Designing Local-Scale Marine Protected Area Networks in the Central Saudi Arabian Red Sea

Thesis by

Maha T. Khalil

In Partial Fulfillment of the Requirements

For the Degree of

Doctor of Philosophy

King Abdullah University of Science and Technology, Thuwal,

Kingdom of Saudi Arabia

EXAMINATION COMMITTEE APPROVAL FORM

The dissertation/thesis of Maha Khalil is approved by the examination committee.

Committee Chairperson: Dr. Michael Berumen

Committee members: Dr. Xabier Irigoyen
Dr. Marc Genton
Dr. Maria Beger

ABSTRACT

Coral reefs around the world are at risk from overexploitation and climate change, and coral reefs of the Red Sea are no exception. Science-based designation of marine protected areas (MPAs), within which human activities are restricted, has become a popular method for conserving biodiversity, restoring degraded habitats, and replenishing depleted populations. The aim of this project was to explore adaptable methods for designing locally-manageable MPAs for various conservation goals near Thuwal in the central Saudi Arabian Red Sea while allowing human activities to continue. First, the potential for using simple spatial habitat distribution metrics to aid in designing MPAs that are well-connected with larval supply was explored. Results showed that the degree of habitat patchiness may be positively correlated with realized dispersal distances, making it possible to space MPAs further apart in patchier habitats while still maintaining larval connectivity. However, this relationship requires further study and may be informative to MPA design only in the absence of spatially-explicit empirical dispersal data. Next, biological data was collected, and the spatial variation in biomass, trophic structure, biodiversity, and community assemblages on Thuwal reefs was analyzed in order to inform the process of prioritizing reefs for inclusion in MPA networks. Inshore and offshore reef community assemblages were found to be different and indicated relatively degraded inshore habitats. These trends were used to select species and benthic categories that would be important to conserve in a local MPA. The abundances of these “conservation features” were then modeled throughout the study area, and the decision support software “Marxan” was used to design MPA networks in Thuwal that included these features to achieve quantitative objectives. While achieving objectives relevant to fisheries concerns was relatively more challenging, results showed that it is possible to design a local MPA that achieves fisheries and biodiversity goals simultaneously. However, future work should focus on expanding the biological dataset and on acquiring socio-economic data in order to formulate a comprehensive local management plan.

ACKNOWLEDGEMENTS

I would like to express my sincere gratitude to my supervisor Dr. Michael Berumen for funding this project, assisting in the collection of visual survey data, and providing academic and moral support from the start of the project until the very end.

Many thanks go to my committee members: Dr. Xabier Irigoyen, Dr. Marc Genton, and Dr. Maria Beger for their feedback on the project and the dissertation. Prof. Robert Pressey and Dr. Rebecca Weeks contributed to planning parts of the project and gave valuable feedback on early drafts. Dr. Pablo Saenz-Agudelo, Dr. Michael Bode, and the late Dr. Glenn Almany provided data from Papua New Guinea.

Jessica Bouwmeester assisted in the collection of benthic data, provided feedback on parts of the manuscript, and occasionally played music with me, all of which are highly appreciated!

Dr. Peng Zhan and Dr. Gerrit Nanninga provided larval dispersal modeling data, and Dr. Pedro De La Torre provided assistance with MATLAB.

Mr. Syed Omar Pasha (KAUST IT department) repeatedly and very patiently provided technical assistance throughout the years with ArcGIS. Thanks also to Francis Mallon, Phil Allnutt, Perdana Karim, and Camrin Braun for GIS-related assistance.

Norma Serra, Matthew Watts, Virgilio Hermoso, Mara Schmiing, and the Marxan support list provided feedback on preparations for Marxan analyses and/or provided technical assistance with the software. Thanks also to Dr. Ian Ball and the University of Queensland for making Marxan easily and freely available.

I also acknowledge the Red Sea Research Center support staff, particularly Ms. Christine Nelson.

Very special thanks to the late Dr. Temille Porter and to Dr. Todd Pietruszka for invaluable counseling. Special thanks also go to Dr. Joseph DiBattista, Dr. Pablo Saenz-Agudelo, Dr. Elizabeth Tyler, and Prof. Andrea Manica for occasional great advice and moral support.

The following persons, who are dear friends and colleagues, were vital, whether they knew it or not, for my ability to maintain a minimum level of sanity through the PhD journey and emerge a happier person (in no particular order): Jessica Masterman, Ebtihal Shedid, Moshira Hassan, Veronica Chaidez, Marcela Herrera, Julia Spaet, Sarah Al-Mahdali, Jesse Cochran, Jessica Bouwmeester, Emily Giles, Eden Furtak-Cole, Aya Hozumi, Mehreen Mughal, Manalle Al-Salamah, Vanessa Robitzch, Noura Zahran, Marina Costa, Agnese Mancini, Pedro De La Torre, May Roberts, and Remy Gatins.

Thanks also to all the current members and alumni of the Reef Ecology lab.

And to my loving family for tolerating my absence and being supportive.

And thanks to Jorge Cham and the PhD Comics team for reminding me to keep a sense of humor.

Last but not least, this project would not be possible without the generous support of KAUST, KAUST IT, and the KAUST Coastal and Marine Resources Core Lab.

TABLE OF CONTENTS

LIST OF ABBREVIATIONS

FSA: Fish spawning aggregation

GEF: Global Environmental Facility

GIS: Geographic Information Systems

IUCN: International Union for the Conservation of Nature

KAEC: King Abdullah Economic City

KAUST: King Abdullah University of Science and Technology

MPA: Marine Protected Area

NMDS: Non-metric Multidimensional Scaling

PERSGA: Regional Organization for the Conservation of the Environment of the Red Sea and Gulf of Aden

PNG: Papua New Guinea

LIST OF FIGURES

Chapter 1:

Chapter 2:

Chapter 3:

Chapter 4:

Chapter 5:

LIST OF TABLES

Chapter 2:

Chapter 3:

Chapter 4:

CHAPTER 1: GENERAL INTRODUCTION

1.1. Marine Protected Areas as Resource Management Tools

It is well-recognized that marine ecosystems around the world are at risk from overexploitation, pollution, climate change, and other anthropogenic stressors (Hixon et al. 2001; Jackson et al. 2001; Hutchings and Reynolds 2004; Kappel 2005; Lotze et al. 2006). Risks to coral reefs and their supporting ecosystems in particular, such as mangroves and sea grass meadows, have received considerable attention from the scientific community, with predictive models indicating severe declines by the year 2050 (Ellison and Farmsworth 1996; Knowlton 2001; Duarte 2002; Hughes et al. 2003; Bellwood et al. 2004; Bellwood et al. 2006; Hughes et al. 2011).

In the attempt to slow or stop the decline of coral reefs, many governments have adopted different strategies to manage their marine resources in a sustainable manner. Such strategies include various types of restrictions on fishing, tourist activities, coastal development, and different levels of spatial closure of sensitive areas to different kinds of activities. Such marine protected areas (MPAs) have become one of the most popular and highly recommended tools used for managing marine resources to achieve different goals depending on the interests of local stakeholders (Game et al. 2009; McCook et al. 2010).

Many MPAs around the world have been shown to be successful in achieving their intended goals. For example, it has been shown that MPAs have direct benefits to locally exploited marine populations (Roberts and Polunin 1991; Halpern 2003; Halpern et al. 2003; Almany et al. 2007; Planes et al. 2009), rapidly allowing stocks to recover (Halpern and Warner

2002). Examples of MPAs that have achieved varying levels of success can be seen in locations such as Kenya (McClanahan et al. 2007; McClanahan 2011), Chile (Manriquez and Castilla 2001), the Bahamas (Stoffle et al. 2010), Egypt (Samy et al. 2011), and the Philippines (Russ and Alcala 1996), among others (Edgar et al. 2014).

However, only 10-15% of MPAs actually achieve their goals (McClanahan 1999; Mora et al. 2009), and there are many reasons why such a large percentage of them fail. For example, if the objectives of an MPA are not clear, it becomes difficult to design efficiently or assess its success (Halpern 2003). Also, MPAs alone may not be sufficient to increase fish stocks or conserve biodiversity. In the absence of management strategies against external stressors such as pollution, habitat loss, and climate change, the benefits of MPAs are very limited (Allison et al. 1998; Jameson et al. 2002; Jones et al. 2004). Species-specific protection strategies must also be in place to protect highly mobile species (e.g., sharks and many marine mammals), as spatial closure cannot feasibly stretch across their entire home ranges (Hilborn et al. 2004). Moreover, MPAs almost always fail in the absence of support from local communities and/or institutional capacity to enforce and maintain those MPAs (Rudd 2000; Hilborn et al. 2004). Without these important factors, MPAs become merely “paper parks”. If community involvement is absent, MPAs will suffer constantly from illegal activities by fishermen and other reef users, and, in the absence of institutional capacity (as in the Fijian example (Cooke et al. 2000)), communities are not capable of preventing outsiders from exploiting their reefs.

MPAs must also be constantly monitored to evaluate their effectiveness, and they should be altered when necessary (Halpern 2003; McCook et al. 2010). Doing so would also allow us to fill in the knowledge gaps needed to understand exactly how effective different designs of MPAs are in achieving their goals (Jones et al. 2007).

1.2. Marine Resource Management in Saudi Arabia

The Kingdom of Saudi Arabia (Figure 1.1) was founded in 1932 after the unification of its four main regions by the now-ruling family of Saud. From then until the mid-1980s, oil production made up more than 91% of Saudi Arabia’s income. However, as oil resources dwindle, oil production now accounts for about 75% of state revenue. This led to other sectors, for example fisheries (IUCN/UNEP 1988), becoming somewhat more significant sources of income. Fisheries are the primary form of exploitation of marine resources in Saudi Arabia, as international dive tourism is limited and coastal development remains minimal. However, there is a growing interest in internal SCUBA diving and freediving tourism for both locals and expatriates. Moreover, there is a growing interest in cutting-edge scientific research in the Red Sea, which is evident from the sizeable investments in universities such as the King Abdullah University of Science and Technology (KAUST) (Mervis 2009) and organizations such as the Living Oceans Foundation. Thus, the value of marine resources for Saudi Arabia are becoming gradually more recognized.

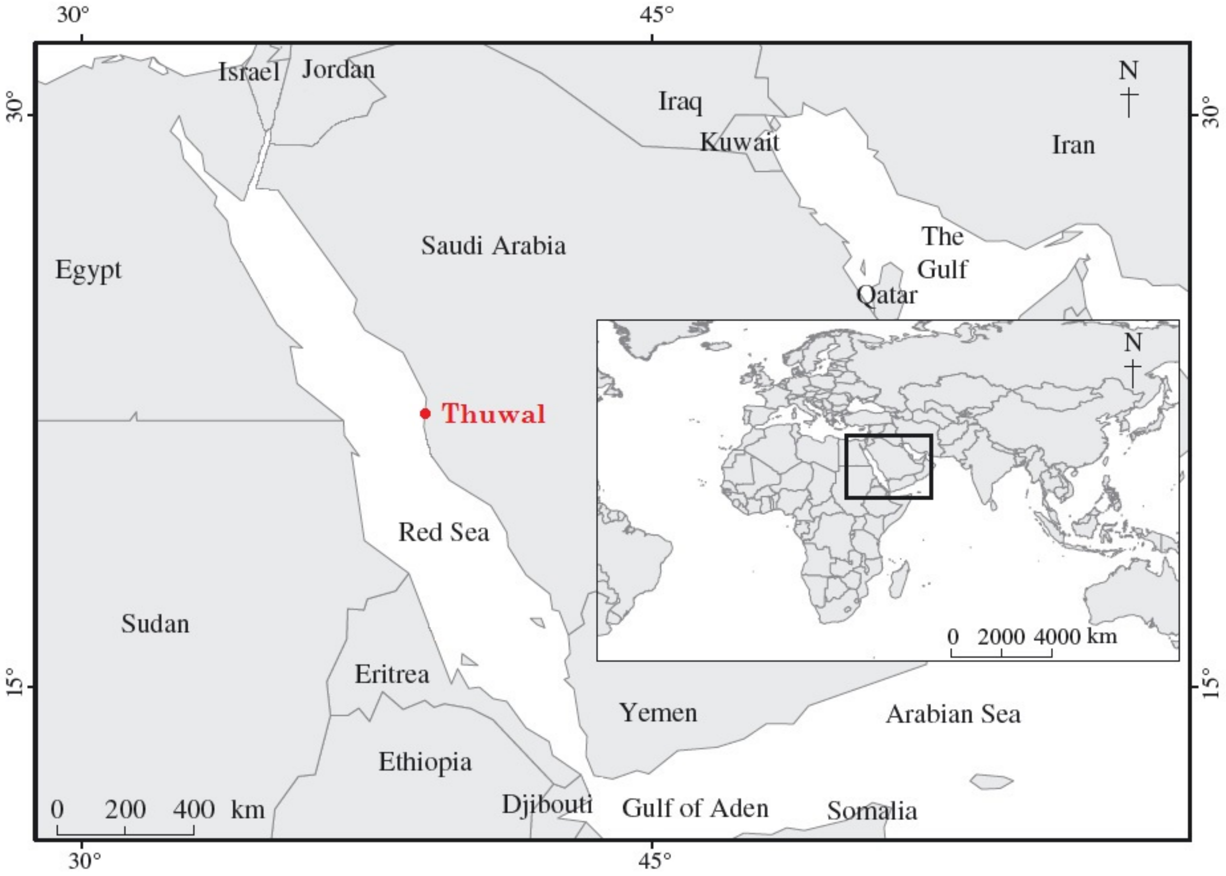


Figure 1.1: Map showing the location of Saudi Arabia and all countries bordering the Red Sea. The location of Thuwal, which is the main study area of this thesis, is shown in red.

There are many reasons to believe that Saudi Arabia is in dire need of a comprehensive plan for managing its marine resources. First, the fisheries of Saudi Arabia are thought to be heavily overexploited (Jin et al. 2012), with significantly reduced populations of large predators such as sharks throughout the country’s waters (Spaet et al. 2012; Spaet 2014; Spaet and Berumen 2015). Also, a bleaching event has reduced coral cover from formerly 60% to 5% on many inshore reefs in the central region down to 10 meters of depth (Furby et al. 2013), and the abundance of herbivorous fishes and large fishes in general is surprisingly low compared to unexploited parts of the Red Sea and the world (Khalil et al. 2013; Kattan 2014). If fish stocks are to recover, and if reefs are to retain adequate resilience to cope with disturbances, science-based, interdisciplinary, and goal-oriented resource management should be established. Such management should take into consideration a comprehensive view of the country's economic and cultural interests.

Overfishing seems to be the most serious threat to Saudi Arabian marine resources, as both tourism and coastal development are, so far, limited (Gladstone 2000). Most (70%) of the landings are from artisanal fishing carried out by nets and hand-lines on small, open, single-engine boats (Jin et al. 2012). However, aquaculture and imports account for the majority of actual seafood consumption within the country (Alruwais and Elhendy 2007). A conservative estimate of the fishing fleet size is minimum 8-10,000 boats, and there is no net economic benefit, while the recommended fleet size for sustainable exploitation is 3,200 boats (Jin et al. 2012). A major challenge (perhaps unique to Saudi Arabia) is presented by the fact that more than half of the fishermen fishing the Saudi Red Sea are of non-Saudi nationalities. Fishermen who are Bengali, Phillippino, Indian, Pakistani, Egyptian, and other nationalities are sponsored by Saudi fleet owners to whom the fishermen pay boat rental fees. A recent "Saudization" movement that was initiated by the Department of Fisheries Management is now requiring fleet owners to hire more Saudi locals (Talal AbuShusha, personal communication), but at present, the situation remains that most of the fishermen are non-local. They work with the aim of accumulating enough savings to return to their home countries as quickly as possible or to continuously send as much money as possible home to their families. Therefore, they are eager to be fishing heavily and diligently all year round (Gladstone 2000). Thus, obtaining the support of expat fishermen to serve the goals of a long-term fisheries management plan may be challenging, while approaching the Saudi fleet owners who sponsor them, as well as the small percentage of local Saudi fishermen who often form exclusive local cooperatives, may be more fruitful.

The Saudi Arabian government has previously been advised to designate up to 46 MPAs, 40 of which were proposed to be in the Red Sea and six in the Arabian Gulf (IUCN/UNEP 1988; McClanahan 1999; PERSGA/GEF 2003). These recommendations were based mostly on large-scale rapid ecological surveys focused on regional trends and patterns, carried out by regional and international organizations such as the Regional Organization for the Conservation of the Environment of the Red Sea and Gulf of Aden (PERSGA), the Global Environmental Facility (GEF), and the International Union for Conservation of Nature (IUCN). Only 2 of the MPAs proposed for the Red Sea were designated on paper and can be found by searching the online MPA Global Database (Wood 2007):

1. The Farasan Islands: Designated in 1996 with an area of 3,310 km^2 (Wood 2007). The area is known for a unique seasonal aggregation of the parrotfish *Hipposcarus harid* (Gladstone 1996). This MPA briefly achieved relative success due to strong community involvement. However, its success was short-lived. Lack of long-term training and awareness programs for the locals and growing commercial fisheries in

the area led to a decline in the effectiveness of the MPA (Gladstone 2000), the status of which, at the moment, hardly surpasses that of a paper park.

2. Um Al-Qamari island: Designated in 1977, with an area of 2 km^2 (Wood 2007). It was designated to protect a resident population of seabirds, and it is not clear whether the protection also extends to the waters surrounding the island or if any enforcement is taking place.

In addition to designated MPAs, Saudi Arabia has officially banned the fishing of sharks (Department of Fisheries 2008). However, little to no enforcement of this ban takes place. Shark fishing occurs on a daily basis, and hundreds of sharks are landed in the Jeddah fish market every week (Spaet 2014; Spaet and Berumen 2015).

1.3. Thesis Objectives

The main aim of this dissertation research is to explore good practices for designing a science-based locally-manageable network of MPAs in the central Saudi Arabian Red Sea. First, I employ a comparative approach to explore the adequacy of using simple and easily-accessible information about spatial habitat distribution in designing small-scale reserve networks that are well-connected by fish larval supply. Then, I describe and analyze the spatial variation in basic ecological variables (e.g. fish biomass, fish and benthic diversity, and benthic cover) and community assemblages on the reefs of Thuwal, a small fishing village in the central Saudi Arabian Red Sea (Figure 1.1). This information is required to provide a scientific basis on which to prioritize local reefs for inclusion in MPA networks. Finally, I make use of a globally popular decision-making software program (Marxan) to optimize reserve network designs for multiple conservation goals and target levels while aiming to minimize the costs of spatial closure. This optimization exercise incorporates the ecological data as well as some basic information on reef use by fishermen and the local dive operator. I also discuss the limitations of the project and the knowledge gaps that should be filled in order to enhance the comprehensiveness of the proposed networks to achieve different goals.

This work provides a model for designing locally-manageable MPAs in the Red Sea using basic biological and spatial information and a free software tool that is useable by reef managers with different scientific and non-scientific backgrounds. It also includes the first application of Marxan in the Arabian region.

References

Agostini VN, Grantham HS, Wilson J, Mangubhai S, Rotinsulu C, Hidayat N, Muljadi A, Muhajir, Mongdong M, Darmawan A, Rumetna L, Erdmann MV, Possingham HP (2012) Achieving fisheries and conservation objectives within marine protected areas: zoning the Raja Ampat network. The Nature Conservancy, Indo-Pacific Division. Report No. 2/12, Denpasar, Indonesia 71 pp

Allison G, Lubchenco J, Carr M (1998) Marine reserves are necessary but not sufficient for marine conservation. Ecological Applications 8:S79-S92

Almany G, Connolly S, Heath D, Hogan J, Jones G, McCook L, Mills M, Pressey R, Williamson D (2009) Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. Coral Reefs 28:339-351

Almany GR, Berumen ML, Thorrold SR, Planes S, Jones GP (2007) Local replenishment of coral reef fish populations in a marine reserve. Science 316:742-744

Alruwais KN, Elhendy AM (2007) Measurement of productivity changes in traditional fishery sector at Red Sea, Saudi Arabia: the Malmquist productivity index approach. Journal of the Saudi Society for Agricultural Sciences 6:87-98

Ban NC, Adams V, Pressey RL, Hicks J (2011) Promise and problems for estimating management costs of marine protected areas. Conservation Letters 4:241-252

Bellwood DR, Hoey AS, Ackerman JL, Depczynski M (2006) Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. Global Change Biology 12:1587-1594

Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. Nature 429:827-833

Berumen M, Almany G, Planes S, Jones G, Thorrold S (2012) Persistence of self-recruitment and patterns of larval connectivity in a marine protected area network. Ecology and Evolution 2:444-452

Bode M, Bode L, Armsworth PR (2006) Larval dispersal reveals regional sources and sinks in the Great Barrier Reef. Marine Ecology Progress Series 308:17-25

Botsford LW, Hastings A, Gaines SD (2001) Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. Ecology Letters 4:144-150

Cooke AJ, Polunin NVC, Moce K (2000) Comparative assessment of stakeholder management in traditional Fijian fishing-grounds. Environmental Conservation 27:291-299

Cowen RK, Lwiza KMM, Sponaugle S, Paris CB, Olson DB (2000) Connectivity of marine populations: open or closed? Science 287:857-859

Cowen RK, Paris CB, Srinivasan A (2006) Scaling of connectivity in marine populations. Science 311:522-527

Cowen RK, Sponaugle S (2009) Larval dispersal and marine population connectivity. Annual Review of Marine Science 1:443-466

Department of Fisheries, Ministry of Agriculture (2008) Protection of sharks. Regulation 50020000, Kingdom of Saudi Arabia

Duarte CM (2002) The future of seagrass meadows. Environmental Conservation 29:192-206

Edgar GJ, Stuart-Smith RD, Willis TJ, Kininmonth S, Baker SC, Banks S, Barrett NS, Becerro MA, Bernard ATF, Berkhout J, Buxton CD, Campbell SJ, Cooper AT, Davey M, Edgar SC, Forsterra G, Galvan DE, Irigoyen AJ, Kushner DJ, Moura R, Parnell PE, Shears NT, Soler G, Strain EMA, Thomson RJ (2014) Global conservation outcomes depend on marine protected areas with five key features. Nature 506:216-220Ellison AM, Farmsworth EI (1996) Anthropogenic disturbance of Caribbean mangrove ecosystems: Past impacts, present trends, and future predictions. Biotropica 28:549-565

Furby KA, Bouwmeester J, Berumen ML (2013) Susceptibility of central Red Sea corals during a major bleaching event. Coral Reefs 32:505-513

Game ET, Grantham HS, Hobday AJ, Pressey RL, Lombard AT, Beckley LE, Gjerde K, Bustamante R, Possingham HP, Richardson AJ (2009) Pelagic protected areas: the missing dimension in ocean conservation. Trends in Ecology & Evolution 24:360-369

Gerlach G, Atema J, Kingsford MJ, Black KP, Miller-Sims V (2007) Smelling home can prevent dispersal of reef fish larvae. Proceedings of the National Academy of Sciences of the United States of America 104:858-863

Gladstone W (1996) Unique annual aggregation of longnose parrotfish (Hipposcarus harid) at Farasan Island (Saudi Arabia, Red Sea). Copeia 1996:483-485

Gladstone W (2000) The ecological and social basis for management of a Red Sea marine-protected area. Ocean & Coastal Management 43:1015-1032

Halpern BS (2003) The impact of marine reserves: Do reserves work and does reserve size matter? Ecological Applications 13:117-137

Halpern BS, Gaines SD, Warner RR (2003) Export of production and the displacement of effort from marine reserves: effects on fisheries and monitoring programs. Oceans 2003 Celebrating the Past Teaming Toward the Future (IEEE Cat No03CH37492)

Halpern BS, Warner RR (2002) Marine reserves have rapid and lasting effects. Ecology Letters 5:361-366

Harrison PL, Babcock RC, Bill GD, Oliver JK, Wallace CC, Willis BL (1984) Mass spawning in tropical reef corals. Science 223:1186-1189

Hastings A, Botsford LW (2003) Comparing designs of marine reserves for fisheries and for biodiversity. Ecological Applications 13:S65-S70

Hilborn R, Stokes K, Maguire J-J, Smith T, Botsford LW, Mangel M, Orensanz J, Parma A, Rice J, Bell J, Cochrane KL, Garcia S, Hall SJ, Kirkwood GP, Sainsbury K, Stefansson G, Walters C (2004) When can marine reserves improve fisheries management? Ocean & Coastal Management 47:197-205

Hixon M, Boersma P, Hunter Jr. M, Micheli F, Norse E, Possingham H, Snelgrove P (2001) Oceans at risk. In: Soulé M, Orians G (eds) Conservation biology: research priorities for the next decade. Island Press, Washington, DC, pp125-154

Hughes T, Bellwood D, Baird A, Brodie J, Bruno J, Pandolfi J (2011) Shifting base-lines, declining coral cover, and the erosion of reef resilience: comment on Sweatman et al. (2011). Coral Reefs 30:653-660

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nystrom M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301:929-933

Hutchings J, Reynolds J (2004) Marine fish population collapses: consequences for recovery and extinction risk. Bioscience 54:297-309

IUCN/UNEP (1988) Coral reefs of the world: Volume 2: Indian Ocea, Red Sea and Gulf. UNEP/IUCN, Gland, Switzerland and Cambridge UK/UNEP, Nairobi, Kenya

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629-637

Jameson SC, Tupper MH, Ridley JM (2002) The three screen doors: can marine “protected” areas be effective? Marine Pollution Bulletin 44:1177-1183

Jin D, Kite-Powell HL, Hoagland P, Solow AR (2012) A bioeconomic analysis of traditional fisheries in the Red Sea off the coast of the Kingdom of Saudi Arabia. Marine Resource Economics 27:137-148

Jones GP, McCormick MI, Srinivasan M, Eagle JV (2004) Coral decline threatens fish biodiversity in marine reserves. Proceedings of the National Academy of Sciences of the United States of America 101:8251-8253

Jones GP, Milicich MJ, Emslie MJ, Lunow C (1999) Self-recruitment in a coral reef fish population. Nature 402:802-804

Jones GP, Planes S, Thorrold SR (2005) Coral reef fish larvae settle close to home. Current biology : CB 15:1314-1318

Jones GP, Srinivasan M, Almany GR (2007) Population connectivity and conservation of marine biodiversity. Oceanography 20:100-111

Kaplan D, Botsford L (2005) Effects of variability in spacing of coastal marine reserves on fisheries yield and sustainability. Canadian Journal of Fisheries and Aquatic Sciences 62:905-912

Kappel C (2005) Losing pieces of the puzzle: Threats to marine, estuarine, and diadromous species. Frontiers in Ecology and the Environment 3:275-282

Khalil M, Cochran JM, Berumen M (2013) The abundance of herbivorous fish on an inshore Red Sea reef following a mass coral bleaching event. Environmental Biology of Fishes 96:1065-1072

Kinlan BP, Gaines SD (2003) Propagule dispersal in marine and terrestrial environments: A community perspective. Ecology 84:2007-2020

Knowlton N (2001) The future of coral reefs. Proceedings of the National Academy of Sciences 98:5419-5425

Levin LA (2006) Recent progress in understanding larval dispersal: new directions and digressions. Integrative and Comparative Biology 46:282-297

Lockwood DR, Hastings A, Botsford LW (2002) The effects of dispersal patterns on marine reserves: Does the tail wag the dog? Theoretical Population Biology 61:297-309

Lomolino MV (1994) An evaluation of alternative strategies for building networks of nature reserves. Biological Conservation 69:243-249

Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG, Kay MC, Kidwell SM, Kirby MX, Peterson CH, Jackson JBC (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312:1806-1809

Manriquez P, Castilla J (2001) Significance of marine protected areas in central Chile as seeding grounds for the gastropod Concholepas concholepas. Mar Ecol Prog Ser 215:201

McClanahan TR (1999) Is there a future for coral reef parks in poor tropical countries? Coral Reefs 18:321-325

McClanahan TR (2011) Coral reef fish communities in management systems with unregulated fishing and small fisheries closures compared with lightly fished reefs – Maldives vs. Kenya. Aquatic Conservation: Marine and Freshwater Ecosystems 21:186-198

McClanahan TR, Graham NAJ, Calnan JM, MacNeil MA (2007) Toward pristine biomass: Reef fish recovery in coral reef marine protected areas in Kenya. Ecological Applications 17:1055-1067

McCook L, Almany G, Berumen M, Day J, Green A, Jones G, Leis J, Planes S, Russ G, Sale P, Thorrold S (2009) Management under uncertainty: guide-lines for incorporating connectivity into the protection of coral reefs. Coral Reefs 28:353-366

McCook LJ, Ayling T, Cappo M, Choat JH, Evans RD, De Freitas DM, Heupel M, Hughes TP, Jones GP, Mapstone B, Marsh H, Mills M, Molloy FJ, Pitcher CR, Pressey RL, Russ GR, Sutton S, Sweatman H, Tobin R, Wachenfeld DR, Williamson DH (2010) Adaptive management of the Great Barrier Reef: A globally significant demonstration of the benefits of networks of marine reserves. Proceedings of the National Academy of Sciences

Mervis J (2009) The big gamble in the Saudi desert. Science 326:354-357

Mora C, Myers RA, Coll M, Libralato S, Pitcher TJ, Sumaila RU, Zeller D, Watson R, Gaston KJ, Worm B (2009) Management Effectiveness of the World's Marine Fisheries. Plos Biology 7

Palumbi SR (2004) Marine reserves and ocean neighborhoods: The spatial scale of marine populations and their management. Annual Review of Environment and Resources 29:31-68

PERSGA/GEF (2003) Coral reefs in the Red Sea and Gulf of Aden: Surveys 1990 to 2000 Summary and recommendations PERSGA Technical Series No 7. PERSGA, Jeddah

Planes S, Jones GP, Thorrold SR (2009) Larval dispersal connects fish populations in a network of marine protected areas. Proceedings of the National Academy of Sciences 106:5693-5697

Roberts CM (1997) Connectivity and management of Caribbean coral reefs. Science 278:1454-1457

Roberts CM, Polunin NVC (1991) Are marine reserves effective in management of reef fisheries? Reviews in Fish Biology and Fisheries 1:65-91

Roberts CM, Reynolds JD, Côté IM, Hawkins JP (2006) Redesigning coral reef conservation. In: Reynolds JD, Côté IM (eds) Coral Reef Conservation. Cambridge University Press, pp515-537

Rudd MA (2000) Live long and prosper: collective action, social capital and social vision. Ecological Economics 34:131-144

Russ G, Alcala A (1996) Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. Marine Ecology Progress Series 132:1-9

Sale PF, Cowen RK, Danilowicz BS, Jones GP, Kritzer JP, Lindeman KC, Planes S, Polunin NVC, Russ GR, Sadovy YJ, Steneck RS (2005) Critical science gaps impede use of no-take fishery reserves. Trends in Ecology & Evolution 20:74-80

Samy M, Sanchez Lizaso JL, Forcada A (2011) Status of marine protected areas in Egypt. Animal Biodiversity and Conservation 34:165-177

Sarkar S, Pressey RL, Faith DP, Margules CR, Fuller T, Stoms DM, Moffett A, Wilson KA, Williams KJ, Williams PH, Andelman S (2006) Biodiversity Conservation Planning Tools: Present Status and Challenges for the Future. Annual Review of Environment and Resources 31:123-159

Shanks AL (2009) Pelagic larval duration and dispersal distance revisited. The Biological Bulletin 216:373-385

Shanks AL, Grantham BA, Carr MH (2003) Propagule dispersal distance and the size and spacing of marine reserves. Ecological Applications 13:S159-S169

Spaet JL (2014) Integrating fisheries dependent and independent approaches to assess fisheries, abundance, diversity, distribution and genetic connectivity of Red Sea elasmobranch populations. PhD Thesis. King Abdullah University of Science and Technology, Saudi Arabia,

Spaet JLY, Berumen ML (2015) Fish market surveys indicate unsustainable elasmobranch fisheries in the Saudi Arabian Red Sea. Fisheries Research 161:356-364

Spaet JLY, Thorrold SR, Berumen ML (2012) A review of elasmobranch research in the Red Sea. Journal of Fish Biology 80:952-965

Stoffle RW, Minnis J, Murphy A, Van Vlack K, O'Meara N, Smith T, McDonald T (2010) Two-MPA Model for Siting a Marine Protected Area: Bahamian Case. Coastal Management 38:501-517

Thorrold SR, Jones GP, Hellberg ME, Burton RS, Swearer SE, Neigel JE, Morgan SG, Warner RR (2002) Quantifying larval retention and connectivity in marine populations with artificial and natural markers. Bulletin of Marine Science 70:291-308

Wood LJ (2007) MPA global: A database of the world's marine protected areas. Sea Around Us Project, UNEP-WCMC & WWF www.mpaglobal.org

Worthen WB (1996) Community composition and nested-subset analyses: Basic descriptors for community ecology. Oikos 76:417-426

CHAPTER 2: CAN SPATIAL HABITAT DISTRIBUTION PREDICT LARVAL DISPERSAL PATTERNS AND INFORM MPA DESIGN?

