speed, and therefore can quickly respond to temporal and spatial fluctuations in prey fish density (Stewart and Jones, 2001). As for Fistularidae, members of this family are generalist, usually very broad ranging inhabiting habitats from reefs to sandy habitats and depths reaching 100 m (Watson and Sandknop, 1996).

4.6 The north, central and south differences

Coral reefs in the WIO region have shown declines in coral cover due to climate change causing coral bleaching and subsequent coral mortality, and are predicted to decrease further (Obura *et al.*, 2017; McClanahan *et al.*, 2020). Critically, healthy coral habitats are essential for different groups of predatory fish. Therefore, future habitat loss through destructive fishing activities like dynamite fishing, which has previously been reported in Pemba Island (Slade and Kalangahe, 2015), will adversely affect the abundance of predatory species. Dynamite fishing and bleaching damage create accumulation of rubble, which could hamper recruitment and re-growth of coral. The cover of rubble can be used to disentangle these effects, particularly if one driver like dynamite fishing is localised and the other like bleaching is widespread. In our study, the cover of rubble was relatively high in the north (15%) and central (10%) sectors compared to the south (4%). However, the low cover in the south is potentially due to artefacts of sampling, which was hindered by logistical constraints of rough sea conditions. Alternately, the differences between the north and south sectors could be due to effects of historical dynamite fishing that was more prevalent in the shallow areas of the northern sector (pers. obs. Melita Samoilys).

Excessive absence of predators is an indication of widespread overfishing (Myers and Worms, 2003). The relatively high proportion of zero counts in the southern and central reef sectors of Pemba Island may therefore indicate overfishing, particularly for emperor reef species:

Lethrinus harak, and *L. rubrioperculatus.* Previous studies in the southern sector (i.e., Misali Island) point to relatively healthy habitats and fish diversity but a disproportionately decreased abundance and diversity of large reef-associated predators (Grimsditch et al., 2009; Jones et al., 2019; Osuka *et al.*, 2021). Indeed, in 2017, estimates of species richness drawn from six families: Carangidae, Epinephelinae, Lethrinidae, Lutjanidae, Carcharhinidae and Sphyraenidae at Misali stood at 15 species, down from 46 species in 2004 (Daniels et al., 2004; Jones et al., 2019). In combination these studies suggest overfishing may have worsened in recent decades.

The central sector was the only sector where Vulnerable (silvertip shark, *Carcharhinus albimarginatus,* brown-marbled grouper, *Epinephelus fuscoguttatus)* IUCN Red Listed species were recorded. Also recorded in the central and southern sectors was the Vulnerable spotted eagle ray *Aetobatus ocellatus*. The appearance of these species in the central sector could be connected to the relatively high habitat quality (Harborne et al., 2011), which is critical in maintaining the remaining populations of threatened species (Root 1998; Friedlander et al., 2007). The central sector had a continuous forereef area making the area ideal for reef predators like sharks and groupers (Papastamatiou et al., 2018; Skinner et al., 2020). Further, the sector's isolation from the main island through an extensive inner reef also imply fishing pressure is relatively low and thus future species and area protection measures would certainly be beneficial.

Studies have documented algal dominated habitats to have fewer predators than coral-dominated habitats (Connell and Kingsford, 1998) possibly due to low densities of prey (Beukers-Stewart et al., 2011). From the SIMPER dissimilarity results, the three sectors differed in terms of common species contributing most to the abundance differences. Fewer predator species occurred in the southern sector potentially due to the relatively high algal cover. This coupled with high turbidity in the sector (pers. obs. Kennedy Osuka) may have decreased the hunting efficiency of predators (Robertson and Blaber, 1993; Mallela et al., 2007) therefore affecting our ability to detect them using BRUVs.

4.7 Using BRUVs to survey predatory coral reef fish

This study joins a growing number illustrating the utility of BRUVs for gaining unique insights into coral reef fish communities across a range of depths and environments. However, it is appropriate to recognize limitations of the method. Our study deployed mono-videos and thus it was not able to estimate fish size and subsequently fish biomass (Bernard et al., 2014; Langlois et al., 2018). An important, but unanswered, question is how biomass of reef-associated predators would change across the sectors. Despite this limitation, we are confident that the central sector had a higher biomass than the other sectors. This is due to the presence of large-sized reef predators including sharks, rays, groupers and trevally in that area.

The rarefaction curves showed that our BRUVs surveys were reasonably adequate to estimate the species richness of predatory reef fish of the outer reefs of Pemba Island. However, the asymptote of the curve had not yet been fully reached suggesting that the observed species richness was somewhat underestimated. As such, it is possible that our sampling might have missed observing some of the rarer, cryptic and more wary reef predators (Asher et al., 2017; Skinner et al., 2020).

In the future it would be useful to extend the reef studies using BRUVs by examining predators at Misali Island. Additional research using stereo-BRUVs would provide further insight into spatial and depth related variation in predatory reef fish biomass (Langlois et al., 2018). Of particular relevance would be the mid-water stereo BRUVs (Santana-Garcon et al., 2014), which may be appropriate for the outer reefs with ledges and walls that make it difficult for BRUV units to settle. The addition of Misali Island (see Figure 1) as a study site would also be informative, as this area is known to support high coral cover (Grimsditch et al., 2009). Future work especially in the outer reefs of Pemba Island would also benefit from application of complementary coral reef survey methods able to survey shallow and mesophotic depths (e.g., AUVs, Osuka et al., 2021). Undoubtedly, such an effort would provide a much comprehensive insight into the drivers of the diversity, distribution, density and biomass of predatory reef fish in the area.

Predatory reef fish populations are facing immense pressures worldwide, leading to alarming losses in abundance and diversity. The present study has shed light on abundance and distribution of predatory reef fish populations off the under-researched oceanic island of Pemba Island. Clearly, different types of predators are discordantly predicted by depth and habitat type with three to six key species within the resident and transient predator categories being responsible for the patterns. Habitats dominated by hard and soft corals, and in relatively deeper waters, hosted high species richness and abundance of reef-associated predators. Our findings add to the growing evidence that deep waters around coral reefs are acting as ‘refuge’ for fish predators and coral habitats. Thus, careful management, through effective area and species protection measures, are needed to prevent further impending reductions in their populations.

Acknowledgements

This work was funded by the Sustainable Oceans, Livelihoods, and food Security Through Increased Capacity in Ecosystem research in the Western Indian Ocean (SOLSTICE-WIO) Programme (www.solstice-wio.org), a collaborative project funded through the UK Global Challenges Research Fund (GCRF) under NERC grant NE/ P021050/1. KEO acknowledges additional support from Norwegian agency for development cooperation (Norad), Perivoli Philanthropy and Dev Joory for funding this work as part of his PhD research. We are grateful to Phil Platts for his critical review of an early draft.

Appendix 1: Image of a BRUV unit being deployed off the coast of Pemba Island.

© Kennedy Osuka

Appendix 2: Species list and their IUCN Red List Categories and minimum and maximum depths sampled

Family	**Species**	**Predator type**	**IUCN Red List Category**	**Min depth (m)**	**Max depth (m)**
Carcharhinidae	*Carcharhinus albimarginatus (Rüppell, 1837)*	Transient	VU	39	39
Carcharhinidae	*Carcharhinus sp*	Transient	VU	10	40
Dasyatidae	*Neotrygon kuhlii (Muller & Henle 1841)*	Resident	DD	23	23
Dasyatidae	*Himantura uarnak (Gmelin 1789)*	Resident	EN	40	40
Myliobatidae	*Aetobatus ocellatus (Kuhl 1823)*	Transient	VU	20	22
Muraenidae	*Gymnothorax buroensis (Bleeker 1857)*	Resident	LC	22	28
Muraenidae	*Gymnothorax eurostus (Abbott 1860)*	Resident	LC	23	23
Muraenidae	*Gymnothorax favagineus Bloch & Schneider 1801*	Resident	LC	16	40
Muraenidae	*Gymnothorax fimbriatus (Bennett 1832)*	Resident	LC	35	35
Muraenidae	*Gymnothorax flavimarginatus (Rüppell 1830)*	Resident	LC	10	15
Muraenidae	*Gymnothorax javanicus (Bleeker 1859)*	Resident	LC	10	45
Muraenidae	*Gymnothorax meleagris (Shaw 1795)*	Resident	LC	10	23
Muraenidae	*Gymnothorax nudivomer (Günther 1867)*	Resident	LC	40	40
Muraenidae	*Gymnothorax undulatus (Lacepède 1803)*	Resident	LC	25	25
Muraenidae	*Gymnothorax griseus (Lacepède 1803)*	Resident	LC	10	21
Congridae	*Heteroconger hassi (Klausewitz & Eibl-Eibesfeldt 1959)*	Resident	LC	20	32
Aulostomidae	*Aulostomus chinensis (Linnaeus, 1766)*	Transient	LC	5.8	35
Echeneidae	*Echeneis naucrates Linnaeus 1758*	Transient	LC	11	20
Fistulariidae	*Fistularia commersonii Ruppell 1838*	Transient	LC	7	28
Epinephelinae	*Aethaloperca rogaa (Fabricius 1775)*	Resident	LC	7	32
Epinephelinae	*Cephalopholis argus Schneider 1801*	Resident	LC	5.8	32
Epinephelinae	*Cephalopholis cyanostigma (Valenciennes 1828)*	Resident	LC	20	20
Epinephelinae	*Cephalopholis boenak (Bloch 1790)*	Resident	LC	10	40
Epinephelinae	*Epinephelus caeruleopunctatus (Bloch 1790)*	Resident	LC	23	23
Epinephelinae	*Epinephelus fuscoguttatus (Forsskal 1775)*	Resident	VU	32	32
Epinephelinae	*Epinephelus sp.*	Resident	LC	25	39
Epinephelinae	*Epinephelus tukula Morgans 1959*	Resident	LC	47	47
Epinephelinae	*Plectropomus laevis (Lacepede 1801)*	Resident	LC	23	23
Epinephelinae	*Variola albimarginata Baissac 1953*	Resident	LC	10	45
Epinephelinae	*Variola louti (Fabricius 1775)*	Resident	LC	15	28
Carangidae	*Carangoides dinema Bleeker, 1851*	Transient	LC	25	25
Carangidae	*Carangoides ferdau (Forsskål, 1775)*	Transient	LC	12	40
Carangidae	*Carangoides fulvoguttatus (Forsskål, 1775)*	Transient	LC	40	40
Carangidae	*Carangoides gymnostethus (Cuvier, 1833)*	Transient	LC	28	28

Carangidae	*Carangoides orthogrammus (Jordan & Gilbert, 1882)*	Transient	LC	10	40
Carangidae	*Carangoides sp.*	Transient	LC	21	45
Carangidae	*Caranx ignobilis (Forsskål, 1775)*	Transient	LC	10	15
Carangidae	*Caranx melampygus Cuvier, 1833*	Transient	LC	10	22
Carangidae	*Caranx sexfasciatus Quoy & Gaimard, 1825*	Transient	LC	5.8	40
Carangidae	*Caranx sp*	Transient	LC	17	22
Carangidae	*Caranx tille Cuvier, 1833*	Transient	LC	8	35
Carangidae	*Trachinotus blochii (Lacepède, 1801)*	Transient	LC	11	40
Lutjanidae	*Macolor niger (Forsskal 1775)*	Resident	LC	10	27
Lutjanidae	*Aphareus furca (Lacepède 1801)*	Transient	LC	6	43
Lutjanidae	*Aprion virescens Valenciennes 1830*	Transient	LC	7	47
Lutjanidae	*Lutjanus bohar (Fabricius 1775)*	Transient	LC	10	40
Lutjanidae	*Lutjanus gibbus (Forsskal 1775)*	Resident	LC	23	25
Lutjanidae	*Lutjanus kasmira (Fabricius 1775)*	Resident	LC	10	16
Lutjanidae	*Lutjanus monostigma (Cuvier 1828)*	Resident	LC	16	16
Lutjanidae	*Lutjanus quinquelineatus (Bloch 1790)*	Resident	LC	16	16
Lutjanidae	*Lutjanus rivulatus (Cuvier 1828)*	Resident	LC	10	10
Lutjanidae	*Lutjanus russellii (Bleeker 1849)*	Resident	LC	40	40
Lutjanidae	*Lutjanus vitta (Quoy & Gaimard 1824)*	Resident	LC	40	40
Haemulidae	*Plectorhinchus gaterinus Fabricius 1775*	Resident	LC	22	25
Haemulidae	*Plectorhinchus vittatus (Linnaeus 1758)*	Resident	LC	23	23
Lethrinidae	*Lethrinus erythropterus Valenciennes 1830*	Resident	LC	40	40
Lethrinidae	*Lethrinus harak (Fabricius 1775)*	Resident	LC	7	28
Lethrinidae	*Lethrinus mahsena (Fabricius 1775)*	Resident	EN	25	25
Lethrinidae	*Lethrinus microdon Valenciennes 1830*	Resident	LC	14	14
Lethrinidae	*Lethrinus nebulosus (Forsskal 1775)*	Resident	LC	28	28
Lethrinidae	*Lethrinus obsoletus (Forsskal 1775)*	Resident	LC	7	7
Lethrinidae	*Lethrinus olivaceus Valenciennes 1830*	Resident	LC	10	45
Lethrinidae	*Lethrinus rubrioperculatus Sato 1978*	Resident	LC	7	45
Lethrinidae	*Lethrinus sp*	Resident	LC	25	25
Lethrinidae	*Lethrinus xanthochilus Klunzinger 1870*	Resident	LC	22	35
Lethrinidae	*Monotaxis grandoculis (Forsskal 1775)*	Resident	LC	11	40
Sphyraenidae	*Sphyraena barracuda (Edwards 1771)*	Transient	LC	40	40
Sphyraenidae	*Sphyraena forsteri Cuvier 1829*	Transient	LC	15	15
Scombridae	*Gymnosarda unicolor (Rüppell 1836)*	Transient	LC	15	25
Scombridae	*Rastrelliger kanagurta (Cuvier 1816)*	Transient	DD	10	40
Scombridae	*Scomberomorus commerson (Lacepède 1800)*	Transient	NT	12	12

References

Anderson, W.D. Jr. and Allen, G.R., 2001. Lutjanidae. Jobfishes. In: Carpenter K.E. and Niem V. (eds.) *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific. Vol. 5. Bony fishes part 3 (Menidae to Pomacentridae)*. FAO, Rome. p. 2840-2918.

Asher, J., Williams, I.D. and Harvey, E.S., 2017. An assessment of mobile predator populations along shallow and mesophotic depth gradients in the Hawaiian Archipelago. *Scientific reports*, *7*(1), pp.1-18.

Bascompte, J., Melián, C.J. and Sala, E., 2005. Interaction strength combinations and the overfishing of a marine food web. *Proceedings of the National Academy of Sciences*, 102(15), pp. 5443–5447.

Bacheler, N.M., Geraldi, N.R., Burton, M.L., Muñoz, R.C. and Kellison, G.T., 2017. Comparing relative abundance, lengths, and habitat of temperate reef fishes using simultaneous underwater visual census, video, and trap sampling. *Marine Ecology Progress Series*, *574*, 141-155.

Bacheler, N.M., Runde, B.J., Shertzer, K.W., Buckel, J.A. and Rudershausen, P.J., 2021. Fine scale behavior of red snapper (*Lutjanus campechanus*) around bait: approach distances, bait plume dynamics, and effective fishing area. *Canadian Journal of Fisheries and Aquatic Sciences*, (ja).

Baum, J. K. and Worm, B., 2009. Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology*, *78*(4), pp. 699–714.

Bell, J., Cheung, W., De Silva, S., Gasalla, M., Frusher, S., Hobday, A., Lam, V., Lehodey, P., Pecl, G., Samoilys, M. and Senina, I., 2016. Impacts and effects of ocean warming on the contributions of fisheries and aquaculture to food security. In: Laffoley D, Baxter JM (eds), *Explaining ocean warming: causes, scale, effects and consequences*. Gland, Switzerland: International Union for the Conservation of Nature.

Bernard, A.T., Götz, A., Parker, D., Heyns, E.R., Halse, S.J., Riddin, N.A., Smith, M.K., Paterson, A.W., Winker, H., Fullwood, L. and Langlois, T.J., 2014. New possibilities for research on reef fish across the continental shelf of South Africa. *South African Journal of Science*, *110*(9-10), pp.01-05.

Beukers-Stewart, B.D., Beukers-Stewart, J.S. and Jones, G.P., 2011. Behavioural and developmental responses of predatory coral reef fish to variation in the abundance of prey. *Coral Reefs* 30:855–864.

Bongaerts, P., Ridgway, T., Sampayo, E.M. and Hoegh-Guldberg, O., 2010. Assessing the 'deep reef refugia' hypothesis: focus on Caribbean reefs. *Coral Reefs* 29, 309–327.

Bowen, B.W., Bass, A.L., Rocha, L.A., Grant, W.S. and Robertson, D.R., 2001. Phylogeography of the trumpetfishes (Aulostomus): ring species complex on a global scale. *Evolution*, *55*(5), pp.1029-1039.

Burkepile, D.E. and Hay, M.E., 2008. Coral Reefs. Encyclopedia of Ecology Pages 784-796

Cappo, M., De'ath, G. and Speare, P., 2007. Inter-reef vertebrate communities of the Great Barrier Reef Marine Park determined by baited remote underwater video stations. *Marine Ecology Progress Series*, 350, pp. 209–221.

Carpenter, K.E. and Allen., G.R. 1989. *FAO Species Catalogue. Vol. 9. Emperor fishes and large-eye breams of the world (family Lethrinidae). An annotated and illustrated catalogue of lethrinid species known to date*. FAO Fish. Synop. 125(9):118 p. Rome: FAO.

Chong-Seng, K. M., Mannering, T. D., Pratchett, M. S., Bellwood, D. R. and Graham, N.A., 2012. The influence of coral reef benthic condition on associated fish assemblages. *PLoS One*, *7*(8), e42167.

Clarke, K.R. and Warwick, R.M., 2001. Change in marine communities: an approach to statistical analysis and interpretation (2nd edn). Plymouth, UK: PRIMER-E.

Collins, M.R., 1990. A comparison of three fish trap designs. *Fish Res 9*:325−332

Connell, S.D. and Kingsford, M.J., 1998. Spatial, temporal and habitat-related variation in the abundance of large predatory fish at One Tree Reef, Australia. *Coral Reefs* 17:49–57.

Dance, M.A., Patterson III, W.F. and Addis, D.T., 2011. Fish community and trophic structure at artificial reef sites in the northeastern Gulf of Mexico. *Bulletin of Marine Science*, 87(3), pp. 301–324.

Daniels C., Fanning E. and Redding D., 2003. Marine resource management for Misali Island: preliminary analysis by Frontier-Tanzania. *West Indian Ocean J Mar Sci.* 2:85–93.

de Mitcheson, Y.J.S., Linardich, C., Barreiros, J.P., Ralph, G.M., Aguilar-Perera, A., Afonso, P., Erisman, B.E., Pollard, D.A., Fennessy, S.T., Bertoncini, A.A. and Nair, R.J., 2020. Valuable but vulnerable: Over-fishing and under-management continue to threaten groupers so what now?. *Marine Policy*, *116*, p.103909.

Espinoza, M., Cappo, M., Heupel, M.R., Tobin, A.J. and Simpfendorfer, C.A., 2014. Quantifying shark distribution patterns and species-habitat associations: implications of marine park zoning. *PloS one*, *9*(9), p.e106885.

Filous, A., Friedlander, A., Wolfe, B., Stamoulis, K., Scherrer, S., Wong, A., Stone, K. and Sparks, R., 2017. Movement patterns of reef predators in a small isolated marine protected area with implications for resource management. *Marine Biology*, *164*(1), pp.1-16.

Fischer, W., Sousa, I., Silva, C., de Freitas, A., Poutiers, J.M., Schneider, W., Borges, T.C., Feral, J.P. and Massinga, A., 1990. Field guide to commercial marine and brackishwater species of Mozambique. 230.

Fricke, R., Eschmeyer, W. N. and van der Laan R., (eds) 2021. Eschmeyer's Catlog of Fishes: Genera, Species, References. http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp

Fricke, R., Kulbicki, M. and Wantiez, L., 2011. Checklist of the fishes of New Caledonia, and their distribution in the Southwest Pacific Ocean (Pisces). *Stuttgarter Beiträge zur Naturkunde A, Neue Serie*, *4*, pp.341-463.

Friedlander, A.M., Brown, E. and Monaco, M.E., 2007. Defining reef fish habitat utilization patterns in Hawaii: comparisons between marine protected areas and areas open to fishing. *Marine Ecology Progress Series*, *351*, pp.221-233.

Frisch, A.J., Ireland, M. and Baker, R., 2014. Trophic ecology of large predatory reef fishes: energy pathways, trophic level, and implications for fisheries in a changing climate. *Marine Biology*, *161*(1), pp.61-73.

Froese, R. and Pauly, D., 2020. FishBase. World Wide Web electronic publication. www.fishbase.org, (06/2020)

Gerrodette, T.I.M., 1987. A power analysis for detecting trends. *Ecology*. Wiley Online Library, 68(5), pp. 1364–1372.

Green, A.L., Maypa, A.P., Almany, G.R., Rhodes, K.L., Weeks, R., Abesamis, R.A., Gleason, M.G., Mumby, P.J. and White, A.T., 2015. Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biological Reviews*, *90*(4), pp.1215-1247.

Graham, N.A., Jennings, S., MacNeil, M.A., Mouillot, D. and Wilson, S.K., 2015. Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature*, *518*(7537), pp.94-97.

Grimsditch, G.D., Tamelander, J., Mwaura, J., Zavagli, M., Takata, Y. and Gomez, T. 2009. *Coral reef resilience assessment of the Pemba channel conservation area, Tanzania*. Gland, Switzerland: IUCN. 40pp.

Hammer, Ø., Harper, D.A. and Ryan, P.D., 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia electronica*, *4*(1), p.9.

Hammerschlag, N., Schmitz, O.J., Flecker, A.S., Lafferty, K.D., Sih, A., Atwood, T.B., Gallagher, A.J., Irschick, D.J., Skubel, R. and Cooke, S.J., 2019. Ecosystem function and services of aquatic predators in the Anthropocene. *Trends in ecology & evolution*, *34*(4), pp.369-

383.

Harborne, A. R., Mumby, P. J., Kennedy, E. V. and Ferrari, R., 2011. Biotic and multi-scale abiotic controls of habitat quality: their effect on coral-reef fishes. *Marine Ecology Progress Series*, *437*, 201-214.