2.1. Introduction

Marine protected areas (MPAs) that are well-connected with larval supply are pivotal when managing coral reef systems to enhance their long-term persistence (Palumbi 2003; Green et al. 2015). This is based on the idea that MPAs can serve as protected stepping-stones that ensure the supply and survival of adequate proportions of marine larvae; and, thus, appropriate spacing and sizing of MPAs to ensure good connectivity becomes an important consideration (Almany et al. 2009; McCook et al. 2009). However, habitat area suitable for settlement is naturally patchy on many reef systems, and such heterogeneity and patchiness is likely to increase in the future as reef areas experience mortality events and habitat loss through climate change and destructive human activities (e.g., Bell et al. 2001; Howel 2003). A good understanding of the influence of habitat patchiness on larval dispersal patterns is, therefore, valuable for MPA network design but has never been thoroughly explored (D’Aloia et al. 2013). Here, I tackle this problem using a combined modeling and empirical approach to make a preliminary investigation of the relationship between habitat patchiness and larval dispersal and the potential implications of this relationship to MPA design.

In terrestrial ecology, studies that explored whether and how habitat distribution may affect the dispersal patterns of species reported conflicting results (Fahrig 2003). For example, Bowler and Benton (2005) found that the size of a habitat patch and its isolation affected the likelihood of a disperser encountering the edge of the habitat, and thus impacting migration patterns and dispersal success. Habitat patch isolation was found to be negatively correlated with species occupancy, while patch size is positively correlated with the same variable (Hanski and Thomas 1994). Other terrestrial studies, however, found that the sizes of habitat patches and distances between them (habitat clustering) had a complex relationship with dispersal success (e.g., increasing or decreasing search time or the likelihood of encountering a habitat edge) that depended on the scale of clustering and on species-specific parameters, such as dispersal potential and larval behavior (Doak et al. 1992; Cattarino et al. 2013). Others still found no relationships between spatial habitat features and dispersal patterns (Bender et al. 2003) or concluded that, for widely-dispersing species (which would include many marine species, such as corals) and species that are incapable of remotely detecting their target habitat, habitat clustering had little or no impact (Fahrig and Paloheimo 1988; Fahrig 2001; Drew and Eggleston 2006). In marine ecosystems, on the other hand, this work lags far behind terrestrial studies. This is mostly due to the inherent technological and biological challenges associated with studying organisms that reproduce by spawning nearly untraceable larvae in a vast three-dimensional aquatic environment. Nevertheless, considerable effort has been dedicated to studying larval dispersal in marine organisms in order to inform the effective design of MPAs (McCook et al. 2009; Gaines et al. 2010). Relevant studies in coral reef ecosystems, aided by advances in genetics and other technologies, have focused on questions such as: Where do fish larvae go? Is self-recruitment sufficient to replenish protected areas and isolated habitats? Can MPAs replenish unprotected areas via larval export? How far from the source do larvae actually settle (e.g., Almany et al. 2007; Berumen et al. 2012; Harrison et al. 2012; Almany et al. 2013)? However, the relationship between the extent of habitat fragmentation (patchiness) and larval dispersal in marine ecosystem, while acknowledged to be important (e.g., Jones et al. 2007; D'Aloia et al. 2013), remains poorly understood. This chapter is a preliminary exploration of the relationship between habitat patchiness and larval dispersal distances and includes a discussion of how knowledge of spatial habitat distribution may be informative to MPA design.

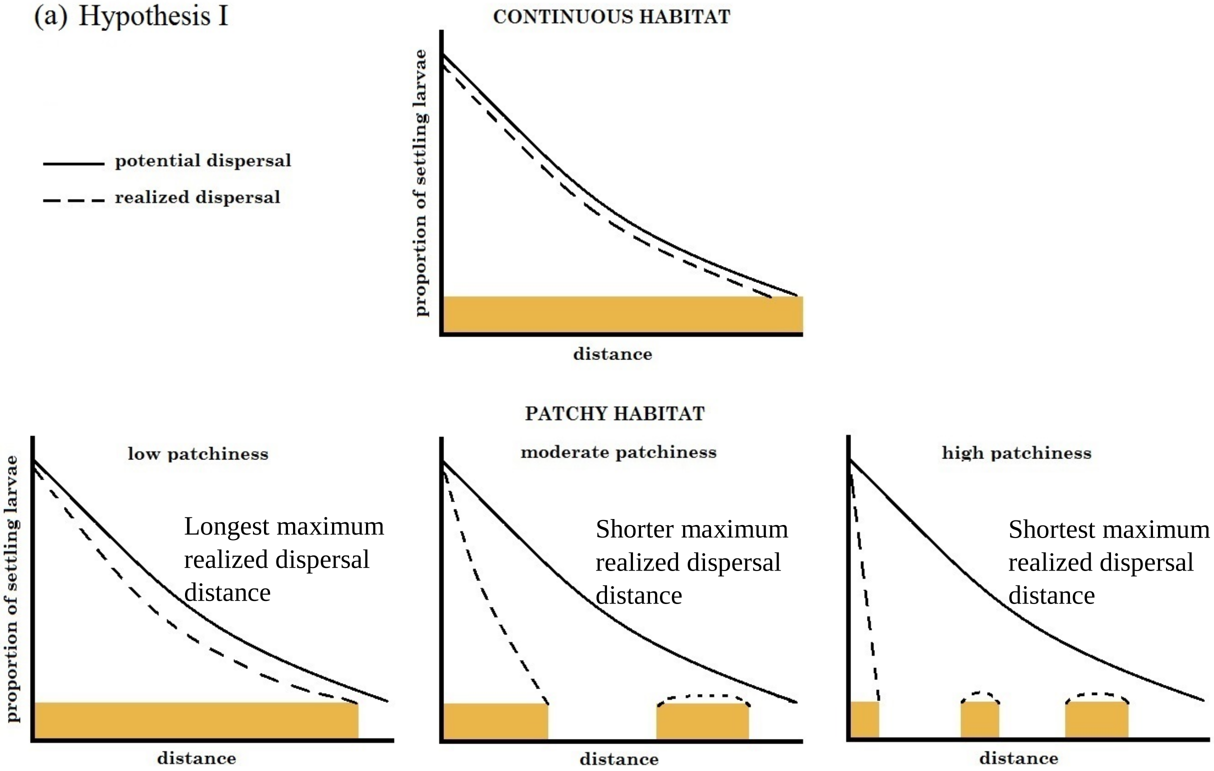
2.2. Conceptual Framework

Here, I define the maximum *potential dispersal distance* as the maximum distance that larvae are hypothetically capable of traveling during their pelagic phase in a given environment based on their inherent energy stores and motility. Potential dispersal distances are usually estimated based on laboratory studies of the pelagic larval phase (e.g., Heyward and Negri 2010). The maximum *realized dispersal distance*, on the other hand, is defined as the actual dispersal distance observed in the same environment and measured or estimated from empirical data (e.g., Almany et al. 2013). The maximum realized dispersal distance is the main focus of this study.

Hypothesis I: Assuming all other variables are equal, if habitat is continuous, then maximum potential and realized dispersal distances would be equal (Jones et al. 2007). Habitat patchiness could thus only *shorten* maximum realized dispersal distances (simply due to habitat unavailability) or have no impact on them. In this scenario, increased habitat patchiness cannot lead to realized dispersal distances being *longer* (Figure 2.1 a). This view assumes that, given the opportunity, a proportion of larvae would always disperse as far as they are inherently capable of dispersing, reaching their maximum potential.

Hypothesis II: Alternatively, in a continuous habitat and assuming all other variables are equal, maximum realized and potential dispersal distances would not be equal. Rather, maximum realized dispersal distances would be much shorter in a continuous habitat, as larvae would attempt to settle as soon as they are competent and as close to their spawning grounds as possible. It has already been shown that fish larvae seem to generally prefer to settle close to home, and that recruitment declines sharply with distance from original spawning grounds (Buston et al. 2012; D’Aloia et al. 2013). By this hypothesis, maximum realized dispersal distances would be expected to be positively correlated with habitat patchiness, as a patchy habitat would “force” some larvae to travel further within the limits of their maximum potential in order to find suitable habitat (Figure 2.1 b).

(a) Hypothesis I



(b) Hypothesis II

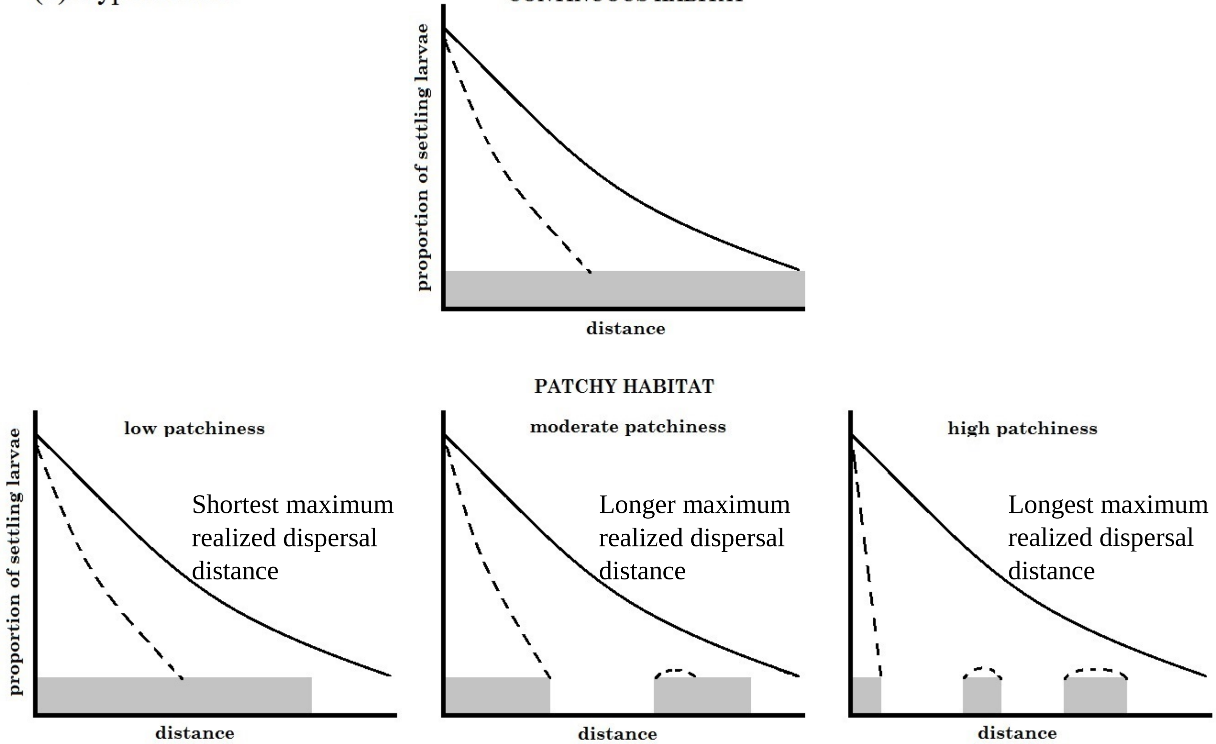


Figure 2.1: An illustration of two hypotheses of the effect of habitat patchiness on realized larval dispersal distances. The top panels in both (a) and (b) demonstrate the relationship between realized and potential dispersal patterns according to two different hypotheses in a continuous habitat. The lower panels demonstrate 3 different scenarios of habitat patchiness and how they would affect realized dispersal. (a) Hypothesis I: Realized dispersal distances strive to reach the maximum potential dispersal distance unless shortened by habitat patchiness; (b) Hypothesis II: If habitat is available, realized dispersal tends to be as short as possible. Thus, under Hypothesis II, habitat patchiness may cause realized dispersal distances to be longer than they would be in a continuous habitat while remaining within the maximum potential limit.

In this chapter, I test how habitat patchiness may be affecting maximum realized dispersal distances. The question is approached using a comparison between three locations for which empirical dispersal data as well as habitat maps are available. The three locations are: Thuwal, in the central Saudi Arabian Red Sea, and Kimbe Bay and Manus Island, both in Papua New Guinea (PNG). I describe the relative habitat patchiness of the three locations, using multiple spatial indices, and then identify whether there may be a relationship between patchiness and maximum realized dispersal distances. If Hypothesis I is true, I expect the longest maximum realized dispersal distances to occur in the location with the least patchy (most continuous) habitat distribution, whereas, if the alternative Hypothesis II is true, the longest realized maximum dispersal distances should occur in the location with the patchiest (least continuous) habitat distribution.

2.3. Methods

2.3.1. Study Sites

In order to test the hypotheses above, three sites within the Indo-Pacific were selected in which a) patchy reef habitat occurs and has been mapped, and b) larval dispersal patterns were studied using empirical data.

Thuwal

The Thuwal area includes 355 patch reefs of varying sizes distributed within an area of about 2200 km^2 along approximately 70 km of central Saudi Arabian Red Sea coastline (Figure 2.2 a). The furthest reef is about 25 km from shore, and the area is close to two large coastal establishments (the King Abdullah University of Science and Technology (KAUST) and the King Abdullah Economic City (KAEC)) as well as a small fishing town called Thuwal (22.28° N, 39.10° E), just south of KAUST. As is common for this region, these reefs are arranged in small clusters, with relatively large, elongated, patches oriented on a north-south axis and surrounded by smaller patches.

Kimbe Bay

The second location includes the west half of Kimbe Bay (150.00° S, -5.60° E), PNG, which is a partially-implemented MPA. This area contains 298 reef patches along approximately 140 km of coastline (Figure 2.2 b).

Manus Island

The third location (Figure 2.2 c) includes reefs along the south coast of Manus Island (2.06° S, 147.00° E), PNG, spanning the waters of (from west to east) Timonai, Tawi, Locha, and Pere, which are artisanal fishing villages with autonomous control of their marine resources. This range covers about 50 km of the island’s coastline. A total of 559 reef patches are found in this area and used in this study.

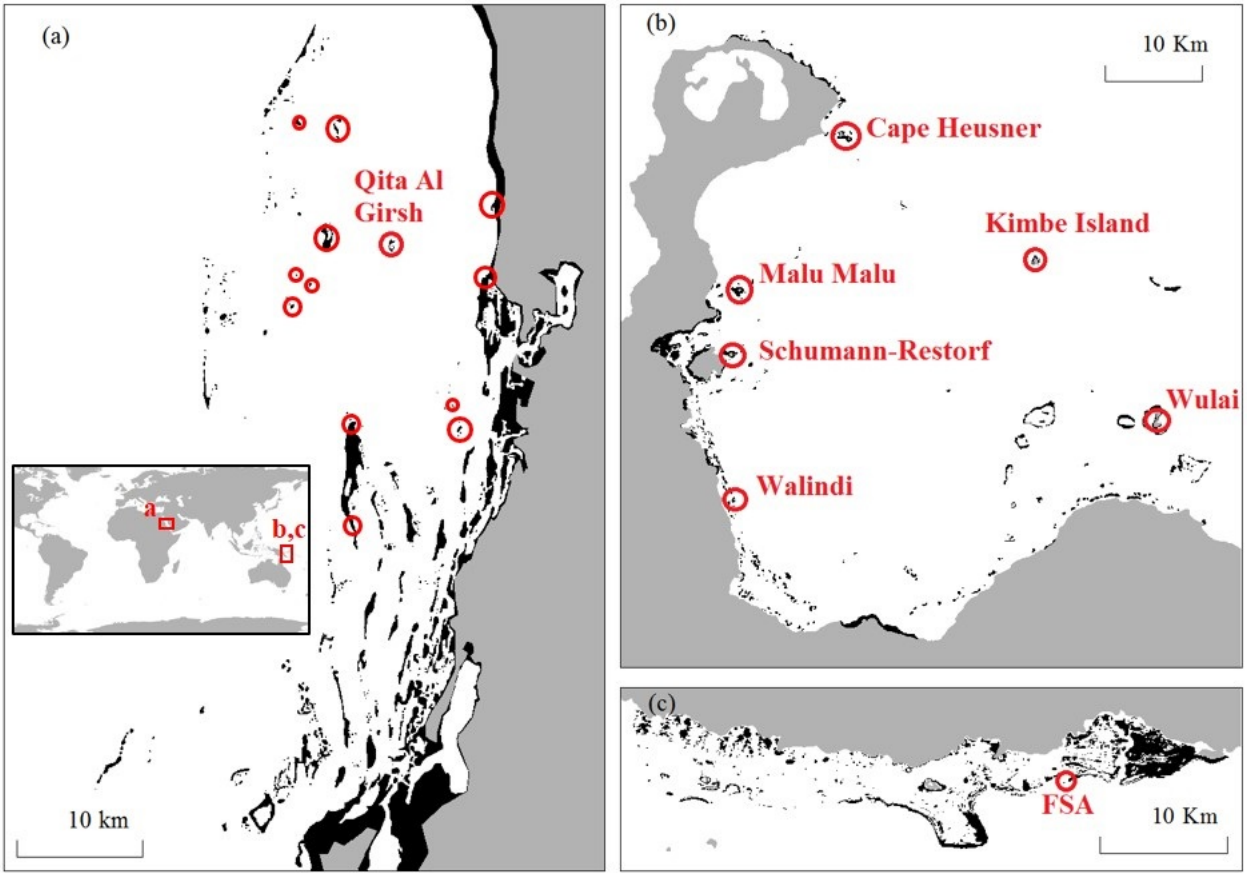


Figure 2.2: Study sites: (a) Thuwal, Saudi Arabian Red Sea; (b) Kimbe Bay, Papua New Guinea (PNG); (c) Manus Island, PNG. Labeled locations mark the sites where adults were sampled for parentage analysis, and FSA stands for fish spawning aggregation. In the case of Kimbe Bay, the labeled locations also mark where juveniles were sampled, and in Thuwal, unlabeled red circles mark locations other than Qita Al Girsh where juveniles were sampled (Nanninga et al. 2015). In Manus Island, juveniles were sampled in many locations along the coast (see Almany et al. 2013).

2.3.2. Spatial Habitat Distribution

Reef habitat is the only habitat type considered in this study, and fragments of reef habitat are referred to as patches or reefs. Patchiness is defined as the degree to which the habitat departs from being continuous, taking into account the sizes (surface areas) of patches as well as the distances between them in each of the study sites. Most patches considered in this study range from having a perimeter of about 120 m to 6000 m, with a few outliers that are much larger. A list of spatial parameters relating to patchiness (potentially affecting the likelihood of a disperser encountering or detecting a habitat edge) was considered in the comparison across the three sites. These parameters were calculated in ArcMap 10.2 (ESRI 2014) and are summarized in Table 2.1.

Table 1.1: A summary of spatial parameters used to compare patchiness across the three study areas, a description of each parameter, mathematical equations where applicable, and an explanation of how each is used to assess patchiness. All parameters were calculated using ArcMap 10.2.

Parameter	Description	Equation (if applicable)	Relevance to patchiness
Patch surface area distribution	Summaries of the sizes of patches in the form of descriptive statistics of reef patch areas.		High proportions of smaller patches indicate more patchiness, while high proportions of large reefs indicate less patchiness.
Patch compactness distribution	Summaries of the compactness of reef patches in the form of descriptive statistics.	$C = p/a$ Where *C* is patch compactness, *p* is perimeter, and *a* is patch area.	High proportions of more compact patches indicate more patchiness, while high proportions of less compact (complex) patches indicate less patchiness.
Clustering	A description of the spatial pattern in which the reef patch matrix is organized. Done by calculating the Average Nearest Neighbor	$ANN = D_O / D_E$ where D_o is the observed mean distance between patches and D_E is the	-1 = Perfectly dispersed spatial distribution (distances between two neighboring patches is always constant, most patchy) 0 = random distribution

	ratio (ANN).	expected mean distance in a random distribution.	1 = highly clustered distribution (least patchy)
Patch proximity	The distribution of the distances between every possible pair of patches.		High proportions of long distances indicate more patchiness, while high proportions of short distances indicate less patchiness.
Proximity of habitat area	The distributions of the total reef areas available within 14 km of any given patch.		High proportions of smaller areas indicate more patchiness, while high proportions of large areas indicate less patchiness
Change in detection zone area as detection radius changes (Figure 2.3)	An analysis of the rate at which the summed total of detection zone areas around all patches changes as a hypothetical detection radius increases. If patches are close enough to each other, detection zone areas will overlap when detection radius is increased, leading to a smaller increase in total detection zone area (Figure	$P_{2r} = (A_{2r} – A_r)/A_r$ where P_{2r} is the change in detection zone area A as the radius is increased from r to $2r$.	An increasing P indicates more patchiness, while a lower or decreasing P indicates less patchiness.

	2.3).

Patch Surface Area Distributions

Using some of the analysis tools available in ArcMap 10.2 (ESRI 2014), the surface areas of reefs were calculated and exported, and the distribution of areas were summarized. Reefs were represented by polygons in vector files that were acquired from various mapping sources for PNG and Saudi Arabia.

Patch Compactness

Approximate patch perimeters represented by polygon perimeters in ArcMap were also exported and summarized for each location. The reef perimeter-to-area ratio was used as a measure of the "compactness" of a patch. A high perimeter-to-area ratio indicates a less compact (long or complex) reef shape, and a high frequency of non-compact reefs within a location potentially indicates higher rates of habitat-edge encounters by dispersing larvae.

Clustering

An Average Nearest Neighbor (ANN) test was performed in ArcMap to determine the degree and pattern of habitat clustering. The ANN index calculates the observed divided by the expected mean Euclidean distance between patches and ranks the distribution of the geometric centers of patches on a scale of -1 to 1, where -1 indicates a perfectly dispersed habitat distribution, zero indicates a random distribution of distances, and 1 indicates a highly clustered and, ordered, distribution (Clark and Evans 1954).

Patch Proximity (distances between patches)

We performed a proximity analysis using the Generate Near Table (GNT) tool to measure the distances between all patches in each location, summarized these distances, and compared them across locations. The GNT tool measures the nearest distance (edge to nearest edge) between each possible pair of patches. Thus, for each location with N number of reefs, there were N × (N – 1) distances. However, I limited the comparison between locations to distances only within a maximum of 45 km. This was to correct for the differences in the total sizes of the study sites.

Proximity of Habitat Area

We also performed another proximity analysis that takes into account the total area of habitat (as opposed to number of patches) found within a 14 km radius of each patch. This was done in order to compare the areas available for settlement in each location within the first few kilometers of any potential source of larval supply. The 14 km radius was chosen based on the results found in Almany et al. (2013) in Manus Island, which showed that 50% of larvae dispersed within this approximate distance (see Dispersal Data below).

Change in Detection Zone Area as Detection Radius Changes

Because larvae have been shown to be capable of remotely detecting reefs using various sensory cues (Tolimieri et al. 2000; Atema et al. 2002; Lecchini et al. 2005; Gerlach et al. 2007), habitat patchiness was explored while taking this into consideration. Using the Buffer tool in ArcMap, a detection zone was created with a radius of 500 m from each reef edge, and its total area was calculated in each location. This was carried out in such a way so that, if the detection zones of two reefs overlapped, their areas would merge into one plane (Figure 2.3). The proportion of increase in the total area of detection zones was then calculated as the radius was increased to 1000, 2000, and 4000 m (Table 2.1). The detection zones of two separate habitat patches would not overlap unless the detection radius is larger than half the distance between their edges. Therefore, when there is no overlap, as in a highly dispersed pattern of habitat distribution, the proportion of increase in detection area would be relatively larger than it would be in the presence of overlap, as in a highly clustered distribution (Figure 2.3). Therefore, the smaller the proportion *P* of increase in detection area in one location, the less patchy (and thus easier to detect) its habitat would be for a disperser that is able to detect habitat from 500, 1000, 2000, or 4000 m away.

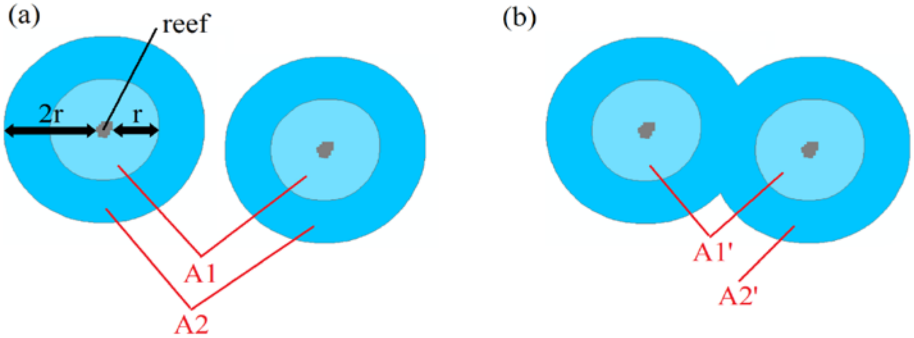


Figure 2.3: A demonstration of how the proportion of increase in habitat detection zone areas is used in this study to compare habitat patchiness across locations. In a widely dispersed (very patchy) habitat distribution, as in (a), the total area *A1* of a detection zone with a radius *r* from the edge of the habitat patches will increase to *A2* if the radius is doubled. There would be no overlap between the detection zones of separate patches, leaving gaps where habitat cannot be detected by dispersing larvae. However, if patches are close enough together, as in (b), the proportion of

increase in the area of the detection zone (from *A1'* to *A2'*) will be smaller, as the detection zones will overlap and merge, leaving fewer gaps in which dispersers are unable to detect habitat (see equation in Table 2.1).

2.3.3. Dispersal Distances

In Thuwal, the model organism used was the two-band anemonefish, *Amphiprion bicinctus*, (Figure 2.4 a) which lays benthic eggs that hatch into larvae with a pelagic larval duration (PLD) of approximately 11 days (Nanninga 2013; Nanninga et al. 2015). One potential source reef within the Thuwal system was thoroughly sampled to create a unique genotype of nearly all adults on the reef. Juveniles were collected throughout the study area, were genotyped, and subsequently were screened against the parent pool to identify parent-offspring relationships (see Nanninga et al. (2015) for full methodology). Using this maximum-likelihood parentage analysis, Nanninga and colleagues assigned only 2 out of 342 sampled recruits to parents on Qita Al Girsh (QG) one of which was self-recruited on the home reef (0.6% self-recruitment). This extremely low self-recruitment is contrary to other studies of anemonefish connectivity, all of which reported between 16-64% self-recruitment (Almany et al. 2007; Planes et al. 2009; Saenz-Agudelo et al. 2011; Berumen et al. 2012). With such low percent assignment of juveniles to parents in QG, it was not possible to accurately estimate dispersal distances for *A. bicinctus* larvae in Thuwal based solely on the empirical data. However, connectivity model simulations matched the empirical data and predicted that most surviving larvae in 2012 and 2013 were located at fringing reefs 8 – 11 km to the east of QG when they reached settlement competency (Nanninga et al. 2015). Unfortunately, none of the recruits sampled on fringing reefs (Figure 2.2 a) were successfully matched to parents on QG, and therefore, it is not possible to comment on recruitment from QG on the fringing reefs. However, for the purpose of this analysis, 11 km was used as the maximum realized dispersal distance for *A. bicinctus* in Thuwal (Table 2.2).

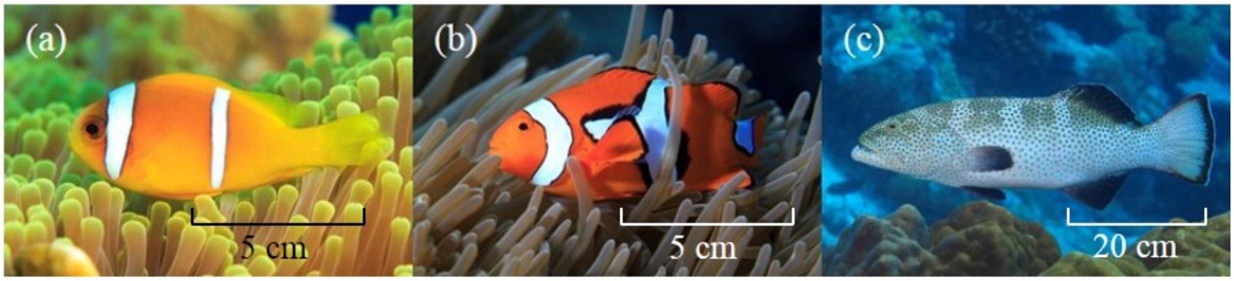


Figure 2.4: The three species included in the study and for which parentage analyses had been carried out. *Amphiprion bicinctus* (a) was studied in Thuwal, Red Sea (Nanninga et al. 2015); *A. percula* (b) was studied in Kimbe Bay, Papua New Guinea (PNG); and the grouper *Plectropomus areolatus* (c) was studied in Manus Island, PNG (Almany et al. 2013). Photos by Tane Sinclair-Taylor.

Another anemonefish species, *Amphiprion percula* (Figure 2.4 b), was extensively studied in Kimbe Bay, PNG, in 2009 and 2011. This species has a comparable PLD to *A. bicinctus* (10 – 13 days) (Almany et al. 2007; Berumen et al. 2012). There was a major effort to sample nearly 100% of adult fish on island reefs within the entire bay. Out of 1447 juveniles screened, 407 (28.1%) were successfully matched to parents within the bay. The best estimates of the potential dispersal distance in 2009 predicted that 50% and 95% of surviving larvae settled within 25.0 and 73.0 km, respectively. In 2011, 50% and 95% of surviving larvae settled within 18.5 and 53.5 km (M Bode, unpublished data). Thus, 53.5 and 73.5 km are used as the maximum realized dispersal distances for *A. percula* in Kimbe Bay (Table 2.2).

In Manus Island, a similar study was conducted using a commercially valuable species of grouper, *Plectropomus areolatus* (Figure 2.4 c). This species is a pelagic spawner and has a PLD of about 4 weeks (2 – 3 times longer than *A. bicinctus* and *A. percula*). Adult aggregate to spawn from April to May at known sites near the island (Almany et al. 2013). Adults were collected at spawning aggregation sites, and juveniles were collected throughout the study area. Out of 782 juveniles sampled, 76 (9.7%) were successfully assigned to parents from the spawning aggregation site. The Ribbens function was used to estimate dispersal distances for *P. areolatus* larvae. It was estimated that 50% and 95% of larvae recruited within 13 and 33 km of the spawning site, respectively, with a mean dispersal distance of 14.4 km. Thus, 33 km was used as the maximum realized dispersal distance for this species in Manus Island (Table 2.2).

Table 2.2: A summary listing the species for which larval dispersal distances were estimated in each location along with their pelagic larval durations (PLDs), the maximum realized dispersal distances estimated, and an indication of whether the estimates were fully validated with empirical genetic data.

Location	Species (PLD in days)	Maximum realized dispersal distance (km)	Empirical validation?
Thuwal	*Amphiprion bicinctus* (11)	11	Incomplete
Kimbe Bay	*A. percula* (10 – 13)	53.5 and 73.5	Yes
Manus Island	*Plectropomus areolatus* (15 – 30)	33	Yes

2.3.4. Hypothesis Testing

The habitat patchiness of the three study sites was ranked on a relative scale from 1 to 3, where 1 = least patchy, 2 = moderately patchy, and 3 = highly patchy. Next, I examined how the available maximum dispersal distance estimates in each location correlate with the rank of patchiness in order to determine if the observations verify either of the hypotheses described (see section 2.2 Conceptual Framework).

2.4. Results

2.4.1. Habitat Distribution

Patch Surface Area Distributions

In all three locations, most habitat patches were smaller than or equal to 0.016 km^2. Manus Island had the largest percentage of reefs within this bin (64%), followed by Thuwal (46%), then by Kimbe Bay (19%). The distribution of patch areas was highly skewed towards smaller patches with a very small number of reefs larger than or equal to 1 km^2 (Figure 2.5). However, Kimbe Bay was the least skewed, having the highest proportion of relatively larger patches.

Patch Compactness

Only Manus Island had the highest proportion of its reefs (12%) with a relatively high perimeter to area ratio (higher than 0.1), indicating that, compared to Thuwal and Kimbe Bay, Manus Island contained the least compact reefs (Figure 2.6). Thuwal and Kimbe Bay reefs, on the other hand, had a skewed distribution towards much lower ratios (more compact reefs), with Thuwal being less skewed (skewness = 0.9) than Kimbe Bay (skewness = 1.4). Thus, Kimbe Bay had the highest proportion of compact reefs.

Clustering

With regards to the spatial pattern of reef patch distribution, the ANN index was largest (most clustered) in Manus Island (0.68), smaller in Thuwal (0.50), and smallest (closest to a random distribution) in Kimbe Bay (0.42). However, all three values were above zero, which indicates a clustered distribution in all three locations with Kimbe Bay being the least clustered and Manus Island being the most clustered.

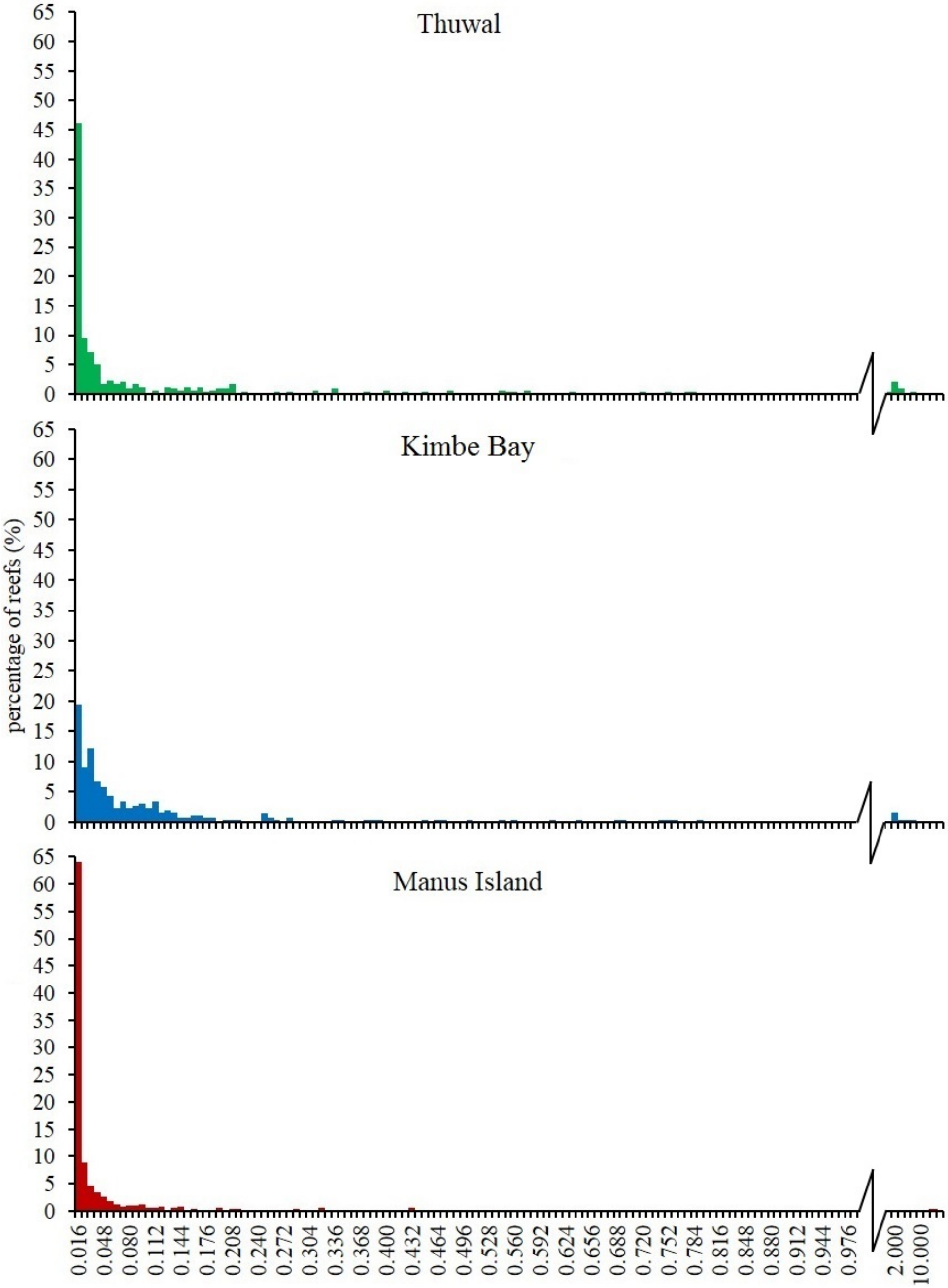


Figure 2.5: The frequency distribution of reef sizes (in km^2) in the three study sites (green = Thuwal, blue = Kimbe Bay, red = Manus Island). In order to correct for differences in the number of reefs in each location, the percentage of reefs is shown on the vertical axis. The break in the horizontal axis indicates a jump to much larger area bins as well as a change in intervals to allow for showing outliers.

Patch Proximity (distances between patches)

Most of the distances between Manus Island reefs ranged from 2 to 5 km, whereas in Thuwal, most distances ranged from 5 to 11 km. On the other hand, in Kimbe Bay, the distribution of distances between reefs was relatively more even with a slight peak within the range of 32 to 37 km (Figure 2.7 a), which further supports a more random distribution of reefs in Kimbe Bay.

Area Available within a Fixed Distance from Patches

Similarly, within a fixed radius of 14 km from any reef patch, Manus Island had larger reef areas (31 – 33 km^2) available more frequently than in Thuwal or Kimbe Bay; Kimbe Bay's most frequently occurring range of available area was considerably smaller (9 – 12 km^2), and Thuwal did not have any comparable peaks, indicating a more even distribution of the amount of area available (Figure 2.7 b).

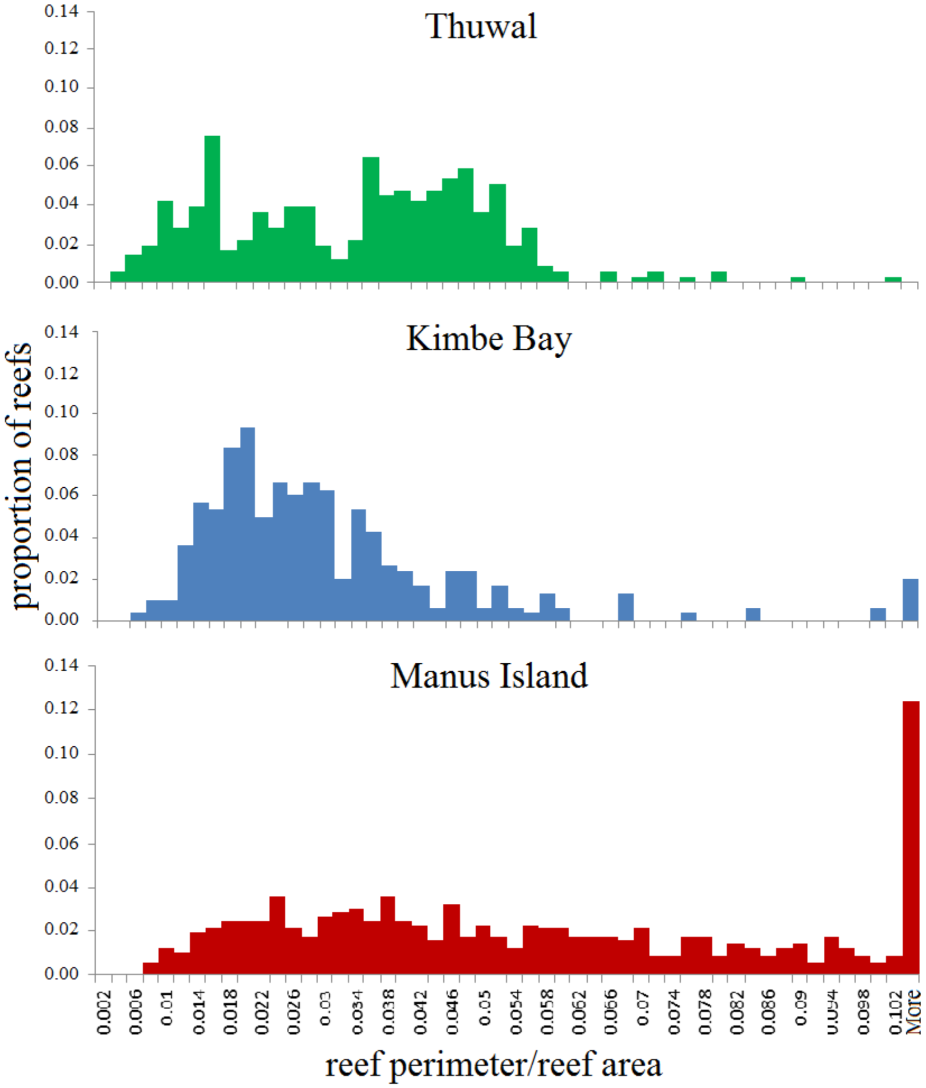
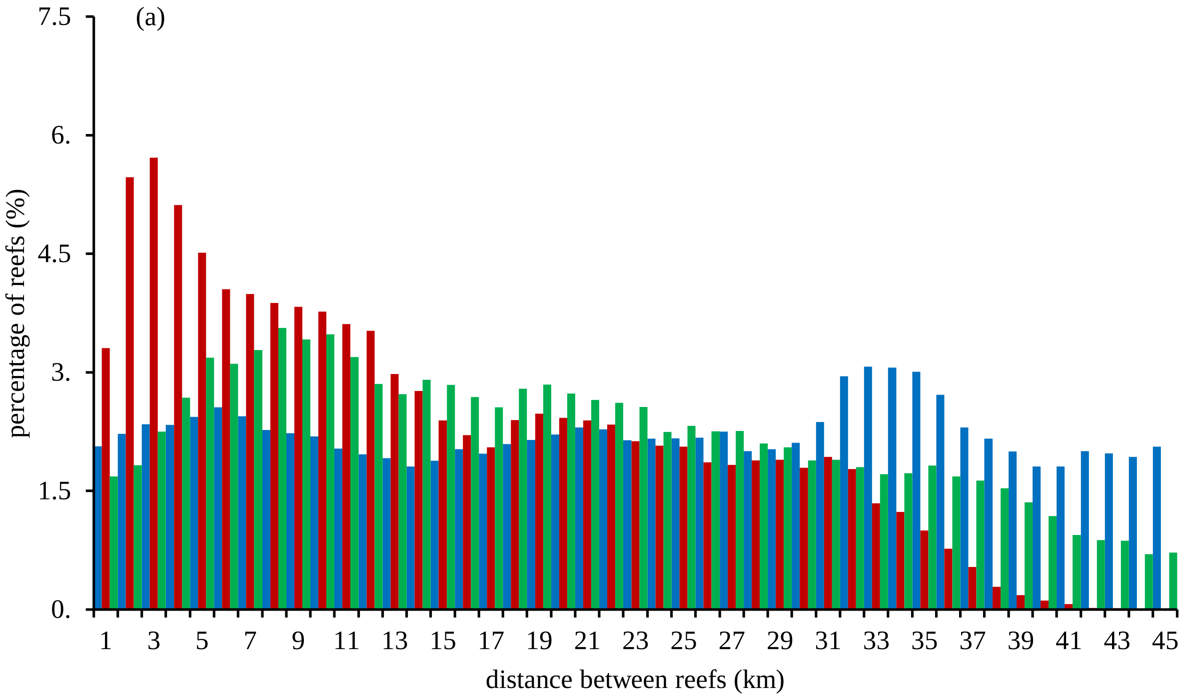


Figure 2.6: Frequency distribution of reef perimeter to area ratios in the three study sites: Thuwal (green), Kimbe Bay (blue), and Manus Island (red). Peaks toward the left of the graph indicate higher proportions of compact reefs, while peaks toward the right of the graph indicate relatively less compact reefs..

Change in Detection Zone Area as Detection Radius Changes When the hypothetical radius of habitat detection by larvae increased from 500 to 1000 m, the total detection areas increased by similar proportions in Thuwal and Kimbe Bay (Figure 2.8). Manus Island, on the other hand, maintained a much smaller proportional increase at all detection radii, indicating more overlap of detection zones in Manus Island. This is due to reef patches being generally much closer together in Manus Island. When the detection radius was increased from 1000 to 2000 m, the proportional increase in Thuwal dropped to an intermediate value between Kimbe Bay and Manus Island, indicating that patches were considerably closer together in Thuwal with this detection radius (Figure 2.8). Therefore, dispersing larvae that can detect habitat from a distance of 1000, 2000, or 4000 m should generally be able to detect habitat at a higher rate in Manus Island than either Thuwal or Kimbe Bay, and if its detection radius is 2000 m, the detection rate would be higher in Thuwal than in Kimbe Bay.



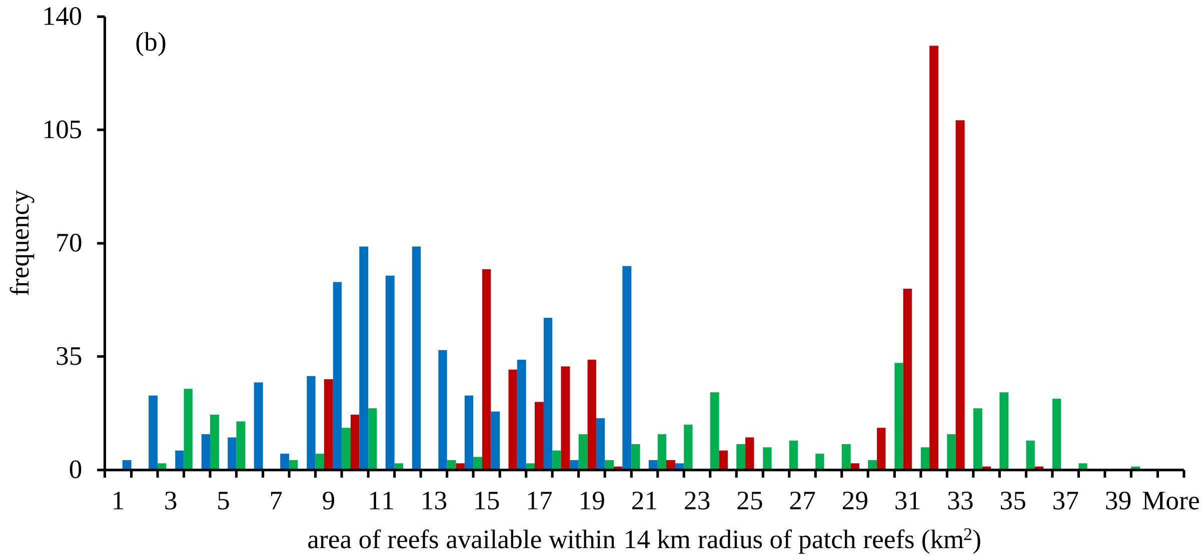


Figure 2.7: Two measures of habitat proximity shown across the three study sites: Thuwal (green), Kimbe Bay (blue), and Manus Island (red): (a) shows the percentage of reefs found at different distance bins from each other. A distribution that is skewed to the left indicates that a higher percentage of reefs are closer to each other, while a flat curve indicates an even distribution of close and far distances; (b) shows the frequency distribution of different area bins found within 14 km of any habitat patch. A peak at higher area bins indicates that large areas of habitat are available more frequently within a distance of 14 km of any patch in that location. The distances in (a) were calculated using the Generate Near Table tool in ArcMap. The areas in (b) were calculated by joining each "near table" produced in (a), according to a unique reef ID number, to a corresponding table in which reef areas were previously calculated. The analysis was then limited to a maximum of 14 km and the frequencies summarized.

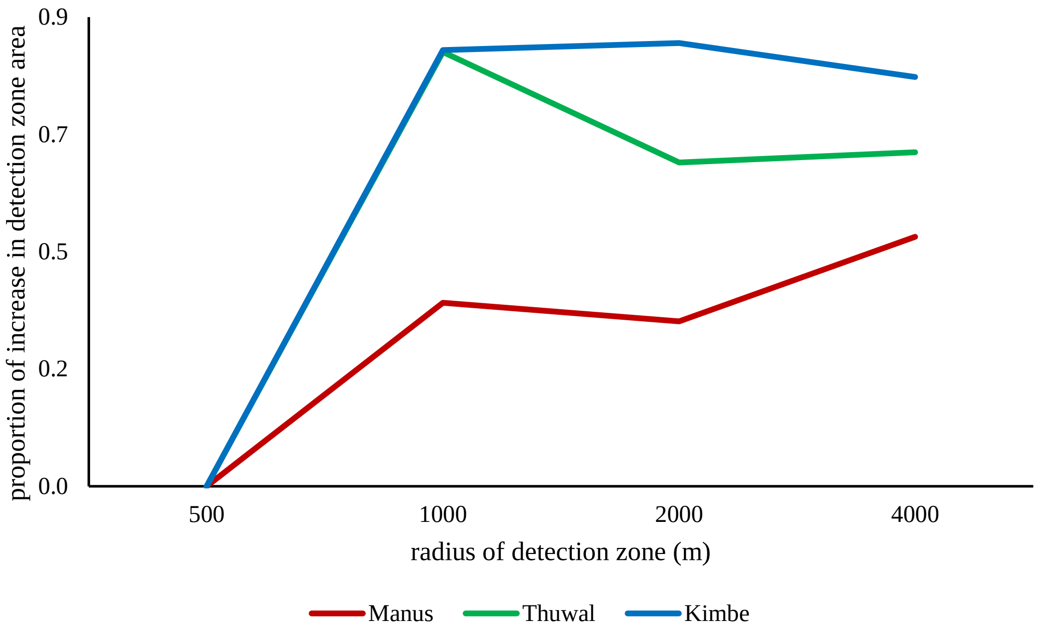


Figure 2.8: The relationship between increasing the radius at which a larva could detect habitat and the proportional increase in the total area of the detection zone in Thuwal (green), Kimbe Bay (blue), and Manus Island (red). A low or decreasing ratio in one location indicates the presence of more overlap between detection zones with an increase in radius, which indicates that habitat patches are closer together at the given location and/or at a given radius. This, in turn, indicates that dispersing larvae would have relatively higher detection rates at locations and radii where the ratio of increase is lower.

2.4.2. Hypothesis Testing

Based on all six spatial distribution parameters described above, Manus Island was ranked as the least patchy site (rank = 1, closest to being continuous), followed by Thuwal (rank = 2), followed by Kimbe Bay as the patchiest habitat (rank = 3, least continuous) (Figure 2.9).

As predicted by Hypothesis II, the location with the most continuous habitat distribution, Manus Island, had a shorter estimated maximum realized dispersal distance (33 km for 95% of *P. areolatus* larvae) than the location with the least continuous habitat, Kimbe Bay, which had the longest estimated maximum dispersal distance (73.5 and 53.5 km for 95% of *A. percula* larvae in 2009 and 2011, respectively). However, Thuwal, which has an intermediate habitat patchiness between Manus Island and Kimbe Bay, did not also have an intermediate maximum realized dispersal distance (8 – 11 km for simulated *A. bicinctus* larvae) (Figure 2.9). Instead, the maximum predicted distance in Thuwal was shorter than that estimated in Manus Island.

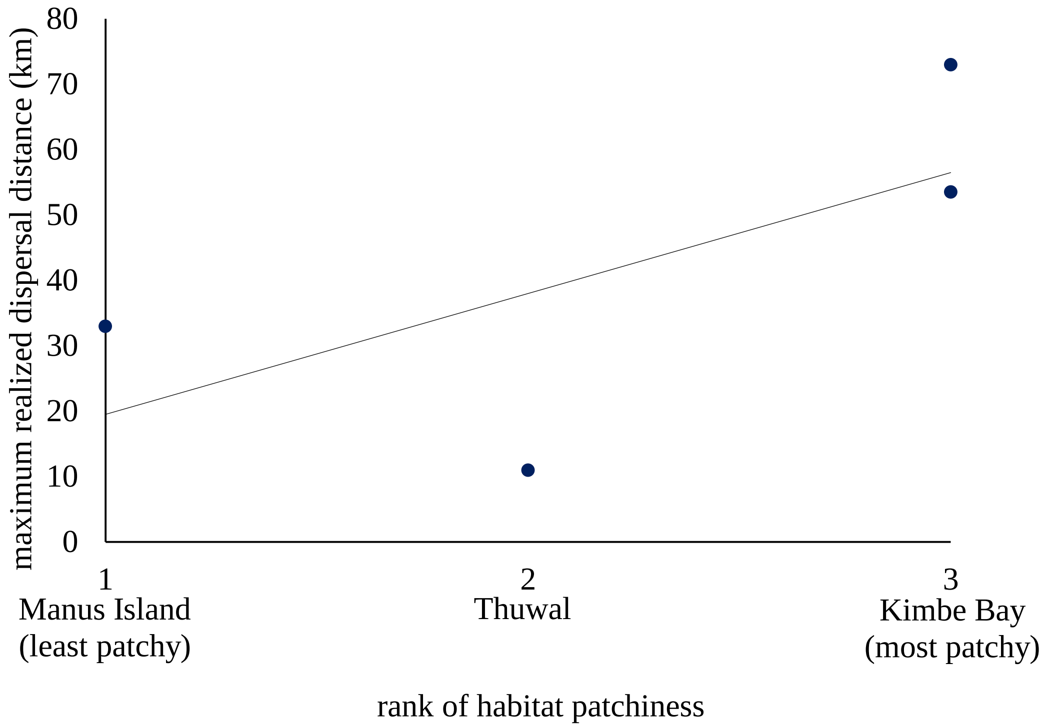


Figure 2.9: An illustration of how the relative degree of patchiness in each of the three study sites relates to the maximum realized dispersal distances estimated for the same locations. The least patchy and the patchiest locations corresponded to the shortest and longest maximum realized dispersal distances, indicating that patchiness might have a positive correlation with realized dispersal distances. However, the location with intermediate patchiness (Thuwal) did not fit the model.

2.5. Discussion

The results of this study point to the relationship between habitat patchiness and larval dispersal distances being more in agreement with Hypothesis II rather than Hypothesis I; it seems more likely that increased habitat patchiness leads to realized dispersal distances being *longer* than they would be in a continuous habitat. The least patchy (Manus Island) and the patchiest (Kimbe Bay) location in this analysis had the shortest and longest maximum realized dispersal distances derived from empirical dispersal data, respectively. However, the dispersal distance predicted by the biophysical model in Thuwal, which had intermediate habitat patchiness, was even shorter than the dispersal estimate in Manus Island, and so, did not fit within this model, which indicates that further study of this relationship is needed to confirm this finding.

Nonetheless, the results offer a preliminary glance at the relationship between habitat patchiness and dispersal, with potential implications to MPA network design. For instance, if the goal of an MPA is the inclusion of the full range of dispersal for a particular species of interest, a single reserve encompassing a potential good source of larvae and large enough to include most of the dispersal range may be adequate in a more continuous habitat, whereas, in a patchy habitat, achieving this goal would require the closure of multiple patches, creating a less compact and more difficult MPA to manage. Moreover, a different tradeoff exists in a scenario where the goal is to increase larval supply to unprotected areas (e.g., for the purpose of enhancing fisheries). In such a scenario, it is generally advised to place multiple, small, MPAs that are far enough apart to allow fishermen to fish between them but still close enough to ensure that larvae from one MPA can reach another (Hastings and Botsford 2003; Jones et al. 2009). If MPAs are too dense, they become difficult to manage and create difficulties for fishermen, and if they are too far apart, they risk being unconnected with larval supply. The findings of this study suggest that: 1) MPAs could be spaced further apart in more patchy habitats while remaining connected, and 2) MPA spacing guidelines should differ from one location to another depending on the degree of habitat patchiness and the species of interest.