Harvey, E., McLean, D., Frusher, S., Haywood, M., Newman, S.J. and Williams, A., 2013. The use of BRUVs as a tool for assessing marine fisheries and ecosystems: a review of the hurdles and potential. *University of Western Australia*, (2010/002).

Harvey, E.S., Newman, S.J., McLean, D.L., Cappo, M., Meeuwig, J.J. and Skepper, C.L., 2012. Comparison of the relative efficiencies of stereo-BRUVs and traps for sampling tropical continental shelf demersal fishes. *Fisheries Research*, *125*, pp.108-120.

Hempson, T.N., Graham, N.A., MacNeil, M.A., Williamson, D.H., Jones, G.P. and Almany, G.R., 2017. Coral reef mesopredators switch prey, shortening food chains, in response to habitat degradation. *Ecology and Evolution*, *7*(8), pp.2626-2635.

Hill, S.L., Hinke, J., Bertrand, S., Fritz, L., Furness, R.W., Ianelli, J.N., Murphy, M., Oliveros-Ramos, R., Pichegru, L., Sharp, R. and Stillman, R.A., 2020. Reference points for predators will progress ecosystem-based management of fisheries. *Fish and Fisheries*, *21*(2), pp.368-378.

Hixon, M.A., 2015. Predation: piscivory and the ecology of coral-reef fishes. In: Mora C. (Ed.) *Ecology of fishes on coral reefs*. Cambridge University Press Cambridge, UK, pp. 41–53.

Hussey, N.E., MacNeil, M.A., McMeans, B.C., Olin, J.A., Dudley, S.F., Cliff, G., Wintner, S.P., Fennessy, S.T. and Fisk, A.T., 2014. Rescaling the trophic structure of marine food webs. *Ecology letters*, *17*(2), pp.239-250.

IUCN (2021). The IUCN Red List of Threatened Species. Version 2021-1. https://www.iucnredlist.org

Jacquet, J. L. and Zeller, D. 2007. Putting the ’United’ in the United Republic of Tanzania: Reconstructing marine fisheries catches’. Putting the ‘United’ in the United Republic of Tanzania: Reconstructing marine fisheries catches. In: Zeller D. and Pauly D., (Ed) *Reconstruction of marine fisheries catches for key countries and regions (1950-2005) Fisheries Centre Research Reports 15(2) Fisheries Centre*, University of British Columbia.

Jennings, S., Boullé, D.P. and Polunin, N.V.C., 1996. Habitat correlates of the distribution and biomass of Seychelles’ reef fishes. *Environmental Biology of fishes*. Springer, 46(1), pp. 15–25.

Jones, S.T., Levine, A. and Jiddawi, N.S., 2019. Effective co-management and long-term reef fish recovery from severe coral bleaching: Insights from Misali Island, PECCA, Tanzania. *Ocean & Coastal Management*, *178*, 104843.

Karisa, J. F., Obura, D. O. and Chen, C.A., 2020. Spatial heterogeneity of coral reef benthic communities in Kenya. *PloS one*. 15(8), p. e0237397.

Kulbicki, M., Bozec, Y.M., Labrosse, P., Letourneur, Y., Mou-Tham, G. and Wantiez, L., 2005. Diet composition of carnivorous fishes from coral reef lagoons of New Caledonia. *Aquatic Living Resources*, *18*(3), pp.231-250.

Langlois, T., Williams, J., Monk, J., Bouchet, P., Currey, L., Goetze, J., Harasti, D., Huveneers, C., Malcolm, H. and Whitmarsh, S., 2018. Marine Sampling Field Manual for Benthic Stereo BRUVS (Baited Remote Underwater Videos). In: Przeslawski, R. and Foster, S. (Eds). *Field Manuals for Marine Sampling to Monitor Australian Waters*, National Environmental Science Programme (NESP). pp. 82-104.

Lieske, E. and Myers, R., 1994. *Collins Pocket Guide. Coral reef fishes. Indo-Pacific & Caribbean including the Red Sea*. Harper Collins Publishers, 400 p.

Long, J.S. and Long, J.S., 1997. *Regression models for categorical and limited dependent variables*. Sage.

MacNeil, M.A., Chapman, D.D., Heupel, M., Simpfendorfer, C.A., Heithaus, M., Meekan, M., Harvey, E., Goetze, J., Kiszka, J., Bond, M.E. and Currey-Randall, L.M., 2020. Global status and conservation potential of reef sharks. *Nature*, *583*(7818), pp.801-806.

Mallela, J., Roberts, C., Harrod, C. and Goldspink, C.R., 2007. Distributional patterns and community structure of Caribbean coral reef fishes within a river-impacted bay. *Journal of Fish Biology*, *70*(2), 523-537.

McClanahan, T.R., Graham, N.A., MacNeil, M.A., Muthiga, N.A., Cinner, J.E., Bruggemann, J.H. and Wilson, S.K., 2011. Critical thresholds and tangible targets for ecosystem-based management of coral reef fisheries. *Proceedings of the National Academy of Sciences*, *108*(41), pp.17230-17233.

McClanahan, T.R., Maina, J.M., Darling, E.S., Guillaume, M.M., Muthiga, N.A., D’agata, S., Leblond, J., Arthur, R., Jupiter, S.D., Wilson, S.K. and Mangubhai, S., 2020. Large geographic variability in the resistance of corals to thermal stress. *Global Ecology and Biogeography*, *29*(12), pp.2229-2247.

McGratten, K. and Pollom, R., 2015. *Aulostomus chinensis*. The IUCN Red List of Threatened Species 2015: e. T65134886A82934000.

Moberg, F. and Folke, C., 1999. Ecological goods and services of coral reef ecosystems.

Ecological economics. Elsevier, 29(2), pp. 215–233.

Myers, R.A. and Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. *Nature*, *423*(6937), pp.280-283.

Nagelkerken, I., Van der Velde, G., Gorissen, M. W., Meijer, G. J., Van't Hof, T. and Den Hartog, C., 2000. Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. *Estuarine, coastal and shelf science*, *51*(1), 31-44.

Nash, K.L., Welsh, J.Q., Graham, N.A. and Bellwood, D.R., 2015. Home-range allometry in coral reef fishes: comparison to other vertebrates, methodological issues and management implications. *Oecologia*, *177*(1), pp.73-83.

Nagelkerken, I., Dorenbosch, M., Verberk, W.C.E.P., De La Morinière, E.C. and Van Der Velde, G., 2000. Day-night shifts of fishes between shallow-water biotopes of a Caribbean bay, with emphasis on the nocturnal feeding of Haemulidae and Lutjanidae. *Marine Ecology Progress Series*, *194*, pp.55-64.

NBS. 2018. Tanzania in Figures 2017 National Bureau of Statistics, Dar es Salaam, Tanzania. p. 1–105.

Obura, D., Gudka, M., Rabi, F.A., Gian, S.B., Bijoux, J., Freed, S., Maharavo, J., Mwaura, J., Porter, S., Sola, E. and Wickel, J., 2017. *Coral reef status report for the Western Indian Ocean (2017).* Nairobi Convention, Global Coral Reef Monitoring Network (GCRMN)/International Coral Reef Initiative (ICRI).

Osuka, K.E., McClean, C., Stewart, B.D., Bett, B.J., Le Bas, T., Howe, J., Abernerthy, C., Yahya, S., Obura, D. and Samoilys, M., 2021. Characteristics of shallow and mesophotic environments of the Pemba Channel, Tanzania: Implications for management and conservation. *Ocean & Coastal Management*, *200*, p.105463.

Papastamatiou, Y.P., Lowe, C.G., Caselle, J.E. and Friedlander, A.M., 2009. Scale-dependent effects of habitat on movements and path structure of reef sharks at a predator-dominated atoll. *Ecology*, *90*(4), pp.996-1008.

Papastamatiou, Y.P., Bodey, T.W., Friedlander, A.M., Lowe, C.G., Bradley, D., Weng, K., Priestley, V. and Caselle, J.E., 2018. Spatial separation without territoriality in shark communities. *Oikos*, *127*(6), pp.767-779.

Paxton, A.B., Newton, E.A., Adler, A.M., Van Hoeck, R.V., Iversen Jr, E.S., Taylor, J.C., Peterson, C.H. and Silliman, B.R., 2020. Artificial habitats host elevated densities of large reef-associated predators. *PloS one*, *15*(9), p.e0237374.

Pinheiro, H.T., Goodbody-Gringley, G., Jessup, M.E., Shepherd, B., Chequer, A.D. and Rocha, L.A., 2016. Upper and lower mesophotic coral reef fish communities evaluated by underwater visual censuses in two Caribbean locations. *Coral Reefs*, *35*(1), pp.139-151.

Rasher, D.B., Hoey, A.S. and Hay, M.E., 2017. Cascading predator effects in a Fijian coral reef ecosystem. *Scientific Reports*, 7(1), pp. 1–10.

Rehren, J., Samoilys, M., Reuter, H., Jiddawi, N. and Wolff, M., 2020. Integrating Resource Perception, Ecological Surveys, and Fisheries Statistics: A Review of the Fisheries in Zanzibar. *Reviews in Fisheries Science & Aquaculture*, pp.1-18.

Robertson, A.I. and Blaber, S.J.M., 1993. Plankton, epibenthos and fish communities. *Coastal and estuarine studies*, pp.173-173.

Root, K. V., 1998. Evaluating the effects of habitat quality, connectivity, and catastrophes on a threatened species. *Ecological Applications*, *8*(3), 854-865.

Sancho, G., 2000. Predatory behaviors of *Caranx melampygus* (Carangidae) feeding on spawning reef fishes: a novel ambushing strategy. *Bulletin of Marine Science*. University of Miami-Rosenstiel School of Marine and Atmospheric Science, 66(2), pp. 487–496.

Sandin, S. A. and Zgliczynski, B., 2015. Inverted trophic pyramids. *In:* Mora, C. (ed.) *Ecology of Fishes on Coral Reefs*. Cambridge: Cambridge University Press, pp. 247–251.

Santana-Garcon, J., Newman, S.J. and Harvey, E.S., 2014. Development and validation of a mid-water baited stereo-video technique for investigating pelagic fish assemblages. *Journal of Experimental Marine Biology and Ecology*, *452*, pp.82-90.

Semba, M., Lumpkin, R., Kimirei, I., Shaghude, Y. and Nyandwi, N., 2019. Seasonal and spatial variation of surface current in the Pemba Channel, Tanzania. *PloS one*, *14*(1), p.e0210303.

Skinner, C., Mill, A.C., Newman, S.P., Alsagoff, S.N. and Polunin, N.V., 2020. The importance of oceanic atoll lagoons for coral reef predators. *Marine Biology*, *167*(2), pp.1-16.

Slade, L.M. and Kalangahe, B., 2015. Dynamite fishing in Tanzania. *Marine pollution bulletin*, *101*(2), pp.491-496.

Sommer, C., Schneider, W. and Poutiers, J. M. 1996. *FAO species identification field guide for fishery purposes: The living marine resources of Somalia.*

Stefanoudis, P.V., Gress, E., Pitt, J.M., Smith, S.R., Kincaid, T., Rivers, M., Andradi-Brown, D.A., Rowlands, G., Woodall, L.C. and Rogers, A.D., 2019. Depth-dependent structuring of reef fish assemblages from the shallows to the rariphotic zone. *Frontiers in Marine Science*, *6*, p.307.

Stewart, B.D. and Jones, G.P., 2001. Associations between the abundance of piscivorous fishes and their prey on coral reefs: implications for prey-fish mortality. *Marine Biology*, 138(2), pp. 383–397.

Taquet, M. and Diringer, A., 2012. Fishes of the Indian Ocean and the Red Sea. Éditions Quæ RD 1078026 Versailles Cedex, France 707p.

Tyler, E.H., Speight, M.R., Henderson, P. and Manica, A., 2009. Evidence for a depth refuge effect in artisanal coral reef fisheries. *Biological Conservation*, *142*(3), pp.652-667.

Vuong, Q.H., 1989. Likelihood ratio tests for model selection and non-nested hypotheses. *Econometrica: Journal of the Econometric Society*. JSTOR, pp. 307–333.

Wanyonyi, I.N., Wamukota, A., Tuda, P., Mwakha, V.A and Nguti, L.M., 2016. Migrant fishers of Pemba: Drivers, impacts and mediating factors. *Marine Policy*, *71*, pp.242-255.

Watson, W. and Sandknop, E.M., 1996. Fistulariidae: cornetfishes. p. 718-723. In Moser, H.G. (ed.) *The early stages of fishes in the California Current Region*. California Cooperative Oceanic Fisheries Investigations (CalCOFI) Atlas No. 33. Allen Press, Inc., Lawrence, Kansas. 1505 p.

Wells, S., Samoilys, M., Makoloweka, S. and Kalombo, H., 2010. Lessons learnt from a collaborative management programme in coastal Tanzania. *Ocean & Coastal Management*, *53*(4), pp.161-168.

White, J., Simpfendorfer, C.A., Tobin, A.J. and Heupel, M.R., 2013. Application of baited remote underwater video surveys to quantify spatial distribution of elasmobranchs at an ecosystem scale. *Journal of Experimental Marine Biology and Ecology*, *448*, pp.281-288.

Wilson, R.J., Sailley, S.F., Jacobs, Z.L., Kamau, J., Mgeleka, S., Okemwa, G.M., Omukoto, J.O., Osuka, K.E., Samoilys, M., Sauer, W., Silas, M.O., Sululu, J.S. and Roberts, M.J., 2021. Large projected reductions in marine fish biomass for Kenya and Tanzania in the absence of climate mitigation. *Ocean & Coastal Management*, *215*, p.105921.

Worm, B., Davis, B., Kettemer, L., Ward-Paige, C.A., Chapman, D., Heithaus, M.R., Kessel, S.T. and Gruber, S.H., 2013. Global catches, exploitation rates, and rebuilding options for sharks. *Marine Policy*, *40*, pp.194-204.

Wyatt, A.S., Lowe, R.J., Humphries, S. and Waite, A.M., 2013. Particulate nutrient fluxes over a fringing coral reef: Source-sink dynamics inferred from carbon to nitrogen ratios and stable isotopes. *Limnology and Oceanography*, *58*(1), pp.409-427.

CHAPTER 5

(DIS)SIMILARITY OF BAITED REMOTE UNDERWATER VIDEOS (BRUVS) AND 'LONG SWIMS' UNDERWATER VISUAL CENSUS (UVC) IN MEASURING LARGE REEF ASSOCIATED FISH OF PEMBA ISLAND

5.1 Preface

Coral reef survey methods such as the historic and widely applied standard underwater visual censuses (UVC) done on SCUBA are prone to underestimate species which either have large home ranges (Leujak and Ormond, 2007; Cheal et al., 2021), are cryptic (Stewart and Beukers, 2000) or are affected by the behaviour of divers (Emslie et al., 2018). Consequently, baited remote underwater videos (BRUVs) are increasingly being applied to survey large-sized predatory species due to their ability to survey habitats in a wide variety of depths and areas, by attracting fish into view (Harvey et al., 2012; White et al., 2013). The use of videography also provides a permanent record that can be reviewed wherever necessary. However, since all reef survey methods are associated with certain biases, combining survey methods is becoming regarded as the best way to gain a comprehensive picture of reef fish communities.

In this chapter, I investigate the similarity and dissimilarity of BRUVS and 'long swim' UVC method for measuring abundance and diversity of large-sized predators from nine selected fish families in order to assess the strengths and weaknesses of each method and their potential for being viewed in combination.

This chapter has been written in the style of Western Indian Ocean Journal of Marine Science.

I declare that the work submitted is my own. The contribution by co-authors was as follows:
Bryce Stewart, Melita Samoilys and Colin McClean: Supervision, review and editing.
Peter Musembi, Saleh Yahya: Assistance in the field.

5.2 References

Cheal, A.J., Emslie, M.J., Currey-Randall, L.M. and Heupel, M.R. 2021. Comparability and complementarity of reef fish measures from underwater visual census (UVC) and baited remote underwater video stations (BRUVS). *Journal of Environmental Management*, *289*, 112375.

Emslie, M.J., Cheal, A.J., MacNeil, M.A., Miller, I.R. and Sweatman, H.P. 2018. Reef fish communities are spooked by scuba surveys and may take hours to recover. *PeerJ*, *6*, e4886.

Harvey, E.S., Newman, S.J., McLean, D.L., Cappo, M., Meeuwig, J.J. and Skepper, C.L. 2012. Comparison of the relative efficiencies of stereo-BRUVs and traps for sampling tropical continental shelf demersal fishes. *Fisheries Research*, *125*, 108-120.

Leujak, W. and Ormond, R.F.G. 2007. Comparative accuracy and efficiency of six coral community survey methods. *Journal of Experimental Marine Biology and Ecology*, *351*(1-2), 168-187.

Stewart, B.D. and Beukers, J.S. 2000. Baited technique improves censuses of cryptic fish in complex habitats. *Marine Ecology Progress Series*, *197*, pp.259-272.

White, J., Simpfendorfer, C.A., Tobin, A.J. and Heupel, M.R. 2013. Application of baited remote underwater video surveys to quantify spatial distribution of elasmobranchs at an ecosystem scale. *Journal of Experimental Marine Biology and Ecology*, *448*, 281-288.

(DIS)SIMILARITY OF BAITED REMOTE UNDERWATER VIDEOS (BRUVS) AND 'LONG SWIMS' UNDERWATER VISUAL CENSUS (UVC) IN MEASURING LARGE REEF ASSOCIATED FISH OF PEMBA ISLAND

Kennedy E. Osuka[1,2], Bryce Stewart[1], Melita Samoilys[2], Colin McClean[1], Peter Musembi[2] and Saleh Yahya[3]

Affiliations

[1.] Department of Environment and Geography, University of York, Heslington, York, YO10 5NG, United Kingdom

[2.] Coastal Oceans Research and Development – Indian Ocean (CORDIO East Africa). 9 Kibaki Flats P.O. Box 10135-80101, Mombasa, Kenya

[3.] Institute of Marine Sciences, University of Dar es Salaam, Zanzibar, Tanzania

* Corresponding author.

E-mail address: koe503@york.ac.uk (K.E. Osuka).

Abstract

Coral reef survey methods such as the historic and widely applied standard underwater visual census (UVC) are prone to underestimate fish species with large home ranges or are cryptic. Here, we assess the similarity and dissimilarity of baited remote underwater videos (BRUVS) and 'long swim (LS)' UVC method for measuring abundance and diversity of large sized predators from nine selected fish families, in order to assess the strengths and weaknesses of each method and their potential for being viewed in combination. BRUVS and LS showed identical estimates of species richness and fish community structure. BRUVS were better than LS at sampling the family Carangidae, *Aphareus furca* and 28 unique large sized predatory species. LS were superior at sampling Lethrinidae, *Monotaxis grandoculis* and only five unique species. BRUVS outmatched LS when measuring occurrence of large sized predatory species while LS appeared beneficial at measuring absolute abundance of species. Therefore, the methods are complementary, providing a more complete assessment of reef fish communities over a wider range of habitats and depths. The combination of both methods should be considered in future monitoring of the abundance and diversity of the predatory reef fish community.

Keywords: Fish monitoring; videography; divers; fish community; tradeoffs

1 Introduction

Large predatory reef fish are an important protein food source to millions of coastal people around the world (de Mitcheson et al., 2020). Their large body size makes them an easy target and a highly preferred trophic group among fishers. However, the slow growth and late maturation of species within this category of fishes, also makes them highly vulnerable to being overexploited and subsequently becoming rare in marine ecosystems (Worm *et al.*, 2013). Such rarity of large predatory reef fish, particularly where fishing pressure is high, calls for robust methods to accurately assess their population sizes.

Coral reef survey methods such as the historic and widely applied standard underwater visual census (UVC) done on SCUBA are prone to underestimate species which either have large home ranges (Leujak and Ormond, 2007; Cheal et al., 2021), are cryptic (Stewart and Beukers, 2000) or are frightened by the behaviour of divers and some fishes (Emslie et al., 2018). In addition, UVC is not feasible in depths or areas that are inaccessible or challenging for divers (Harvey et al., 2001). Consequently, baited remote underwater videos (BRUVs) are increasingly being applied to survey large-sized species due to their ability to survey habitats in a wide variety of depths and attract rare species (Harvey et al., 2012; White et al., 2013). The use of videography provides a permanent record that can be reviewed wherever necessary. However, the long processing times of the video footage and the difficulties of estimating the area in the field of view are still key methodological challenges. Since all reef survey methods are associated with certain biases, combining survey methods is becoming regarded as the best way to gain a comprehensive picture of reef fish communities.

Integration of methods could enable surveys of large defined reef areas in relatively shallow habitats using UVC, helping overcome the challenges of restricted field of view linked to BRUVS. At the same time fish communities occurring in shallow and relatively deeper habitats can be surveyed using BRUVS. This creates an opportunity to compare the in-situ records collected through UVC with the BRUVS video records (Cappo et al., 2004). Certainly, combining BRUVS and UVC is likely to enlarge the extent of existing monitoring efforts thereby providing additional details of reef fish communities (Schramm et al., 2020). Despite the apparent inter-method biases, studies on the Great Barrier Reef have empirically assessed the potential of combining BRUVS and UVC, and the results have shown integration of methods was beneficial at providing managers with a complete assessment of reef fish (Cheal et al., 2021). It therefore appears likely that such a combination of survey methods could also be beneficial in other coral reef areas, such as the oceanic island of Pemba in the Western Indian Ocean.

Coral reefs of Pemba Island are amongst the most biodiverse in the region (Grimsditch et al., 2009). However, they face significant threats from local fishing including the effects of historic dynamite fishing that is considered to have led to heavy degradation, particularly in unprotected sites. To date there have been a limited number of studies that have examined the reefs of Pemba Island (Horrill, 1992; Horrill et al., 1994; Daniels et al 2004; Grimsditch et al., 2009; Jones et al., 2019), with the majority of these studies conducted at Misali Island in the south. Therefore, research is needed to identify a practical and cost-effective monitoring method to support management and conservation of this biologically important area.

This study aimed to identify the most suitable methods, or combination of methods for surveying large predatory fish off Pemba Island. To this end the similarity and dissimilarity of fish assemblages counted during BRUV deployments (Chapter 4) and UVC transects (Samoilys, unpublished data) were assessed to evaluate the potential benefits of combining these two methods. Given the focus on large and potentially rare species, this study applied a large UVC transect measuring 150m x 20m (hereafter called long swims UVC), which are identified to be more suitable than standard UVC transects (e.g., 50m x 5m) (Mapstone and Ayling, 1998).

2 Materials and methods

2.1 Study area

The baited remote underwater videos (BRUVS) and long swim UVC surveys were conducted in the outer reefs of the western margins of Pemba Island. Reefs were selected for sampling based on previous surveys conducted in the Greater Pemba Channel within the Pemba Community Conservation Area using SCUBA (Grimsditch *et al.*, 2009) and autonomous underwater vehicles (Chapter 3). Sites were chosen to include areas representative of different reef habitats utilised by fish predators (Figure 1).

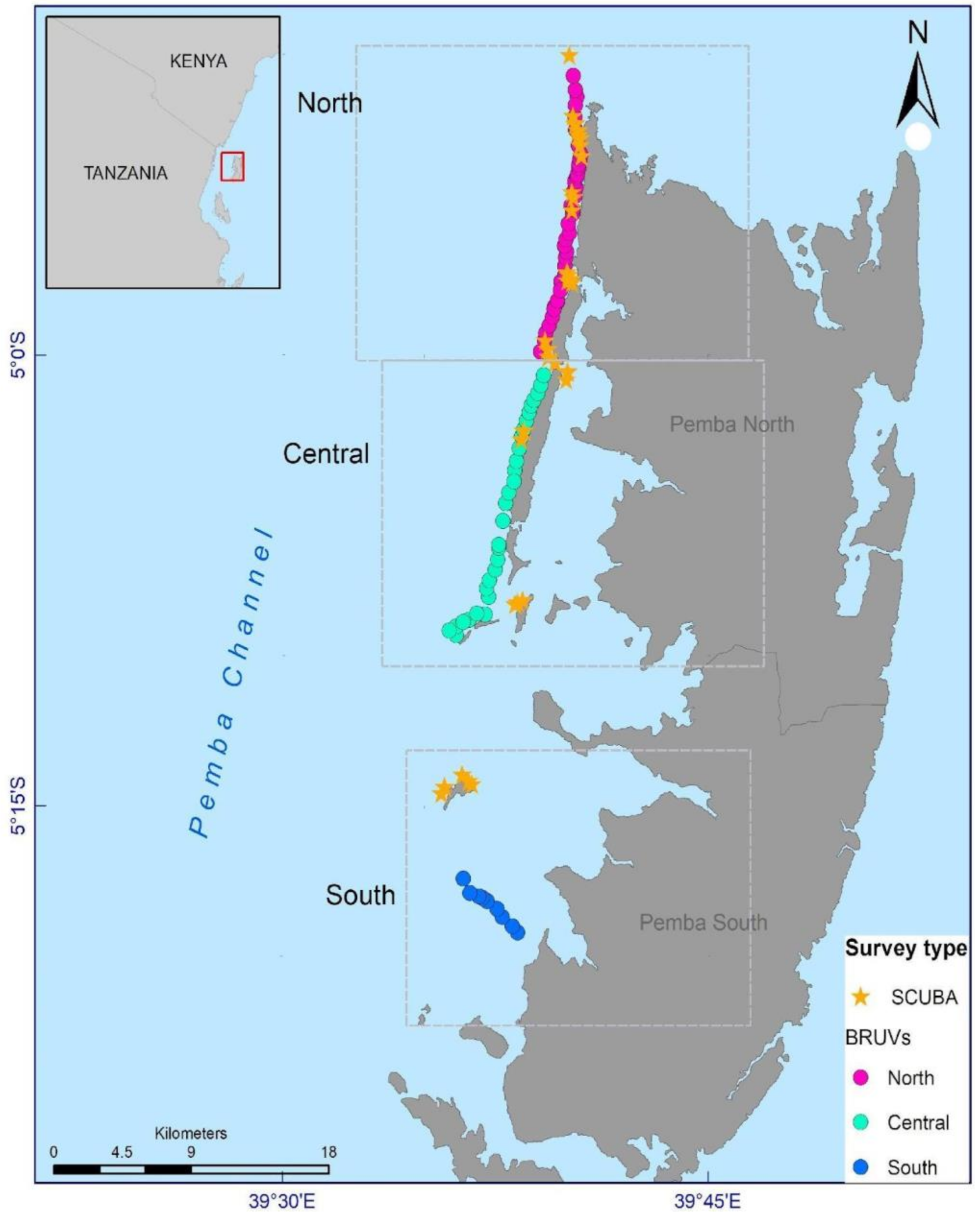


Figure 1: Map of the study stations where baited remote underwater videos were deployed, and long swim underwater visual census conducted in Pemba Island.

2.2 Description of the surveys

This study utilised a total of 61 BRUVS and 23 LS underwater visual transects deployed or laid at seven sites spread from the north to the south of the western margins of Pemba Island (Table 1; Figure 1). Each BRUV sampling event involved deployment of a BRUV unit consisting of a video camera, GoPro Hero4 Silver, set on a medium field of view (FOV). It was assumed that each BRUVS deployment sampled an equal area. At least five replicate deployments were done approximately 500m away from each other but along the reef. Each BRUV unit was retrieved after at least 1-hour of recording (Table 2).

A ten-minute LS underwater visual census covering 150m x 20m along the reef (Samoilys et al., 2011) was undertaken at selected reef sites. At each reef site, at least two replicate LS surveys were undertaken approximately 470 m away from each other (Table 2). Both survey methods overlapped at some reef sites but also included sites far from LS stations. The maximum number of individuals (MaxN) and absolute counts of each species of predatory reef fish encountered were quantified for BRUV and LS surveys respectively (Chapter 4; Samoilys and Carlos, 2000; Langlois et al., 2018).

Table 1: Number of replicates and depth range per site for baited remote underwater videos (BRUVS) and 'long swims' (LS) underwater visual census undertaken on coral reefs of the Pemba Island.

Site	**BRUVs**		**LS**	
	No. of replicates	**Depth range (m)**	**No. of replicates**	**Depth range (m)**
Misali - Vikunguni	5	10 - 39	2	8 - 16
Kokota - Uvinje	7	6 - 40	2	2 - 14
Fundo	15	8 - 43	6	4 - 17
Mandela	5	15 - 47	2	7 -17
Njao	11	7 - 40	4	7 – 18
Paradise	8	10 - 45	2	5 - 15
Shimba - Scorpion Secret	10	7 - 40	3	4 - 16
Total	**61**	**6 - 47**	**23**	**4 - 18**

Table 2: List of variables and their measurements for baited remote underwater videos (BRUVS) and 'long swims' (LS) underwater visual census. NA - not applicable, FOV - field of view.

Variable	**BRUVs**	**LS**

Time	~1hr video recording	10 min swims
Replicates per reef	At least 5	At least 2
Distance between replicates/stations	~500 m	~ 470 m
Reef area	NA	~ 150 m x 20 m (3000 m^2)
Resolution	Medium FOV [1080]	NA
Measurement of abundance	Maximum number (MaxN) seen in a video footage	Absolute counts (N)

2.3 Target taxa

Selection of target taxa to be surveyed is driven by the presence of species of ecological importance, exploited in the artisanal fisheries and large or rare individuals (Samoilys and Carlos, 2000; Kawaka et al., 2016). The target taxa were relatively large and fast swimming epipelagic species that are rare or expected to be in low abundance or attracted by bait such as species from families of Carangidae, Carcharhinidae, Dasyatilidae, Myliobatidae, Scombridae, Sphyraenidae (Chapter 4; Mapstone and Ayling, 1998; White et al., 2013). Suggestions have been made to assign fish predators by size (Haupel et al., 2013; Paxton et al., 2020). Consequently, for species within the families of Lethrinidae, Lutjanidae and Serranidae, which are widely surveyed in the standard UVC, the study only focussed on species with a maximum total length of greater than or equal to 55cm.

2.3 Data processing and analysis

2.3.1 Effect of distance from Long swim station to BRUV station

Generalized additive modelling (GAM) was used to test the effect of distance from LS station to BRUV station on total abundance and species richness (Cheal , et al 2021). Results showed no effect on total abundance but a significant effect on species richness. Species richness tended to decrease significantly at BRUVs stations located >4 kms away from LS (Appendix 1). As such BRUVs stations 4 km away from the nearest LS station were excluded from the analysis.

Species accumulation curves were utilised in order to compare the expected species richness for each method given a particular sample size. Further, species data from both methods were combined and a species accumulation curve generated with a purpose of highlighting additional benefits of using both methods to characterise predator fish community.

The mean abundance for fish species and families was calculated from replicate data (Table 1). Since abundance data from each method was processed using a different measure of abundance (MaxN and N), we calculated a comparable measure called frequency of occurrence. This was determined by dividing the species/family mean by cumulative site mean. Frequency of occurrence of common species found in both methods were compared to display their uniformity in estimating the relative abundance of different species. Likewise, frequency of occurrence of rare species were graphed to highlight differences in the methods.

Generalized linear mixed models utilising the *glmer.nb* function of the negative binomial error distribution in R package (R Core Team, 2021) were applied to assess the differences in the estimates of abundance and species richness between BRUVs and LS.

Non-metric dimensional scaling (nMDS) was conducted on the relative abundance data of common species sampled by both survey methods. This was intended to determine (di)similarity of the assemblage structure of reef fishes sampled by both LS and BRUVS. A one-way analysis of similarity (ANOSIM) was then performed to showcase any differences (Clarke and Gorley, 2006).

The abundance estimates (i.e., relative abundance) of each of the species common in both BRUVS and LS were matched by sites. A paired t-test was then used to compare the methods in recording the species. The test was also conducted for the target families using estimates of relative abundance derived from cumulative abundance of species.

3 Results

3.1 Species frequency of occurrence

A total of 48 species were encountered across both methods. Of these, 89.6% and 39.6% were observed in BRUVs and LS respectively. Fourteen species were common in both methods (Figure 2), and a further 28 and five species were unique to BRUVs and LS respectively (Figure 3). Results on frequency of occurrence of common species revealed the presence of *Monotaxis grandoculis* and *Lethrinus harak* in all sites sampled by LS compared to 42.9% and

57.1% respectively, in sites surveyed by BRUVs. The occurrence of *Aprion virescens* showed the least difference between LS and BRUVS, being present in more than 70% of the sites. Other species that frequently occurred in BRUVS were *Aphareus furca* and *Aethaloperca rogaa,* both occurring in 71.4% of sites compared to <43.0% of sites surveyed by LS.

Two conspicuous species unique to BRUVS were *Cephalopholis argus* and *Lethrinus olivaceus* that were recorded in more than 70% of sites. The majority (56%) of unique species recorded in BRUVS were sampled in 14.3% of the sites (Figure 3a). Unique species sampled by LS were *Lutjanus fulviflamma* in 42.9% of sites, and four other species which each were found in 14.3% of the sites (Figure 3b).

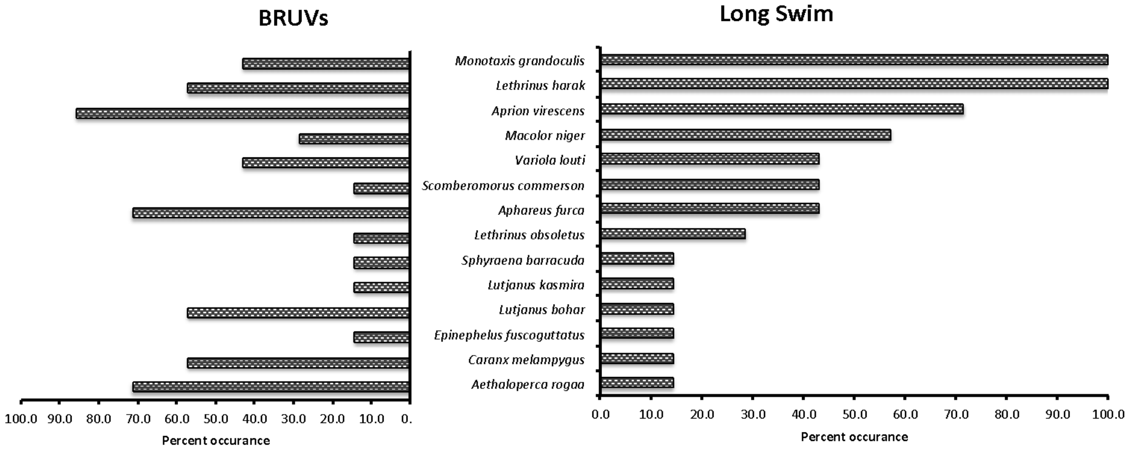


Figure 2: Frequency of occurrence of fish species common to both baited remote underwater videos (BRUVS) and ‘long swims’ (LS) underwater visual census.

3.2 Species accumulation curves

Species accumulation curves showed BRUVS were associated with relatively more species compared to LS. For example, rarefaction based on 20 stations yielded a median of 27 species with BRUVs compared to 19 species with LS. When data from the two methods were combined, the number of species recorded in 20 stations was identical to those recorded by BRUVS (Figure 4). However, there were no statistical differences between BRUVS and LS in terms of species richness (glmer: z value = 0.986, p = 0.324). In contrast, the relative abundance of large predatory fish was significantly different (glmer: z value = 2.427, p = 0.015) with LS showing 60% higher estimates than BRUVS. A further analysis of relative abundance of fish families showed Lethrinidae was 41% more in LS than in BRUVS deployments (glmer: z value = 2.077, p = 0.0378). Other families showed no clear significant differences across the methods.

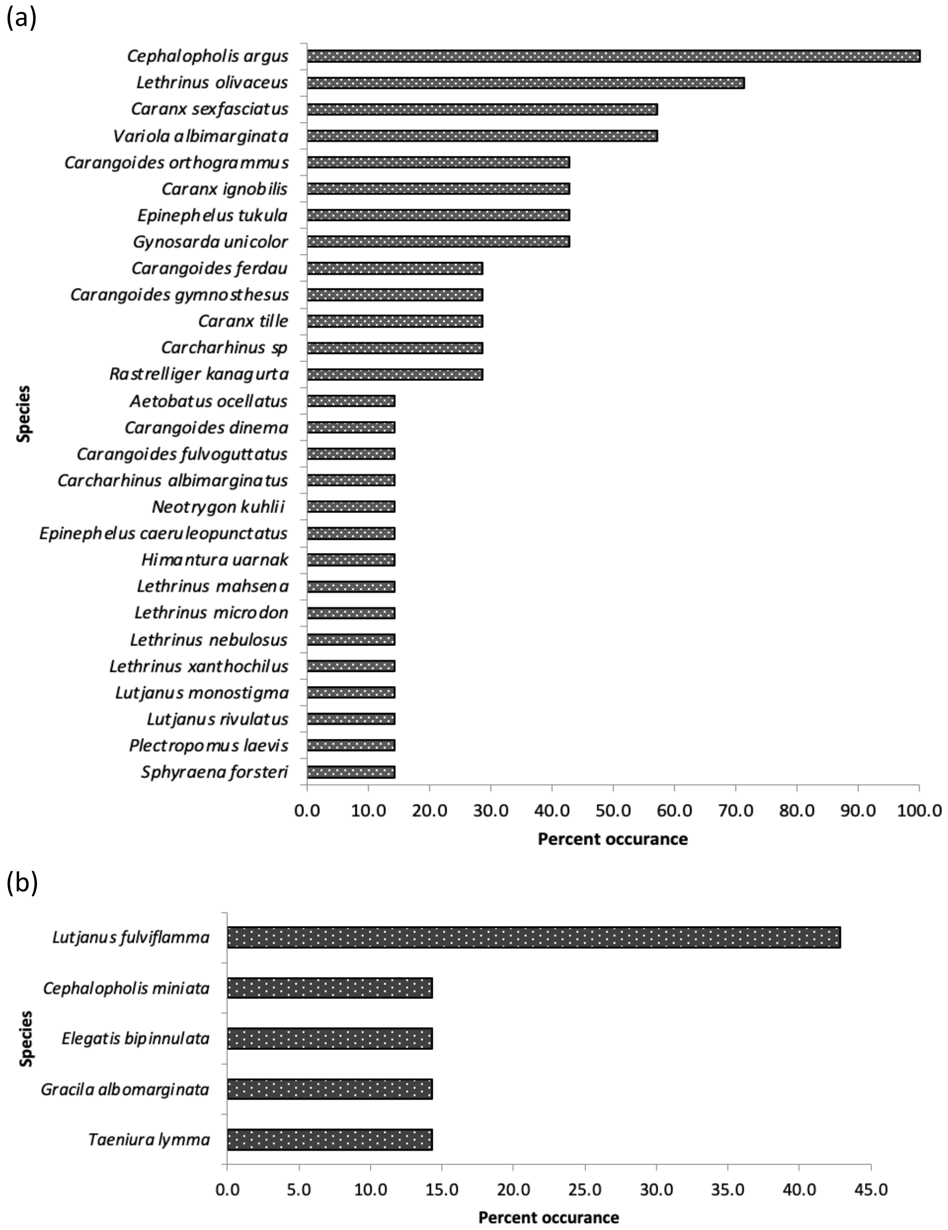


Figure 3: Frequency of occurrence of fish species unique to (a) baited remote underwater videos (BRUVS) and, (b) ‘long swims’ (LS) underwater visual census.

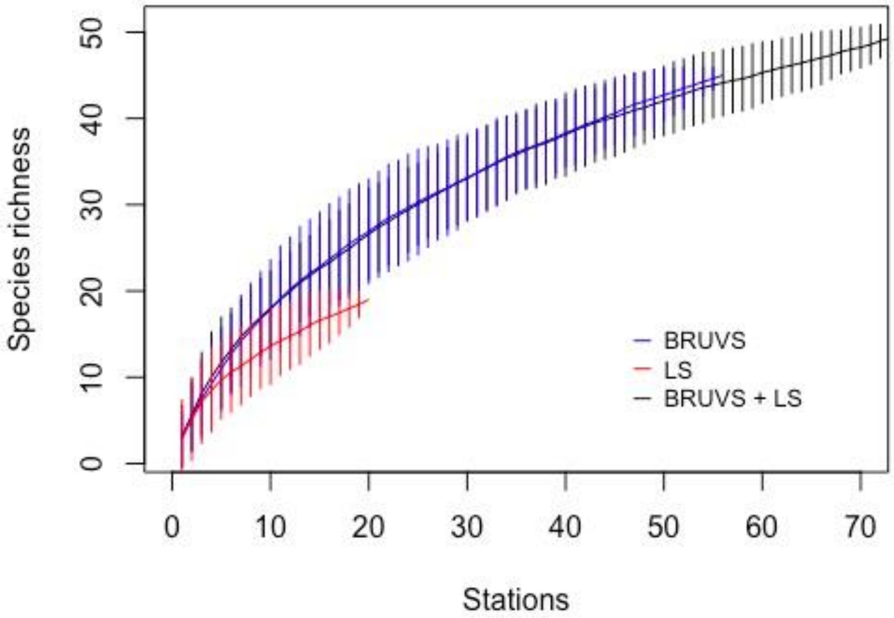


Figure 4: Species accumulation curves from BRUVS deployments, long swims (LS) and combined survey methods.

3.3 Family and species abundance

Out of the nine families surveyed, only Carangidae and Lethrinidae showed significant differences across the two survey methods (Figure 5). The relative abundance of Carangidae was higher in BRUVs than LS [(t-test t = 3.169; p =0.019) Figure 5a], while an opposite pattern was observed for Lethrinidae [(t-test t = -2.725; p = 0.034), Figure 5b].

Paired t-tests revealed that LS and BRUVs were only different in recording the abundance of two out of the 14 species (Figure 5). The relative abundance of *Aphareus furca* was higher in BRUVS than LS [(t-test, t = 2.560; *p* = 0.042), Figure 5c], while *Monotaxis grandoculis* showed higher abundance in LS than BRUVS [(t-test, t =4.800; p =0.003), Figure 5d].

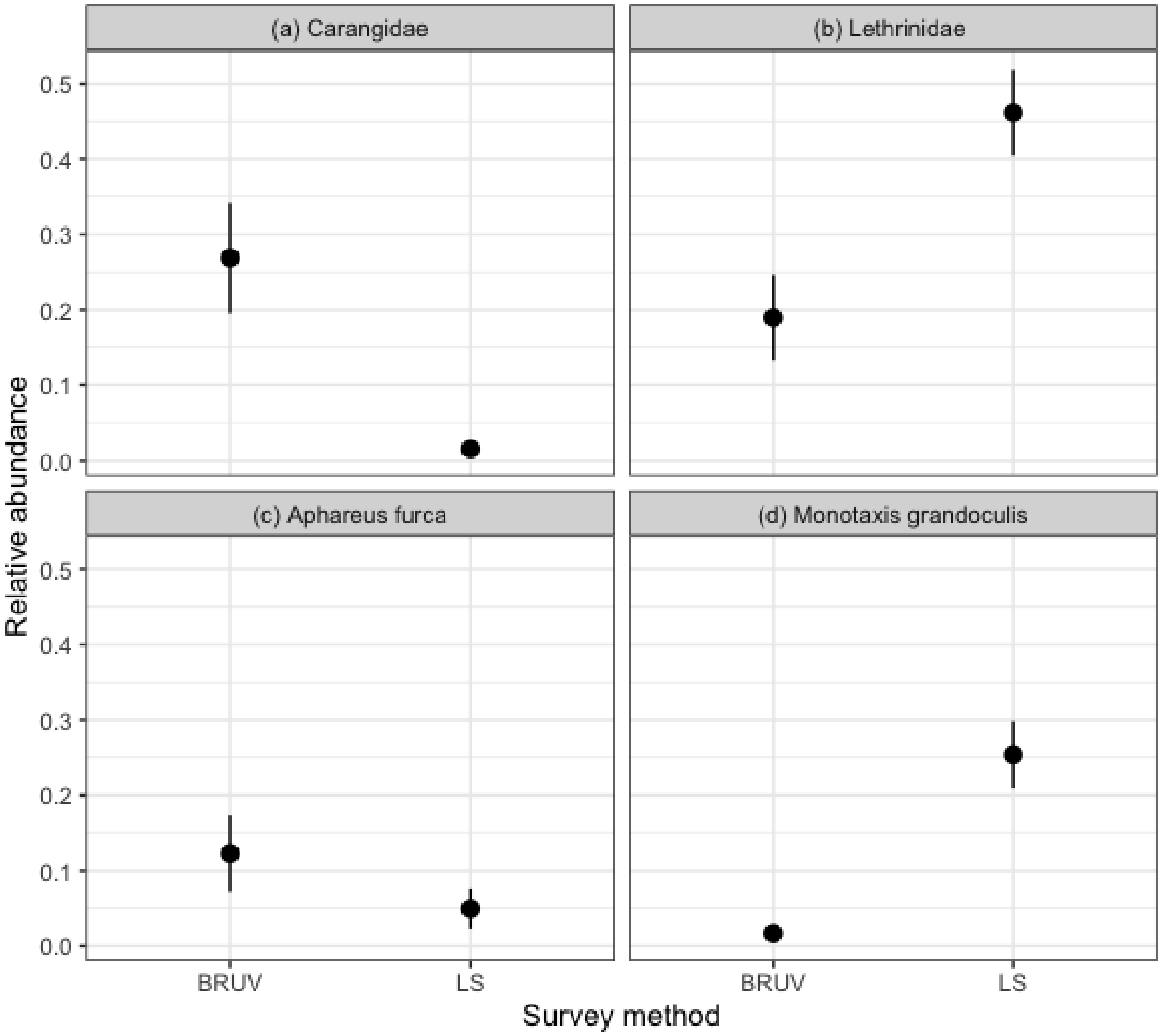


Figure 5: Mean relative abundance of (a) Carangidae, (b) Lethrinidae, (c) *Aphareus furca* and (d) *Monotaxis grandoculis* for baited remote underwater videos (BRUVS) and long swims (LS) underwater visual census undertaken in Pemba Island, Tanzania. Error bars are standard error.