It has been previously stated that a pressing issue to address in current larval dispersal research is the influence of factors driving variation in dispersal patterns (including habitat patchiness) by expanding research efforts to multiple locations and species (D'Aloia et al. 2013). The focus thus far in marine connectivity research has been on self-recruitment, where results tend to show higher rates of self-recruitment in isolated habitats (Jones et al. 2009; Berumen et al. 2012; Pinsky 2012). However, it is recognized that this trend is observed due, at least partly, to the increase in the denominator of the self-recruitment fraction in continuous habitats (higher influx of total recruits) (D'Aloia et al. 2013). By focusing on overall dispersal distances rather than self-recruitment, and by including several locations and species, the comparative approach used in this study may be more appropriate for studying the relationship between habitat patchiness and dispersal.

However, while habitat patchiness does appear to have potential implications to dispersal and reserve design, simple spatial parameters alone probably cannot replace empirical dispersal information. It is still essential, whenever possible, to use empirical studies to increase knowledge of the dispersal patterns of species that are important for conservation, as this leads to much more efficient management (e.g., Costello et al. 2010). However, in the absence of empirical data and models (both of which are costly and challenging to produce), spatial habitat distribution parameters may at least provide a general guidance in designing MPAs that have larval connectivity goals.

It is also important to note that there are several uncontrolled variables in this analysis which could have impacted the results. First, the sampling effort for parentage analysis in Thuwal was much smaller than that of Kimbe Bay and Manus Island. This difference in sampling effort and lack of replicate reefs for adult sampling in Thuwal could mean that the variability of dispersal patterns in the Thuwal area was not adequately captured. A larger sampling effort may have led to successful empirical estimates of dispersal rather than the reliance on partially-validated model predictions.

The species considered in this study were also different, and species-specific variables may have played a role in the differences found across locations. Anemonefish are restricted to reefs where anemones are available for settlement, and therefore the density of anemones on reefs within the study area, among other variables, could have impacted recruitment (Buston 2003). A grouper such as *P. areolatus*, on the other hand, may recruit mostly to inner lagoons and reefs with rich coral growth where adequate shelter is available for their style of predation (Froese and Pauly 2014). Also, depending on the environment and the species, mortality in the first few days after settlement may have been very different between the three locations (Almany and Webster 2006). Such aspects of microhabitat availability and post-settlement mortality could have influenced recruitment patterns, and in turn, the results of parentage analyses and the estimations of dispersal kernels. The inclusion of multiple species and locations in this analysis, however, is, in principle, a positive aspect for testing the universality of the relationship between patchiness and dispersal, and one that has been called for in the literature (e.g., D'Aloia et al. 2013). However, a larger number of replicates would make the analysis more robust and allow for more conclusive results. This could be made possible in the future as more empirical estimations of dispersal become available for different species and locations.

Finally, the scale at which habitat patchiness and clustering needs to differ in order to impact dispersal remains to be explored and would depend on a variety of environmental and species-specific factors (e.g., Doak et al. 1992; Cattarino et al. 2013). It is possible, for instance, that the differences in habitat distribution patterns between Thuwal and Manus Island are not significant enough to clearly impact dispersal, but that Kimbe Bay's habitat distribution is significantly different from both other locations. A larger number of comparable studies to be used in such a comparative analysis would make it possible to explore the strength of the correlation between habitat distribution and dispersal patterns, and it could possibly lead to a more quantitative and less relative understanding of the correlation.

2.6. Conclusions

This study suggests that increased habitat patchiness may be causing larvae to travel further than they would in a continuous habitat, leading to longer overall realized dispersal distances. While further exploration of the connection between habitat distribution and dispersal is needed, these results have potential use in guiding simple MPA placement decisions; they indicate that, in patchier habitats, MPAs could potentially be spaced further apart while remaining connected with larval supply. The use of empirical dispersal data whenever possible should remain the first choice for guiding decision-making on the placement of MPAs that aim to achieve larval connectivity. However, in the absence of funds and effort to produce such data or to produce validated models, the use of a combination of simple spatial features of habitat distribution, such as clustering and habitat proximity, may provide a general comparative guide.

References

Almany G, Connolly S, Heath D, Hogan J, Jones G, McCook L, Mills M, Pressey R, Williamson D (2009) Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. Coral Reefs 28:339-351

Almany Glenn R, Hamilton Richard J, Bode M, Matawai M, Potuku T, Saenz-Agudelo P, Planes S, Berumen Michael L, Rhodes Kevin L, Thorrold Simon R, Russ Garry R, Jones Geoffrey P (2013) Dispersal of Grouper Larvae Drives Local Resource Sharing in a Coral Reef Fishery. Current biology : CB 23:626-630

Bell SS, Brooks RA, Robbins BD, Fonseca MS, Hall MO (2001) Faunal response to fragmentation in seagrass habitats: implications for seagrass conservation. Biological Conservation 100:115-123

Berumen M, Almany G, Planes S, Jones G, Thorrold S (2012) Persistence of self-recruitment and patterns of larval connectivity in a marine protected area network. Ecology and Evolution 2:444-452

Buston P (2003) Forcible eviction and prevention of recruitment in the clown anemonefish. Behavioral Ecology 14:576-582

Buston PM, Jones GP, Planes S, Thorrold SR (2012) Probability of successful larval dispersal declines fivefold over 1 km in a coral reef fish. Proceedings of the Royal Society of London B: Biological Sciences 279:1883-1888

Cattarino L, McAlpine C, Rhodes J (2013) The consequences of interactions between dispersal distance and resolution of habitat clustering for dispersal success. Landscape Ecol 28:1321-1334

Costello C, Rassweiler A, Siegel D, De Leo G, Micheli F, Rosenberg A (2010) The value of spatial information in MPA network design. Proceedings of the National Academy of Sciences 107:18294-18299

Doak DF, Marino PC, Kareiva PM (1992) Spatial scale mediates the influence of habitat fragmentation on dispersal success: implications for conservation. Theoretical Population Biology 41:315-336

Drew CA, Eggleston D (2006) Currents, landscape structure, and recruitment success along a passive–active dispersal gradient. Landscape Ecol 21:917-931

Fahrig L (2001) How much habitat is enough? Biological Conservation 100:65-74

Fahrig L, Paloheimo J (1988) Effect of spatial arrangement of habitat patches on local population size. Ecology:468-475

Froese R, Pauly D (2014) Fishbase World Wide Web electronic publication. www.fishbase.org

Gaines SD, White C, Carr MH, Palumbi SR (2010) Designing marine reserve networks for both conservation and fisheries management. Proceedings of the National Academy of Sciences 107:18286-18293

Gerlach G, Atema J, Kingsford MJ, Black KP, Miller-Sims V (2007) Smelling home can prevent dispersal of reef fish larvae. Proceedings of the National Academy of Sciences of the United States of America 104:858-863

Green AL, Maypa AP, Almany GR, Rhodes KL, Weeks R, Abesamis RA, Gleason MG, Mumby PJ, White AT (2015) Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. Biological Reviews 90:1215-1247

Hanski I, Thomas CD (1994) Metapopulation dynamics and conservation: a spatially explicit model applied to butterflies. Biological Conservation 68:167-180

Harrison Hugo B, Williamson David H, Evans Richard D, Almany Glenn R, Thorrold Simon R, Russ Garry R, Feldheim Kevin A, van Herwerden L, Planes S, Srinivasan M, Berumen Michael L, Jones Geoffrey P (2012) Larval Export from Marine Reserves and the Recruitment Benefit for Fish and Fisheries. Current biology : CB 22:1023-1028

Hovel KA (2003) Habitat fragmentation in marine landscapes: relative effects of habitat cover and configuration on juvenile crab survival in California and North Carolina seagrass beds. Biological Conservation 110:401-412

Jones GP, Almany GR, Russ GR, Sale PF, Steneck RS, van Oppen MJH, Willis BL (2009) Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. Coral Reefs 28:307-325

Jones GP, Srinivasan M, Almany GR (2007) Population connectivity and conservation of marine biodiversity. Oceanography 20:100-111

Kaplan D, Botsford L (2005) Effects of variability in spacing of coastal marine reserves on fisheries yield and sustainability. Canadian Journal of Fisheries and Aquatic Sciences 62:905-912

Lecchini D, Planes S, Galzin R (2005) Experimental Assessment of Sensory Modalities of Coral-Reef Fish Larvae in the Recognition of Their Settlement Habitat. Behavioral Ecology and Sociobiology 58:18-26

Lindsay M, Patterson H, Swearer S (2008) Habitat as a surrogate measure of reef fish diversity in the zoning of the Lord Howe Island Marine Park, Australia. Marine Ecology Progress Series 353:265-273

McCook L, Almany G, Berumen M, Day J, Green A, Jones G, Leis J, Planes S, Russ G, Sale P, Thorrold S (2009) Management under uncertainty: guide-lines for incorporating connectivity into the protection of coral reefs. Coral Reefs 28:353-366

Nanninga GB (2013) Merging approaches to explore connectivity in the Anemonefish, Amphiprion bicinctus, along the Saudi Arabian Coast of the Red Sea. King Abdullah University of Science and Technology, p186

Nanninga GB, Saenz-Agudelo P, Zhan P, Hoteit I, Berumen ML (2015) Not finding Nemo: limited reef-scale retention in a coral reef fish. Coral Reefs:1-10

Palumbi S (2003) Population genetics, demographic connectivity, and the design of marine reserves. Ecol Appl 13:S146

Pinsky ML, Palumbi SR, Andréfouët S, Purkis SJ (2012) Open and closed seascapes: Where does habitat patchiness create populations with high fractions of self-recruitment? Ecological Applications 22:1257-1267

Planes S, Jones GP, Thorrold SR (2009) Larval dispersal connects fish populations in a network of marine protected areas. Proceedings of the National Academy of Sciences 106:5693-5697

Richards ZT (2013) A comparison of proxy performance in coral biodiversity monitoring. Coral Reefs 32:287-292

Saenz-Agudelo P, Jones GP, Thorrold SR, Planes S (2009) Estimating connectivity in marine populations: an empirical evaluation of assignment tests and parentage analysis under different gene flow scenarios. Molecular Ecology 18:1765-1776

Saenz-Agudelo P, Jones GP, Thorrold SR, Planes S (2011) Connectivity dominates larval replenishment in a coastal reef fish metapopulation. Proceedings of the Royal Society of London B: Biological Sciences

Sala E, Aburto-Oropeza O, Paredes G, Parra I, Barrera JC, Dayton PK (2002) A general model for designing networks of marine reserves. Science 298:1991-1993

Tolimieri N, Jeffs A, Montgomery JC (2000) Ambient sound as a cue for navigation by the pelagic larvae of reef fishes. Marine Ecology Progress Series 207:219-224

CHAPTER 3: SPATIAL VARIATION OF CORAL REEF COMMUNITIES IN THUWAL

The previous chapter explored the potential for using simple information on spatial habitat distribution in guiding basic decision-making for designing MPAs that aim to achieve larval connectivity goals. It did not take into account any biological or ecological factors that could indicate which reefs may be potential suppliers of larvae. Also, the empirical dispersal results in Thuwal were atypical and less informative than the other two locations considered. Moreover, many MPAs aim to conserve particular species that play important roles in the ecosystem, the maximum number of species possible, or, for instance, a percentage of the available biomass of commercially important species. In order to be able to address any of these goals, there is no substitute for acquiring direct knowledge of the reef communities and describing spatial patterns in factors such as biomass, biodiversity, and community assemblages. In this chapter, I explore and describe some of these spatial patterns on Thuwal reefs in order to provide the necessary information to guide the design of a local network of reserves for several potential goals, which is the subject of the following chapter.

3.1. Introduction

Despite the uniqueness of its environment and the fact that it possesses one of the longest coral reef systems in the world, the Red Sea remains a relatively understudied region of the world with regards to coral reef ecology (Berumen et al. 2013). Detailed information on spatial patterns of fish biomass, fish densities, and benthic and fish community assemblages are available only for some parts of the Red Sea, mostly the Gulf of Aqaba and parts of Egypt (e.g., Bouchon-Navaro and Bouchon 1989; Alwany and Stachowitsch 2007). Saudi Arabia has the largest stretch of Red Sea coastline (approximately 1700 km), and yet there are relatively few publications in coral reef ecology available from the Saudi Arabian Red Sea (Berumen et al. 2013).

Previous ecological information from the Saudi Arabian Red Sea is mostly confined either to reports prepared by collaborating regional and international organizations and published in grey literature (e.g., PERSGA/GEF 2003) or to large-scale studies focused on regional trends and patterns (e.g., Roberts et al. 1992; Price et al. 1998; DeVantier et al. 2000). With the exception of a few recent studies (e.g., Furby et al. 2013), little work was done to characterize reef communities on small, local, scales, which could be used to inform local resource-managers and decision makers (e.g., Green et al. 2009; Almany et al. 2013).

However, recent expansion of research activity in Saudi Arabia (Mervis 2009) has begun to address questions about the functioning of Red Sea reefs at local scales (e.g., Davis et al. 2011; Jessen et al. 2013; van der Merwe et al. 2014). One example is the thermal bleaching event that occurred in summer 2010 (Furby et al. 2013, Pineda et al. 2013), which raised questions about the potential local impact of human activities on reef resilience in the presence of climate change (Khalil et al. 2013). Ongoing research efforts increasingly highlight the need for detailed assessments of local, and regional (e.g., Roberts et al. in review), reef communities.

This study aims to describe the reef communities off the coast of Thuwal by exploring spatial patterns of the biomass, density, and diversity of reef fishes, with focus on important trophic and commercial groups. I also describe the spatial variation in benthic cover and in fish and benthic community assemblages. Finally, potential interpretations are suggested of what the drivers of some of these spatial patterns may be, based on comparisons with other parts of the world and information available in the literature. I expected to find a cross-shore gradient of increasing fish biomass and diversity with distance from shore due to typical environmental gradients in reef topography, depth, sedimentation, food availability, or human impact, which are recurring patterns found in previous studies around the world (e.g., Fabricius 2005; Aguilar-Perera and Appeldoorn 2008; Nemeth and Appeldoorn 2009; Malcolm et al. 2010) I also expected to find clear differences in fish species richness and assemblages along a gradient of live coral cover, richness, and algal cover (Roberts and Ormond 1987; Chabanet et al. 1997; Chong-Seng et al. 2012).

3.2. Methods

3.2.1. Study Site

The Thuwal area includes 355 patch reefs of varying sizes distributed within an area of about 2200 km^2 along approximately 70 km of the central Saudi Arabian coast (Figure 3.1). The furthest reef is about 25 km from shore. The study area also encompasses two large coastal establishments (KAUST and the King Abdullah Economic City (KAEC)) as well as Thuwal itself, which a small fishing town (22.28° N, 39.10° E). The area suffered from a severe bleaching event in summer 2010, which had the highest impact on reefs closest to shore. Inshore reefs lost most of their adult coral cover up to a depth of 10 meters and experienced a change in coral community assemblage (Furby et al. 2013).

We surveyed 9 reefs, three each at three different distances from shore (Figure 3.1). The three offshore reefs (more than 15 km from shore and adjacent to waters deeper than 200 m) were, from north to south, Abu Romah Reef (RR), Shib Nazar (NR), and Abu Madafi Reef (AMR). Midshelf reefs (10 – 14 km from shore and adjacent to waters 50 – 200 m deep) were Al-Fahal Reef (FR), Al-Taweel Reef (TWR), and Abu-Henshan Reef (AHR). Inshore reefs (less than 5 km from shore and surrounded by waters around 20 m deep) were Abu Shosha Reef (ASR), Tahla Reef (TR), and East Fsar Reef (EFR). The reefs are arranged in small clusters, with relatively large elongated reef patches oriented on a north-south axis surrounded by smaller patches. All study reefs have relatively steep walls dropping down to 20 m or deeper and shallow reef tops, with the exception of inshore reefs which drop to a sloping seabed at 10 – 15 m (Sheppard et al., 1992).

3.2.2. Fish and Benthic Surveys

Surveys were conducted in May 2013 at two depths (10 m and between 1 – 3 m (on the reef crest)) at each of the 9 reefs. All transects were located on the west sides of the reefs, exposed to prevailing winds, currents, and waves. Fish surveys were conducted along three 25 m transects at each depth (a total of 6 transects per reef), where a diver swam along the transects twice; first to record larger (> 18 cm) vagile fish in 25 x 8 m belts (while simultaneously laying out the transect tape), and a second time, swimming in the opposite direction, to record smaller (< 18 cm), less mobile fish in 25 x 4 m belts. This method was chosen following Sandin et al. (2008) in order to allow for comparability. Individual fishes were counted and their sizes were estimated and placed in categories of total length in cm (0 – 3, 4 – 5, 6 – 10, 11 – 15, 16 – 20…61 – 70, 71 – 80…101 – 150, 151 – 200 cm). Categories larger than 100 cm were merged as only two species (the moray eel *Gymnothorax javanicus* and the white tip reef shark *Triaenodon obesus*) were observed in these categories, and there was less confidence in the accuracy of estimating these sizes. Cryptic species were also not counted (see Table 3.1 for a list of species observed), as these are poorly described in the Red Sea and require specific sampling methods (e.g., Tornabene et al. 2012).

Benthic surveys to determine live scleractinian (hard) coral cover, coral genus richness, and other categories were conducted on the same transects as the fish surveys using the line-intercept method. Apart from hard coral genera, soft coral cover was also recorded (to genus level when possible), sponges, crustose coralline algae (CCA), turf algae, and “other” algae. Transects for benthic surveys were 10 m long and located in the middle of each of the 25 m transects used for counting fish, making a total of 6 transects per reef, 3 at each depth. The transect length was chosen for its convenience in the field, to be comparable to previous studies done in this region (Furby et al. 2013), and because it has been previously shown to be adequate for quantitative studies of coral cover (Beenaerts and Berghe 2005). In order to minimize the impact of any potential observer bias, all data were collected by the same divers (Jessica Bouwmeester collected benthos data, Michael Berumen collected fish data).

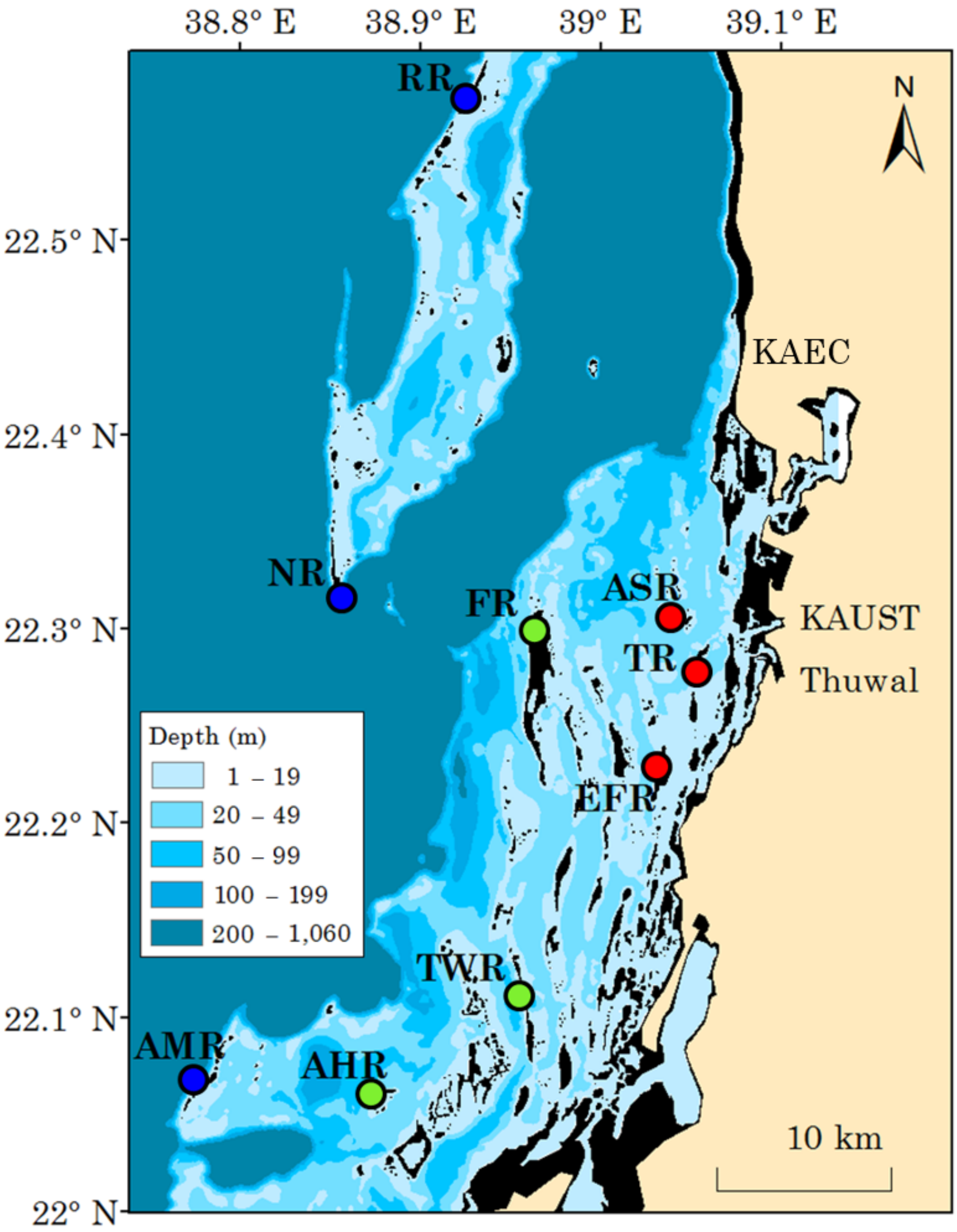


Figure 3.1: The study area and locations of survey reefs near the town of Thuwal, the King Abdullah University of Science and Technology (KAUST), and the King Abdullah Economic City (KAEC). Depth is color coded as noted in the inset key. The black color represents the shallowest portion of reef areas. Reef name abbreviations (see main text) are shown next to their respective, color-coded marker circles: red = inshore reefs; green = midshelf reefs; blue = offshore reefs. Geographic location is indicated by a decimal-degree grid on the left and top margins.

3.2.3. Biomass, Abundance, and Diversity Calculations

3.2.3.1. Fish Biomass and Abundance

Fish biomass was calculated following Friedlander and DeMartini (2002) using the equation: $W = a \times L^b$, where W is the weight of the fish in grams, L is its total length (TL) in cm and a and b are species-specific constants obtained from FishBase (2014) (Table 3.1). For the L value, I used the mid-range value of each TL size category. When several values of a and b were present in the database for a given species, I used an average of the available values, and when values were absent, I used values based on length-weight relationship models for sister species, the genus, or the family as provided by FishBase.

Table 3.1: List of all fish species found on the 9 study reefs, the families or sub-families they belong to, and the trophic groups to which they were assigned, with corresponding a and b values obtained from FishBase (2014) and used in biomass calculations. All data were collected in May 2013 from reefs near Thuwal in the central Saudi Arabian Red Sea, with six 25 x 8 m belt transect replicates on each reef: 3 at 10 meters' depth, and 3 at 2 meters' depth.

Family/Sub-family	Species	Trophic group	a	b
Acanthurinae	*Acanthurus gahhm*	Herbivore	0.023	3.060
Acanthurinae	*Acanthurus nigrofuscus*	Herbivore	0.023	3.060
Acanthurinae	*Acanthurus sohal*	Herbivore	0.023	3.060
Acanthurinae	*Ctenochaetus striatus*	Herbivore	0.023	3.060
Acanthurinae	*Zebrasoma desjardinii*	Herbivore	0.034	2.861
Acanthurinae	*Zebrasoma xanthurum*	Herbivore	0.034	2.861
Amphiprioninae	*Amphiprion bicinctus*	Herbivore	0.020	3.000
Anthiinae	*Pseudanthias squamipinnis*	Planktivore	0.057	2.650
Balistidae	*Balistapus undulatus*	Carnivore	0.026	3.010
Balistidae	*Pseudobalistes flavimarginatus*	Carnivore	0.073	2.760
Balistidae	*Sufflamen albicaudatus*	Carnivore	0.030	2.957
Belonidae	*Tylosurus choram*	Carnivore	0.001	3.090
Bodianinae	*Bodianus axillaris*	Carnivore	0.011	3.039
Bodianinae	*Bodianus diana*	Carnivore	0.011	3.039
Caesioninae	*Caesio lunaris*	Planktivore	0.011	3.080
Caesioninae	*Caesio striata*	Planktivore	0.011	3.080

Carangidae	*Atule mate*	Top Predator	0.009	3.052
Carangidae	*Carangoides bajad*	Top Predator	0.009	3.052
Carangidae	*Caranx melampygus*	Top Predator	0.009	3.052
Carcharhinidae	*Triaenodon obesus*	Top Predator	0.009	3.052
Chaetodontidae	*Chaetodon auriga*	Carnivore	0.032	2.920
Chaetodontidae	*Chaetodon austriacus*	Carnivore	0.023	3.130
Chaetodontidae	*Chaetodon fasciatus*	Carnivore	0.023	3.130
Chaetodontidae	*Chaetodon larvatus*	Carnivore	0.026	3.100
Chaetodontidae	*Chaetodon melannotus*	Carnivore	0.027	3.049
Chaetodontidae	*Chaetodon paucifasciatus*	Carnivore	0.023	3.130
Chaetodontidae	*Chaetodon semilarvatus*	Carnivore	0.023	3.130
Chaetodontidae	*Chaetodon trifascialis*	Carnivore	0.035	2.860
Chaetodontidae	*Heniochus intermedius*	Carnivore	0.017	3.211
Cheilininae	*Cheilinus abudjubbe*	Carnivore	0.015	3.070
Cheilininae	*Cheilinus quinquecinctus*	Carnivore	0.015	3.000
Cheilininae	*Epibulus insidiator*	Carnivore	0.016	3.081
Cirrhitidae	*Cirrhitus pinnulatus*	Carnivore	0.021	3.000
Cirrhitidae	*Paracirrhites forsteri*	Carnivore	0.009	3.070
Corinae	*Anampses twistii*	Carnivore	0.020	3.000
Corinae	*Coris cuvieri*	Carnivore	0.003	3.489
Corinae	*Halichoeres hortulanus*	Carnivore	0.012	3.064
Corinae	*Halichoeres scapularis*	Carnivore	0.005	3.382
Corinae	*Hemigymnus fasciatus*	Carnivore	0.017	3.000
Corinae	*Hologymnosus annulatus*	Carnivore	0.004	3.010
Corinae	*Stethojulis albavittata*	Carnivore	0.013	3.077
Corinae	*Thalassoma lunare*	Carnivore	0.021	2.814
Corinae	*Thalassoma purpureum*	Carnivore	0.026	3.000
Corinae	*Thalassoma rueppellii*	Carnivore	0.021	2.814
Dasyatidae	*Taeniura lymma*	Carnivore	0.013	3.100
Diodontidae	*Diodon hystrix*	Carnivore	0.337	2.364
Ephippidae	*Platax teira*	Herbivore	0.043	2.975
Epinephelinae	*Aethaloperca rogaa*	Carnivore	0.030	3.000
Epinephelinae	*Cephalopholis argus*	Carnivore	0.012	3.120
Epinephelinae	*Cephalopholis hemistiktos*	Carnivore	0.022	3.000
Epinephelinae	*Cephalopholis miniata*	Carnivore	0.017	2.990
Epinephelinae	*Epinephelus chlorostigma*	Carnivore	0.011	3.078
Epinephelinae	*Epinephelus stoliczkae*	Top Predator	0.011	3.040
Epinephelinae	*Epinephelus summana*	Top Predator	0.021	3.000

Epinephelinae	*Variola louti*	Carnivore	0.014	3.117
Fistulariidae	*Fistularia commersonii*	Carnivore	0.001	3.000
Holocentrinae	*Myripristis murdjan*	Planktivore	0.019	3.034
Holocentrinae	*Neoniphon sammara*	Carnivore	0.021	3.036
Holocentrinae	*Sargocentron caudimaculatum*	Carnivore	0.019	3.050
Holocentrinae	*Sargocentron diadema*	Carnivore	0.012	3.120
Holocentrinae	*Sargocentron spiniferum*	Carnivore	0.019	3.050
Kyphosinae	*Kyphosus sp.*	Herbivore	0.023	3.055
Labridae	*Gomphosus caeruleus*	Carnivore	0.024	2.703
Labridae	*Labroides dimidiatus*	Carnivore	0.006	3.231
Labridae	*Larabicus quadrilineatus*	Carnivore	0.011	3.039
Labridae	*Novaculichthys taeniourus*	Carnivore	0.011	3.039
Labridae	*Oxycheilinus digramma*	Carnivore	0.049	2.450
Labridae	*Oxycheilinus mentalis*	Carnivore	0.049	2.450
Labridae	*Paracheilinus octotaenia*	Carnivore	0.011	3.039
Lethrininae	*Lethrinus harak*	Carnivore	0.017	3.037
Lethrininae	*Lethrinus xanthochilus*	Carnivore	0.022	2.940
Lutjaninae	*Lutjanus bohar*	Top Predator	0.016	3.059
Lutjaninae	*Lutjanus ehrenbergii*	Top Predator	0.003	3.335
Lutjaninae	*Lutjanus fulviflamma*	Top Predator	0.027	2.935
Lutjaninae	*Lutjanus gibbus*	Top Predator	0.023	3.060
Lutjaninae	*Lutjanus kasmira*	Top Predator	0.011	3.154
Lutjaninae	*Lutjanus monostigma*	Top Predator	0.022	2.913
Monacanthidae	*Aluterus scriptus*	Carnivore	0.823	1.814
Monacanthidae	*Amanses scopas*	Carnivore	0.022	2.922
Monacanthidae	*Paraluteres arqat*	Carnivore	0.010	3.150
Monotaxinae	*Monotaxis grandoculis*	Carnivore	0.027	2.960
Mullidae	*Mulloidichthys vanicolensis*	Carnivore	0.012	3.167
Mullidae	*Parupeneus forsskali*	Carnivore	0.010	3.110
Muraeninae	*Gymnothorax javanicus*	Top Predator	0.001	3.100
Nasinae	*Naso brevirostris*	Herbivore	0.060	2.743
Nasinae	*Naso elegans*	Herbivore	0.023	3.060
Nasinae	*Naso hexacanthus*	Planktivore	0.042	2.854
Nasinae	*Naso unicornis*	Herbivore	0.028	2.980
Nemipteridae	*Scolopsis ghanam*	Carnivore	0.012	2.990
Ostraciidae	*Ostracion cubicus*	Carnivore	0.115	2.550
Pempheridae	*Pempheris sp.*	Carnivore	0.012	3.064
Pempheridae	*Pempheris vanicolensis*	Carnivore	0.012	3.064