4 Discussion

Methods applied to survey coral reef fish populations are inherently characterised by biases related to either methodological approach or estimation of abundance (Leujak and Ormond, 2007; Emslie et al., 2018). However, combining methods can help overcome these limitations, provide more accurate estimates, and help make an informed decision of the best method to apply to match management and conservation goals (Cheal et al., 2021). This study found BRUVS, and LS were similar in providing estimates of species richness, fish community structure and relative abundance of most of the target fish families and species. Nonetheless, BRUVS were better than LS at estimating the abundance of Carangidae and *Aphareus furca* and sampled 28 unique predatory species. On the contrary, LS were superior at sampling the family Lethrinidae, *Monotaxis grandoculis* and five unique species. The results strongly imply that the two methods are complementary, together providing a more complete assessment of reef fish communities. They also highlight which method is better at measuring the abundance of transient (fast moving mobile pelagic species) and resident (species showing strong association with the reef structure or seafloor) taxa (Chapter 4). Therefore, when the fish monitoring objectives are aimed at assessing the occurrence of large reef-associated predators then BRUVS should be applied. Similarly, when the objective is to assess the abundance of resident families and species then LS would be most appropriate. This highlights the need for strategic application of BRUVS and LS either individually or collectively to assess the status and the distributions of predatory reef fish communities over a wider range of habitats and depths.

BRUVS and LS showed different patterns in estimating relative abundance of Carangidae and Lethrinidae. Carangidae are transient predators that move in schools and at faster speeds and respond quickly to temporal and spatial fluctuations in prey fish density (Stewart and Jones, 2001; Hixon 2015). It is plausible that the high relative abundance of Carangidae in BRUVS was driven by depths and habitat types where BRUVS were deployed (Chapter 4). The family Lethrinidae has a considerable number of species with some species like humpnose big-eye bream *Monotaxis grandoculis* usually forming aggregations exceeding 50 individuals (Lieske and Myers, 1994). Despite a shorter sampling time of 10 minutes, LS surveys were associated with elevated abundance of Lethrinidae. This suggests LS surveys are more suited for sampling fish families with residential behaviour.

Common species recorded by BRUVS, and LS showed under representation of frequently occurring species in one method over the other. This was certainly the case for *Monotaxis grandoculis* and *Lethrinus harak,* which were ubiquitous in LS but poorly represented in BRUVS. Generally, emperors are residential fish associated with sandy and coral reef habitats where they feed by hunting less mobile prey (Kulbicki et al., 2005). Therefore, the low frequency of occurrence in BRUVS could be because these species do not respond to the bait (Chapter 4). It could also point to the inability of BRUVS to record common residential predators notwithstanding the influence of the camera's field of view on the relative abundance of species (Colton and Swearer, 2010). However, BRUVS provided the benefit of being able to sample both roving species - e.g., two-spot red snapper *Lutjanus bohar* and small-toothed jobfish *Aphareus furca* - and shy species like redmouth grouper *Aethaloperca rogaa* (Chapter 4; Cheal et al., 2021). This appears to be because the bait plume disperses enough to reach roving species, while the one-hour soak time is sufficient to allow shy species to enter BRUVS field of view (Harvey et al., 2012; Espinoza et al., 2014). Since the adults of small-toothed jobfish are pelagic, occurring singly or in groups (Anderson and Allen, 2001), it is plausible that the presence of bait attracts them to frequently enter video frames. This coupled with a long soak time increased the likelihood of recording large mobile species.

Estimates of species richness were considerably similar between the two methods, although BRUVS sampled more unique species than LS. When the two methods were combined a similar number of species was recorded as by BRUVS alone. This implies that unique species recorded by LS were not sufficient to result in greater species richness. Therefore, despite their difference, each method sampled the selected predatory species in similar ways. The results on species richness were consistent with Cheal and colleagues (2021) that compared BRUVS and standard (250 m^2) UVCs. However, it is suspected that more sampling effort would yield clearer methodological differences. Indeed, species accumulation curves for each method and combined methods had not plateaued, suggesting that more species would have been recorded with a higher sampling effort. Through converting the MaxN and count data to estimates of relative abundance, the study was able to make a direct comparison of BRUVS and LS. In terms of future research, it would be useful to extend the current findings by using stereo-BRUVS (Langlois et al., 2018) to enable estimation of biomass, and increase the level of replication for LS.

Survey methods introduce different biases that need to be acknowledged and/or corrected. For instance, the size of the area surveyed, and use of bait can influence abundance estimates, when utilising BRUVS (Cheal and Thompson, 1997; Harvey et al., 2007). Regarding LS surveys, potential bias would emerge from avoidance effects from divers by fishes leading to poor detectability and underestimation of targeted species (Kulbicki et al. 2010, Gray et al., 2016; Bradley et al. 2017, Heenan et al. 2020). Both methods are also characterised by measurement errors. Worth noting are the potential trade-offs (i.e., pros and cons) associated with each method (Table 3). These should guide the choice of method to be applied.

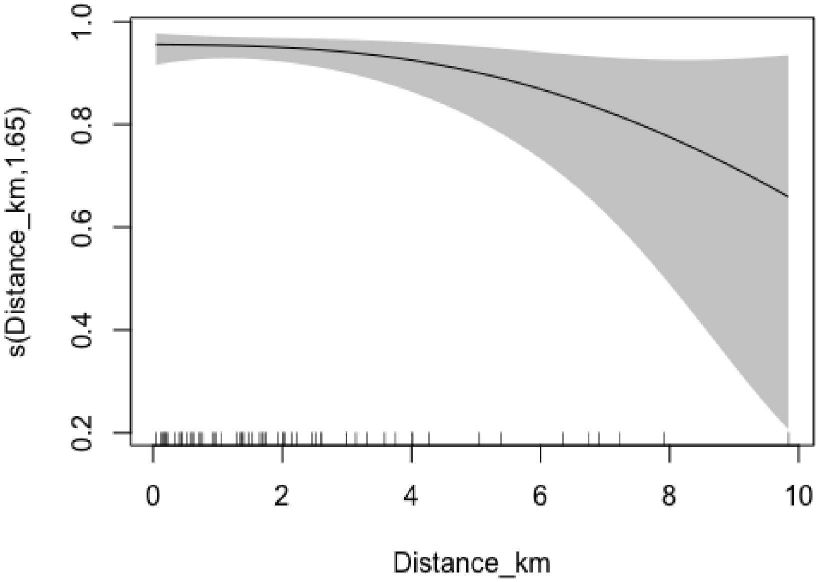
Table 3: Summary of the trade-offs between baited remote underwater videos and long swim underwater visual census.

Criteria	**BRUVs**	**LS**
Sampling area	Cannot be estimated but relies on the field of view (FOV) set on the camera	Based on the transect size (e.g. 3,000m^2).
Depth limitations	Applied to remotely assess fish found in deeper areas.	LS on SCUBA find it logistically difficult or even impossible to reach deeper areas.
Permanent record	Offers a permanent video record that can be reviewed by other scientists at other times.	Collect data in-situ meaning full reliance on diver expertise.
Cost	Relatively high cost associated with insurance costs for divers and diving gear due to medium risks that require mitigation plans.	Relatively low costs due to low level of qualifications and expertise.
Labour	Labour intensive due to the high number of replicates each requiring the same amount of time to analyse the videos as the recording time.	Associated with less processing time, particularly because of in-situ data collection.

Five of these trade-offs merit comment. First is the sampling area, which was known for LS but could not be estimated for BRUVs. Each LS survey was conducted over a defined area of reef of approximately 3,000m^2, implying that estimation of area-related variables such as biomass and productivity was possible (Samoilys and Carlos, 2000; Heenan et al., 2017). On the other hand, BRUVS relied on the field of view (FOV) set on the camera, and this can be extensively diminished if features on the reef such as coral bommies obstruct the camera. Secondly, BRUVS may be applied to remotely assess fish found in deeper areas where divers conducting LS on SCUBA find it logistically difficult or even impossible to reach. This indicates that BRUVs are essential for revealing potential depth refugia, especially in areas facing high fishing pressure at shallower depths (Chapter 4). Thirdly, BRUVS offer a permanent video record that can be reviewed by other scientists at other times (e.g., for species ID), whereas LS, like standard UVC, collect data in-situ meaning full reliance on diver expertise (Heenan et al., 2017). Fourthly, the costs associated with conducting LS are considered to be slightly higher than BRUVS due to medium risks that require mitigation plans. These warrant safe diving protocols that are associated with insurance costs for divers and diving gear (Osuka, unpublished data). The dive personnel need to be suitably qualified and experienced to conduct the surveys safely and have sufficient expertise to identify a wide range of species quickly underwater (Heenan et al., 2017). In comparison, BRUVs require a lower level of qualifications and expertise. Even with well-established health safety protocols for diving, BRUV surveys inherently involve less risk to personnel. Costs for conducting BRUVS can be met within national monitoring funding budgets, but with LS the costs will continue to increase as the level of replication increases. Lastly, BRUVS are labour intensive due to the high number of replicates each requiring the same amount of time to analyse the videos as the recording time (Langlois et al., 2018). On the contrary, LS are associated with less processing time, particularly because of in-situ data collection. Taken together, the findings indicate that between the two methods, BRUVS are the better choice. However, the best option is to use a combination of BRUVS and LS.

The study provides data that can underpin conservation and management decisions including spatial closures and gear restrictions. In particular, the data can help in the designation of Marine Protected Areas and protection of vulnerable large predatory species through fisheries management measures such as species and gear restrictions. Ultimately, the ability to accurately assess predatory reef fish communities not only allows development of conservation and management strategies, but it also allows assessment of their effectiveness over time and adapt them as necessary.

Appendix 1: Generalised additive model plot showing the relationship between distance of sampling stations (Distance_km) and the probability (s(Distance_km, 1.65)) of species richness.



References

Anderson, WD Jr, Allen GR (2001) Lutjanidae. Jobfishes. p. 2840-2918. In Carpenter KE, Niem V (eds.) *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific. Vol. 5. Bony fishes part 3 (Menidae to Pomacentridae)*. FAO, Rome.

Bradley D, Conklin E, Papastamatiou YP, McCauley DJ, Pollock K, Kendall BE, Gaines SD, Caselle JE (2017) Growth and life history variability of the grey reef shark (*Carcharhinus amblyrhynchos*) across its range. PLoS One. 12(2):e0172370.

Cappo M, Speare P, De'ath G (2004) Comparison of baited remote underwater video stations (BRUVS) and prawn (shrimp) trawls for assessments of fish biodiversity in inter-reef areas of the Great Barrier Reef Marine Park. *Journal of Experimental Marine Biology and Ecology*, *302*(2), 123-152.

Cheal AJ, Thompson AA (1997) Comparing visual counts of coral reef fish: implications of transect width and species selection. *Marine Ecology Progress Series*, *158*, 241-248.

Cheal AJ, Emslie MJ, Currey-Randall LM, Heupel MR (2021) Comparability and complementarity of reef fish measures from underwater visual census (UVC) and baited remote underwater video stations (BRUVS). *Journal of Environmental Management*, *289*, 112375.

Clarke KR, Gorley RN (2006) User manual/tutorial. *Primer-E Ltd.,* Plymouth Marine Laboratory, 93

Colton MA, Swearer SE (2010) A comparison of two survey methods: differences between underwater visual census and baited remote underwater video. *Marine Ecology Progress Series*, *400*, 19-36.

Daniels C, Fanning E, Jiddawi N (2004) Misali Island: A detailed description of the subtidal regions. *Frontier-Tanzania Environmental Research. Society for Environmental Exploration, UK, with the University of Dar es Salaam including the Institute of Marine Sciences and the Ministry of Agriculture Natural Resources and Environment Co-operatives, Zanzibar*

de Mitcheson, Y.J.S., Linardich, C., Barreiros, J.P., Ralph, G.M., Aguilar-Perera, A., Afonso, P., Erisman, B.E., Pollard, D.A., Fennessy, S.T., Bertoncini, A.A., Nair, R.J., 2020. Valuable but vulnerable: Over-fishing and under-management continue to threaten groupers so what now? *Marine Policy*, *116*, p.103909.

Emslie MJ, Cheal AJ, MacNeil MA, Miller IR, Sweatman HP (2018) Reef fish communities are spooked by scuba surveys and may take hours to recover. *PeerJ*, *6*, e4886.

Espinoza M, Cappo M, Heupel MR, Tobin AJ, Simpfendorfer CA, (2014) Quantifying shark distribution patterns and species-habitat associations: implications of marine park zoning. *PloS one*, *9*(9), p.e106885.

Gray AE, Williams ID, Stamoulis KA, Boland RC, Lino KC, Hauk BB, Leonard JC, Rooney JJ, Asher JM, Lopes Jr KH, Kosaki RK (2016) Comparison of reef fish survey data gathered by open and closed circuit SCUBA divers reveals differences in areas with higher fishing pressure. *PLoS One.* e0167724.

Grimsditch, G.D., Tamelander, J., Mwaura, J., Zavagli, M., Takata, Y. and Gomez, T. (2009). *Coral reef resilience assessment of the Pemba channel conservation area, Tanzania*. Gland, Switzerland: IUCN. 40pp.

Harvey E, Fletcher D, Shortis M (2001) A comparison of the precision and accuracy of estimates of reef-fish lengths determined visually by divers with estimates produced by a stereo-video system. *Fishery Bulletin*, *99*(1), 63-63.

Harvey ES, Cappo M, Butler JJ, Hall N, Kendrick GA (2007) Bait attraction affects the performance of remote underwater video stations in assessment of demersal fish community structure. *Marine Ecology Progress Series*, *350*, 245-254.

Harvey ES, Newman SJ, McLean DL, Cappo M, Meeuwig JJ, Skepper CL (2012) Comparison of the relative efficiencies of stereo-BRUVs and traps for sampling tropical continental shelf demersal fishes. *Fisheries Research*, *125*, 108-120.

Heenan A, Williams ID, Acoba T, DesRochers A, Kosaki RK, Kanemura T, Nadon MO, Brainard RE (2017) Long-term monitoring of coral reef fish assemblages in the Western central pacific. *Scientific data*, *4*(1), pp.1-12.

Heenan A, Williams GJ, Williams ID (2020). Natural variation in coral reef trophic structure across environmental gradients. Frontiers in Ecology and the Environment. *Frontiers in Ecology and the Environment*, *18*(2), pp.69-75.

Heupel M, Knip D, Simpfendorfer C, Dulvy N (2013) Sizing up the ecological role of sharks as predators. *Marine Ecology Progress Series*. *495*:291–8.

Hixon, M.A., 2015. Predation: piscivory and the ecology of coral-reef fishes. In: Mora C. (Ed.) *Ecology of fishes on coral reefs*. Cambridge University Press Cambridge, UK, pp. 41–53.

Horrill JC (1992) The status of coral reefs of Misali Island, Pemba. The Commission for Lands and Environment, Zanzibar. *Zanzibar Environmental Study Series*, (13), 12.

Horrill JC, Machano H, Omar SH (1994) *Misali Island: Rationale for a marine protected area*. The Commission.

Jones ST, Levine A, Jiddawi NS (2019) Effective co-management and long-term reef fish recovery from severe coral bleaching: Insights from Misali Island, PECCA, Tanzania. *Ocean & Coastal Management*, *178*, 104843.

Kawaka J, Samoilys M, Murunga M, Maina GW, King J, Michelmore F (2016) Coral reef monitoring in Eastern Africa: a guide for communities. TNC/CORDIO. 64pp

Kulbicki M, Bozec YM, Labrosse P, Letourneur Y, Mou-Tham G, Wantiez L (2005) Diet composition of carnivorous fishes from coral reef lagoons of New Caledonia. *Aquatic Living Resources*, *18*(3), pp.231-250.

Kulbicki M, Cornuet N, Vigliola L, Wantiez L, Moutham G, Chabanet P (2010) Counting coral reef fishes: interaction between fish life-history traits and transect design. Journal of *Experimental Marine Biology and Ecology*387(1-2):15-23.

Langlois T, Williams J, Monk J, Bouchet P, Curre L, Goetze J, Harasti D, Huveneers C, Malcolm H, Whitmarsh S (2018) Marine Sampling Field Manual for Benthic Stereo BRUVS (Baited Remote Underwater Videos). *In* Przeslawski, R., Foster, S. (Eds). Field Manuals for Marine Sampling to Monitor Australian Waters, National Environmental Science Programme (NESP). pp. 82-104.

Leujak W, Ormond RFG (2007) Comparative accuracy and efficiency of six coral community survey methods. *Journal of experimental marine biology and ecology*, *351*(1-2), 168-187.

Lieske E, Myers R (1994) Collins Pocket Guide. Coral reef fishes. Indo-Pacific & Caribbean including the Red Sea. Haper Collins Publishers, 400 p.

Mapstone BD, Ayling AM (1998) An investigation of optimum methods and unit sizes for the visual estimation of abundances of some coral reef organisms. A Report to the Great Barrier Reef Marine Park Authority. 71 pp.

Paxton AB, Newton EA, Adler AM, Van Hoeck RV, Iversen Jr ES, Taylor JC, Peterson CH, Silliman BR (2020) Artificial habitats host elevated densities of large reef-associated predators. *PloS one*, *15*(9), p.e0237374.

R Core Team. (2021). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Samoilys MA, Carlos G (2000) Determining methods of underwater visual census for estimating the abundance of coral reef fishes. *Environmental Biology of Fishes.* 57(3):289-304.

Samoilys MA, Ndagala J, Macharia D, da Silva I, Mucave S, Obura D (2011) A rapid assessment of coral reefs at Metundo Island, Cabo Delgado, northern Mozambique. In: Obura DO, Samoilys MA (eds) CORDIO status report 2011. CORDIO East Africa. 36 pp

Schramm KD, Harvey ES, Goetze JS, Travers MJ, Warnock B, Saunders BJ (2020) A comparison of stereo-BRUV, diver-operated, and remote stereo-video transects for assessing reef fish assemblages. *Journal of Experimental Marine Biology and Ecology*, *524*, 151273.

Stewart BD, Beukers JS (2000) Baited technique improves censuses of cryptic fish in complex habitats. *Marine Ecology Progress Series*, *197*, pp.259-272.

Stewart BD, Jones GP (2001) Associations between the abundance of piscivorous fishes and their prey on coral reefs: implications for prey-fish mortality', *Marine Biology*. Springer, 138(2), pp. 383–397.

White J, Simpfendorfer CA, Tobin AJ, Heupel MR (2013) Application of baited remote underwater video surveys to quantify spatial distribution of elasmobranchs at an ecosystem scale. *Journal of Experimental Marine Biology and Ecology*, *448*, 281-288.

Worm B, Davis B, Kettemer L, Ward-Paige CA, Chapman D, Heithaus MR, Kessel ST, Gruber, SH (2013). Global catches, exploitation rates, and rebuilding options for sharks. *Marine Policy*, *40*, pp.194-204.

CHAPTER 6

GENERAL DISCUSSION

6.1. Summary of thesis aims and results

This study aimed to assess the shallow and mesophotic reef communities occurring in the Greater Pemba Channel, Tanzania and provide recommendations for their management and conservation. In particular, the study assessed (a) what level of protection provides enhanced outcomes for different fish sizes sampled at the interphase between shallow and mesophotic depths, (b) what key factors/variables influence the presence of seafloor substrates and benthic communities transcending from shallow to mesophotic depths, and whether the patterns occurring in Pemba Channel are similar to those reported elsewhere, (c) how fish taxa targeted by artisanal fisheries are influenced by depth and habitat types, and (d) which reef survey method provides the most accurate and cost-effective estimates of the abundance of large-sized predatory reef fish.

The first chapter introduced my research by highlighting what knowledge gaps exist for deeper waters of Tanzania, particularly in the mesophotic depths (30-150 m). This chapter also highlighted the key themes and questions the research aimed to contribute and answer, and approaches applied to achieve the results. Finally, other related contributions I have made to coral reef ecology and conservation during my doctoral research were highlighted.

The second chapter set the scene for the rest of the thesis by examining the effect of different levels of marine protection through utilising fish density and size data from studies published in the western and central Indian Ocean. The study employed size spectra analysis to assess the importance of protection to different fish communities. Overall, the results from this chapter showed that effective Marine Protected Areas (MPAs) in the Indian Ocean are more productive and have more small fish. It also highlighted the increasing need to invest in MPAs and strengthen and support management systems, acutely for the moderately protected MPAs, and particularly in areas of high human population density. It was noted that doing so would increase the resilience of coral reef fish communities and contribute towards sustainable livelihood security.

A depth refugia effect was evidenced in Chapters 3 and 4, highlighting the importance of deeper environments in maintaining biodiversity of the ecological important area of Pemba

Island. In particular, the third chapter showcased how application of an autonomous underwater vehicle (AUV) had great potential for mapping the photic and mesophotic coral ecosystems (MCEs) of the Greater Pemba Channel, thereby starting to fill the knowledge gap on MCEs in this area of the western Indian Ocean. This was made possible by the utilities offered by AUVs of being able to: autonomously follow a pre-designed track, go to deeper areas of 150 m, and collect a wide range of high-resolution data within the water column and on the seafloor. Through modelling of the various streams of data collected by the AUV, the study determined that submarine walls occurring in water depths greater than 40 m were potential hotspots of MCE biodiversity. Therefore, management agencies in Tanzania and the larger WIO region should consider directing more efforts towards their management and conservation. However, AUVs were less successful at providing estimates of fish abundance, thus baited remote underwater videos (BRUVS) and long swim (LS) underwater visual census were employed in the subsequent chapters.