Plectorhinchinae	*Plectorhinchus gaterinus*	Carnivore	0.017	3.040
Pomacanthidae	*Centropyge multispinis*	Carnivore	0.031	2.885
Pomacanthidae	*Pomacanthus asfur*	Carnivore	0.034	2.968
Pomacanthidae	*Pomacanthus imperator*	Carnivore	0.034	2.968
Pomacanthidae	*Pomacanthus maculosus*	Carnivore	0.034	2.968
Pomacanthidae	*Pygoplites diacanthus*	Herbivore	0.031	2.885
Pomacentrinae	*Abudefduf sexfasciatus*	Herbivore	0.023	3.130
Pomacentrinae	*Abudefduf vaigiensis*	Herbivore	0.020	3.034
Pomacentrinae	*Amblyglyphidodon flavilatus*	Planktivore	0.023	3.130
Pomacentrinae	*Amblyglyphidodon indicus*	Planktivore	0.023	3.130
Pomacentrinae	*Chromis dimidiata*	Planktivore	0.057	2.650
Pomacentrinae	*Chromis flavaxilla*	Planktivore	0.057	2.650
Pomacentrinae	*Chromis viridis*	Planktivore	0.048	2.710
Pomacentrinae	*Chromis weberi*	Planktivore	0.057	2.650
Pomacentrinae	*Dascyllus aruanus*	Planktivore	0.050	2.736
Pomacentrinae	*Dascyllus marginatus*	Planktivore	0.018	3.000
Pomacentrinae	*Dascyllus trimaculatus*	Planktivore	0.060	2.850
Pomacentrinae	*Neoglyphidodon melas*	Carnivore	0.018	3.182
Pomacentrinae	*Plectroglyphididon lacrymatus*	Herbivore	0.061	2.635
Pomacentrinae	*Pomacentrus sulfureus*	Herbivore	0.030	2.870
Pomacentrinae	*Pomacentrus trichrourus*	Herbivore	0.031	3.000
Pomacentrinae	*Stegastes nigricans*	Omnivore	0.030	3.048
Priacanthidae	*Priacanthus hamrur*	Carnivore	0.031	2.788
Pseudodacinae	*Pseudodax moluccanus*	Carnivore	0.011	3.039
Ptereleotridae	*Ptereleotris heteroptera*	Planktivore	0.004	3.120
Pteroinae	*Pterois miles*	Carnivore	0.011	3.270
Pteroinae	*Pterois radiata*	Carnivore	0.011	3.270
Scarinae	*Cetoscarus bicolor*	Herbivore	0.020	3.000
Scarinae	*Chlorurus gibbus*	Herbivore	0.019	3.100
Scarinae	*Chlorurus sordidus*	Herbivore	0.019	3.100
Scarinae	*Hipposcarus harid*	Herbivore	0.013	3.050
Scarinae	*Scarus ferrugineus*	Herbivore	0.025	3.000
Scarinae	*Scarus frenatus*	Herbivore	0.025	3.000
Scarinae	*Scarus niger*	Herbivore	0.018	3.130
Scarinae	*Scarus rivulatus*	Herbivore	0.020	3.091
Scarinae	*Scarus rubroviolaceus*	Herbivore	0.014	3.109
Serranidae	*Plectropomus areolatus*	Top Predator	0.012	3.060
Siganidae	*Siganus luridus*	Herbivore	0.019	2.956

Siganidae	*Siganus rivulatus*	Herbivore	0.013	3.014
Siganidae	*Siganus stellatus*	Herbivore	0.014	3.138
Sparidae	*Acanthopagrus bifasciatus*	Carnivore	0.023	3.130
Sparisomatinae	*Calotomus viridescens*	Herbivore	0.012	3.167
Tetraodontidae	*Arothron diadematus*	Carnivore	0.017	2.960
Total:	136 species 44 families			

The average biomass of all species was then calculated in kg/100 m^2 for each reef, and, from these values, I extracted and summarized the biomass of four trophic guilds (top predators, carnivores, herbivores, and planktivores) and 3 major groups of commercial fish, which included 25 species in 5 subfamilies: parrotfishes (Scarinae and Sparisomatinae: 10 species), snappers (Lutjaninae: 6 species), and groupers (Serraninae and Epinephelinae: 9 species) (Table 3.2). The study species were assigned to the most appropriate one of the four trophic guilds defined by Sandin et al. (2008). The mean number of fish (hereafter, density) was also calculated per 100 m^2.

Table 3.2: A list of fish species found during the surveys and that were assigned to 3 of the most commercially valued and heavily-targeted fish groups by fishermen in Saudi Arabia: parrotfish, snappers, and groupers, and the subfamilies to which they belong.

Group	**Sub-family**	**Species**
Parrotfishes	Scarinae	*Cetoscarus bicolor*
	Scarinae	*Chlorurus gibbus*
	Scarinae	*Chlorurus sordidus*
	Scarinae	*Hipposcarus harid*
	Scarinae	*Scarus ferrugineus*
	Scarinae	*Scarus frenatus*
	Scarinae	*Scarus niger*
	Scarinae	*Scarus rivulatus*
	Scarinae	*Scarus rubroviolaceus*

	Sparisomatinae	*Calotomus viridescens*
Snappers	Lutjaninae	*Lutjanus bohar*
	Lutjaninae	*Lutjanus ehrenbergii*
	Lutjaninae	*Lutjanus fulviflamma*
	Lutjaninae	*Lutjanus gibbus*
	Lutjaninae	*Lutjanus kasmira*
	Lutjaninae	*Lutjanus monostigma*
Groupers	Epinephelinae	*Aethaloperca rogaa*
	Epinephelinae	*Cephalopholis argus*
	Epinephelinae	*Cephalopholis hemistiktos*
	Epinephelinae	*Cephalopholis miniata*
	Epinephelinae	*Epinephelus chlorostigma*
	Epinephelinae	*Epinephelus stoliczkae*
	Epinephelinae	*Epinephelus summana*
	Epinephelinae	*Variola louti*
	Serraninae	*Plectropomus areolatus*
Parrotfish Total:	10 species	
Snappers Total:	6 species	
Groupers Total:	9 species	
Grand Total:	25 pecies	

3.2.3.2. Fish and Coral Diversity

The total number of fish species (species richness) per reef was determined (i.e., if an individual was recorded on any one of the six transects per reef). Species richness was then used to calculate Shannon's Diversity Index *(H)*, which was in turn used to calculate species evenness using the equations: $H_{(R)} = -\sum_{i=1}^{S} \left(P_{(i)} \text{ x} \ln P_{(i)} \right)$ and $E_{(R)} = H_{(R)} / \ln S$, where $H_{(R)}$ is Shannon's Diversity Index for a reef *R*, which has $1 \rightarrow S$ number of species (thus, *S* is species richness), *P* is the proportion of species *i* (number of individuals of the species/total number of individuals of all species), and $E_{(R)}$ is species evenness for reef *R* (Heip et al. 1998). The only diversity index measured for scleractinian corals was total genus richness per reef, which has been shown to be an adequate surrogate for species richness, (Balmford et al. 1996; Bett and Narayanaswamy 2013). Species richness was not measured directly for the sake of convenience in the field and due to the high probability of identification errors encountered within many genera present in the Red Sea. Several recent studies in the region have revealed troublesome scleractinian groups and new taxonomic discoveries (e.g., Huang et al. 2014; Terraneo et al. 2014; Arrigoni et al. 2015; Bouwmeester et al. 2015), highlighting the need for caution when working at the species level in this region until coral taxonomy is formally revised.

3.2.4. Spatial Trends and Statistical Analysis

The data collected were examined for cross-shore patterns and differences between reefs using Pearson’s correlation and Kruskal-Wallis tests (KW) with post-hoc Mann-Whitney U tests (MW). One-way ANOVA tests and post-hoc Tukey’s tests were used with datasets that met assumptions of normality. I also examined whether coral cover or coral genus richness correlated with either fish biomass or species richness. SPSS Statistics®, version 21, was used for these statistical analyses.

3.2.5. Fish and Benthic Community Assemblages

In order to identify and analyze patterns of similarity in community assemblages across reefs, I created non-metric multidimensional scaling (NMDS) plots using fish biomass, fish densities, and benthic cover data. All data were log-transformed ($\mathrm{Log}(x + 1)$) to ensure that all species have similar influence on the analysis regardless of the abundance range in which they occur, and the Bray-Curtis method was used to create all resemblance matrices. As per guidelines provided by Clarke (1993) for ecological data, I considered plots with 2D stress values higher than 0.2 to be poor representations of the data in 2-dimensional space, while stress values lower than 0.1 to be excellent representations. Most analyses were followed up by analyses of similarity (ANOSIM) to test for significant clustering and similarity percentage (SIMPER) analyses to identify the top species or categories contributing to dissimilarity between clusters (Clarke 1993). The software PRIMER, version 6, was used for these analyses (Clarke and Gorley 2006).

3.3. Results

3.3.1. Fish Biomass and Trophic Composition

A grand total of 13,792 fish from 136 species and 44 families/sub-families (Table 3.1) were counted on the surveys. Two of the offshore reefs, NR and AMR, had the highest mean fish biomass values of 17.2 (±6.1) and 16.2 (±4.3) kg/100 m^2, respectively (Table 3.3, Figure 3.2 a). However, while AMR also had a relatively high mean numerical density of fish compared to the other reefs (308.2 ±55.6 fish/100 m^2), NR had one of the lowest (140.4 ±25.3 fish/100 m^2). The reefs that had the highest mean fish densities were the midshelf reef TWR with 361.8 ±48.1 fish/100 m^2 and the inshore reef TR with 354.0 (±40.1) fish/100 m^2 (Figure 3.2 b).

Overall, mean fish biomass increased significantly with distance from shore (Figure 3.3) measured to the nearest kilometer (R = 0.804, R^2 = 0.646, p = 0.009) and differed between individual reefs (p_{KW} = 0.004). Multiple MW comparisons showed significant differences between the offshore reef AMR and the two midshelf reefs, FR and TWR (z = -3.12 and -2.82, and p_{MW} = 0.002 and 0.005, respectively; corrected alpha value = 0.012). With regards to density, the inshore reef ASR differed significantly from TWR (midshelf) and TR (inshore) (p_{Tukey} = 0.003 and 0.005, respectively).

Table 3.3: Mean and total fish biomass from 9 reefs near Thuwal in the central Saudi Arabian Red Sea, expressed as mean kg/100 m^2 (± SE) on each of the surveyed reefs. Each reef was surveyed using six replicate visual belt transects. Distance from shore indicates the location of each reef on the continental shelf, Reef is the name of each study reef (see main text for abbreviations). Values are divided into trophic groups (planktivores, herbivores, carnivores, and top predators) and shown as a Total for all groups combined.

Distance from shore	Reef	Biomass				
		Planktivores	Herbivores	Carnivores	Top Predators	Total
offshore	RR	1.51 (±0.4)	5.65 (±1.3)	1.89 (±0.5)	1.10 (±0.4)	10.09 (±1.3)
	NR	1.10 (±0.6)	7.99 (±2.6)	2.02 (±0.4)	6.12 (±4.8)	17.22 (±6.1)
	AMR	2.45 (±0.6)	11.96 (±3.7)	1.55 (±0.4)	0.26 (±0.1)	16.22 (±4.3)
midshelf	FR	0.58 (±0.2)	3.15 (±1.0)	2.03 (±0.4)	0.74 (±0.5)	6.50 (±1.2)
	TWR	0.58 (±0.4)	3.71 (±1.2)	2.00 (±0.3)	0.34 (±0.1)	6.63 (±1.2)
	AHR	1.29 (±0.4)	6.80 (±2.7)	2.37 (±0.4)	1.01 (±0.7)	11.46 (±2.6)
inshore	ASR	0.18 (±0.1)	7.62 (±4.5)	1.65 (±0.4)	0.10 (±0.1)	9.54 (±1.6)
	TR	1.33 (±0.8)	6.77 (±2.3)	2.00 (±0.2)	0.41 (±0.1)	10.51 (±4.9)
	EFR	0.01 (±0.0)	7.67 (±3.5)	1.72 (±0.3)	0.40 (±0.2)	9.80 (±4.1)

Although the biomass of all four trophic guilds increased slightly with distance from shore, only herbivores showed a moderate and significant positive correlation (R = 0.675, R^2 = 0.47, p = 0.046). Trophic composition on all reefs is dominated by herbivorous fishes with few to no top predators. Only two sharks (two *Triaenodon obesus* individuals) were observed during the surveys, both of which were on the same transect on the offshore reef NR. Other observed fish that were considered top predators were grouper, snapper, eel, and jack species.

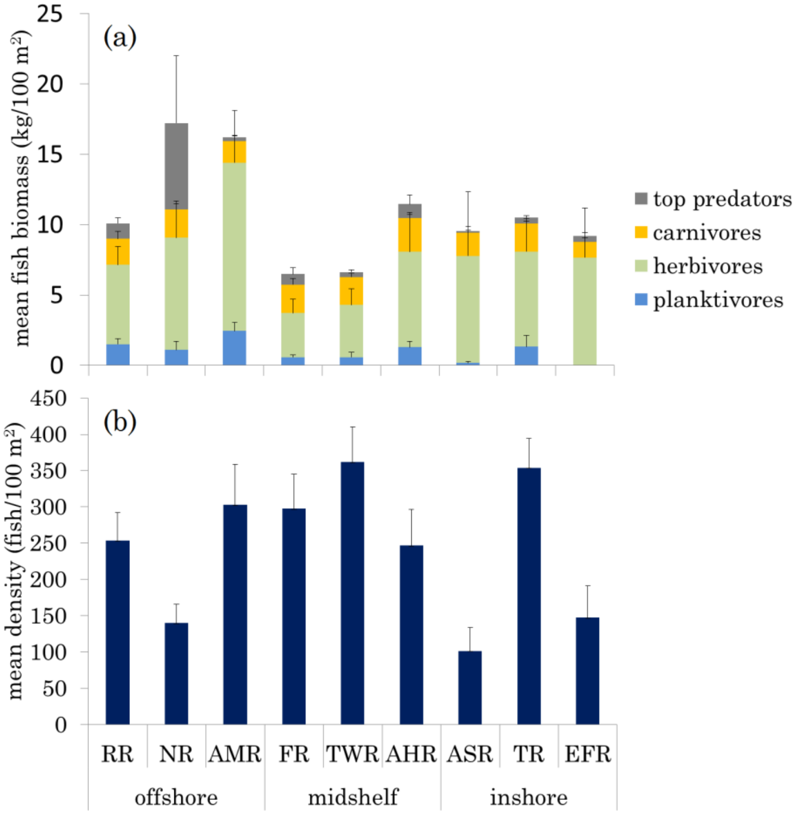


Figure 3.2: Fish biomass: (a) Mean fish biomass in kg/100 m^2 for each of the 9 study reefs, color-coded according to stacked trophic group as per the inset key (planktivores, herbivores, carnivores, or top predators); significant differences were found only between overall biomass on AMR and FR, and between AMR and TWR ($p_{\text{Mann-Whitney}} < 0.01$); (b) mean fish density (fish/100 m^2) for each reef (no significant differences found, $p_{\text{Kruskal-Wallis}} > 0.05$). Reef name abbreviations are presented on the x-axis (see main text for full names) and separated according to distance from shore into offshore, midshelf, and inshore reefs. All data were collected in May 2013 from the central Saudi Red Sea.

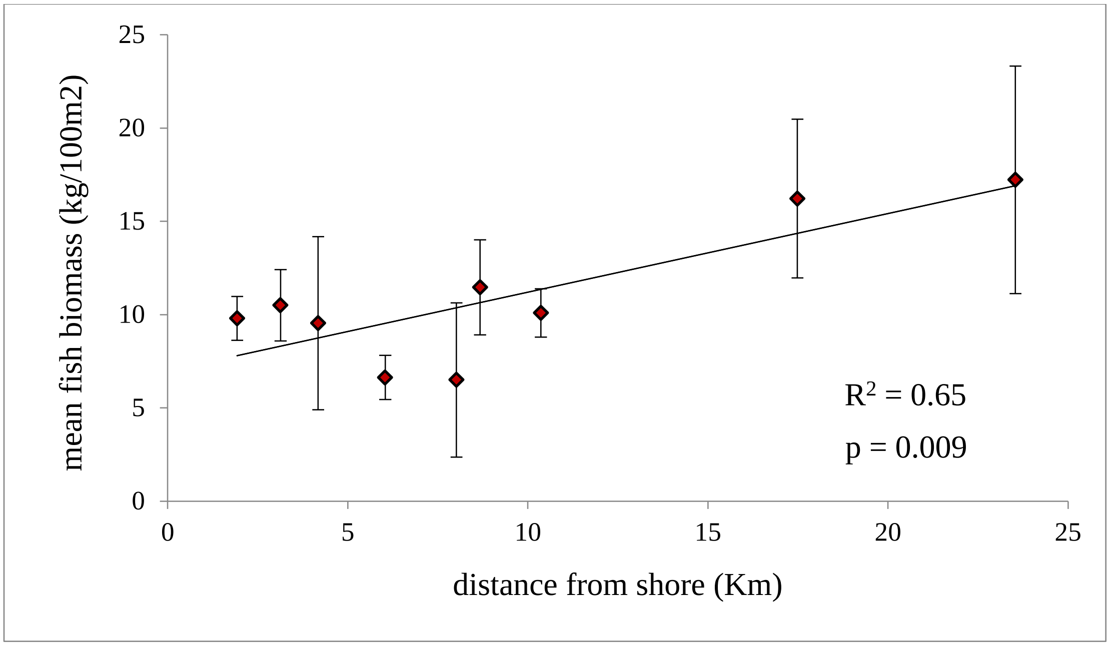


Figure 3.3: A scatterplot showing the relationship between mean fish biomass in Kg/100m^2 and distance from shore to the nearest kilometer. Mean values for each point were calculated from 6 transects on one reef, 3 at 2 m depth, and 3 at 10 m depth. Error bars represent standard error of the mean.

3.3.2. Commercial Fish

The reefs RR (offshore) and TR (inshore) had the highest biomass of parrotfish and groupers, respectively, and RR had the highest overall mean biomass of the three commercial fish groups combined with 3.1 ±0.9 kg/100 m^2 (Figure 3.4 a). However, none of these observations were statistically significant (KW, $p > 0.05$ for all tests). Regression analyses showed insignificant correlations with distance from the Thuwal fishing port for all 3 groups (parrotfish: $R = 0.307$, $R^2 = 0.094$, $p = 0.422$; snappers: $R = 0.599$, $R^2 = 0.359$, $p = 0.088$; groupers: $R = 0.025$, $R^2 = 0.001$, $p = 0.950$; Figure 3.4 b).

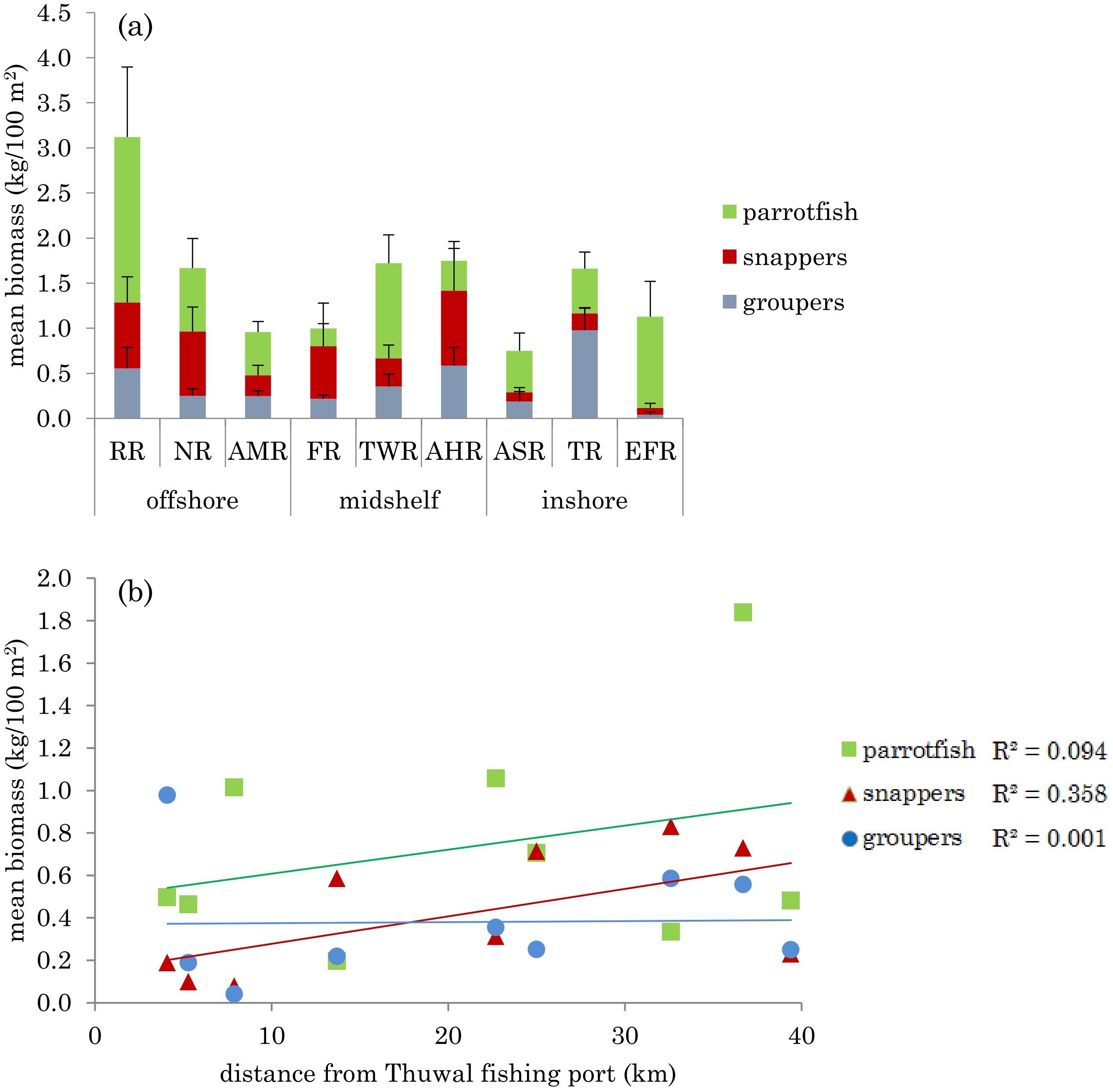


Figure 3.4: Commercial fish biomass. (a) Mean biomass from the 9 study reefs of the 3 most targeted commercial fish groups: parrotfish, snappers, and groupers, color-coded as indicated by the inset key. Bars represent standard error, and reef name abbreviations are presented on the x-axis and separated according to distance from shore into offshore, midshelf, and inshore reefs; (b) scatterplot of the mean biomass per 100 m^2 of the three fish groups in (a) for each reef against distance from the Thuwal port. Increasing distance from port is used as a proxy for decreasing fishing pressure. R^2 values are shown on the right indicate no strong correlations. All data were collected in May 2013 near Thuwal in the central Saudi Red Sea. Mean values are calculated from six visual belt transects per reef; 3 at 10 m and 3 at 2 m.

3.3.3. Coral and Algal Cover

We recorded a total of 38 benthic categories, including 25 genera of scleractinian corals (listed in Table 3.4). Mean percent coral cover ranged from 8.35 % (±3.3) on inshore reef ASR to 30.70 % (±3.7) on midshelf reef TWR (Table 3.5). There was no strong correlation between coral cover and distance from shore ($R = 0.470$, $R^2 = 0.221$, $p = 0.202$). However, One-way ANOVA tests showed significant difference between reefs ($F = 16.7$, $p = 3 \times 10^{-6}$), and post-hocs showed that coral cover on inshore reefs was significantly lower than that of midshelf reefs ($p_{\mathrm{Tukey}} = 2 \times 10^{-5}$) and offshore reefs ($p_{\mathrm{Tukey}} = 7 \times 10^{-6}$). Coral cover also did not correlate strongly with fish species richness or with fish biomass ($R^2 = 0.10$ and 0.01, respectively).

Table 3.4: List of benthic categories recorded on the 9 study reefs. The taxonomic sub-categories (mostly genera) are listed in the second column as recorded during the surveys. A total of 25 scleractinian genera were recorded, at least 6 soft coral genera (the sub-category “Xenidae” may have included more than one genus which were unidentifiable in the field), and one genus of hydrozoan. Sponges and algae were recorded as general categories and the rest are non-living substrate categories. All data were collected using the line-intercept method in May 2013 near Thual in the central Saudi Arabian Red Sea on shorter (10 m long) subsets of the same transects used to collect fish data. There were 3 replicates at 10 m, and 3 at 2 m.

Benthic Category	Genus/Sub-category
Scleractinia	*Acropora*
	Astreopora
	Ctenactis
	Cyphastrea
	Diploastrea
	Echinopora
	Echinophyllia
	Dipsastraea
	Favites
	Fungia
	Galaxea
	Gardineroseris
	Goniastrea

	Goniopora
	Gyrosmilia
	Leptastrea
	Lobophyllia
	Montipora
	Pavona
	Playtgyra
	Pocillopora
	Porites
	Psammocora
	Stylocoeniella
	Stylophora
Soft corals	*Palythoa*
	Rhytisma
	Sarcophyton
	Sinularia
	Tubipora
	Xenidae
Hydrozoans	*Millepora*
Sponge	
Crustose coralline algae (CCA)	
Turf algae	
Other algae	
Rock	
Rubble	
Sand	

Table 3.5: Mean cover (±SE) of benthic categories recorded on the 9 study reefs near Thuwal in the central Saudi Arabian Red Sea in May 2013. Reef names are shown as abbreviations in column headers and separated according to distance from shore. Data were collected on 10 m long transects at 10 m and 2 m depths using the line-intercept method. The category Hard corals summarizes values for 25 scleractinian coral genera that were observed (listed in Table 3.4); Soft corals summarize at least 6 genera; Hydrozoans contained only the genus Millepora; and the remaining categories were recorded as shown in the table.

Benthic category	Mean percent cover (±SE)								
	offshore			midshore			inshore		
	RR	NR	AMR	FR	TWR	AHR	ASR	TR	EFR

Hard corals	26.4 (±4.6)	21.3 (±2.5)	28.6 (±2.0)	26.3 (±4.3)	24.8 (±4.9)	30.7 (±3.7)	8.4 (±3.3)	14.9 (±2.8)	13.2 (±1.8)
Soft corals	0.3 (±0.3)	15.7 (±2.0)	8.2 (±2.8)	16.7 (±5.1)	5.4 (±0.9)	5.8 (±2.3)	3 (±1.4)	7.6 (±3.5)	3.7 (±2.6)
Hydrozoans	1.5 (±1.2)	0.3 (±0.2)	1.8 (±1.2)	1.7 (±1.7)	0.0 (±0.0)	0.6 (±0.3)	0.0 (±0.0)	0.2 (±0.2)	0.0 (±0.0)
Sponges	0.6 (±0.6)	0.2 (±0.2)	0.7 (±0.4)	0.5 (±0.5)	3.8 (±2.5)	1.6 (±0.5)	0.9 (±0.5)	0.3 (±0.3)	2.6 (±1.5)
CCA	21.9 (±9.7)	9.4 (±2.1)	29.3 (±6.5)	8.1 (±3.9)	2.5 (±1.5)	26.1 (±8.2)	9.7 (±5.0)	9.8 (±3.7)	0.2 (±0.2)
Turf algae	0.0 (±0.0)	0.0 (±0.0)	0.3 (±0.3)	1.8 (±1.8)	3.7 (±0.8)	7.9 (±5.1)	2.4 (±1.1)	11.7 (±5.1)	14.3 (±6.5)
Other algae	0.0 (±0.0)	0.0 (±0.0)	0.2 (±0.2)	0.1 (±0.1)	0.3 (±0.3)	0.4 (±0.4)	0.0 (±0.0)	0.2 (±0.2)	0.0 (±0.0)
Rock	35.5 (±4.0)	52.8 (±2.3)	30.5 (±7.0)	31.3 (±6.0)	36.6 (±5.7)	26.9 (±7.6)	40.9 (±7.6)	43.4 (±3.6)	50.2 (±5.3)
Rubble	14 (±7.6)	0.4 (±0.3)	0.5 (±0.5)	6.9 (±5.4)	13.1 (±2.4)	0.0 (±0.0)	12.6 (±4.6)	8.6 (±3.6)	2.8 (±0.9)
Sand	0.0 (±0.0)	0.0 (±0.0)	0.0 (±0.0)	6.5 (±3.5)	9.8 (±6.2)	0.0 (±0.0)	22.2 (±9.9)	3.3 (±2.0)	13 (±7.3)

3.3.4. Fish and Coral Diversity

A grand total of 136 species of fish were counted on the surveys (Table 3.1). Fish species richness ranged from 54 on ASR (an inshore reef) to 70 species in TR (inshore) and TWR (midshelf), and species evenness, which was calculated from Shannon's Index for each reef, ranged narrowly from 0.59 to 0.77, indicating a fairly even number of individuals per species on all reefs (Table 3.6). Species richness was highest on average on midshelf reefs, but no statistical significance was found (One-way ANOVA, $F = 2.461$, $p = 0.166$).

Table 3.6: A summary of fish and hard coral diversity indices for each of the 9 study reefs near Thuwal in the central Saudi Arabian Red Sea. For coral genus and fish species richness, the numbers shown are the total numbers of genera and species found on each reef, respectively. Fish species evenness was calculated from Shannon's Diversity Index for each reef, which was based on the reported species richness. Each reef was surveyed using six replicate

visual belt transects. Distance from shore indicates the location of each reef on the continental shelf, Reef is the abbreviated name of each study reef.

Distance from shore	Reef	Hard coral genus richness	Fish species richness	Fish species evenness
offshore	RR	14	60	0.68
	NR	16	59	0.76
	AMR	20	55	0.59
midshelf	FR	23	69	0.62
	TWR	18	70	0.66
	AHR	20	64	0.61
inshore	ASR	10	54	0.77
	TR	18	70	0.72
	EFR	20	55	0.59

A midshelf reef, FR, had the highest number of hard coral genera (23), while an inshore reef, ASR, had the lowest (10 genera). MW tests showed ASR to have significantly lower coral genus richness than all other reefs ($p_{\mathrm{MW}} < 0.005$) except NR and TR. Coral genus richness was also a poor predictor of fish species richness ($R = 0.224$, $R^2 = 0.050$, $p = 0.562$) and fish biomass ($R = 0.096$, $R^2 = 0.009$, $p = 0.806$).

3.3.5. Fish and Benthic Community Assemblages

A number of iterations were attempted to identify any significant differences in fish and benthic assemblages between the reefs and between the two depths at which the data were collected. These analyses used fish biomass, fish densities, benthic cover, and a combination of fish biomass and benthic cover. The most significant NMDS results (all of which have very low 2D stress) are shown in Figure 3.5, while a summary of all NMDS, ANOSIM, and SIMPER results is shown in Table 3.7.

Preliminary analyses including all replicates consistently showed a slight (2D stress > 0.2 for fish and 0.17 for benthos) yet significant (ANOSIM significance 0.1 %) separation of 10 m assemblages from 2 m assemblages. These preliminary analyses also showed a great reduction in 2D stress (< 0.1) when mean values, rather than all replicates, were used.

The NMDS plots for fish biomass and densities at 10 m (Figure 3.5 a and c) are very similar to each other with a very clear and tight clustering of all reefs in one cluster except for two inshore reefs (ASR and EFR), which separated from the other reefs but did not cluster closely together. This shows very high similarity (ANOSIM R = 0.9, sig. 2.8) at 10 m depth in fish assemblages (by biomass as well as densities) among all reefs except ASR and EFR. In terms of biomass, *Caesio lunaris* contributed the most to the dissimilarity (SIMPER dissimilarity contribution (hereafter Contrib.) = 7.9 %), being more abundant in the group containing offshore reefs, midshelf reefs, and TR.

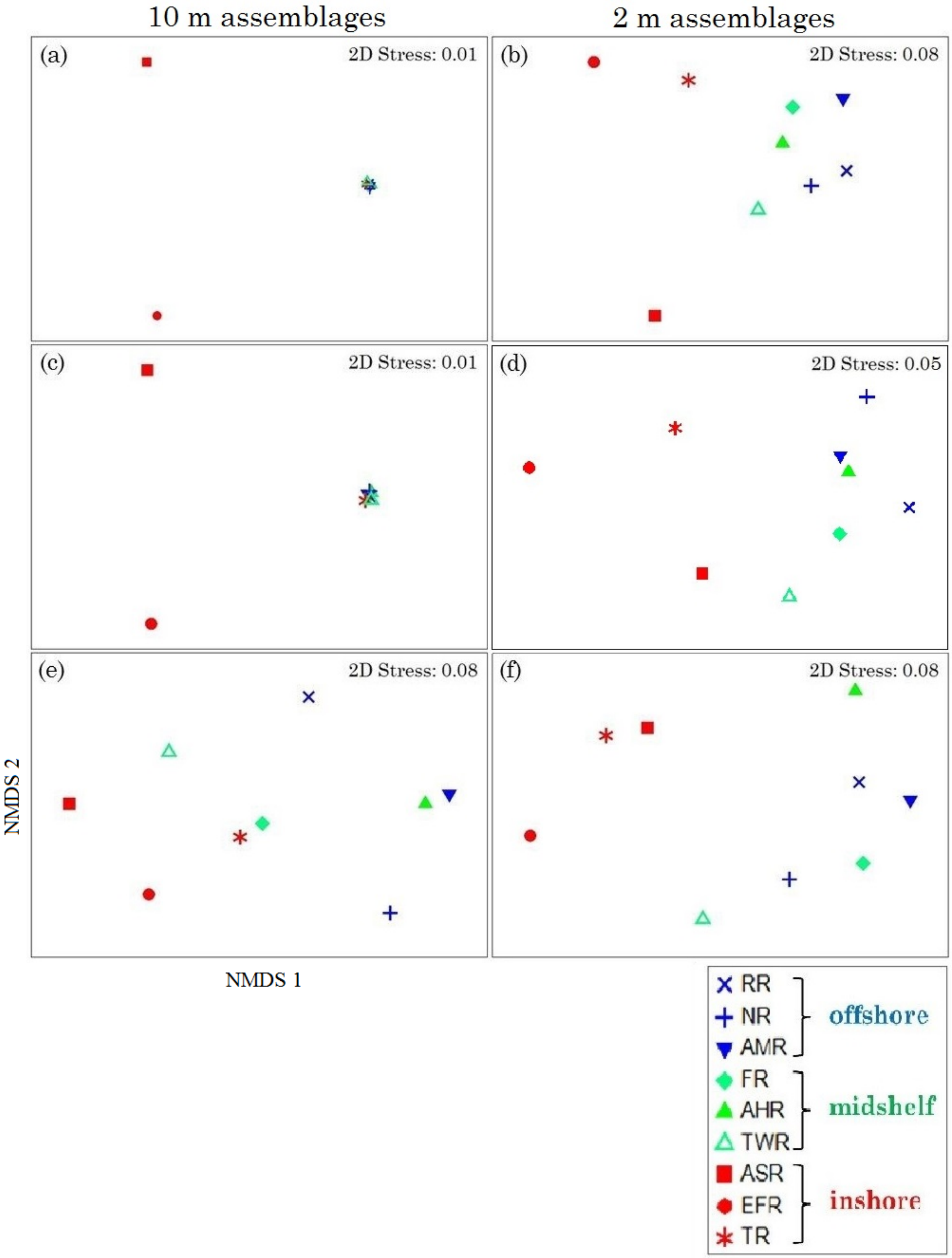

10 m assemblages
2 m assemblages
(a)
2D Stress: 0.01
(b)
2D Stress: 0.08
(c)
2D Stress: 0.01
(d)
2D Stress: 0.05
(e)
2D Stress: 0.08
(f)
2D Stress: 0.08
NMDS 2
NMDS 1
RR
NR
AMR
offshore
FR
AHR
TWR
midshelf
ASR
EFR
TR
inshore

Figure 3.5: NMDS plots from Bray-Curtis resemblance matrices based on log (x+1)-transformed reef averages for fish biomass (a and b), fish densities (c and d), and benthic cover (e and f); a, c, and e show10 m assemblages, while b, d, and f show 2m assemblages. X-axes represent NMDS1 and y-axes represent NMDS2. Reef name abbreviations are shown in the inset key next to their representative symbols, and the 9 reefs are color-coded according to distance from shore as shown by the key. 2D stress values are shown in the upper right corner of each plot. All data were averaged across the relevant replicates for each reef. Fish and benthic data were originally collected on the same transects (6 per reef in total) at the same time from the central Saudi Arabian Red Sea.

However, looking at fish assemblages at 2 m (Figure 3.5 b and d), all inshore reefs separated (including TR) from all other reefs, which clustered together, though less closely than at 10 m, indicating more dissimilarity within shallow inshore and offshore fish communities despite significant separation between the two groups (ANOSIM sig. 1.2 % for both biomass and densities). The farming *Stegastes nigricans* contributed highly to the dissimilarity in terms of both biomass and numerical density (Contrib. 14.6 and 6.8 %, respectively), being abundant on inshore reefs and nearly absent on other reefs. Another damselfish, *Chromis dimidiata*, also contributed by being more abundant on midshelf and offshore reefs (Contrib. 4.3 %).

As for benthic assemblages at 10 m (Figure 3.5 e), inshore reefs in addition to two midshelf reefs (TWR and FR) separated from the remaining four reefs (ANOSIM *R* = 0.78, sig. 0.8 %), with sand and rubble (collective Contrib. 32.0 %) and CCA (9.2 %) contributing the most to the separation. Sand and rubble were more abundant in the group containing the inshore reefs, while CCA was more abundant in the group containing the offshore reefs. However, at 2 m (Figure 3.5 f), there was a clearer separation once again between inshore reefs and all other reefs (ANOSIM *R* = 0.82, sig. 1.8 %). Turf algae (Contrib. 14.6 %), rock (10.4 %), and *Porites* (10.0 %) were more abundant on inshore reefs, contributing highly to the dissimilarity, while *Pocillopora* (14.3 %), CCA (13.5 %), and Xenidae soft corals (9.6 %) were more abundant on offshore and midshelf reefs (Table 3.7).

Table 3.7: A list of all non-metric multidimensional scaling (NMDS), analyses of similarity (ANOSIM), and similarity percentage (SIMPER) analyses performed on the fish and benthic data collected on the 9 study reefs near Thuwal in the central Saudi Arabian Red Sea. The first column indicates which dataset was used (all data were log (x+1)-transformed); the second column indicates which subset of the data was included in the analysis (whether all replicates were used, replicates from a certain depth were used, and/or reef averages were used); the third column contains brief descriptions of NMDS plots produced; the fourth column shows the 2D stress for the plots described in the third column (> 0.2 indicates poor representation of data in 2-dimensional space, < 0.1 indicates excellent representation); the fifth column shows the global R statistic for ANOSIM (as the value approaches 1, the separation of groups analyzed is larger); the sixth column shows the significance of the separation indicated by the R statistic (values below 5% are considered significant); the seventh column shows the SIMPER percent average dissimilarity between the groups analyzed; and the last column lists some of the highest-contributing species/categories to the dissimilarity and the percent of their contribution between parentheses. Cells that are filled with dashes indicate that ANOSIM and SIMPER were not performed for the corresponding analyses indicated in the second column.

				ANOSIM		SIMPER	
Data analyzed	Analysis	NMDS results/comments	2D stress	Global R statistic	Significance (%)	Average dissimilarity (%)	Top contributing species/categories (%)
Fish biomass (kg/transect)							
	All replicates, all depths	Poor but significant separation between shallow and deep replicates with more dissimilarity within groups than between them.	0.27	0.31	0.1	85.2	*Acanthurus sohal (11.6), Stegastes nigricans (5.8), Caesio lunaris (4.6)*
	Reef averages, all depths	Poor separation between inshore and other reefs, with more dissimilarity within groups than between them.	0.04	0.6	2.4	56	*Stegastes nigricans (8.3), Pseudanthias squamipinnis (6.2), Thalassoma ruepellii (4.1)*
	10 m replicates only	Poor separation between 2 inshore reefs and all other reefs with more dissimilarity within groups than between them.	0.24	-	-	-	-

	10 m reef averages	Strong significant separation between 2 inshore reefs and all other reefs with high dissimilarity between the 2 inshore reefs.	0.01	0.94	2.8	83.7	*Caesio lunaris (7.9), Abudefduf sexfasciatus (5.0), Naso unicornis (4.6)*
	2 m replicates only	Poor separation between inshore reefs and all other reefs with more dissimilarity within groups than between them.	0.21	-	-	-	-
	2 m reef averages	Slight separation between inshore and other reefs with more dissimilarity within groups than between them.	0.08	0.78	1.2	71	*Stegastes nigricans (14.6), Acanthurus sohal (10.8), Naso unicornis (5.4)*
Fish density (fish/transect)							
	All replicates, all depths	Poor but significant separation between shallow and deep replicates with more dissimilarity within groups than between them.	0.21	0.23	0.1	72.7	*Chromis dimidiata (4.2), C. flavaxilla (3.9), Acanthurus sohal (3.5)*
	Reef averages, all depths	Poor but significant separation between inshore and other reefs with more dissimilarity within groups than between them.	0.07	0.75	1.2	56.7	*Chromis dimidiata (9.5), Caesio lunaris (7.9), Chromis flavaxilla (6.7)*
	10 m replicates	Clear separation between 2 inshore reefs and all other reefs with more dissimilarity between the 2 inshore reefs than between groups.	0.12	-	-	-	-
	10 m reef averages	Clear and significant separation between 2 inshore reefs and all other reefs with more dissimilarity between the 2 inshore reefs than between groups.	0.01	0.99	2.8	75.3	*Chromis dimidiata + C. flavaxilla (14.4), Caesio lunaris + Pseudanthias squamipinnis*

							(10.8)
	2 m replicates	Poor separation between inshore reefs and all other reefs with more dissimilarity within groups than between them.	0.19	-	-	-	-
	2 m reef averages	Slight, yet significant, separation between inshore and other reefs with more dissimilarity within groups than between them.	0.05	0.77	1.2	56.8	*Stegastes nigricans (6.8), Chromis dimidiata + C. flavaxilla (8.5), Acanthurus nigrofuscus (3.8)*
Benthic cover (%)							
	All replicates, all depths	Poor but significant separation between shallow and deep replicates with more dissimilarity within groups than between them.	0.17	0.45	0.1	57.4	CCA *(14.0)*, rubble + sand *(18.8)*, turf algae *(7.4)*, *Pocillopora (7.0)*
	Reef averages, all depths	Poor separation between inshore reefs and all other reefs with more dissimilarity within groups than between them.	0.08	0.65	1.2	41.3	Sand *(13.1)*, *Pocillopora (12.2)*, CCA *(11.3)*, turf algae *(10.2)*
	10 m replicates	No clear separation of groups.	0.15	-	-	-	-
	10 m reef averages	Separation of inshore plus 2 midshelf reefs from all other reefs, with more dissimilarity within than between groups.	0.08	0.78	0.8	48.7	Sand + rubble *(32)*, *CCA (9.2)*, Xenidae *(5.1)*, *Porites (5.1)*

	2 m replicates	Poor separation between inshore reefs and all other reefs with more dissimilarity within groups than between them.	0.15	-	-	-	-
	2 m reef averages	Clear separation between inshore reefs and all other reefs with more dissimilarity within groups than between them.	0.08	0.82	1.2	50.8	Turf algae *(14.6)*, *Pocillopora (14.3)*, CCA *(13.5)*, rock *(10.4)*, *Porites (10.0)*, Xenidae *(9.6)*
Fish density (fish/transect) and benthic cover (%)	Reef averages, all depths	Slightly better separation between inshore and other reefs compared to fish counts or benthic cover alone.	0.04	0.74	1.2	49.8	*Stegastes nigricans (4.9)*, *Chromis dimidiata (4.6)*, *Caesio lunaris (3.8)*

3.4. Discussion

I presented a description of the spatial trends in fish biomass, trophic structure, and fish and benthic community assemblages on 9 reefs in Thuwal, with particular focus on differences in community assemblages along a cross-shelf gradient. Results show a moderate increase in fish biomass with distance from shore and that trophic structure is dominated by herbivorous fishes at all sites. Fish communities are characterized by planktivorous fishes and branching corals on offshore reefs and by farming damselfishes, turf algae, and massive corals on inshore reefs. Shallow inshore benthic communities still appear to be showing the impacts of the bleaching event that occurred three years prior to this study (Furby et al. 2013). The following sections discuss these results in detail.

3.4.1. Fish Biomass, Trophic Composition, and Commercial Fish

Compared to relatively remote and nominally pristine locations around the world, including sites in the central Pacific (Sandin et al. 2008; Williams et al. 2011; Friedlander et al. 2014), the North-Western Hawaiian Islands (Friedlander and DeMartini 2002; Williams et al. 2011), and even some relatively remote and unfished parts of the Red Sea (Kattan 2014), Thuwal reefs have very low fish biomass. This is true even if only Nazar Reef (NR) is compared to these sites. NR had the highest biomass in this study, but is still several times lower than most other locations considered in this comparison (Table 3.8). Although Ducie Island in the Pacific had a comparable biomass to that of NR, 63 % of this biomass on Ducie Island was attributed to top predators compared to NR’s 36 %. In fact, the trophic composition of all locations listed in Table

3.8, including the Sudanese Red Sea site, is that of an inverted pyramid with most of the biomass contributed by top predators, as opposed to Thuwal reefs where the bulk of the biomass is attributed to herbivores (Figure 3.2 a).

Our survey design (using relatively short belt transects for visual census and having only 6 replicates per reef) is not adequate for accurately capturing the abundances of large mobile predators such as sharks, trevallies, and barracudas, which are typically surveyed using much longer and wider transects or using baited cameras (e.g., Robbins et al. 2005; Goetze and Fullwood 2013), and the non-Red Sea studies shown in Table 3.8 are located in vastly different physical environments from that of the Red Sea, which could partly account for the observed differences in biomass. Nevertheless, the method used in this study was the same that was applied by Kattan (2014) in the Sudanese Red Sea, where much higher abundances of top predators were still recorded despite the shortness of transects and small number of replicates. Some of the other studies listed in Table 3.8 also used a similar transect length (e.g., Sandin 2008) and captured much higher abundances of top predators. Therefore, it is possible that the absence of top predators in this study reflects actual low abundances rather than a mere drawback of methodology. This is also confirmed by recent studies that specifically aimed to quantify shark abundances in the Red Sea and found evidence of low abundances and severe fishing pressure (Spaet 2014; Spaet and Berumen 2015). Therefore, it follows that the presence of fishing in Thuwal waters could be driving the differences between this location and the others mentioned above.

Table 3.8: A comparison of mean fish biomass and top predator composition between the reef with the highest biomass in this study (Nazar Reef) and reefs with high biomass from various studies in other regions. Mean fish biomass (standardized to kg/100 m^2) from each site is shown in the fourth column, while Top predator composition indicates the percentage of top predator biomass compared to total fish biomass. There were no major differences in the way in which top predators were defined as a group across the studies.

Site	Region	Mean fish biomass (kg/100 m^2)	Top predator composition (%)	Study
Kingman Reef	Pacific	53	81	Sandin et al. 2008
Pearl & Hermes Atoll	North-Western Hawaiian Islands	47	81	Friedlander and DeMartini 2002
Kure Atoll	North-Western Hawaiian Islands	35	66	Williams et al. 2011
Jarvis Reef	Pacific	25	68	Williams et al. 2011
French Frigate Shoals	North-Western Hawaiian Islands	26	62	Friedlander and DeMartini 2002
Palmyra Atoll	Pacific	25	64	Sandin et al. 2008
Ducie Island	Pacific	16	63	Friedlander et al. 2014
Deep South	Red Sea, Sudan	43	67	Kattan (2014)
Nazar Reef	Red Sea, Saudi Arabia	17	35	This study

Top predators such as sharks, jacks, and groupers are critical in forming and maintaining the structure of reef communities, and overfishing these groups can lead to trophic cascades and overall loss of diversity (Friedlander and DeMartini 2002; Sandin et al. 2008; Salomon et al.

2010; Houk and Musburger 2013). Thus, the trophic structure on Thuwal reefs suggests potentially poor resilience and points to a possible overfishing problem. Currently, there is substantial and growing evidence of severe overfishing in the Saudi Arabian Red Sea. Jin et al. (2012) have shown in a study based on several decades of fishing data that Saudi Arabian fisheries have been operating beyond sustainable levels since the 1990s, and Spaet and Berumen (2015) have shown evidence of unsustainable elasmobranch fisheries based on two years of fish market surveys. The biomass and trophic structure observed on Thuwal reefs in this study, therefore, could be a confirmation of overfishing.

Herbivores are an essential functional group for maintaining the resilience of reefs, as they assist coral recruitment and recovery from disturbances by keeping macroalgae under control (Williams and Polunin 2001; Hughes et al. 2007; Ledlie et al. 2007). The higher biomass of herbivores on offshore compared to inshore reefs in Thuwal (Figure 3.2 a) indicates that offshore reefs may be relatively more resilient to disturbances than inshore reefs. However, it is unknown whether the biomass of herbivores on Thuwal reefs, while large relative to other trophic groups, is sufficient to maintain reef resilience (Khalil et al. 2013).

The lack of a relationship between distance from the Thuwal fishing port and commercial fish biomass (Figure 3.4) may suggest that the fishing pressure in the area is relatively homogeneous. Similarly, in the Sudanese Red Sea, where fishing is also mostly artisanal and done using similar equipment and boats, Kattan (2014) did not find an increase in top predator biomass with increasing distance from port except for sites that were further than 100 km.

Therefore, it is likely that all Thuwal reefs, which are no more than about 25 km from port, are within easy access to local fishermen. The observed lack of top predators at all sites, that are also preferred fisheries species (Spaet and Berumen 2015), supports this interpretation of more-or-less equal impacts across these reefs.

3.4.2. Coral and Algal Cover

Coral cover differed significantly between inshore reefs as a group and other reefs, which could be due to the impact of the 2010 bleaching event (Furby et al. 2013; Pineda et al. 2013). It appears that these inshore reefs have not yet recovered their coral cover in the top 10 meters in the ~3 years that passed between the bleaching event and the commencement of data collection for this study. Studies from other locations, such as the Great Barrier Reef, have also found that coral cover on inshore reefs tended to decline more severely than on offshore reefs following disturbances (e.g., Sweatman et al. 2007). However, recovery time was found to be highly variable; while some studies reported relatively rapid recovery of coral cover following disturbance (e.g., ~2.5 years reported by Hughes et al. (2007)), others reported that, even after six years, many inshore reefs hardly recovered any lost coral cover (Sweatman et al. 2011). Others still have found that, in Moorea, several decades following repeated disturbances, considerable coral cover was recovered; however, there were long-term changes in coral community structure that indicated low resilience (Pratchett et al. 2011). However, in the absence of benthic data from before the bleaching event, it is difficult to confirm that the impact of the bleaching drove the difference between inshore and offshore reefs.

At the same time, inshore reefs in this study have higher coverage of turf algae, which could be explained by the high abundance of the farming damselfish species, *Stegastes nigricans* (see section 3.4.4) as well as relatively low herbivore biomass. This supports the previous speculation that offshore reefs in the Thuwal area may be more resilient relative to inshore reefs, since high abundances of turf algae and *S. nigricans* are often considered indicators of a degraded habitat (White and O'Donnell 2010). Continued monitoring of the reefs and larger datasets may allow stronger inferences about the level of reef resilience in Thuwal to be made in the future (Bellwood et al. 2004; Pratchett et al. 2011).

3.4.3. Diversity

Although previous studies have found benthic cover, diversity, and complexity to be correlated with fish species richness (e.g., Roberts and Ormond 1987; Chabanet et al. 1997; Chong-Seng et al. 2012), I found no such patterns on Thuwal reefs neither with coral cover nor genus richness. This could be due to different stresses impacting the fish and benthic communities in different ways. Fishing pressure has less direct impact on benthic communities, and a bleaching event has less direct impact on fish communities. Alternatively, the lack of correlation between fish and benthic diversity here could be due to inadequate sampling. Therefore, for this study, the relationship between fish and benthic diversity may be observable only on the level of qualitative assemblage rather than total quantitative richness.

3.4.4. Fish and Benthic Community Assemblages

It appears that, especially in the shallow depths, inshore reefs are markedly different in fish and benthic community assemblage from other reefs in the area, and it is likely that the change in the benthic community that was brought about by the bleaching event of 2010 is the main driver of these differences.

Furby et al. (2013) had found that, prior to the bleaching, coral assemblages (genus level abundances and coral cover) were similar on inshore and offshore Thuwal reefs, and that the post-bleaching differences were mostly caused by a decline in acroporids and pocilloporids on inshore reefs, which are faster-growing corals that tend to be more susceptible to bleaching (Marshall and Baird 2000). Very similar trends were also reported in other locations, e.g., in Moorea by Berumen and Pratchett (2006). This study supports these findings and also shows turf algae to be one of the main contributors to the dissimilarity between inshore and offshore shallow communities. Similarly, the slow-growing genus *Porites* was found to be a more characteristic community component on inshore reefs, while *Acropora, Pocillopora,* and *Stylophora* were important components of distinguishing assemblages only on midshelf and offshore shallow communities. Further, the higher abundance of sand and rubble observed at 10 m inshore assemblages could be explained by the difference in the surrounding bathymetry between inshore and offshore reefs; at 10 m, inshore reefs are closer to the bottom of the slope where there is more sedimentation, while offshore reefs are surrounded by deeper water.

Herbivore assemblages are commonly recognized as a key functional component of coral reef communities (Lewis 1986; Hughes et al. 2007; Adam et al. 2011). On Thuwal reefs, very similar herbivore assemblages were found on all reefs except the inshore reefs. Offshore communities were characterized by the surgeonfishes *Acanthurus sohal, Naso unicornis, Ctenochaetus striatus,* and *A. nigrofuscus,* while inshore communities were dominated mostly by the farming damselfish *Stegastes nigricans.* This correlates well with the higher abundance of turf algae inshore and presents a potential difficulty for the recovery process of inshore reefs. These territorial damselfish promote the mono-cultural growth of algae on reef flats and crests, subsequently preventing settlement by corals and other invertebrates (e.g., White and O'Donnell 2010), whereas other types of grazers, such as surgeonfishes and parrotfishes, tend to remove algae and promote invertebrate settlement (Vine 1974; Jones et al. 2006). Thus, functional diversity is compromised on inshore reefs, potentially lowering their resilience (Bellwood et al. 2004).

On the deeper transects, fish assemblages were very similar across all reefs except for two of the inshore reefs. With regards to both biomass and numerical density, the offshore communities seem to be dominated by planktivorous fishes, such as *Caesio lunaris*, *Chromis dimidiata, Chromis flavaxilla,* and *Pseudanthias squamipinnis*; these contributed the most to the similarity within the offshore reef cluster. This may be due to a higher influx of zooplankton on more exposed reefs.

3.5. Conclusions

The findings of this study can be summarized as follows:

1) Fish biomass on Thuwal reefs increases moderately with distance from shore.
2) Fish biomass on Thuwal reefs is low compared to other reef systems around the world that are considered "healthy" as well as relative to some sites within the Red Sea itself.
3) Most of the fish biomass on all reefs belonging to herbivores; top-predators are sparse in abundance.
4) Commercially valuable fish are low in abundance throughout the area.
5) There are a few dissimilarities in benthic and fish assemblages which are mostly found between inshore reefs as a group and all other reefs:
    a. Inshore benthic communities are characterized by having more turf algae and slow-growing corals compared to offshore reefs.
    b. Farming damselfish dominate shallow inshore herbivore communities compared to more diverse herbivore communities on offshore reefs.
    c. A few planktivorous species characterize offshore reef assemblages and are much less abundant on inshore reefs.

The findings of this study are somewhat limited by the sample size and methodology. Longer transects and more depth and reef replicates could allow for more spatial trends to be discovered and would also be more appropriate for capturing the abundance of top predators. Nevertheless, the results point to several general issues which should be taken into account while considering the spatial prioritization of reefs for designing a local MPA in Thuwal, depending on the goals of this MPA. The results could even be used to help in deciding what the goals for such an MPA should be. For example, since the study highlighted the possibility that Thuwal reefs may be overexploited by fishing, it could be concluded that one of the main goals of a local MPA should be to lower the fishing pressure and preserve or increase fish biomass; and, by showing that offshore reefs tended to have higher fish biomass, the study suggests that offshore reefs should potentially be prioritized in a management plan that has these goals.

These considerations regarding the potential goals of a local MPA in Thuwal as well as multiple possible designs to meet these goals are the focus of the next chapter.