Predatory reef fish populations are facing immense pressures worldwide, leading to alarming losses in abundance and diversity. The fourth chapter applied BRUVS in order to shed light on abundance and distribution of predatory reef fish populations off the under-researched oceanic island of Pemba Island. Predator reef fish types (transient/mobile and resident) were discordantly predicted by depth and habitat types. However, habitats dominated by hard and soft corals, and in relatively deeper waters, hosted higher species richness and abundance of reef-associated predators. These findings add to the growing evidence that deep waters around coral reefs are acting as ‘refuges’ for fish predators and coral habitats. Thus, careful management, through effective area and species protection measures, are needed to prevent impending reductions in their populations.

The fifth chapter explored similarities and differences between BRUVS and LS underwater visual census in order to identify the most accurate and cost-effective method. The study documented similar estimates between the survey methods in measuring species richness, fish community structure and relative abundance of common predatory reef fish species. The results suggested that the two methods were complementary, together providing a more complete assessment of reef fish communities. It was therefore concluded that independent surveys using BRUVS should be conducted when the monitoring goal is to estimate species richness and abundance of transient taxa, while LS should be applied when estimating the abundance of resident taxa. While BRUVS appears to be the better choice, the best option was found to incorporate a combination of both BRUVS and LS.

Apart from the five chapters summarised above, knowledge contributions were made in the fields of marine survey technology (Jacobs et al., 2020; Obura et al., 2019; Palmer et al., 2021), coral reef fish ecology and vulnerability of coral reef ecosystem of the Red Sea and Western Indian Ocean (Cowburn et al., 2019; Samoilys et al., 2019a; Obura et al., 2021), management of artisanal fisheries in Kenya and Mozambique (Alati et al., 2020; Samoilys et al., 2019b; Osuka et al., 2021; Wanyonyi et al., 2021), influence of climate change on East Africa's coastal fisheries (Jacobs et al., 2021; Wilson et al., 2021), management and conservation of reef sharks (MacNeil et al., 2020), socio-ecological systems of Mozambique's fisheries (Osuka et al., 2020), implications of COVID-19 on MPAs (Phua et al., 2021), and policy pathways for rebuilding coral reefs (Knowlton et al., 2021). The results from these studies are expected to feed directly into addressing issues around sustainability and food security and threats of climate change to coral reefs.

Based on the findings established, there are key research themes that will be important to address to advance our comprehension of shallow and deeper marine environments to establish pathways for their improved management and conservation.

6.2 Marine Protected Areas (MPAs)

MPAs are a critical management tool with an all-important role in balancing between biodiversity conservation and fisheries management (Sala et al., 2021). However, to achieve the maximum benefits of MPAs will require large enough areas that are well enforced (Edgar, et al., 2014). This implies the importance of having habitats that are relatively undamaged and protected from overexploitation (Hilborn and Sinclair, 2021). In the WIO, where there is a long fishing history, achievement of the full benefits of MPAs is likely to be a challenge particularly because MPAs are generally not large enough to protect all the species. However, their effectiveness is more apparent where social-ecological conditions are considered through adaptive management processes (Osuka et al., 2020). In addition, extension of MPA coverage and fisheries management up to MCEs, is needed to promote sustainable management of the ocean (Eyal et al. 2021; Kriegl et al., 2021).

6.3 Shallow and deep-water research

MCEs occur at a transition zone between shallow and deep-sea environments. Application of marine robots show great potential to collect baseline and routine monitoring data, not least for tackling under-researched ecosystems such as the MCEs of the WIO (Chapter 3). Marine robots would also be relevant in the assessment of distribution and origins of geological structures (Howe et al., 2019), monitoring of MPAs (Benoist et al 2019) and help document threats facing MCEs. Investment in relatively low-cost marine robotics would therefore immensely support monitoring of coral ecosystems spanning from shallow to mesophotic depths. To facilitate research in a deeper environment requires amendment of fisheries and conservation policies, including the associated management plans (Turner et al., 2019). Such an undertaking would require building awareness on depth refugia and existence of MCEs, followed by stakeholder engagement to extend conservation areas up to mesophotic depths.

6.4 Complementarity of survey methods

Use of multiple techniques is critical in accurately measuring marine habitat and fish community composition. The overall utilities provided by multiple survey methods help overcome the biases associated with single methods. This was certainly the case in this study, where AUVs enabled collection of information in the deeper environments where SCUBA UVC seemed inadequate. AUVs are however limited in providing better estimates of fish, which BRUVS and SCUBA-based long swims performed well in the shallow and upper mesophotic depths. Application of multiple methods should therefore be applied in monitoring marine ecosystems in the shallow and deeper zones but perhaps using methods that are readily available and cost-effective. For instance, GoPros offer low-cost option to monitor marine ecosystems through their ability to collect eco-acoustic indices such as temporal variability, acoustic complexity index and acoustic richness (Chapuis et al 2021). Application of BRUVS and LS considerably improve assessments of the status and distribution of the predatory reef fish communities over a wide range of habitats and depths (Chapter 5). In sum, integration of methods would increase the monitoring coverage of marine ecosystems in a cost-effective manner. This has the potential to provide crucial data that would underpin conservation and management decisions, such as the designation of further MPAs but more importantly in the deeper environments.

6.5 Distribution, behaviour, and roles of fishes

Results on trophic group and reef predatory provide critical insights into the effects of fishing and habitat degradation on coral reefs. Of importance, is the evidence on varying effects of fisheries exploitation on multiple trophic groups. The findings pinpoint the complexity of fisheries management and biodiversity conservation. This further highlights the need for monitoring and management of coral reef ecosystems through the lenses of multi-trophic group approach (Zgliczynski and Sandin, 2017).

Low biomass of piscivores, plankivores, large- and small excavators were evident in reef areas near high human population densities (Chapter 2). This suggests that these groups may require highly protected MPAs to thrive. Otherwise, the ultimate outcome of a reduction in biomass of trophic groups such as piscivores can lead to changes in food web interactions that may result in prey release (Sandin et al., 2010). Planktivorous fishes are bound to become an important trophic group particularly in areas showing increased availability of suspended food. As anthropogenic impacts become more evident leading to increased suspended particles, this trophic group will be important in supporting local fisheries and livelihoods.

Resident predators show high degrees of site fidelity (Stewart and Jones, 2001), in contrast to transient predators that show the weakest relationships with coral habitat types (Asher et al., 2017). Transient predators can however show strongest habitat-relationships when the abundance of prey increases over certain orders of magnitude. Consequently, management strategies for predatory reef fishes should encompass fish movement behaviour as well as attainment and maintenance of thresholds of prey densities (McClanahan et al., 2011) and protection of habitats that their prey fish rely upon.

6.6 Role of benthic habitats

It is evident that hard and soft coral dominated habitats are strongly correlated with higher structural complexity. This aspect of reef ecology provides shelter and hiding places to small fish that act as food resources to a wide range of piscivorous fish (Stewart and Jones 2002).

Increase in the cover of macroalgal habitats is associated with phase-shifts. Algal dominated habitats tend to have fewer predators possibly due to low densities of prey. Water clarity is usually poor in such habitats making it difficult for predators to hunt. However, there is evidence to highlight the significant role of macro-algal habitats as nursery ground for reef fishes (Eggertsen et al. 2017) and dominated by juvenile fishes. Thus, incorporation of multiple habitat characteristics in reef surveys would certainly reveal new insights into the spatial drivers of fish population. Importantly, the habitat supports a high abundance of herbivorous fishes that support local fisheries.

6.7 Recommendations

The study recommends application of marine robots for collection of baseline and routine monitoring data, not least for tackling under-researched ecosystems such as the MCEs of the Western Indian Ocean (WIO), and assessment of the distribution and origins of geological structures. The robots should also be applied to monitor MPAs and document threats facing MCEs. Thus, management agencies in Tanzania and other WIO countries should consider investing in relatively low-cost marine robotics as opposed to ship-based research vessels to support monitoring of coral ecosystems spanning from shallow to mesophotic depths.

There is a need to amend fisheries and conservation policies to include MCEs in management plans of coral reef environments in the WIO region. As such, stakeholder engagement should be conducted to inform the extension of conservation areas to include mesophotic depths and drop-offs and to ensure they have local support. This should be preceded by activities geared towards building awareness of the existence of MCEs in Pemba Channel and their importance as depth refugia.

Strategic application of BRUVS and LS surveys would considerably improve assessments of the status and distribution of the predatory reef fish communities over a wide range of habitats and depths. This has the potential to provide crucial data that can underpin conservation and management decisions, such as the designation of further MPAs.

6.8 Future research

This study is not shy of limitations that would benefit from further investigations in the future. The data collated from published studies in Chapter 2 did not include abundance and sizes of large-sized families like Carangidae, Carcharhinidae, Dasyatilidae, Myliobatidae, Scombridae, and Sphyraenidae. This implies that the size spectra results were not a full reflection of community size structure. Large MPAs with high levels of protection are generally associated with high fish abundance and large fish sizes (Edgar, et al., 2014). Therefore, inclusion of species from aforementioned families in future size spectra studies would likely yield results that would further showcase the differences between the levels of protection.

While my study recommends management agencies in the WIO to acquire marine robotics, there are still significant challenges around capacity, expertise, and costs of the equipment. Perhaps one way of overcoming these issues is through establishing a marine robotics hub in one of the WIO countries (Palmer et al., 2021). The hub could serve as a Centre of Excellence (CoE) with key mandates of purchasing the AUVs, conducting training on management and deployment of AUVs, and providing hiring services to institutions conducting research or routine monitoring of MPAs. Another critical area of focus should involve making the technology more affordable to management agencies in the WIO region.

Processing of videos and images from BRUVS and AUVs is a very time-consuming activity. However, recent developments in machine learning have shown promising results for processing large amounts of such data (Shafait et al., 2016), and therefore should be adopted for solving this challenge (Marini et al., 2018). In such a case, the CoE would be critical in developing the machine learning algorithms and offering training to scientists and managers.

It would be useful to extend my study of the reefs around Pemba Island by using BRUVs to examine predatory reef fish at the coral-rich site of Misali Island (Grimsditch et al., 2009). The adoption of stereo-BRUVs, which can measure fish size (Langlois et al., 2018), would also enable an assessment of how fish biomass varies across all the sectors of Pemba Island. Of relevance would be the application of mid-water stereo BRUVs (Santana-Garcon et al., 2014), which would likely be more suitable for the outer reefs of Pemba Island, which have ledges and walls that make it difficult for BRUV units to settle.

Future work especially on species distribution of corals, fleshy algae, sponges, and fish in the outer reefs of Pemba Island would also benefit from application of complementary coral reef survey methods able to survey shallow and mesophotic depths. Undoubtedly, such an effort will give comprehensive estimates on diversity, density, and biomass of MCE taxa components.

6.9 Conclusions

In the course of this three-year study in the WIO, new analysis was conducted that showed high levels of protection were most important for small fish and overall community productivity. Through documenting the presence of mesophotic coral ecosystems in Pemba Island, I found that depth and slope were the key predictors of coral and algal communities. In the shallow and upper mesophotic depths around Pemba Island, the abundance of predatory reef fish generally increased with depth while the influence of habitat type depended on the mobility of the species assessed. Finally, due to inherent biases associated with fish sampling methods, I demonstrated that integration of video and diver reef surveys enabled the most complete assessment of large-sized coral reef associated fish predators.

6.10 References

Alati, V.M., Olunga, J., Olendo, M., Daudi, L.N., Osuka, K., Odoli, C., Tuda, P. and Nordlund, L.M., 2020. Mollusc shell fisheries in coastal Kenya: Local ecological knowledge reveals overfishing. *Ocean & Coastal Management*, *195*, p.105285.

Asher, J., Williams, I.D. and Harvey, E.S., 2017. An assessment of mobile predator populations along shallow and mesophotic depth gradients in the Hawaiian Archipelago. *Scientific reports*, *7*(1), pp.1-18.

Benoist, N.M., Morris, K.J., Bett, B.J., Durden, J.M., Huvenne, V.A., Le Bas, T.P., Wynn, R.B., Ware, S.J. and Ruhl, H.A., 2019. Monitoring mosaic biotopes in a marine conservation zone by autonomous underwater vehicle. *Conservation Biology*, *33*(5), pp.1174-1186.

Cowburn, B., Samoilys, M.A., Osuka, K., Klaus, R., Newman, C., Gudka, M. and Obura, D., 2019. Healthy and diverse coral reefs in Djibouti–A resilient reef system or few anthropogenic threats? *Marine pollution bulletin*, *148*, pp.182-193.

Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T., Berkhout, J. and Buxton, C.D., 2014. Global conservation outcomes depend on marine protected areas with five key features. *Nature*, *506*(7487), pp.216-220.

Eggertsen, L., Ferreira, C.E., Fontoura, L., Kautsky, N., Gullström, M. and Berkström, C., 2017. Seaweed beds support more juvenile reef fish than seagrass beds in a south-western Atlantic tropical seascape. *Estuarine, Coastal and Shelf Science*, *196*, pp.97-108.

Eyal, G., Laverick, J.H., Bongaerts, P., Levy, O. and Pandolfi, J.M., 2021. Mesophotic coral ecosystems of the Great Barrier Reef are understudied and underexplored. *Frontiers in Marine Science*, *8*, p.83.

Grimsditch, G.D., Tamelander, J., Mwaura, J., Zavagli, M., Takata, Y. and Gomez, T. 2009. *Coral reef resilience assessment of the Pemba channel conservation area, Tanzania*. Gland, Switzerland: IUCN. 40pp.

Hilborn, R. and Sinclair, A.R., 2021. Biodiversity protection in the 21st century needs intact habitat and protection from overexploitation whether inside or outside parks. *Conservation Letters*, *14*(4).

Howe, J.A., Husum, K., Inall, M.E., Coogan, J., Luckman, A., Arosio, R., Abernethy, C. and Verchili, D., 2019. Autonomous underwater vehicle (AUV) observations of recent tidewater glacier retreat, western Svalbard. Marine Geology, 417, p.106009.

Jacobs, Z.L., Jebri, F., Srokosz, M., Raitsos, D.E., Painter, S.C., Nencioli, F., Osuka, K., Samoilys, M., Sauer, W., Roberts, M., Taylor, S.F., Scott, L., Kizenga, H. and Popova, E., 2020. A major ecosystem shift in coastal East African waters during the 1997/98 Super El Niño as detected using remote sensing data. *Remote Sensing*, *12*(19), p.3127.

Jacobs, Z.L., Yool, A., Jebri, F., Srokosz, M., van Gennip, S., Kelly, S.J., Roberts, M., Sauer, W., Queirós, A.M., Osuka, K.E., Samoilys, M., Becker, A.E. and Popova, E., 2021. Key climate change stressors of marine ecosystems along the path of the East African coastal current. *Ocean & Coastal Management*, *208*, p.105627.

Knowlton, N., Grottoli, A.G., Kleypas, J., Obura, D., Corcoran, E., de Goeij, J.M., Felis, T., Harding, S., Mayfield, A., Miller, M., Osuka, K., Peixoto, R., Randall, C.J., Voolstra, C.R., Wells, S., Wild, C., Ferse, S. 2021. Rebuilding Coral Reefs: A Decadal Grand Challenge. *International Coral Reef Society and Future Earth Coasts* 56 pp.

Kriegl, M., Elías Ilosvay, X.E., von Dorrien, C. and Oesterwind, D., 2021. Marine Protected Areas: At the Crossroads of Nature Conservation and Fisheries Management. *Frontiers in Marine Science*, *8*, p.676264.

Langlois, T., Williams, J., Monk, J., Bouchet, P., Currey, L., Goetze, J., Harasti, D., Huveneers, C., Malcolm, H. and Whitmarsh, S., 2018. *Marine Sampling Field Manual for Benthic Stereo BRUVS (Baited Remote Underwater Videos)*. *In*: Przeslawski, R. and Foster, S. (Eds). *Field Manuals for Marine Sampling to Monitor Australian Waters*, National Environmental Science Programme (NESP). pp. 82-104.

MacNeil, M. A., Chapman, D. D., Heupel, M., Simpfendorfer, C. A., Heithaus, M., Meekan, M., et al., 2020. Global status and conservation potential of reef sharks. *Nature*, *583*(7818), 801-806.

Marini, S., Fanelli, E., Sbragaglia, V., Azzurro, E., Del Rio Fernandez, J. and Aguzzi, J., 2018. Tracking fish abundance by underwater image recognition. *Scientific Reports*, **8**, 13748.

McClanahan, T.R., Graham, N.A., MacNeil, M.A., Muthiga, N.A., Cinner, J.E., Bruggemann, J.H. and Wilson, S.K., 2011. Critical thresholds and tangible targets for ecosystem-based management of coral reef fisheries. *Proceedings of the National Academy of Sciences*, *108*(41), pp.17230-17233.

Obura, D.O., Aeby, G., Amornthammarong, N., Appeltans, W., Bax, N., Bishop, J., Brainard, R.E., Chan, S., Fletcher, P., Gordon, T.A., Gramer, L., Gudka, M., Halas, J., Hendee, J., Hodgson, G., Huang, D., Jankulak, M., Jones, A., Kimura, T., Levy, J., Miloslavich, p., Chou, L.M., Muller-Karger, F., Osuka, K., Samoilys, M., Simpson S.D., Tun, K. and Wongbusarakum, S. 2019. Coral reef monitoring, reef assessment technologies, and ecosystem-based management. *Frontiers in Marine Science*, *6*, p.580.

Obura, D., Gudka, M., Samoilys, M. Osuka, K., Mbugua, J., Keith, A.K., Porter, S. Roche, R, van Hooidonk, R., Ahamada, S., Araman, A., Karisa, J., Komakoma, J., Madi, M., Ravinia, R., Razafindrainibe, H., Yahya, S. Zivane, F. 2021. Vulnerability to collapse of coral reef ecosystems in the Western Indian Ocean. *Nature Sustainabilit*y.

Osuka, K., Kawaka, J.A. and Samoilys, M.A., 2021. Evaluating Kenya's coastal gillnet fishery: trade-offs in recommended mesh-size regulations. *African Journal of Marine Science*, *43*(1), pp.15-29.

Osuka, K., Rosendo, S., Riddell, M., Huet, J., Daide, M., Chauque, E. and Samoilys, M. 2020. Applying a social–ecological systems approach to understanding local marine management trajectories in Northern Mozambique. *Sustainability*, *12*(9), 3904.

Palmer, M.R., Shagude, Y.W., Roberts, M.J., Popova, E., Wihsgott, J.U., Aswani, S., Coupland, J., Howe, J.A., Bett, B.J., Osuka, K.E., Abernethy, C., Alexiou, S., Painter, S.C., Kamau, J.N., Nyandwi, N. and Sekadende, B. 2021. Marine robots for coastal ocean research in the Western Indian Ocean. *Ocean & Coastal Management*, *212*, p.105805.

Phua, C., Andradi-Brown, D.A., Mangubhai, S., Ahmadia, G.N., Mahajan, S.L., Larsen, K., Friel, S., Reichelt, R., Hockings, M., Gill, D., Veverka, L. Anderson, R., Augustave, L.C., Bervoets, A.T., Brayne, K., Djohani, R., Kawaka, J., Kyne, F., Ndagala, J., Oates, J., Osuka, K., Prvan, M., Shah, N., Vallarola, F., Wenzel, L., Widodo, H. and Wells, S., 2021. Marine protected and conserved areas in the time of COVID. *Parks 2.*

Sala, E., Mayorga, J., Bradley, D., Cabral, R.B., Atwood, T.B., Auber, A., Cheung, W., Costello, C., Ferretti, F., Friedlander, A.M. and Gaines, S.D., 2021. Protecting the global ocean for biodiversity, food and climate. *Nature*, *592*(7854), pp.397-402.

Samoilys, M. A., Halford, A., and Osuka, K., 2019a. Disentangling drivers of the abundance of coral reef fishes in the Western Indian Ocean. *Ecology and evolution*, *9*(7), 4149-4167.

Samoilys, M.A., Osuka, K., Mussa, J., Rosendo, S., Riddell, M., Diade, M., Mbugua, J., Kawaka, J., Hill, N. and Koldewey, H., 2019b. An integrated assessment of coastal fisheries in Mozambique for conservation planning. *Ocean & Coastal Management*, *182*, p.104924.

Sandin, S.A., Walsh, S.M. and Jackson, J.B., 2010. Prey release, trophic cascades, and phase shifts in tropical nearshore marine ecosystems. In: Terborgh, J., Estes, J.A. (Eds.), Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature. Island Press, Washington, DC, pp. 71–90.

Santana-Garcon, J., Newman, S.J. and Harvey, E.S., 2014. Development and validation of a mid-water baited stereo-video technique for investigating pelagic fish assemblages. *Journal of Experimental Marine Biology and Ecology*, *452*, pp.82-90

Shafait, F., Mian, A., Shortis, M., Ghanem, B., Culverhouse, P.F., Edgington, D., Cline, D., Ravanbakhsh, M., Seager, J. and Harvey, E.S., 2016. Fish identification from videos captured in uncontrolled underwater environments. *ICES Journal of Marine Science*, *73*(10), pp.2737-2746.

Stewart, B.D. and Jones, G.P., 2001. Associations between the abundance of piscivorous fishes and their prey on coral reefs: implications for prey-fish mortality. *Marine Biology*, 138(2), pp. 383–397.

Turner, J.A., Andradi-Brown, D.A., Gori, A., Bongaerts, P., Burdett, H.L., Ferrier- Pag`es, C., Voolstra, C.R., Weinstein, D.K., Bridge, T.C., Costantini, F., Gress, E., 2019. Key questions for research and conservation of mesophotic coral ecosystems and temperate mesophotic ecosystems. In: Loya, Y., Puglise, K.A., Bridge, T.C.L. (Eds.), Mesophotic Coral Ecosystems. Springer, Cham, pp. 989–1003.

Wanyonyi, I.N., Wamukota, A., Alati, V.M. and Osuka, K., 2021. The influence of 'space' on migrant fisher livelihoods. *African Identities*, pp.1-16.

Wilson, R.J., Sailley, S.F., Jacobs, Z.L., Kamau, J., Mgeleka, S., Okemwa, G.M., Omukoto, J.O., Osuka, K.E., Samoilys, M., Sauer, W., Silas, M.O., Sululu, J.S. and Roberts, M.J., 2021. Large projected reductions in marine fish biomass for Kenya and Tanzania in the absence of climate mitigation. *Ocean & Coastal Management*, *215*, p.105921.

Zgliczynski, B.J. and Sandin, S.A., 2017. Size-structural shifts reveal intensity of exploitation in coral reef fisheries. *Ecol. Indic.* 73, 411–421.