References

Adam TC, Schmitt RJ, Holbrook SJ, Brooks AJ, Edmunds PJ, Carpenter RC, Bernardi G (2011) Herbivory, connectivity, and ecosystem resilience: response of a coral reef to a large-scale perturbation. PLoS One 6:e23717

Alwany MA, Stachowitsch M (2007) Distribution and diversity of six common reef fish families along the Egyptian coast of the Red Sea. Journal of Fisheries and Aquatic Science 2:1-16

Arrigoni R, Berumen ML, Terraneo TI, Caragnano A, Bouwmeester J, Benzoni F (2014) Forgotten in the taxonomic literature: resurrection of the scleractinian coral genus Sclerophyllia (Scleractinia, Lobophylliidae) from the Arabian Peninsula and its phylogenetic relationships. Systematics and Biodiversity 13:140-163

Balmford A, Green MJB, Murray MG (1996) Using Higher-Taxon Richness as a Surrogate for Species Richness: I. Regional Tests. Proceedings B 263:1267-1274

Beenaerts N, Berghe EV (2005) Comparative study of three transect methods to assess coral cover, richness and diversity. Western Indian Ocean J Mar Sci 4:29–37

Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. Nature 429:827-833

Berumen M, Pratchett M (2006) Recovery without resilience: persistent disturbance and long-term shifts in the structure of fish and coral communities at Tiahura Reef, Moorea. Coral Reefs 25:647-653

Berumen ML, Hoey AS, Bass WH, Bouwmeester J, Catania D, Cochran JEM, Khalil MT, Miyake S, Mughal MR, Spaet JLY, Saenz-Agudelo P (2013) The status of coral reef ecology research in the Red Sea. Coral Reefs 32:737-748

Bett BJ, Narayanaswamy BE (2014) Genera as proxies for species and diversity: tested across a deep-water Atlantic-Arctic boundary. Marine Ecology 35:436-444

Bouchon-Navaro Y, Bouchon C (1989) Correlations between chaetodontid fishes and coral communities of the Gulf of Aqaba (Red Sea). In: Motta P (ed) The butterflyfishes: success on the coral reef. Springer Netherlands, pp47-60

Bouwmeester J, Benzoni F, Baird AH, Berumen ML (2015) *Cyphastrea kausti* sp. n. (Cnidaria, Anthozoa, Scleractinia), a new species of reef coral from the Red Sea. ZooKeys:1-13

Chabanet P, Ralambondrainy H, Amanieu M, Faure G, Galzin R (1997) Relationships between coral reef substrata and fish. Coral Reefs 16:93-102

Chong-Seng KM, Mannering TD, Pratchett MS, Bellwood DR, Graham NAJ (2012) The influence of coral reef benthic condition on associated fish assemblages. Plos One 7

Clarke K, Gorley R (2006) PRIMER: User manual/tutorial. PRIMER-E, Plymouth

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18:117-143

Davis KA, Lentz SJ, Pineda J, Farrar JT, Starczak VR, Churchill JH (2011) Observations of the thermal environment on Red Sea platform reefs: a heat budget analysis. Coral Reefs 30:25-36

DesRosiers N (2011) Growth and naturation of *Plectropomus* spp. in the Saudi Arabian Red Sea. Master of Science Thesis. King Abdullah University of Science and Technology, Saudi Arabia

DeVantier L, Turak E, Al-Shaikh K, De ath G (2000) Coral communities of the central-northern Saudi Arabian Red Sea. Fauna of Arabia 18:23-66

Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Marine Pollution Bulletin 50:125-146

Friedlander AM, DeMartini EE (2002) Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. Marine Ecology Progress Series 230:253-264

Friedlander AM, Caselle JE, Ballesteros E, Brown EK, Turchik A, Sala E (2014) The real bounty: Marine biodiversity in the Pitcairn Islands. PLoS ONE 9:e100142

Froese R, Pauly D (2014) FishBase. World Wide Web electronic publication. www.fishbase.org

Furby KA, Bouwmeester J, Berumen ML (2013) Susceptibility of central Red Sea corals during a major bleaching event. Coral Reefs 32:505-513

Goetze JS, Fullwood LAF (2013) Fiji’s largest marine reserve benefits reef sharks. Coral Reefs 32:121-125

Green A, Smith SE, Lipsett-Moore G, Groves C, Peterson N, Sheppard S, Lokani P, Hamilton R, Almany J, Aitsi J, Bualia L (2009) Designing a resilient network of marine protected areas for Kimbe Bay, Papua New Guinea. Oryx 43:488-498

Heip CHR, Herman PMJ, Soetaert K (1998) Indices of diversity and evenness. Océanis 24:61-87

Houk P, Musburger C (2013) Trophic interactions and ecological stability across coral reefs in the Marshall Islands. Marine Ecology Progress Series 488:23-34

Huang D, Benzoni F, Arrigoni R, Baird AH, Berumen ML, Bouwmeester J, Chou LM, Fukami H, Licuanan WY, Lovell ER, Meier R, Todd PA, Budd AF (2014) Towards a phylogenetic classification of reef corals: the Indo-Pacific genera Merulina, Goniastrea and Scapophyllia (Scleractinia, Merulinidae). Zoologica Scripta 43:531-548

Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L, Moltschaniwskyj N, Pratchett MS, Steneck RS, Willis B (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. Current Biology 17:360-365

Jessen C, Lizcano JFV, Bayer T, Roder C, Aranda M, Wild C, Voolstra CR (2013) In-situ effects of eutrophication and overfishing on physiology and bacterial diversity of the Red Sea coral *Acropora hemprichii*. PloS One 8:e62091

Jin D, Kite-Powell HL, Hoagland P, Solow AR (2012) A bioeconomic analysis of traditional fisheries in the Red Sea off the coast of the Kingdom of Saudi Arabia. Marine Resource Economics 27:137-148

Jones GP, Santana L, McCook LJ (2006) Resource use and impact of three herbivorous damselfishes on coral reef communities. Marine Ecology Progress Series 328:215-224

Kattan A (2014) Baselines and comparison of Red Sea fish assemblages in the central Red Sea. Master of Science Thesis. King Abdullah University of Science and Technology, Kingdom of Saudi Arabia

Khalil M, Cochran JM, Berumen M (2013) The abundance of herbivorous fish on an inshore Red Sea reef following a mass coral bleaching event. Environmental Biology of Fishes 96:1065-1072

Ledlie MH, Graham NAJ, Bythell JC, Wilson SK, Jennings S, Polunin NVC, Hardcastle J (2007) Phase shifts and the role of herbivory in the resilience of coral reefs. Coral Reefs 26:641-653

Lewis SM (1986) The role of herbivorous fishes in the organization of a Caribbean reef community. Ecological Monographs 56:183-200

Malcolm H, Jordan A, Smith SA (2010) Biogeographical and cross-shelf patterns of reef fish assemblages in a transition zone. Mar Biodiv 40:181-193

Margules CR, Pressey RL (2000) Systematic conservation planning. Nature 405:243-253

Marshall PA, Baird AH (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. Coral Reefs 19:155-163

Mervis J (2009) The big gamble in the Saudi desert. Science 326:354-357

Nemeth M, Appeldoorn R (2009) The distribution of herbivorous coral reef fishes within fore-reef habitats: the role of depth, light and rugosity Caribbean Journal of Science 45:247-253

PERSGA/GEF (2003) Coral reefs in the Red Sea and Gulf of Aden: Surveys 1990 to 2000 Summary and recommendations PERSGA Technical Series No 7. PERSGA, Jeddah

Pratchett M, Trapon M, Berumen M, Chong-Seng K (2011) Recent disturbances augment community shifts in coral assemblages in Moorea, French Polynesia. Coral Reefs 30:183-193

Price ARG, Jobbins G, Shepherd ARD, Ormond RFG (1998) An integrated environmental assessment of the Red Sea coast of Saudi Arabia. Environmental Conservation 25:65-76

Roberts CM, Alexander RDS, Ormond RFG (1992) Large-scale variation in assemblage structure of Red Sea butterflyfishes and angelfishes. Journal of Biogeography 19:239-250

Roberts MB, Jones GP, McCormick MI, Munday PL, Neale S, Thorrold S, Robitzch VS, Berumen ML (In review) Homogeneity of coral reef communities across 8 degrees of latitude in the Saudi Arabian Red Sea. Marine Pollution Bulletin

Robertson DR, Choat JH, Posada JM, Pitt J, Ackerman JD (2005) Ocean surgeonfish Acanthurus bahianus. II. Fishing effects on longevity, size and abundance? Marine Ecology Progress Series 295:245-256

Robbins WD, Hisano M, Connolly SR, Choat JH (2006) Ongoing collapse of coral-reef shark populations. Current Biology 16:2314-2319

Salomon AK, Gaichas SK, Shears NT, Smith JE, Madin EMP, Gaines SD (2010) Key features and context-dependence of fishery-induced trophic cascades. Conservation Biology 24:382-394

Sandin SA, Smith JE, DeMartini EE, Dinsdale EA, Donner SD, Friedlander AM, Konotchick T, Malay M, Maragos JE, Obura D, Pantos O, Paulay G, Richie M, Rohwer F, Schroeder RE, Walsh S, Jackson JBC, Knowlton N, Sala E (2008) Baselines and degradation of coral reefs in the Northern Line Islands. PLoS ONE 3:e1548

Sheppard C, Price A, Roberts C (1992) Marine ecology of the arabian region: Patterns and processes in extreme tropical environments. Academic Press Ltd., London, England, Uk; San Diego, California, USA

Spaet JL (2014) Integrating fisheries dependent and independent approaches to assess fisheries, abundance, diversity, distribution and genetic connectivity of Red Sea elasmobranch populations. PhD Thesis. King Abdullah University of Science and Technology, Saudi Arabia,

Spaet JLY, Berumen ML (2015) Fish market surveys indicate unsustainable elasmobranch fisheries in the Saudi Arabian Red Sea. Fisheries Research 161:356-364

Spaet JLY, Thorrold SR, Berumen ML (2012) A review of elasmobranch research in the Red Sea. Journal of Fish Biology 80:952-965

Sweatman H, Delean S, Syms C (2011) Assessing loss of coral cover on Australia's Great Barrier Reef over two decades, with implications for longer-term trends. Coral Reefs 30:521-531

Sweatman H, Thompson A, Delean S, Davidson J, Neale S (2007) Status of near-shore reefs of the Great Barrier Reef 2004

Terraneo, TI; Berumen, ML; Arrigoni, R; Waheed, Z; Bouwmeester, J; Caragnano, A; Stefani, F; Benzoni, F (2014) *Pachyseris inattesa* sp. n. (Cnidaria, Anthozoa, Scleractinia): a new reef coral species from the Red Sea and its phylogenetic relationships. ZooKeys 433: 1–30

Tornabene L, Ahmadia GN, Berumen ML, Smith DJ, Jompa J, Pezold F (2013) Evolution of microhabitat association and morphology in a diverse group of cryptobenthic coral reef fishes (Teleostei: Gobiidae: Eviota). Molecular Phylogenetics and Evolution 66:391-400

van der Merwe R, Röthig T, Voolstra CR, Ochsenkühn MA, Lattemann S, Amy GL (2014) High salinity tolerance of the Red Sea coral *Fungia granulosa* under desalination concentrate discharge conditions: An in situ photophysiology experiment. Frontiers in Marine Science 1

Vine PJ (1974) Effects of algal grazing and aggressive behaviour of the fishes *Pomacentrus lividus* and *Acanthurus sohal* on coral-reef ecology. Marine Biology 24:131-136

White J-SS, O'Donnell JL (2010) Indirect effects of a key ecosystem engineer alter survival and growth of foundation coral species. Ecology 91:3538-3548

Williams ID, Richards BL, Sandin SA, Baum JK, Schroeder RE, Nadon MO, Zgliczynski B, Craig P, McIlwain JL, Brainard RE (2011) Differences in reef fish assemblages between populated and remote reefs spanning multiple archipelagos across the central and western Pacific. Journal of Marine Biology 2011:14

Williams IW, Polunin NP (2001) Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. Coral Reefs 19:358-366

CHAPTER 4: EXPLORING SPATIAL MPA PRIORITY SITES FOR MULTIPLE GOALS

4.1. Introduction

The management of reefs with well-designed marine protected areas (MPAs) along with other measures is generally regarded as the best insurance against overexploitation and declines of coral reef ecosystems (Allison et al. 1998; Halpern and Warner 2002; Halpern 2003). Increasing threat levels from climate change and human use, as well as global scale declines, necessitate the establishment of reactive and/ or proactive protected areas (Bellwood et al. 2004; Veron et al. 2009). MPA networks are most effective when they are properly designed, have clear objectives, and are based on sound scientific and socio-economic knowledge of the region of interest (Margules and Pressey 2000; Tear et al. 2005).

Generally, most MPA objectives fall under two main goals: either to maintain biodiversity in order to preserve the environment and maintain ecosystem services (Worm et al. 2006), or to support and enhance fisheries (Barnes and Sidhu 2013; Januchowski-Hartley et al. 2013; Green et al. 2014). These two goals have been previously shown to create trade-offs, influencing the process of spatial prioritization in a conflicting manner depending on the goal being considered (Hastings and Botsford 2003; Klein et al. 2008). Enhancing fisheries typically requires small reserves spaced close enough to each other to allow for the export of larvae to other reserves and fished areas and to allow for the spillover of adult fish into fished areas as biomass increases within reserves (McClanahan and Mangi 2000; Kelly et al. 2002; Tewfik and

Bene 2003; Hilborn et al. 2004; Pelc et al. 2010b). Ultimately, an MPA with a fisheries objective aims to increase the financial income from fishing to benefit fishermen and the local economy. On the other hand, biodiversity conservation goals typically require fewer, larger, reserves that can include full dispersal ranges of species of interest and all habitat types needed in their life cycles (Lomolino 1994; Almany et al. 2009; McCook et al. 2009), and their ultimate purpose is to preserve nature and maintain ecosystem services besides fishing income (e.g. coastal protection, recreational value, etc.). However, recent studies have shown that it may be possible to achieve both fisheries and biodiversity conservation goals simultaneously (e.g., Klein et al. 2009; Gaines et al. 2010; Schmiing et al. 2014).

In Thuwal, there is an opportunity to work out the best MPAs based on social and ecological factors and objectives, given that existing protection is minimal. Since there are no existing local MPAs (see Chapter 1) and hardly any knowledge of stakeholder interest or political will for implementation, it would be particularly beneficial to provide multiple alternative options and present different reserve scenarios for consideration (Tear et al. 2005). In the previous chapter, a considerable amount of information was obtained regarding ecological and biodiversity patterns on Thuwal reefs. Building this foundation of knowledge is one of the essential requirements for science-based systematic conservation planning, following the identification of conservation objectives (Margules and Pressey 2000; Tear et al. 2005). In this chapter, I define fisheries and biodiversity objectives for a potential local MPA in Thuwal, selecting species that would serve these goals and identifying the quantities to be included in MPAs. I then use the data provided by the previous chapter and a decision-making software tool

(Marxan, Ball et al. 2009) to explore whether conservation priority sites differ for fisheries objectives and biodiversity objectives, taking into consideration both the spatial configurations of suggested MPAs and their ability to protect the chosen quantities of different species. Based on the results of the previous chapter, it is expected that fisheries solutions would be more spatially biased towards offshore reefs, while biodiversity solutions would be more biased towards midshelf and inshore reefs. I also answer the questions: How do the best fisheries and biodiversity reserve solutions differ when minimum versus maximum recommended quantitative objectives are considered? And how do various practical considerations specific to the Thuwal area affect the spatial solutions?

4.2. Methods

4.2.1. Study Area

The study area is the same as that described in Chapter 3 (and shown in Figure 3.1) and Chapter 2 (Figure 2.2 a) and includes 355 reefs off the coast of Thuwal in the central Saudi Arabian Red Sea. The individual reefs were used as irregular planning units (PUs) in Marxan input files.

4.2.2. Marxan

The software Marxan (Ball et al. 2009) was used to produce multiple spatial designs for reserve networks in the Thuwal area and analyze the similarities and differences between them. Marxan optimizes solutions for reserve networks that achieve conservation targets defined by the user for the least possible costs (Possingham et al. 2000; Ball et al. 2009). Marxan uses a simulated annealing algorithm to select a set of spatial planning units (PUs) that achieve the conservation targets most efficiently. Every solution produced by Marxan has a score that is the sum of the cost of the reserve system, plus its boundary length (a measure of the spatial compactness of the solution), and a penalty if any conservation target is not fully met in the solution; this is the “objective function” that the algorithm attempts to minimize (Game and Grantham 2008). Marxan was selected for this analysis for several reasons: 1) It has the ability to produce multiple feasible solutions for each scenario of interest and/or for multiple target levels, thus making it possible for users to assess more than one reserve alternative; 2) it can potentially be used in the future to evaluate reserves that may be put in place (e.g., Stewart et al. 2003; Allnutt et al. 2012; Schmiing et al. 2014); and 3) it is a fairly simple, adaptable, and free tool that can be used by scientists and managers alike (Ball et al. 2009). Marxan is now widely used in marine, freshwater, and terrestrial conservation as a highly popular aid in decision-making (Stewart et al. 2003; Klein et al. 2009; Beger et al. 2010; Hermoso et al. 2012; Schmiing et al. 2014).

4.2.3. Conservation Objectives and Conservation Features

The two main conservation objectives considered in this analysis were fisheries and biodiversity objectives. I define fisheries objectives as those that ultimately aim to increase the biomass of species that are commercially important to local fishermen. In this study, achieving this objective required the inclusion of specific biomass proportions of as many commercial fish species as possible depending on data availability. The assumption in this case is that preserving areas with high densities of these fish would improve their reproductive output both inside and outside MPAs (McClanahan and Mangi 2000; Williamson et al. 2004). Biodiversity objectives are defined as those objectives that aim to preserve biodiversity by including adequate proportions of the different fish and benthic community assemblages found locally, as well as all endemic fish species into MPAs.

"Conservation feature" is the term used in Marxan to describe any feature of interest for conservation. In this study, conservation features are the specific fish species and benthic categories (Table 4.1) selected to achieve the above objectives. Each conservation feature is given a "target", which is the quantitative proportion to be included within a reserve network.

The fish species used to prepare conservation features were selected based on one of the following factors: 1) they are important to Thuwal fisheries and are highly targeted by fishermen (thus, including them fulfils fisheries objective), 2) they are endemic to the Red Sea (fulfilling biodiversity objective), or 3) based on previously conducted multivariate analysis (Chapter 3), they contributed highly to dissimilarities between inshore and offshore reef communities within the study area (thus representing different assemblages to fulfil biodiversity objective). The top 11 species shown in Table 4.1 are all fish species which were chosen as representatives of commercial fishes (4 groupers, 5 parrotfish, and 2 snappers). The species *Caesio lunaris, Pseudanthias squamipinnis, Acanthurus sohal,* as well as the grouper *Cephalopholis hemistiktos* (which was also included with the commercial fish species) were chosen based on the results of the multivariate analyses conducted in the previous chapter. Including these species as conservation features ensures that the resulting reserve network would be representative of different communities found in the study area. Finally, the species *Chromis dimidiata, Amphiprion bicinctus,* and *Thalassoma rueppellii* were selected because they are endemic to the Red Sea, and thus, are of high biodiversity conservation value.

Five benthic categories were selected to create the remaining 10 conservation features. Three coral genera, *Acropora, Pocillopora*, and *Porites*, and the categories "rock" (which stands for bare rock substrate) and crustose coralline algae ("CCA"). Similarly to some of the fish species mentioned above, all five categories were found through multivariate analyses (Chapter 3) to contribute to dissimilarities between inshore and offshore communities and selected accordingly. (In order to minimize the inaccuracy of the modeling process described below, species or benthic categories which were very low in abundance or absent in more than 3 of the 9 surveyed reefs were excluded from the selection process.)

The average abundances of the selected fish species and the average percent cover of the selected benthic categories were modeled from the results of visual surveys conducted in the study described in the previous chapter. Nine reefs were surveyed at different distances from shore and spanning the north-south extent of the study area (see Chapter 3, Figure 3.1). A spatial splining function was then used in ArcGIS to approximately predict the abundance of each category on reefs where data were not collected directly. Splining was chosen because it applies a smooth approximation function and is a simple method that can be applied quickly and in regions where environmental data is not sufficient to create sophisticated abundance models. The predicted abundances were then rescaled to a standardized scale of 0 – 100 and categorized into low (0 – 34%), medium (35 – 67%), and high (68 – 100%) abundance for the fish species, and low (0 – 50%) and high (51 – 100%) cover for benthic categories. Thus, each fish species was divided into three conservation features, and each benthic category was divided into two conservation features (total = 60 conservation features).

Table 4.1: A list of conservation features (species and benthic categories), their abundance classes, the conservation scenario types in which they were included in Marxan runs, and their minimum and maximum target levels. FS stands for fisheries scenario, BS stands for biodiversity scenario, and CCA stands for crustose coralline algae. The first 11 species are representatives of species important to fisheries (4 groupers, 5 parrotfish, and 2 snappers). Other fish species and benthic categories listed represent different community assemblages on Thuwal reefs. Endemic species are marked with an (*).

Conservation feature	Abundance (%)/ mean cover (%)	Scenario type	Minimum target (%)	Maximum target (%)
Aethaloperca rogaa	low (0 - 34)	FS	0	0
A. rogaa	medium (35 - 67)	FS	5	15
A. rogaa	high (68 - 100)	FS	10	30
Cephalopholis argus	low	FS	0	0
C. argus	medium	FS	5	15
C. argus	high	FS	10	30
Cephalopholis hemistiktos	low	FS, BS	0	0
C. hemistiktos	medium	FS, BS	5	15
C. hemistiktos	high	FS, BS	10	30
Cephalopholis miniata	low	FS	0	0
C. miniata	medium	FS	5	15
C. miniata	high	FS	10	30
Scarus niger	low	FS	0	0
S. niger	medium	FS	5	15
S. niger	high	FS	10	30
Scarus ferrugineus	low	FS	0	0
S. ferrugineus	medium	FS	5	15
S. ferrugineus	high	FS	10	30
Chlorurus sordidus	low	FS	0	0
C. sordidus	medium	FS	5	15
C. sordidus	high	FS	10	30
Hipposcarus harid	low	FS	0	0
H. harid	medium	FS	5	15
H. harid	high	FS	10	30
Cetoscarus bicolor	low	FS	0	0
C. bicolor	medium	FS	5	15
C. bicolor	high	FS	10	30
Lutjanus bohar	low	FS	0	0
L. bohar	medium	FS	5	15
L. bohar	high	FS	10	30
Lutjanus ehrenbergii	low	FS	0	0
L. ehrenbergii	medium	FS	5	15
L. ehrenbergii	high	FS	10	30

Caesio lunaris	low	BS	0	0
C. lunaris	medium	BS	5	15
C. lunaris	high	BS	10	30
Pseudanthias squamipinnis	low	BS	0	0
P. squamipinnis	high	BS	10	30
Acanthurus sohal	low	BS	0	0
A. sohal	medium	BS	5	15
A. sohal	high	BS	10	30
*Chromis dimidiata**	low	BS	0	0
C. dimidiata	medium	BS	5	15
C. dimidiata	high	BS	10	30
*Amphiprion bicinctus**	low	BS	0	0
A. bicinctus	medium	BS	5	15
A. bicinctus	high	BS	10	30
*Thalassoma rueppellii**	low	BS	0	0
T. rueppellii	medium	BS	5	15
T. rueppellii	high	BS	10	30
Acropora	low (0 - 50)	BS	0	0
Acropora	high (51 - 100)	BS	10	30
Pocillopora	low	BS	0	0
Pocillopora	high	BS	10	30
Porites	low	BS	0	0
Porites	high	BS	10	30
Rock	low	BS	0	0
Rock	high	BS	10	30
CCA	low	BS	0	0
CCA	high	BS	10	30

* Endemic species

4.2.4. Reserve Selection Scenarios and Target Setting for Marxan

Two main questions were explored to contrast two general conservation goals: 1) enhancing fisheries (fisheries scenarios (FSs)), and 2) biodiversity conservation (biodiversity scenarios (BSs)). The objective of fisheries scenarios is to include a set proportion of commercial fish biomass within a no-take reserve, with the assumption that this type of protection may eventually enhance biomass outside the reserve area. The objectives of biodiversity scenarios are to: 1) represent different community assemblages by including key species, and 2) represent endemic species. Two target levels were explored for each scenario type: a “minimum” target (up to 10% of each conservation feature) and a “maximum” target (up to 30% of each conservation feature).

Targets for the conservation features described in the previous section were set in a way to achieve the above objectives under minimum and maximum target levels. Targets were set to 0% for “low” abundances, 5% for “medium” abundances, and 10% for “high” abundances under the minimum target settings, while, under maximum target settings, targets were set to 0% for low abundances, 15% for medium abundances, and 30% for high abundances (Table 4.1). By setting the target for low abundance features to 0%, it is ensured that Marxan will prioritize high abundance areas (it may still “overshoot” targets). These quantities were set based on general conservation guidelines and recommendations (e.g., World Parks Congress 2003; Convention on Biological Diversity 2010) and following a similar method to the study by Schmiing et al. (2014).

For each of the two goals (fisheries and biodiversity) and target levels (minimum and maximum), multiple Marxan scenarios were run with different adjustments that may be of practical relevance to conservation planning in Thuwal, amounting to a total of 22 scenarios: 12 BSs (6 with minimum targets and 6 with maximum targets) and 10 FSs (5 with minimum targets and 5 with maximum targets). Table 4.2 lists all the different scenarios, the justification for running them, and which scenario type they were applied to. Scenario 1 was a “control” in which no reefs were preselected to be included in or excluded from the final reserve solution (locked in or out, respectively). In Scenario 2, inshore reefs (< 5 km from shore) were locked out of the final reserve (the algorithm could not include them in the final solution). This is because inshore reefs in this area have been shown to experience high levels of coral mortality in the event of thermal bleaching (Furby et al. 2013), and, since bleaching cannot be directly prevented via spatial closure, one of the common practices is to devote management resources towards the more resilient reefs in any given area (Jameson et al. 2002). (However, it is important to note that it can also be argued that protecting the less resilient reefs in order to enhance their resilience should be a higher priority, and that deciding to allocate resources towards the "weak" or "strong" areas is a complex process (Game et al. 2008).) Scenario 3 gives higher priority to 3 reefs used as long-term research monitoring sites. Scenario 4 excludes reefs smaller than 0.1 km^2 as managing and policing many such small reefs may be impractical. Scenario 5 halves the value of the largest reef in the area (which also happens to be one of the research monitoring sites) by locking half of it out of the final reserve. This scenario was done because when irregular PUs are used, as is the case in this study, the optimization algorithm is biased towards selecting larger PUs, and, since this reef is significantly larger than all others (almost 7 km^2 while most reefs are less than 1 km^2), there is a strong bias towards selecting it. I tried to remove some of this bias to explore if targets could still be met even if only half of this reef could be included in a reserve. In practice, it may be difficult to enlist local support for a reserve network that closes the whole reef to fishing, whereas closing only half of it may be feasible. Finally, scenario 7, which was only done for biodiversity scenario types locks two inshore reefs (one of which is also one of the research monitoring sites) into the final reserve. These reefs were found to be high priority sites for the objective of representing all endemic species, as 5 of the 23 endemic species recorded in the surveys discussed in Chapter 3 were found only on one of these reefs and none of the others.

Table 4.2: A summary of scenario iterations: their identification numbers, a brief description of the variable altered in each iteration, the justification for running each iteration, and the scenario type(s) and target levels in which they were attempted. FS = fisheries scenario; BS = biodiversity scenario; min = minimum target level; max = maximum target level.

Scenario iteration number	Description	Justification	Scenario type	Target level
1	No PUs were locked in or out of the final reserve.	Control run	FS, BS	min, max
2	All inshore reefs were locked out of the final reserve (status = 3 in PU file).	Inshore reefs are too vulnerable to thermal bleaching to be protected by spatial closure.	FS, BS	min, max
3	Research monitoring sites (3 PUs in total) were locked in.	These reefs are important for ongoing research purposes.	FS, BS	min, max
4	Any PUs smaller than 100000 m^2 (0.1 km^2) were locked out.	Policing the closure of many very small reefs may be impractical.	FS, BS	min, max
5	Half of the largest reef in the area was locked out.	To explore whether targets could still be met even if only half of this reef could be included in a reserve.	FS, BS	min, max
6	Two inshore reefs were locked in (status = 2).	These two reefs are "irreplaceable" for the objective of conserving all endemic species.	BS	min, max

The purpose of running all the different iterations is to explore whether some of these practical considerations would significantly change the spatial solutions generated by Marxan by making them infeasible or by making it impossible to meet all targets. In this study, I define a *feasible solution* as: a reserve network that does not include more than a third (33%) of the total reef area. Targets for each conservation feature had to be met by at least 95%.

Since none of the PUs had shared borders, the spatial compactness of solutions was not considered. Therefore, the boundary length modifier (BLM) was set to 1 in all runs. Each scenario run/iteration was set to generate 100 solutions, and the best solutions (the most feasible solutions that met the maximum number of targets) were imported into QGIS for visualization and included in further statistical analysis (section 4.2.5).

4.2.5. Economic Data

Due to the unavailability of data regarding fishing pressure in the Thuwal area, it was not possible to estimate the cost of closing reefs to fishing or create a precise cost layer. However, based on personal communication with members of the local fishing cooperative (R. Jahdali and H. Jahdali, pers. comm.) and the general ecological patterns described in the previous chapter, an assumption was made that most of the Thuwal reefs are equally heavily exploited by fishing.

In addition to fishing, there are recreational SCUBA diving and snorkeling trips organized by the only dive operator in the area (Coastline) which is based in KAUST. The trips target 34 of the 355 reefs included in this study at a frequency of about 6 – 24 trips per year, depending on weather conditions and site popularity (anonymous Coastline staff, pers. comm.). Based on trip prices per person (including full gear rental) and assuming that trips operate at full capacity (25 persons on SCUBA diving trips and 30 persons on snorkeling trips), a total revenue of approximately 3,002,250 Saudi Riyals per year was estimated from diving and snorkeling trips. However, in preliminary test runs (and assuming that reserves would be closed to recreational activities), incorporating this data as costs in Marxan input files did not appear to make any significant change to the final spatial solutions compared to runs where cost was simply set to 1 for all PUs. The total number of PUs selected and the total area of reserves did not change. This is probably because most of the 34 sites targeted by recreational trips are very small patches which are easily replaced by other small patches in the final solution. Therefore, in order to simplify the analysis, it was decided to set costs to 1 for all PUs until fishing cost data are available to be combined with recreational costs, leaving the focus of the study on biological targets and the iterations described in the previous section (Table 4.2).