CHAPTER 7

SUPPLEMENTARY MATERIALS

Chapter 2: Protection outcomes for fish trophic groups across a range of management regimes

Kennedy E. Osuka[a, b], Bryce D. Stewart[a], Melita A. Samoilys[a,d], Ronan C. Roche[c], John Turner[c] and Colin Mcclean[a]

Institutional affiliation:

[a] Department of Environment and Geography, University of York (York, UK)

[b] CORDIO East Africa (Mombasa, Kenya)

[c] School of Ocean Sciences, Bangor University (Bangor, UK)

[d] Department of Zoology, University of Oxford (Oxford, UK)

Table S 1: Details of fish survey sites in ocean exposed fringing reefs and atolls with their reef type, protection index and depths at each reef site. Protection index: F=Fished – reef with no management in place at all, MP=moderate protection- a gazetted marine protected area (MPA) and established though effectiveness weak due to poor enforcement; P= Well - protected - a gazetted MPA or a tourism zone with informal rules, and good enforcement, HP=high protection - a gazetted MPA in remote location with strong enforcement.

Country	**Location**	**Site**	**Reef type**	**Year**	**Month**	**Protection index**	**No. of fish transects**	**Min. depth**	**Max. depth**
Tanzania	Mafia	Dindini	Forereef	2011	March	P	5	4	17
Tanzania	Mafia	Kifinge	Forereef	2011	March	P	5	1.6	16.5
Tanzania	Mafia	Yuyuni	Forereef	2011	March	P	5	5	20
Tanzania	Mnazi	MnazA	Forereef	2009	October	MP	5	3	22
Tanzania	Mnazi	MnazB	Forereef	2009	October	MP	5	8	17
Tanzania	Mnazi	MnazF	Forereef	2009	October	MP	5	5	15
Tanzania	Zanzibar	Mnemba	Forereef	2009	October	MP	5	6	18
Chagos	Blenheim Reef	Blenheim	Forereef	2014	March	HP	5	7	15
Chagos	Diego Garcia Atoll	DGOuterN	Terrace & forereef	2014	April	HP	4	8	16
Chagos	Great Chagos Bank	Eagle Outer	Forereef	2014	April	HP	5	10	16
Chagos	Great Chagos Bank	EgmontIn	Forereef	2014	April	HP	5	8	17
Chagos	Peros Banhos Atoll	PBIsdela Passe	Terrace & forereef	2014	April	HP	5	7	16
Chagos	Salomon Atoll	SAIsdela Passe	Terrace & forereef	2014	March	HP	3	4	23
Chagos	Salomon Atoll	SAIsle Anglaise	Terrace & forereef	2014	March	HP	5	7	20
Chagos	Great Chagos Bank	Three Brothers	Terrace & forereef	2014	April	HP	5	6	17

Country	**Location**	**Site**	**Reef type**	**Year**	**Month**	**Protection index**	**No. of fish transects**	**Min. depth**	**Max. depth**
Comoros	Grand Comore	Chin	Forereef	2010	March	F	5	5	20
Comoros	Grand Comore	Itsan	Forereef	2010	March	F	5	5	20
Comoros	Grand Comore	Male	Forereef	2010	March	F	3	10	20
Comoros	Grand Comore	Mitsam	Forereef	2010	March	F	5	7	20
Comoros	Grand Comore	Moindz	Forereef	2010	March	F	3	2	17
Comoros	Grand Comore	Shom	Forereef	2015	March	F	3	2	11
Mozambique	Metundo	MetundoE	Forereef	2015	March	P	3	5	14
Mozambique	Metundo	MetundoNE	Forereef	2014/ 2015	March	P	8	5	11
Mozambique	Nacala	Nangata	Terrace & forereef	2011	September	F	5	8	20
Mozambique	Palma	Quifuki1	Forereef	2014	March	F	3	3	6
Mozambique	Palma	Quirindi	Forereef	2015	March	F	5	9	15
Mozambique	Vamizi	VamiziNE	Forereef	2011/ 2015	October/March	P	10	5	17
Mozambique	Vamizi	VamiziNR	Deep terrace	2011	October	P	4	7	17
Madagascar	Ambodivahibe	Ambo Inner	Shallow terrace	2010	March	F	3	3	11
Madagascar	Ambodivahibe	Ambo Outer	Forereef	2010	March	F	5	10	19
Madagascar	Ambodivahibe	Ambo S	Shallow terrace	2010	March	F	5	3	15
Madagascar	Loky	Loky S	Forereef	2010	March/April	F	5	6	20

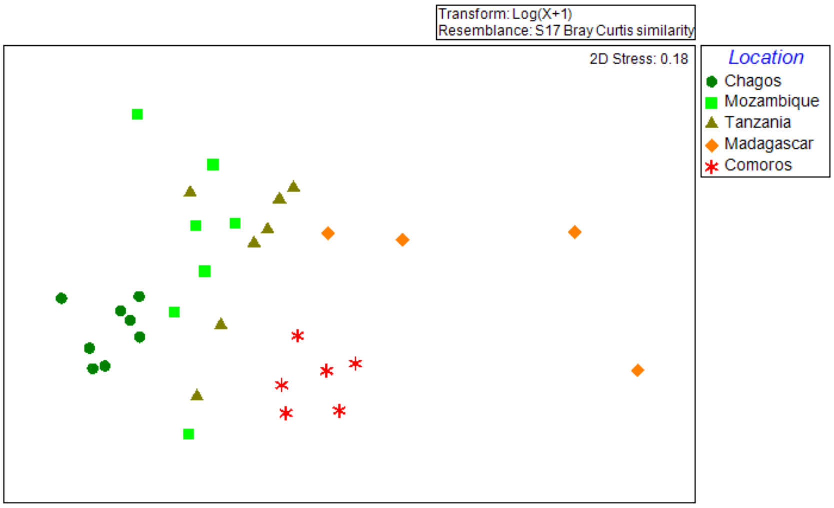
Fish community patterns

Multivariate dimensional scaling (MDS) analyses based on Bray-Curtis similarity index were performed on log (x+1) transformed fish density and biomass data and compared based on location as well as a combined factor of location and protection (Figure S1a-d). A permutation-based hypothesis testing analysis of similarities (ANOSIM) was used to compare fish density and biomass across the four protection levels (Clarke & Gorley, 2006).

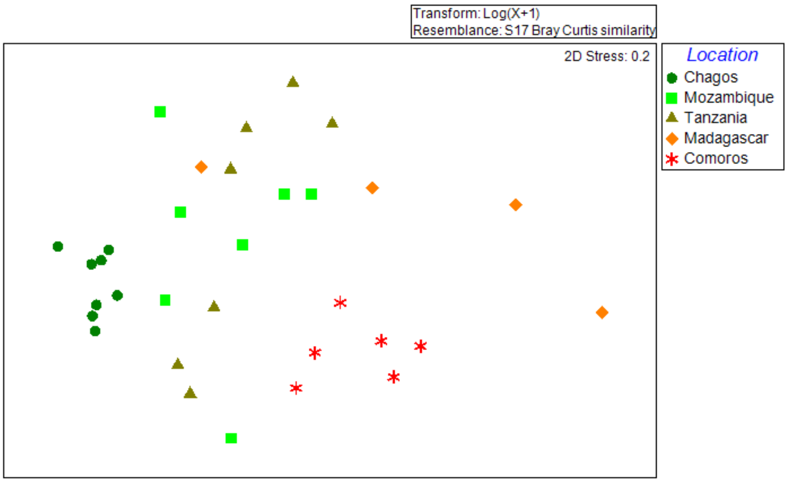
Fish density and biomass showed a significant (p=0.001) strong grouping based on location (ANOSIM: abundance R = 0.726; biomass R = 0.717 Figure S1a-b). The MDS showed clearer differences in groupings of locations with exception of Mozambique and Tanzania that overlapped in the abundance and biomass of fish community (Figure S1a-b). Except for Tanzania – Mozambique comparisons, pairwise ANOSIM results revealed strong geographic differences in abundance (R range 0.619 – 0.999, p<0.01) and biomass (R range 0.593 - 1.000, p<0.01) of fish with greater dissimilarities being between Chagos versus Comoros and Madagascar.

Fish density and biomass showed a significant grouping (p = 0.001) based on combined factor of location and protection (ANOSIM: density R = 0.811; biomass R = 0.844; Figure S1b-c). Greater dissimilarities were found between highly protected sites in Chagos Archipelago versus fished sites from Comoros. Pairwise ANOSIM results revealed strong geographic and protection differences in fish densities and biomass except for pairwise comparisons between protected sites in Mozambique versus fished sites in Mozambique and protected sites in Tanzania; and fished sites in Madagascar versus protected sites in Tanzania and fished sites in Mozambique. Greater dissimilarities were found between highly protected sites in Chagos Archipelago versus fished sites from Comoros. In-country differences in protection index were only evident in Tanzania.

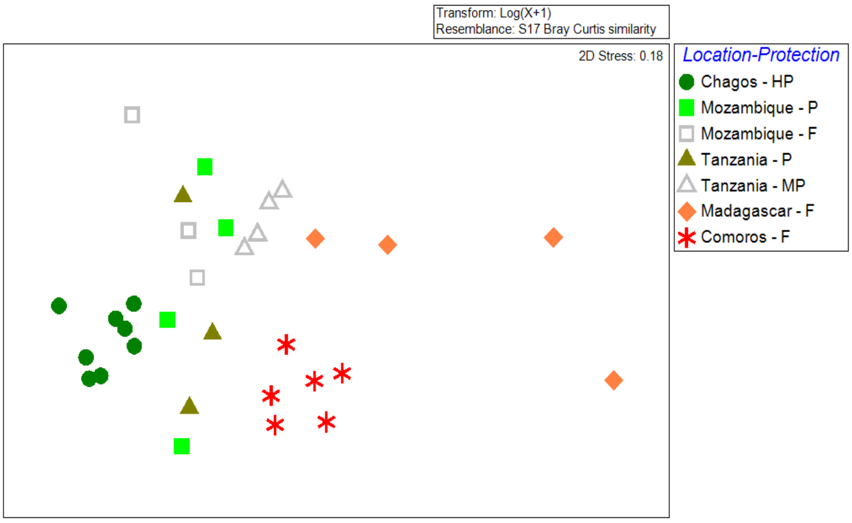
a) Location Abundance



b) Location Biomass



c) Location-protection abundance



d) Location-protection abundance

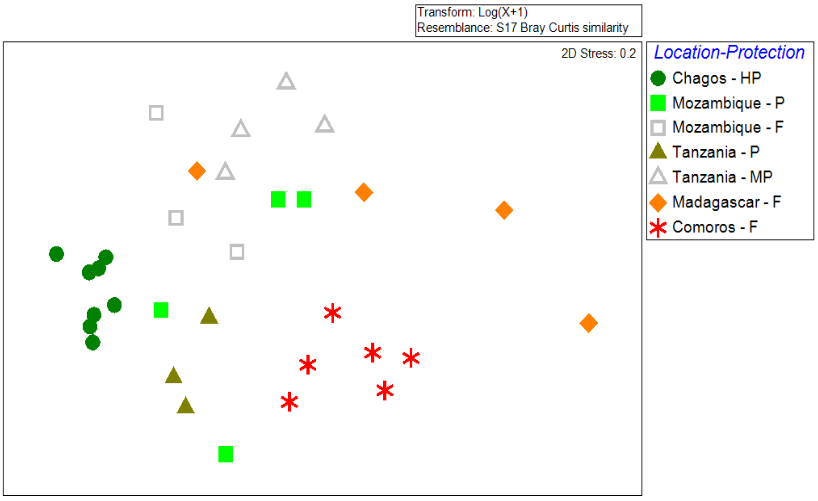


Figure S 1: Multi-dimensional scaling plots based on Bray-Curtis similarity statistic on: a) fish species density b) fish species biomass grouped by five locations in central and western Indian Ocean; c) density and d) biomass across seven combinations of location and protection from five countries HP = high protection, P = well-protected, MP = moderate protection and F = Fished.

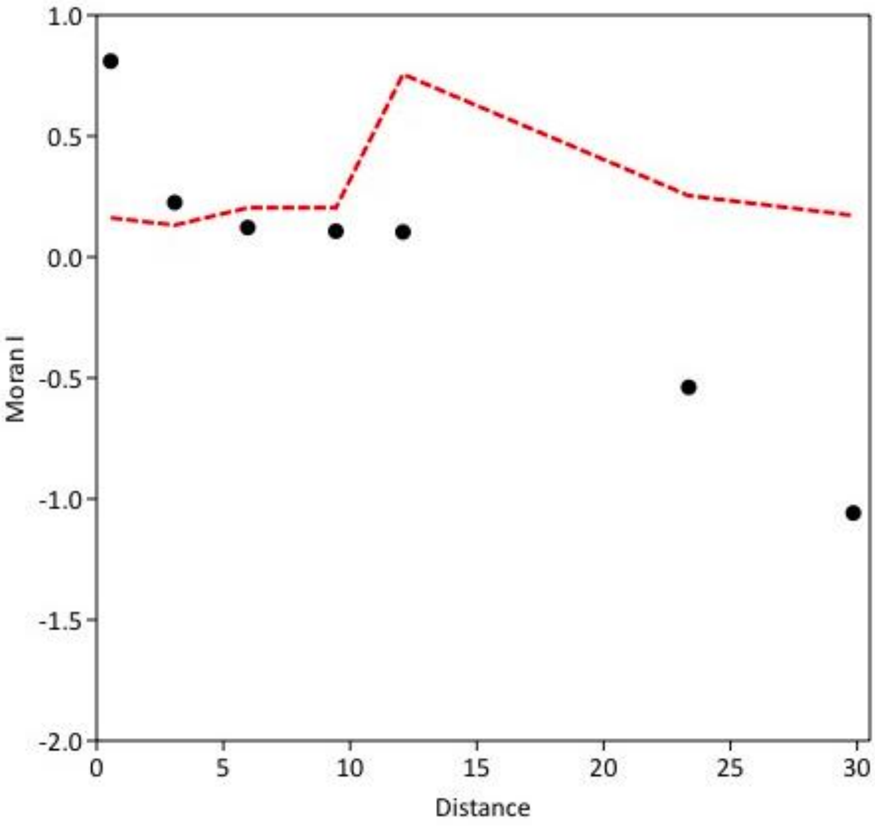


Figure S 2: Plot showing relationship between distance of sampling sites and Moran I critical values. Points above the red dotted line show spatial autocorrelation.

Chapter 3: Characteristics of shallow and mesophotic environments of the Pemba Channel, Tanzania: implications for management and conservation

Authors Kennedy E. Osuka[1, 2, *]; Colin McClean[2], Bryce Stewart[2], Brian J. Bett[3], Tim Le Bas[3], John Howe[4], Colin Abernerthy[4] Saleh Yahya[5], David Obura[1] and Melita Samoilys[1]

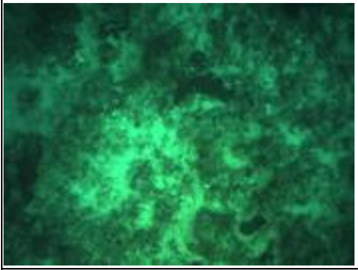
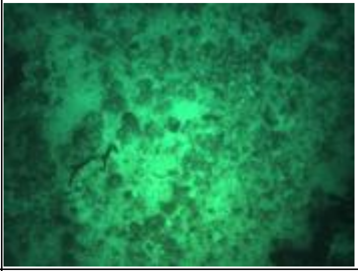
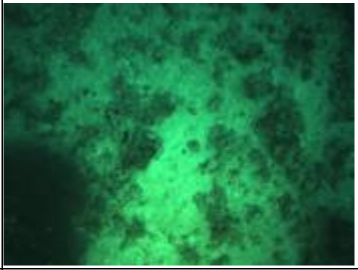
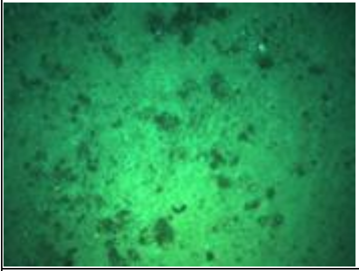
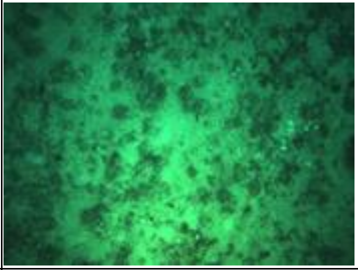
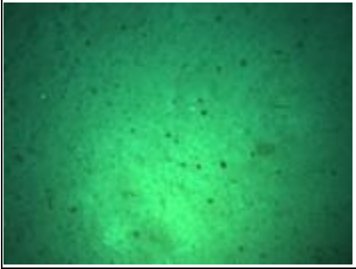
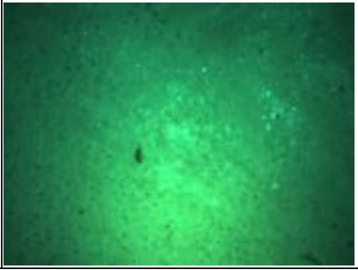
[1.] Coastal Oceans Research and Development – Indian Ocean (CORDIO East Africa). 9 Kibaki Flats P.O. Box 10135-80101, Mombasa, Kenya
[2]. Department of Environment and Geography, University of York, Heslington, York, YO10 5NG, United Kingdom
[3.] National Oceanography Centre, Southampton, SO14 3ZH, United Kingdom
[4.] Scottish Association for Marine Science, Dunbeg, Oban, PA37 1QA, United Kingdom
[5.] Institute of Marine Sciences, Zanzibar, Tanzania

* Corresponding author.
E-mail address: kosuka@cordioea.net; koe503@york.ac.uk (K.E. Osuka).

Table S 1: Locations of SonTek [YSI] CastAway- conductivity temperature depth (CTD) profiles.

Site	Latitude	Longitude	Cast depth (m)
West Misali	-5.2559	39.5779	87
South Misali	-5.2777	39.6021	24
Mkoani	-5.3290	39.6043	23
	-5.3286	39.6080	22
	-5.3195	39.6032	26
	-5.2522	39.5831	23
Tumbatu Shoal	-5.7723	39.1063	69
	-5.7646	39.1079	71
	-5.7643	39.1080	42
	-5.7622	39.1115	64
	-5.7717	39.1078	55

Table S 2: Examples of primary and secondary substratum types identified from autonomous underwater vehicle seabed images from deployment the Greater Pemba Channel.

Primary substratum (≥50%)	Secondary substratum (≥10%)	
Hard (H) 	Hard coarse (Hc) 	Hard sand (Hs) 
Coarse (C) 	Coarse hard (Ch) 	
Sand (S) 	Sand coarse (Sc) 	

Abbreviations: H, 50% seafloor cover by bedrock, boulder, cobbles; h, 10% seafloor cover by bedrock, boulder, cobbles; C, 50% seafloor cover by gravelly sand, granules, pebbles, shells; c, 10% seafloor cover by gravelly sand, granules, pebbles, shells; S, 50% seafloor cover by sand; s, 10% seafloor cover by sand.

Prediction of substrata and benthic community types

1 West Misali

1.1 Hard

Bathymetry affected the probability of occurrence of hard substrata, with increasing probabilities as the water depth reduced reaching 0.9 at 20 m (Figure S1a). Increase in slope increased the probabilities of presence of hard substrata with probabilities of >0.5 at >30° (Figure S1b). Rugosity had a non-linear effect on the occurrence of hard substrata with low probabilities of <0.2 on flat surfaces (Figure S1c).

1.2 Hard sand

Bathymetry affected the probability of occurrence of hard-sandy substrata, with increasing probabilities, as the water depth became shallower reaching 0.6 at 20 m (Figure S1d). Slope had a non-linear effect on the probabilities of presence of hard-sand with generally <0.5 probabilities at < 50° and greater probabilities with increasing slopes (Figure S1e).

Rugosity had a non-linear effect on the occurrence of hard-sand substrata with low probabilities of <0.2 at 0 (Figure S1f).

1.3 Sand

The probability of occurrence of sandy substrata was affected by bathymetry, with greater probabilities of 0.9 in deeper waters (80-140 m) (Figure S1g). From 80 m, probability declined linearly to around 0.1 at 20 m. Acoustic backscatter lowers the probabilities of distribution of sand reducing marginally as backscatter increases (Figure S1h). Slope also lowered the probabilities of presence of sand with probabilities of >0.5 at 0-20° and <0.5 at 20-90° (Figure S1i). Rugosity had a non-linear effect on the occurrence of sandy substrata with higher probabilities of 0.8 on flat surfaces (Figure S1j).

1.4 Sand hard

Bathymetry had a non-linear effect on the occurrence of mixed substrata of sand hard, with greater peak probabilities at depths 70 and 140 m (Figure S1k). Acoustic backscatter lowered the probabilities from around 0.7 when backscatter signal was zero, to about 0.1 at higher backscatter (Figure S1l). Slope of slope affected the probability of presence of sand-hard by marginally increasing it over high slopes (Figure S1m).

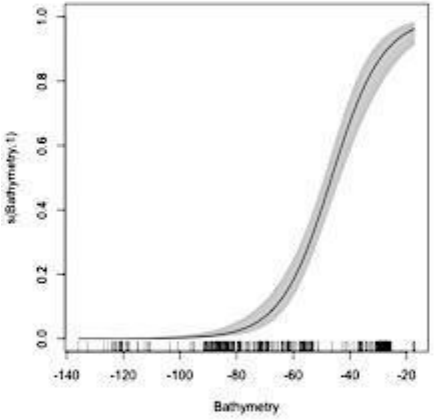
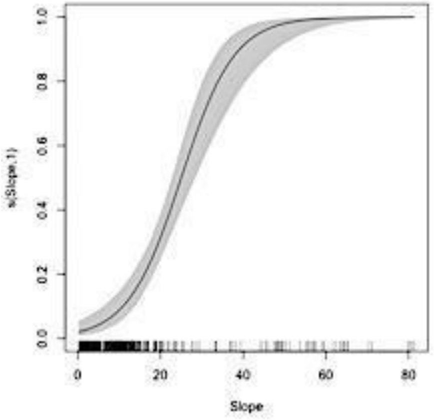
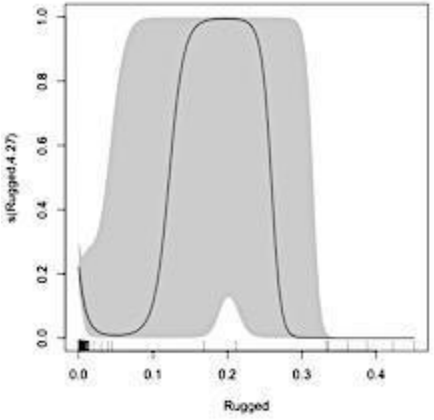
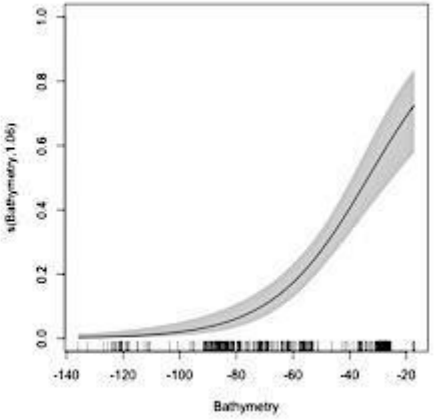
1.5 Sand-coarse

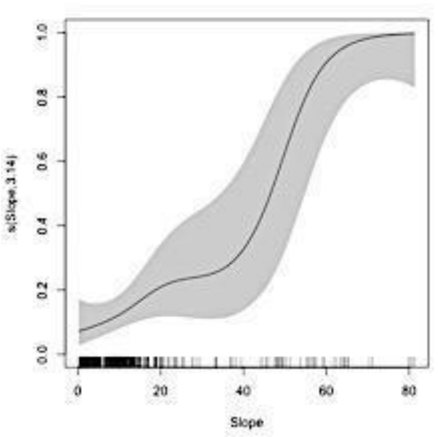
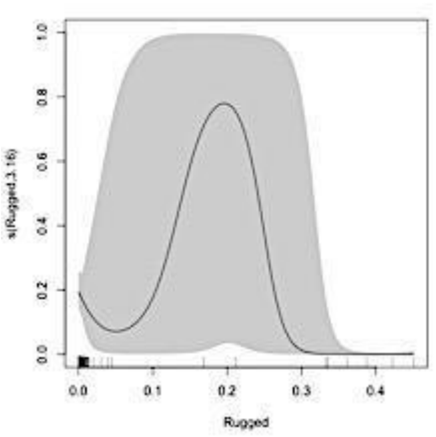
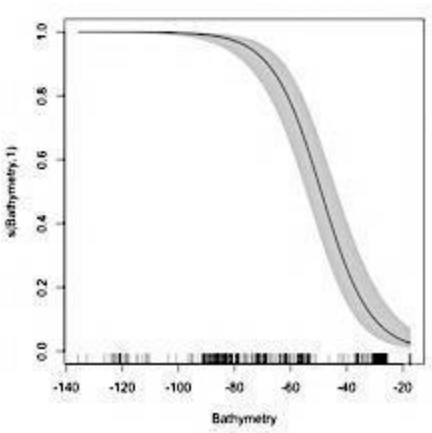
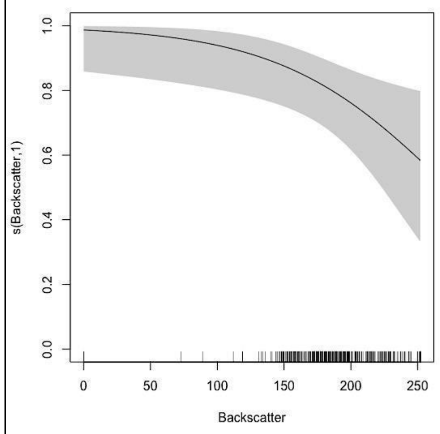
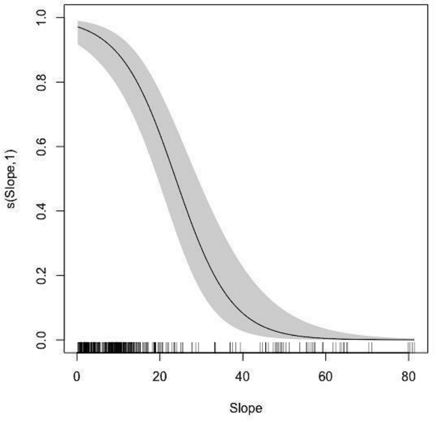
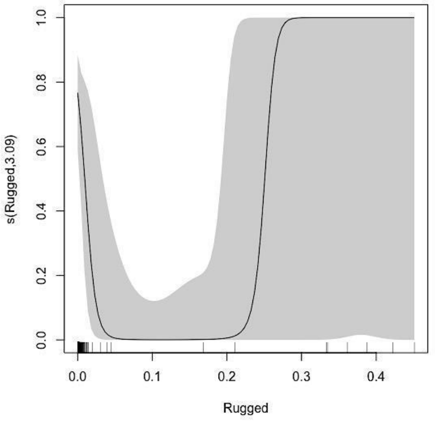
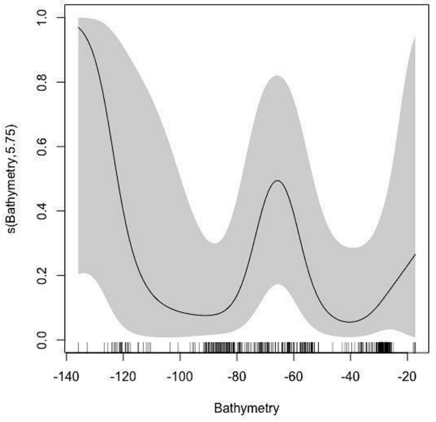
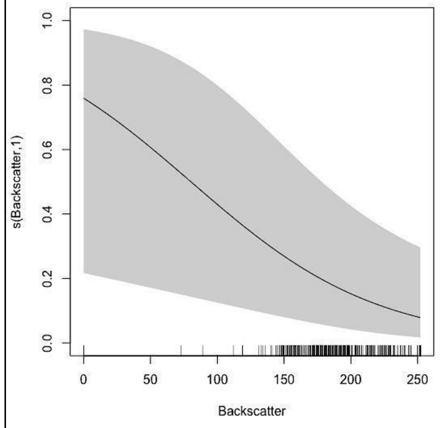
Bathymetry had a non-linear effect on the occurrence of sandy and coarse substrata, with greater probabilities at the depths of 140 m but dramatically reduced to 0.1 at 90 m (Figure S1n). Elevated probabilities of >0.5 were found at 80m.

Table S 3: West Misali site generalised additive logistic model results based on presence-absence of different substrata (hard, sand and mixed substrata), and benthic community types (hard corals, fleshy algae, turf algae, fish), as predicted by Bathymetry, Backscatter, Slope, Slope of slope, Curvature, Aspect and Ruggedness. Only significant predictors are shown. Significance codes: *** < 0.001, ** <0.01, * < 0.05.

Substrata	**Intercept coefficients**				**Significant smoothing terms**		
	Estimate	**se**	**z-value**	**Deviance explained (%)**	**Variable**	**Effective degrees of freedom**	**Chi-square**
Hard	-1.5937	0.2088	-7.634-***	39.7	Bathymetry	1.000	72.198***
					Slope	1.000	41.600***
					Ruggedness	4.266	35.596***
Hard sand	-1.5892	0.1748	-9.09***	22.0	Bathymetry	1.064	40.406***
					Slope	3.141	22.768***
					Ruggedness	3.162	13.839**
Sand	1.3481	0.3381	3.988***	42.0	Bathymetry	1.000	72.294***
					Backscatter	1.000	6.151*
					Slope	1.000	38.757***
					Ruggedness	3.086	16.716**
Sand hard	1.5450	0.7018	-2.202*	18.4	Bathymetry	5.751	30.062***
					Backscatter	1.003	6.938**
					Slope of slope	1.000	3.996*
Sand coarse	-1.4757	0.6007	-2.457*	21.3	Bathymetry	6.847	49.058***
Benthic community							
Hard coral	-1.0959	0.2292	-4.781***	38.2	Bathymetry	5.420	68.820***
					Backscatter	1.000	3.900*
					Slope	1.000	2.901***
Soft coral	-6.880	2.341	-2.939**	42.8	Bathymetry	2.437	11.909**
					Slope of slope	1.000	3.848*
Turf algae	-2.3445	0.4844	-4.84***	20.4	Slope	4.691	12.901*

Fish	0.21751	0.06757	3.219**	5.7	Slope of slope	1.704	6.269**

a	b	c	D
			
e	f	g	h

s(Slope,3.14) 0.0 0.2 0.4 0.6 0.8 1.0 0 20 40 60 80 Slope	s(Rugged,3.16) 0.0 0.2 0.4 0.6 0.8 1.0 0.0 0.1 0.2 0.3 0.4 Rugged	s(Bathymetry,1) 0.0 0.2 0.4 0.6 0.8 1.0 -140 -120 -100 -80 -60 -40 -20 Bathymetry	s(Backscatter,1) 0.0 0.2 0.4 0.6 0.8 1.0 0 50 100 150 200 250 Backscatter
i	j	k	l
s(Slope,1) 0.0 0.2 0.4 0.6 0.8 1.0 0 20 40 60 80 Slope	s(Rugged,3.09) 0.0 0.2 0.4 0.6 0.8 1.0 0.0 0.1 0.2 0.3 0.4 Rugged	s(Bathymetry,5.75) 0.0 0.2 0.4 0.6 0.8 1.0 -140 -120 -100 -80 -60 -40 -20 Bathymetry	s(Backscatter,1) 0.0 0.2 0.4 0.6 0.8 1.0 0 50 100 150 200 250 Backscatter
m	n		

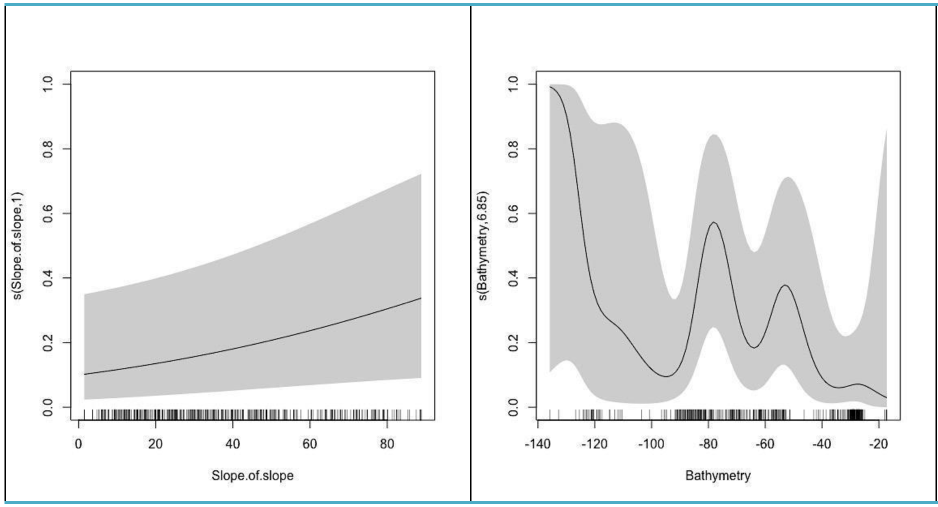


Figure S 1: West Misali GAM plots for significant smoothing terms for hard (a -c), hard sand (d-f), sand (g-j), sand-hard (k-m) and sand coarse (n) substrata.

1.6 Hard coral

Bathymetry had a non-linear effect on the occurrence of hard corals, with greater probabilities of >0.5 between 20m to 60m depth (Figure S2a). Higher probabilities of presence of hard coral were found at higher backscatter signal (Figure S2b). Slope affected presence of reefs, increasing its probability to over 0.5 when slope is >30° (Figure S2c).

1.7 Soft corals

Bathymetry had a non-linear effect on the occurrence of soft coral, however there are greater uncertainties at low and higher depths (Figure S2d). Slope of slope affected the distribution of soft corals, however there were greater uncertainties at higher slopes (Figure S2e).

1.8 Turf algae

Slope had a non-linear effect on the distribution of turf algae, with probabilities of 0.4 at 0°. There was marginal increase in probability reaching 0.1 at 20° (Figure S2f).

1.9 Fish

Slope of slope affected the probability of occurrence of fish, increasing it to just over 0.5 when slope of slope was 0°, to just over 0.7 when slope reached 90° (Figure S2g).

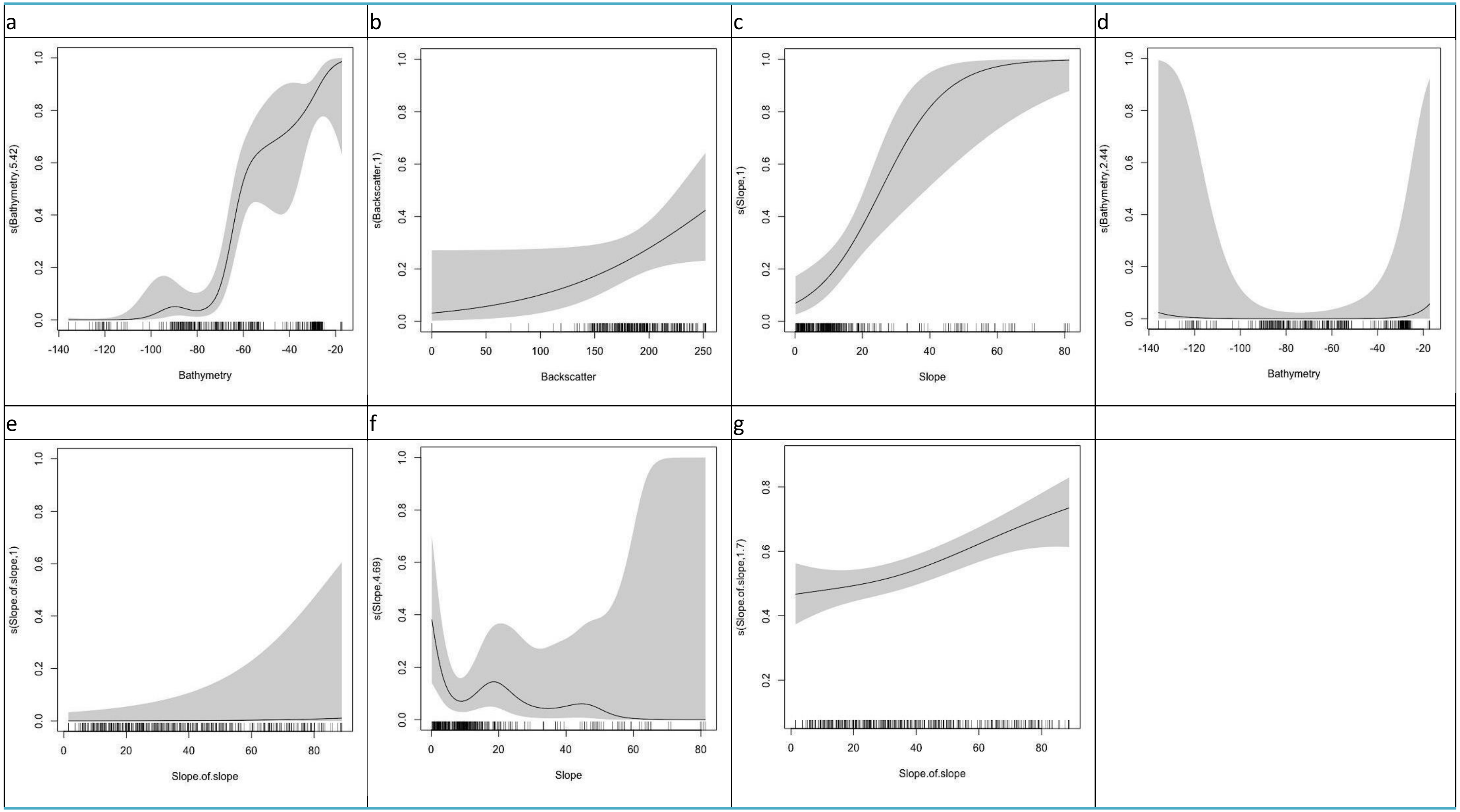


Figure S 2: West Misali GAM plots for significant smoothing terms for hard coral (a-c), soft coral (d-e), turf algae (f) and fish (g).

2 South Misali

2.1 Sand

Bathymetry had a non-linear effect on the occurrence of sandy substrata, with peak probabilities of >0.5 at 21 m (Figure S3a).

2.2 Sand coarse

Bathymetry had a non-linear effect on the occurrence of sand coarse substrata, with increasing probabilities at greater depths >22 m (Figure S3b).

2.3 Sand hard

Bathymetry had a non-linear effect on the occurrence of sand hard substrata, with peak probabilities of 0.7 at 22 m (Figure S3c). Slope affected the distribution of sand hard substrata by increasing probability of occurrence at 2° (Figure S3d).

Table S 4: South Misali generalised additive logistic model results based on presence-absence of different substrata (hard, sand and mixed substrata), and benthic community types (hard corals, fleshy algae, turf algae, fish), as predicted by Bathymetry, Backscatter, Slope, Slope of slope, Curvature, Aspect and Ruggedness. Only significant predictors are shown. Significance codes: *** < 0.001, ** <0.01, * < 0.05.

	Intercept coefficients				**Significant smoothing terms**		
Substrata	**Estimate**	**se**	**z-value**	**Deviance explained (%)**	**Variable**	**Effective degrees of freedom**	**Chi-square**
Sand	-0.750	0.115	-6.544***	13.2	Bathymetry	4.601	51.565***
Sand coarse	-1.032	0.111	-9.266***	8.4	Bathymetry	3.949	23.634***
Sand hard	-0.643	0.107	-6.011***	10.1	Bathymetry	4.258	26.877***
					Slope	3.301	12.245*

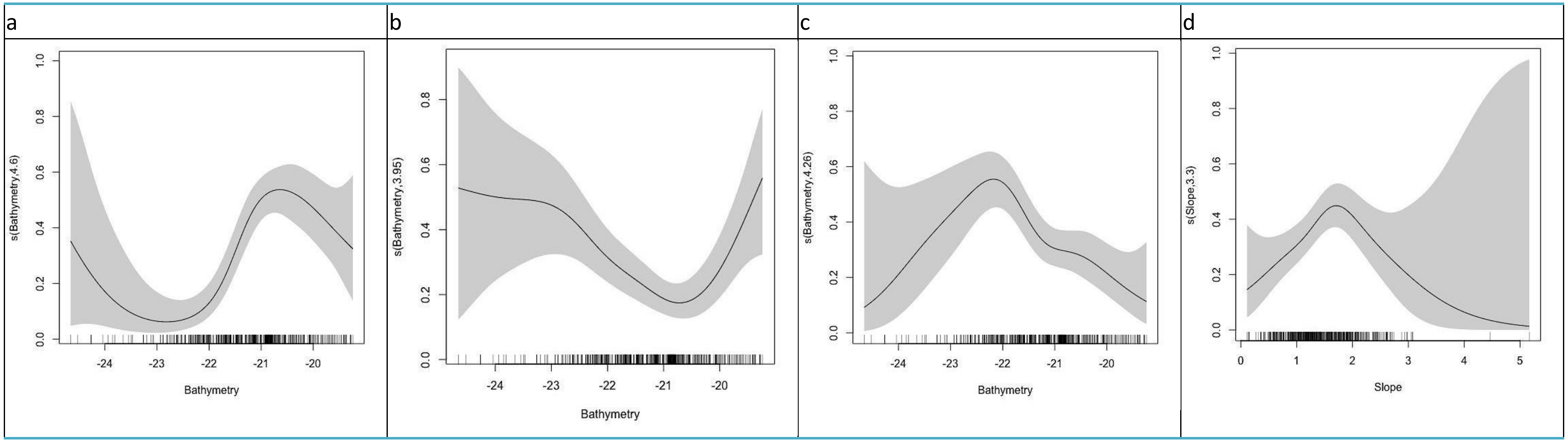


Figure S 3: South Misali GAM plots for significant smoothing terms for sand (a), sand-coarse (b) and sand hard (c-d).

3 Tumbatu Shoal

3.1 Sand

Bathymetry had a non-linear effect on the occurrence of sandy substrata, with greater probabilities of >0.5 at greater depths >55 m and reduced in shallower areas (Figure S4a). Aspect had a non-linear effect on the occurrence of sandy substrata, with higher probabilities of around 0.2 at easterly and westerly aspects (Figure S4b).

3.2 Sand hard

Bathymetry had a non-linear effect on the occurrence of sand hard, with greater probabilities at shallower depths (Figure S4c). Higher probabilities of presence of sand hard were found at higher acoustic backscatter levels (Figure S4d). Slope affected presence of sand hard substrata increasing its probability at higher slopes of 30° (Figure S4e).

3.3 Hard coral

Bathymetry had a non-linear effect on the occurrence of hard coral, with greater probabilities at shallower depths (Figure S5a). Higher probabilities of presence of hard coral were found where backscatter signals were highest (Figure S5b). Slope affected presence of reef increasing its probability at higher slopes of up to 30° (Figure S5c). Curvature affected the probability of occurrence of hard coral, increasing as the surface became concave (Figure S5d).

Table S 5: Tumbatu shoal generalised additive logistic model results based on presence-absence of different substrata (hard, sand and mixed substrata), and benthic community types (hard corals, fleshy algae, turf algae, fish), as predicted by Bathymetry, Backscatter, Slope, Slope of slope, Curvature, Aspect and Ruggedness. Only significant predictors are shown. Significance codes: *** < 0.001, ** <0.01, * < 0.05.

Substrata	**Intercept coefficients**				**Significant smoothing terms**		
	Estimate	**se**	**z-value**	**Deviance explained (%)**	**Variable**	**Effective degrees of freedom**	**Chi-square**
Sand	-1.813	0.403	-4.499***	41.2	Bathymetry	2.696	138.579***
					Aspect	2.610	9.068*
Sand hard	0.802	0.222	3.623***	22.3	Bathymetry	4.182	112.480***
					Backscatter	1.000	5.358*
					Slope	1.000	6.202*
Reef	-0.101	0.274	-0.360	26.0	Bathymetry	6.267	129.084***
					Backscatter	2.175	14.606**
					Slope	2.806	39.023***
					Curvature	2.159	9.487*
Turf algae	-10.737	2.724	-3.942*	36.2	Bathymetry	1.197	21.244***
					Ruggedness	1.000	5.443*

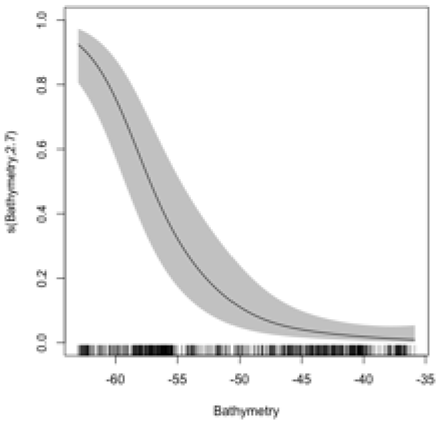
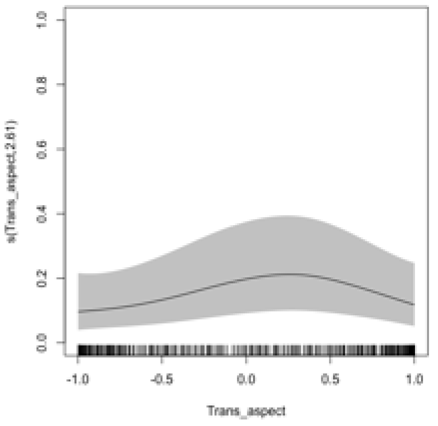
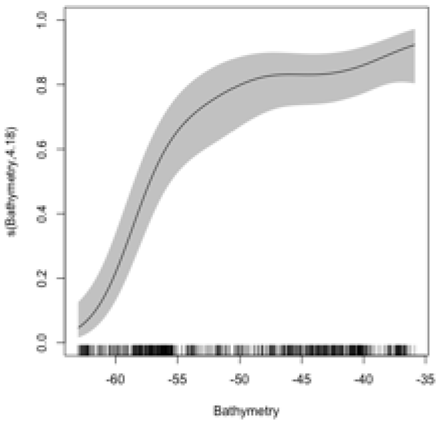
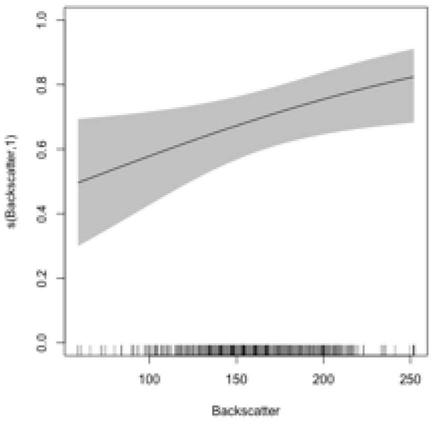
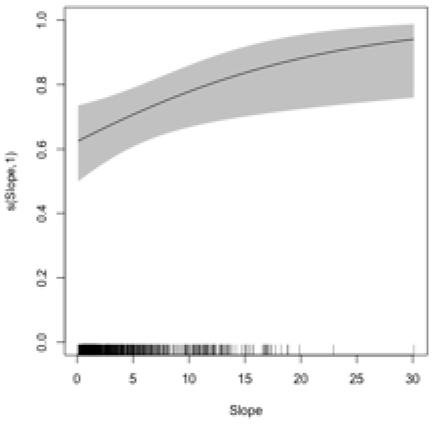
a	b	c	d
s(Bathymetry,2.7) 0.0 0.2 0.4 0.6 0.8 1.0 -60 -55 -50 -45 -40 -35 Bathymetry	s(Trans_aspect,2.61) 0.0 0.2 0.4 0.6 0.8 1.0 -1.0 -0.5 0.0 0.5 1.0 Trans_aspect	s(Bathymetry,4.18) 0.0 0.2 0.4 0.6 0.8 1.0 -60 -55 -50 -45 -40 -35 Bathymetry	s(Backscatter,1) 0.0 0.2 0.4 0.6 0.8 1.0 100 150 200 250 Backscatter
e			
s(Slope,1) 0.0 0.2 0.4 0.6 0.8 1.0 0 5 10 15 20 25 30 Slope			

Figure S 4: Tumbatu Shoal GAM plots for significant smoothing terms for sand (a-b), and sand-hard (c-e) substrata

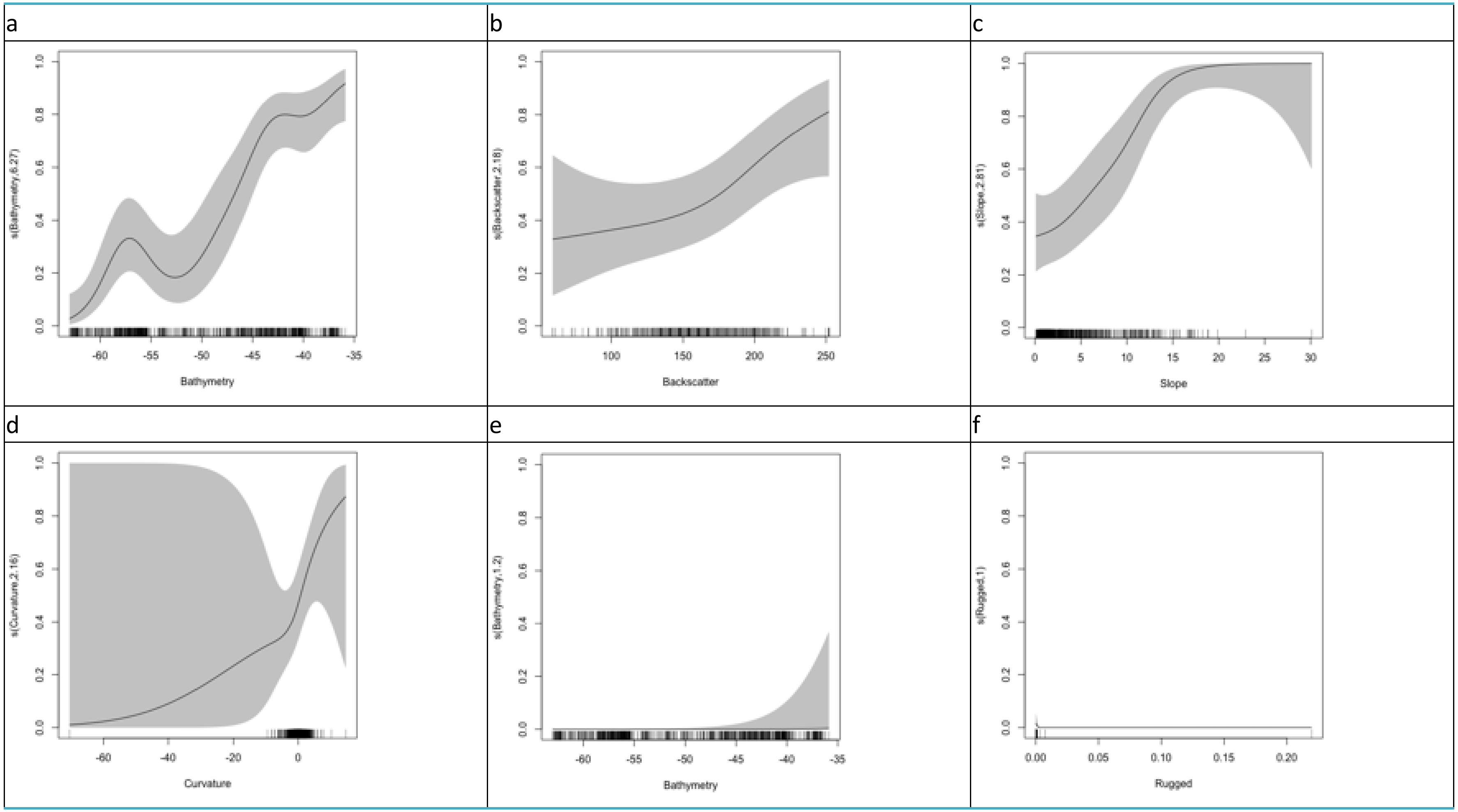


Figure S 5: Tumbatu Shoal GAM plots for significant smoothing terms for hard coral (a -d), and turf algae (e-f)

Chapter 4: Baited remote underwater videos reveal a potential depth refuge for predatory reef fish off Pemba Island, Tanzania

Kennedy E. Osuka[1,2], Bryce Stewart[1], Melita Samoilys[2], Colin McClean[1], Peter Musembi[2], Saleh Yahya[3], Ali Rashid[4], and James Mbugua[2],

Affiliations

[1.] Department of Environment and Geography, University of York, Heslington, York, YO10 5NG, United Kingdom

[2.] Coastal Oceans Research and Development – Indian Ocean (CORDIO East Africa). 9 Kibaki Flats P.O. Box 10135-80101, Mombasa, Kenya

[3.] Institute of Marine Sciences, University of Dar es Salaam, Zanzibar, Tanzania

[4.] Department of Fisheries Development, Zanzibar-Tanzania

Fish community

Nonmetric multidimensional scaling (nMDS) based on Bray–Curtis similarity, was performed on square-root transformed MaxN data to graphically assess patterns in abundance of reef predators across the three sectors (Clarke and Warwick 2001). NMDS revealed overlap in species composition across the three sectors (Figure S1). However, the overlap was greatest between the southern and northern sectors.

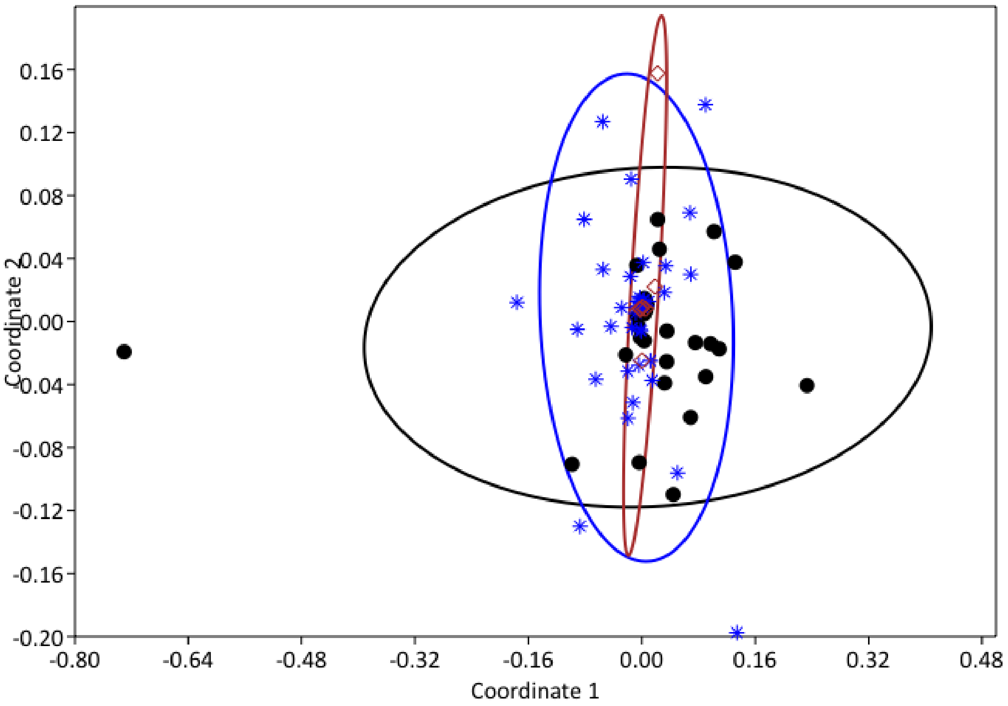


Figure S- 1: Non-metric multidimensional scaling (nMDS) of predator fish population sampled from the outer reefs of Pemba Island using baited remote underwater video (BRUV). North, central and south sectors represented by blue stars, black dots and red diamonds.

Benthic structure

The cover of various benthic variables showed minimal differences between the north and central sectors, but together they differed from the southern sector that had high cover of sand (52%) and fleshy algae (20%) (Figure S2). Hard corals and soft corals averaged 19% and 9% cover respectively in north and central sectors with a 1-2% difference. Overall, sand was dominant in all sectors, although the percent cover was more than half in the southern sector. The cover of rubble was 15%, 10% and 4% in north, central and south sectors respectively.

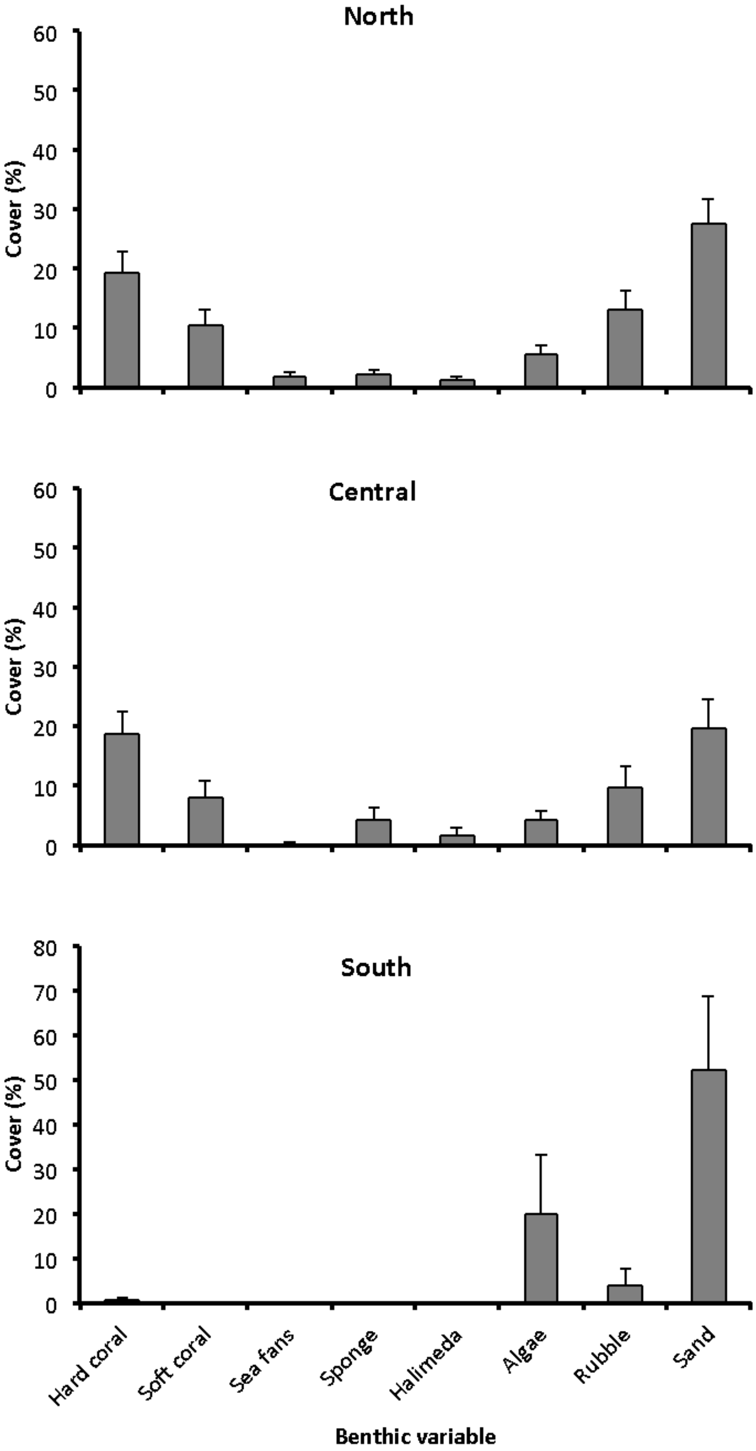


Figure S- 2: Mean cover of benthic variables at three sectors of the Pemba Island assessed from BRUVS. Error bars represent standard error.

Table S 1: Parameter estimates for the zero-inflated poisson model on four groups of fish predator abundance sampled using baited remote underwater videos. Significant codes: '***' = <0.001, '**' = <0.01, '* = <0.05. Hab = habitat type, SA_RU = sand and rubble, Sec = sector. Reference group for Hab was hard coral and soft coral (HC_SC); and Sec was Central.

Group	Count model coefficients			Zero-inflation model coefficients		
	Estimate	Coefficients	S.E	Estimate	Coefficients	S.E
Species richness	Intercept***	1.45	0.12	Intercept***	-2.00	0.58
	Dep**	0.01	0.01	Sec_North	-1.03	1.00
	Hab_SA_RU**	-0.37	0.12	Sec_South	0.63	1.06
All predators	Intercept***	2.26	0.08	Intercept***	-2.61	0.74
	Dep**	0.01	0.01	Sec_North	-0.31	1.04
	Hab_SA_RU***	-0.46	0.08	Sec_South	0.66	1.30
Resident predators	Intercept***	1.75	0.13	Intercept*	-0.92	0.40
	Dep*	0.01	0.01	Sec_North	-0.07	0.55
	Hab_SA_RU***	-0.57	0.14	Sec_South**	2.98	2.63
Transient predators	Intercept***	1.81	0.11	Intercept	-0.46	0.37
	Dep	0.01	0.01	Sec_North*	-1.47	0.61
	Hab_SA_RU	-0.07	0.11	Sec_South	-0.24	0.80

Table S 2: Estimated coefficients of linear and categorical predictors for predator families, pooled predator abundance and species richness with ZIP and their standard errors (S.E.). Significant codes: '***' = <0.001, '**' = <0.01, '* = <0.05. Hab = habitat type, SA_RU = sand and rubble, Sec = sector. Reference group for Hab was hard coral and soft coral (HC_SC); and Sec was Central.

Family	Count model coefficients			Zero-inflation model coefficients		
	Estimate	Coefficients	S.E	Estimate	Coefficients	S.E
Aulostomidae	Intercept	0.16	0.34	Intercept	-9.41	85.60
	Dep*	-0.03	0.02	Sec_North	-3.82	730.89
	Hab_SA_RU	-0.24	0.34	Sec_South	9.89	85.61
Carangidae	Intercept***	0.97	0.23	Intercept*	1.08	0.44
	Dep	-0.00	0.01	Sec_North	-0.81	0.55
	Hab_SA_RU***	1.51	0.23	Sec_South	-0.01	0.93
Carcharhinidae	Intercept	-3.07	3.05	Intercept	-2.14	16.69
	Dep	0.06	0.07	Sec_North	2.48	14.20
	Hab_SA_RU	-11.04	104.26	Sec_South	15.96	2415.07
Congridae	Intercept	-4.25	1.75	Intercept	-6.72	138.33
	Dep	0.05	0.06	Sec_North	5.83	137.87
	Hab_SA_RU	-0.30	1.56	Sec_South	16.27	260.52
Dasyatidae	Intercept*	-5.36	2.18	Intercept	-5.15	63.63
	Dep	0.09	0.07	Sec_North	4.13	62.52
	Hab_SA_RU	-0.81	1.61	Sec_South	16.25	527.61
Haemulidae	Intercept	-8.06	4.50	Intercept*	2.34	1.07
	Dep*	0.40	0.19	Sec_North	-0.69	1.23
	Hab_SA_RU	-1.62	1.35	Sec_South	15.23	3117.04
Fistulariidae	Intercept	0.68	2.12	Intercept	20.28	5769.00
	Dep	-0.03	0.05	Sec_North	-19.34	5769.00
	Hab_SA_RU	-0.22	1.31	Sec_South	0.00	13120.0
Lethrinidae	Intercept	-0.14	0.32	Intercept	-0.11	0.50
	Dep***	0.05	0.01	Sec_North	-0.25	0.60
	Hab_SA_RU	0.05	0.24	Sec_South	1.94	1.19

Family	Count model coefficients			Zero-inflation model coefficients		
	Estimate	Coefficients	S.E	Estimate	Coefficients	S.E
Lutjanidae	Intercept***	2.22	0.15	Intercept	0.33	0.38
	Dep	-0.01	0.01	Sec_North	-0.73	0.51
	Hab_SA_RU***	-0.70	0.17	Sec_South	-0.37	0.82
Muraenidae	Intercept	-0.93	0.56	Intercept	-0.97	1.57
	Dep	0.01	0.02	Sec_North	-1.53	4.12
	Hab_SA_RU	0.08	0.42	Sec_South	16.60	1378.12
Myliobatidae	Intercept	-41.30	544.95	Intercept	1.27	1.15
	Dep	1.88	24.79	Sec_North	18.24	6641.98
	Hab_SA_RU	-49.18	595.77	Sec_South	-13.48	447.35
Scombridae	Intercept***	3.50	0.46	Intercept***	2.11	0.61
	Dep	-0.04	0.04	Sec_North	0.32	0.86
	Hab_SA_RU**	-1.70	0.64	Sec_South	16.41	3877.59
Epinephelidae	Intercept	0.43	0.31	Intercept	-0.97	0.61
	Dep	0.01	0.01	Sec_North	0.46	0.72
	Hab_SA_RU	-0.42	0.29	Sec_South	17.91	1923.57
Sphyraerinidae	Intercept	-11.04	258.38	Intercept	20.09	7551.00
	Dep	-0.06	0.05	Sec_North	-18.13	7551.00
	Hab_SA_RU	12.86	258.38	Sec_South	0.00	12480.00

Table S 3: Estimated coefficients of linear and categorical predictors for predator species that showed significant association with predictor variables together with ZIP and their standard errors (S.E.). Significant codes: '***' = <0.001, '**' = <0.01, '* = <0.05. Hab = habitat type, SA_RU = sand and rubble, Sec = sector. Reference group for Hab was hard coral and soft coral (HC_SC); and Sec was Central.

Species	Count model coefficients			Zero-inflation model coefficients		
	Estimate	Coefficients	S.E	Estimate	Coefficients	S.E
Aulostomous chinensis	Intercept	0.16	0.34	Intercept	-9.36	112.95
	Dep*	-0.04	0.02	Sec_North	-5.29	1276.6
	Hab_SA_RU	-0.19	0.34	Sec_South	10.11	112.95
Caranx melampygus	Intercept***	4.13	0.85	Intercept**	2.37	0.76
	Dep*	-0.17	0.07	Sec_North	0.91	1.26
	Hab_SA_RU	0.19	0.57	Sec_South	16.89	6091.1
Trachinotus blochii	Intercept	-9.42	120.66	Intercept	22.49	22100
	Dep**	0.06	0.02	Sec_North	<-0.01	27700
	Hab_SA_RU	10.42	120.66	Sec_South	-21.39	22100
Lethrinus harak	Intercept	0.43	0.59	Intercept**	2.80	1.05
	Dep	0.01	0.04	Sec_North**	-3.19	1.22
	Hab_SA_RU**	-2.41	0.83	Sec_South	15.17	5797.2
L. rubrioperculatus	Intercept	-9.67	29.34	Intercept*	1.47	0.80
	Dep*	0.04	0.02	Sec_North*	-0.43	0.95
	Hab_SA_RU	9.69	29.34	Sec_South	15.89	2183.3
Aphareus furca	Intercept	0.28	0.45	Intercept**	1.39	0.53
	Dep	-0.01	0.02	Sec_North	-0.39	0.65
	Hab_SA_RU*	0.98	0.46	Sec_South	-1.31	0.88
Aprion virescens	Intercept***	1.35	0.38	Intercept***	2.07	0.62
	Dep	0.01	0.02	Sec_North**	-2.08	0.73
	Hab_SA_RU***	-1.44	0.38	Sec_South	16.33	3994.5

Rastrelliger kanagurta	Intercept***	13.83	2.80	Intercept**	2.20	0.75
	Dep***	-1.00	0.27	Sec_North	1.11	1.26
	Hab_SA_RU***	27.08	8.13	Sec_South	16.89	4972.8