4.2.6. Multivariate Analysis of Solutions

The best solutions identified from each scenario run were then used to create Bray-Curtis similarity matrices using the software PRIMER-E v.6 (Clarke and Gorley 2006) in order to explore the dissimilarity between solutions on the level of scenarios, target levels, and iterations. The original matrix is similar to the example shown in Table 4.3, where a “0” indicates the PU is absent in the solution and a value of “1” indicates the PU was selected in the solution. The Bray-Curtis similarity was chosen because it does not take into account joint absences, which would be desirable when comparing solutions as joint absences occur at high frequencies and the interest here lies in joint presences (Faith et al. 1987; Linke et al. 2011).

Table 4.3: An example of the similarity matrix used in multivariate analyses of best Marxan solutions. Rows list the scenario type, target level, and iteration number: BS = biodiversity scenarios; FS = fisheries scenarios; max = maximum target levels; min = minimum target levels; numbers indicate the iteration (number key shown in Table 4.2). Columns indicate whether planning units (PUs), which are individual reefs (355 in total), were selected (1) or not selected (0) in the best solution of the run indicated in the first column.

Scenario-target-iteration#	PU_1	…	PU_n
FS-max-1	1	…	0
FS-min-1	0	…	1
BS-max-1	1	…	1

The resemblance matrices were then used to create non-metric multidimensional scaling (nMDS) plots similar to those described and shown in Chapter 3 in order to visualize similarities between solutions. The benefit of using nMDS rather than other methods is that it is a space-conserving randomization technique that presents the multidimensional space so that it reflects true similarities (Linke et al. 2011). In addition, I performed in PRIMER a hierarchical agglomerative classification using a complete linkage clustering on the same Bray-Curtis similarity matrices. Complete linkage clustering first takes the two most similar solutions and links them as a mini-cluster. The node that links these two solutions becomes a starting point for the next cluster, and so on. Once the entire dendrogram is completed, a cutoff value of 50% similarity was chosen to identify distinct clusters, meaning, solutions had to be more than 50% similar in order to be considered within a significant cluster. This is a more conservative cutoff point than was suggested and used by Linke et al. (2011).

4.2.7. Reef Selection Frequency

As mentioned above, Marxan was set to generate 100 solutions for each scenario iteration/run. One of Marxan’s output files for each run is a summary of how many times out of 100 each reef was selected into a solution. This selection frequency is a measure of a reefs’ or planning unit's conservation priority (e.g., Schmiing et al. 2014). As a final step in the analysis, the selection frequency of each of the 355 reefs was summed across all iterations for each scenario type and visualized in ArcMap 10.2 (ESRI 2014).

4.3. Results

A summary of the best reserve networks generated by Marxan (henceforth referred to as "solutions") for all 22 scenario runs, including the number of reefs (PUs) selected, number of targets missed, and percent reef area included, is shown in Table 4.4. Maps of all best solutions can be found in Appendix 4.

Table 4.4: Summary of the best solutions of all Marxan runs. The first four columns list scenario type (FS = fisheries scenario; BS = biodiversity scenario), target levels (max = maximum target level; min = minimum target level), scenario number, and a brief description/justification of the scenario, respectively. The last three columns show how many planning units (PUs) or reefs were selected in the best solution, the number of conservation feature targets missed by more 5%, and the percent of total reef area included in the reserve. The maximum feasible limit defined in this study is 33% of reef area included in reserves.

Scenario objective	Target level	Scenario	Brief description of scenario	Number of PUs in best solution	Number of targets missed by more than 5%	Reef area included in solution (%)
FS	max	1	Control (no locks)	10	1	37.7
FS	max	2	Inshore reefs locked out	12	4	32
FS	max	3	Monitoring sites locked in	12	0	41.7
FS	max	4	Reefs < 0.1 km^2 locked out.	9	2	37.5
FS	max	5	Half of largest reef locked out.	10	1	30.2
FS	min	1	Control (no locks)	9	0	31.6
FS	min	2	Inshore reefs locked out	8	4	25.6
FS	min	3	Monitoring sites locked in	9	0	30.6
FS	min	4	Reefs < 0.1 km^2 locked out.	8	1	32.7
FS	min	5	Half of largest reef locked out.	9	0	22.9
BS	max	1	Control (no locks)	9	0	30.6
BS	max	2	Inshore reefs locked out	10	1	32.1
BS	max	3	Monitoring sites locked in	10	0	34.9
BS	max	4	Reefs < 0.1 km^2 locked out.	8	1	30.6
BS	max	5	Half of largest reef locked out.	10	1	33.4
BS	max	6	Two irreplaceable inshore reefs locked in.	10	0	32.1
BS	min	1	Control (no locks)	5	0	21.7
BS	min	2	Inshore reefs locked out	5	0	21.9
BS	min	3	Monitoring sites locked in	6	0	23.9
BS	min	4	Reefs < 0.1 km^2 locked out.	4	1	21.8

BS	min	5	Half of largest reef locked out.	6	0	17.6
BS	min	6	Two irreplaceable inshore reefs locked in.	6	0	24

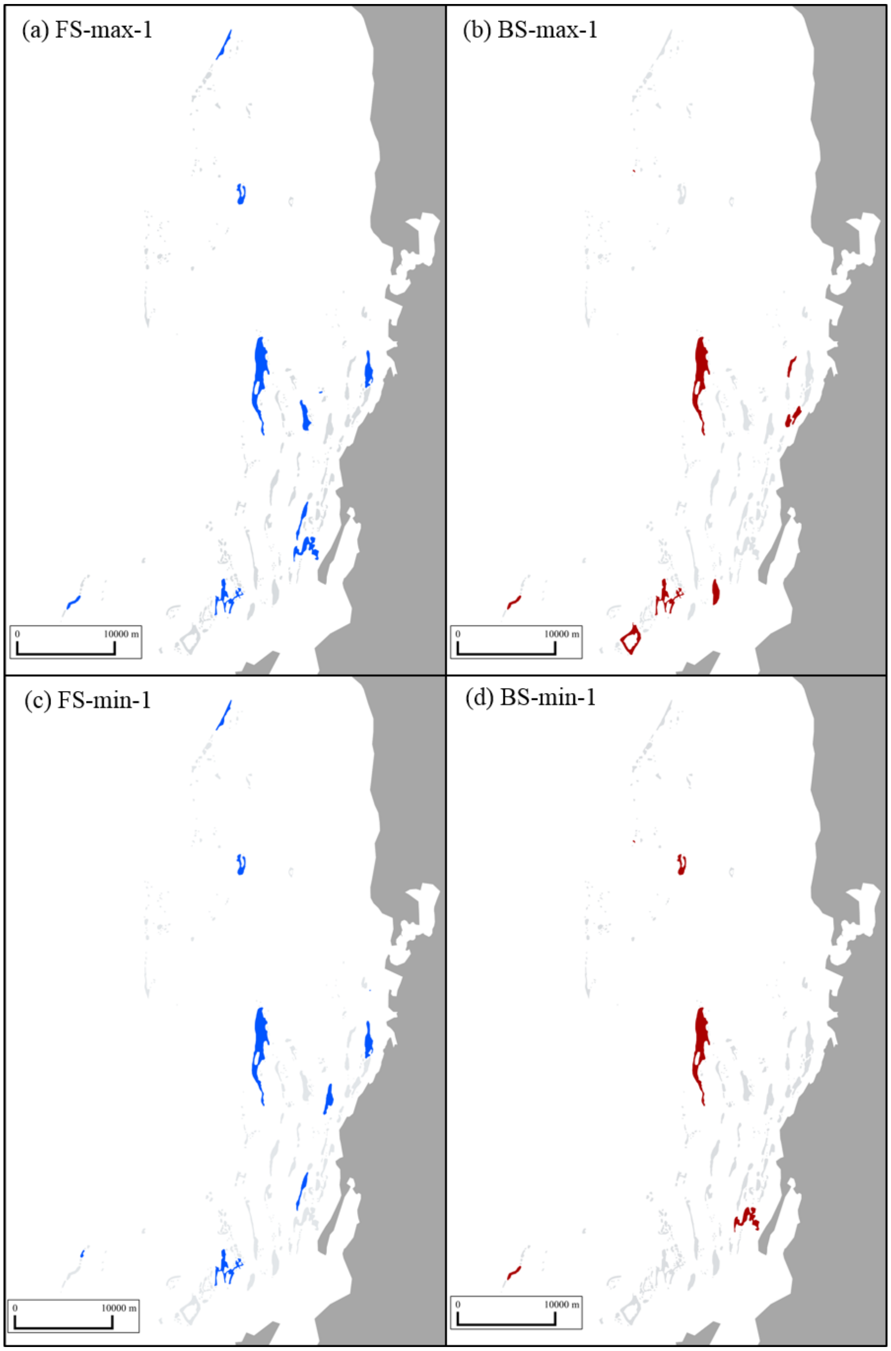


Figure 4.1: Maps of the best Marxan reserve solutions of control scenarios of fisheries and biodiversity scenarios in Thuwal, central Saudi Arabian Red Sea. Colored reef patches indicate reefs that were selected into reserves (blue = fisheries reserves, red = biodiversity reserves) while pale grey patches are non-selected reefs. Dark gray shows the mainland. FS = fisheries scenario; BS = biodiversity scenario; min = minimum target level; max = maximum target level. The number "1" indicates that the reserves shown are for the control scenarios.

4.3.1. Differences between Scenario Objectives: Fisheries vs. Biodiversity Solutions

There were several differences between fisheries and biodiversity solutions both spatially and in terms of feasibility and the ability to meet targets. Fisheries solutions generally tended to miss targets more frequently, and miss a higher number of targets, than biodiversity solutions: 6 out of 10 fisheries solutions missed 1 – 4 targets, while only 4 out of 12 biodiversity solutions missed 1 target each (Table 4.4).

Spatially, fisheries solutions tended to include a larger number of reefs (8 – 12 compared to 4 – 10 reefs for biodiversity solutions), Also, especially when attempting to meet maximum target levels, fisheries solutions selected reefs that were more spatially dispersed throughout the study area (Figure 4.1 a), while biodiversity solutions tended to select midshelf and inshore reefs unless the latter were locked out. Maps of the best solutions for all scenarios (22 maps in total) can be found in Appendix 4.

The Bray-Curtis similarity dendrogram and nMDS plot (Figure 4.2 a and b) do show some separation between fisheries and biodiversity solutions. However, as shown by the rather poor separation and wide scattering of solutions in the nMDS plot and by the mixing of scenario types occurring within clusters, the separation is not strong; there seems to be more variation *within* the two scenario types/objectives than there is between them.

Regarding feasibility, only 4 solutions out of all 22 were unfeasible (3 fisheries solutions and one biodiversity solution), selecting more than 33% of the total reef area to include in a reserve. Fisheries solutions in general were larger and closer to the feasible limit than biodiversity solutions (Table 4.5).

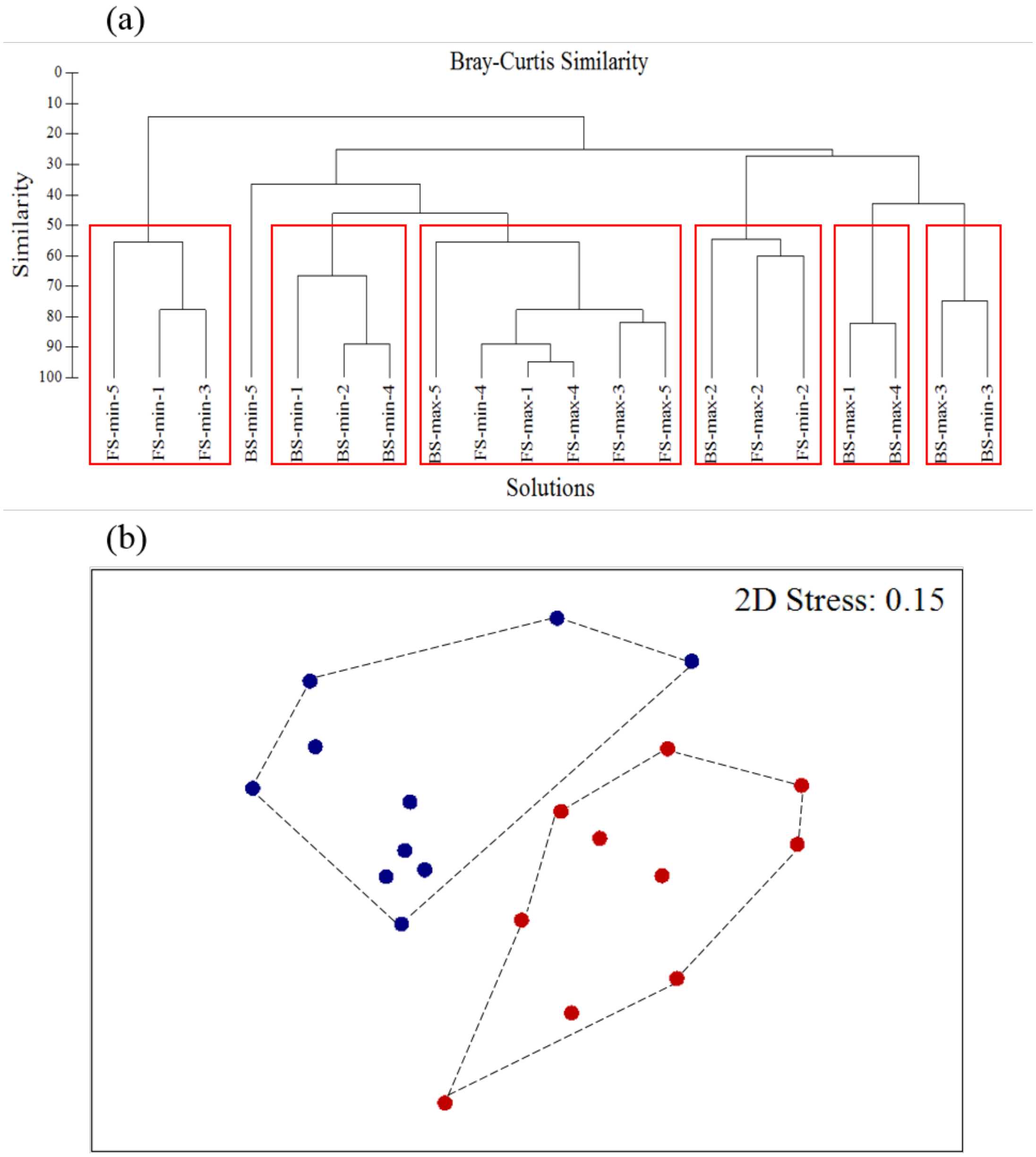


Figure 4.2: Bray-Curtis similarities between FS (fisheries) and BS (biodiversity scenario) best solutions, including maximum (max) and minimum (min) target levels and scenarios 1 – 5 (scenario number key shown in Table 4.2). The top panel (a) shows the dendrogram based on Bray-Curtis similarities. The clusters identified are shown by the

red boxes which start at the cutoff limit of 50% similarity. The bottom panel (b) shows the non-metric multidimensional scaling (nMDS) plot representing the distances between FS and BS solutions based on Bray-Curtis similarities in 2-dimensional space. Blue = FS solutions; red = BS solutions. Dotted lines outline the edges of FS and BS clusters for easier visualization. The 2-D stress value is shown in the top right corner (see main text for interpreting 2-D stress).

The conservation features that tended to have their targets partially or totally missed are shown in Table 4.5. In FS solutions, *Hipposcaris harid*-high and *Cephalopholis hemistiktos*-medium tended to be the most frequently-missed targets, followed by *C. hemistiktos*-high, *Scarus ferrugineus*-medium, and *Chlorurus sordidus*-medium. The target shortfall ranged from 15 – 78%, except for *C. hemistiktos*-medium, which was missed by 100%. As for BS solutions, missed targets were mostly attributed to Rock-high, *Porites*-high, and *C. hemistiktos*-medium. Target shortfall in BS solutions ranged only from 1 – 3%, except for *C. hemistiktos*-medium, which was missed by 100% in some iterations (Table 4.5). In all iterations where targets were missed, Marxan was only able to meet these missed targets by selecting all 355 reefs into the reserve.

4.3.2. Differences between Target Levels: Minimum vs. Maximum Target Level Solutions

Within fisheries solutions, shifting from minimum to maximum target levels added 1 – 2 reefs to the number of reefs selected (compare Figure 4.1 a and c). For 3 out of the 5 iterations, this led to the reserve size exceeding the 33% feasible limit and increased the number of missed targets by 1 (Table 4.5). On the other hand, for biodiversity scenarios, the spatial solutions almost doubled in terms of the number of reefs included (compare Figure 4.1 b and d). However, this affected the number of targets missed only in one scenario (from 0 – 1 target), which was the scenario in which half of the largest reef was locked out (scenario 5). It also led to an increase in reserve size beyond the feasible limit only once (iteration 3, where monitoring sites were locked in) without missing any targets (Table 4.5), and, even then, the feasible limit was exceeded only by about 2%.

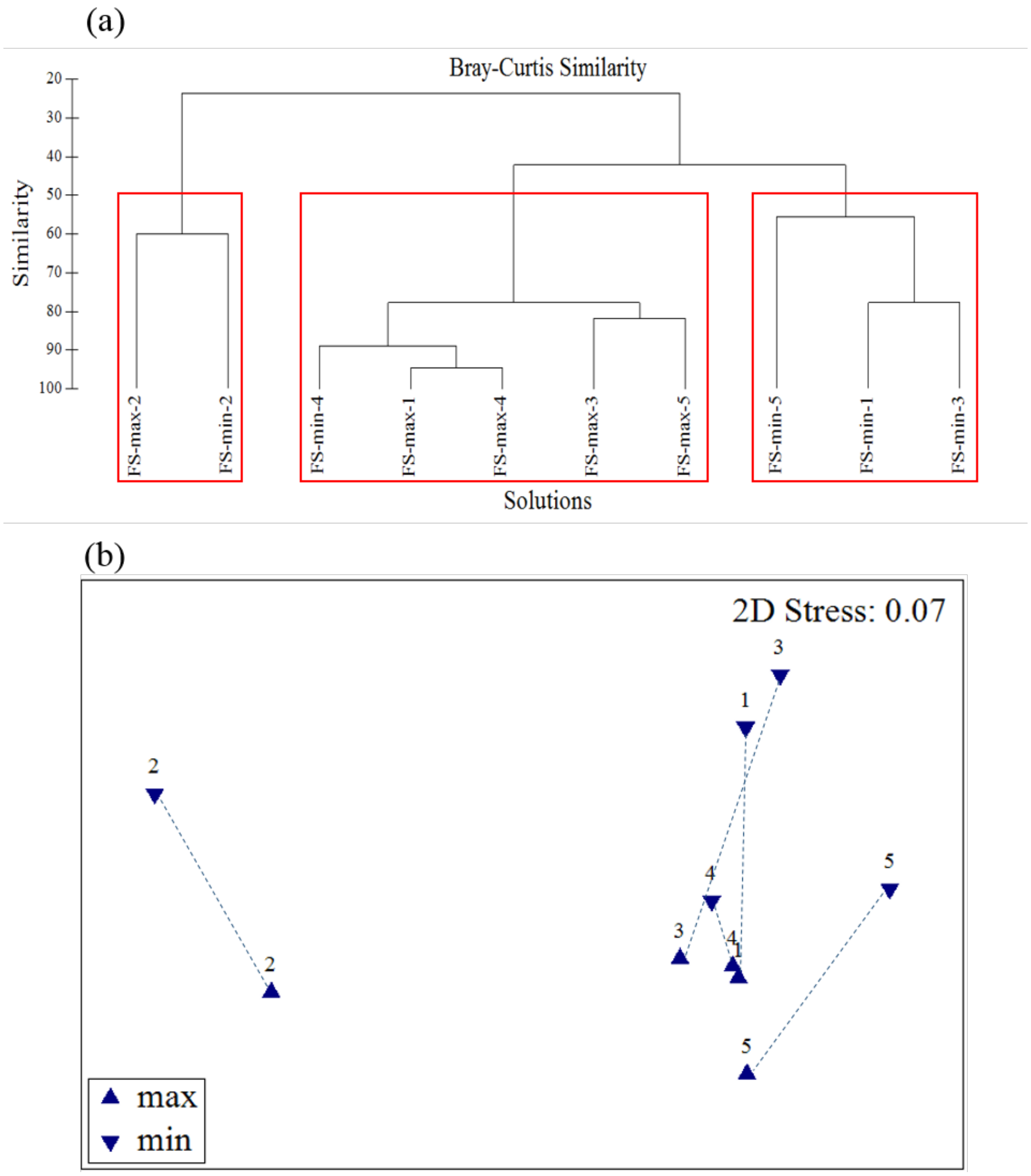


Figure 4.3: Bray-Curtis similarities between FS (fisheries scenario) best solutions, including maximum (max) and minimum (min) target levels and scenarios 1 – 5 (scenario number key shown in Table 4.2). The top panel (a) shows the dendrogram based on Bray-Curtis similarities. The clusters identified are shown by the red boxes which start at the cutoff limit of 50% similarity. The bottom panel (b) shows the nMDS plot representing the distances between solutions based on Bray-Curtis similarities in 2-dimensional space. Minimum and maximum target level solutions are indicated according to the inset key. Dotted lines link max and min solutions of the same scenario. The 2-D stress value is shown in the top right corner (see main text for interpreting 2-D stress).

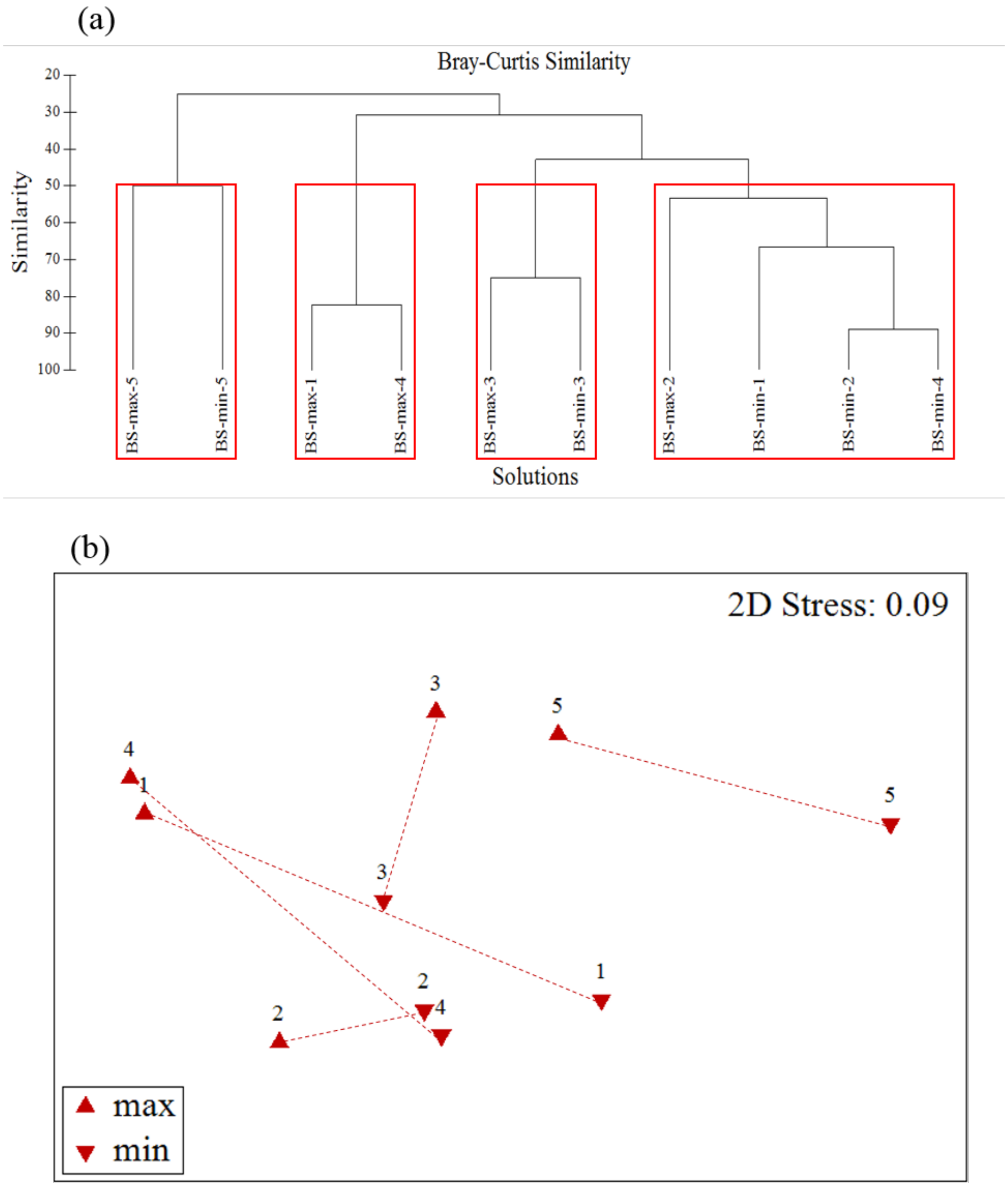


Figure 4.4: Bray-Curtis similarities between BS (biodiversity scenario) best solutions, including maximum (max) and minimum (min) target levels and scenarios 1 – 5 (scenario number key shown in Table 4.2). The top panel (a) shows the dendrogram based on Bray-Curtis similarities. The clusters identified are shown by the red boxes which start at the cutoff limit of 50% similarity. The bottom panel (b) shows the nMDS plot representing the distances between solutions based on Bray-Curtis similarities in 2-dimensional space. Minimum and maximum target level solutions are indicated according to the inset key. Dotted lines link max and min solutions of the same scenario. The 2-D stress value is shown in the top right corner (see main text for interpreting 2-D stress).

However, despite those observed differences, the Bray-Curtis dendrogram and nMDS plots still show there is more variation *within* the minimum and maximum solutions than between them, and this applies for both fisheries (Figure 4.3) and, to a lesser extent, biodiversity (Figures 4.4) solutions. Nevertheless, there was a strong separation between minimum and maximum solutions within several of the iterations (e.g., FS-max-1 and FS-min-1, or BS-max-6 and BS-min-6) as shown by the dotted lines in Figures 4.3 b and 4.4 b), and these solutions sometimes separated into different clusters.

4.3.3. Differences between Scenarios

As shown in the above dendrograms and nMDS, spatial solutions did not cluster together consistently according to scenario number, with three exceptions. The two FS solutions of scenario 2 (where inshore reefs were locked out) were in the same cluster with the maximum target BS solution of the same scenario number (Figure 4.2 a); FS solutions of scenario 4 also clustered together (Figure 4.2 a and 4.3 a), and so did scenarios 2, 3, and 5 of the BS solutions (Figure 4.4 a). Thus, while some solutions of the same scenario number were spatially similar, the pattern was not consistent. The impact of each scenario adjustment on solution feasibility and target achievement is presented below.

Locking out inshore reefs (scenario 2)

Compared to control runs (scenario 1), locking out inshore reefs led to more targets being missed in all scenarios except for the BS minimum target scenario, which was not affected by this adjustment. In FSs, locking out inshore reefs was particularly detrimental to the success of the solutions, as they failed to meet a total of 4 targets, two of which (the conservation features *Hipposcaris harid*-high and *Cephalopholis hemistiktos*-medium) were missed by 100%. However, in terms of the size of the reserve, these solutions were more feasible than the control runs. The BS maximum target solution of this scenario missed only one target (*Porites*-high) by 10%.

Locking in research monitoring sites (scenario 3)

Surprisingly, locking in the three research monitoring sites improved upon the control solution in the FS maximum target run in terms of meeting targets. While the best solution in the control run missed one target (*Hipposcaris harid*-high) by 25%, the best solution of this scenario missed no targets. However, it increased the size of the solution far beyond the predetermined feasible level (from 37.7% in the control run to 41.7%, both of which are infeasible). FS minimum target runs were not affected by this scenario (Table 4.5).

In both maximum and minimum target BS runs, locking in monitoring sites did not affect the ability to meet targets. However, it increased the area of the reserve compared to the control by about 2%. For the maximum target scenario, this resulted in the only unfeasible BS solution, which was 2% larger than the limit.

Locking out reefs smaller than 0.1 km^2 (scenario 4)

Locking out very small reefs did not affect the feasibility of any scenarios. However, for both scenario types and both target levels, it led to an increase in the number of targets missed by 1 target compared to the control runs (Table 4.5). This additional missed target was always *C. hemistiktos*-medium, which was always missed by 100% with this adjustment. Thus, under the current model of species abundances, it seems that this particular conservation feature was only found on those small reefs.

Locking out half of the largest reef (scenario 5)

Locking out half of the largest reef in the study area had no significant impact on the size and feasibility of the best solutions compared to control runs, except for the BS maximum target run, in which one target (Rock-high) was missed by 10%.

Locking in inshore reefs that are high-priority for representing endemics (scenario 6, BSs only)

Locking in the two inshore reefs which were found to be of high-priority for representing all endemic fish species made no significant difference to BS solutions. While it increased the size of the reserve by 1 reef compared to control runs, the solutions remained within the feasible limit and no targets were missed.

4.3.4. Reef Selection Frequency

Figure 4.5 shows a visualization of the frequency at which each reef in the study area was selected in the best solutions of all FSs and BSs. The general selection frequency is very similar for both scenario types, except that a higher number of reefs had a selection frequency higher than 0% in FS solutions, which is the result of FS solutions being generally larger than BS solutions. More importantly, however, this analysis gives an indication of how irreplaceable each reef is according to current biological information.

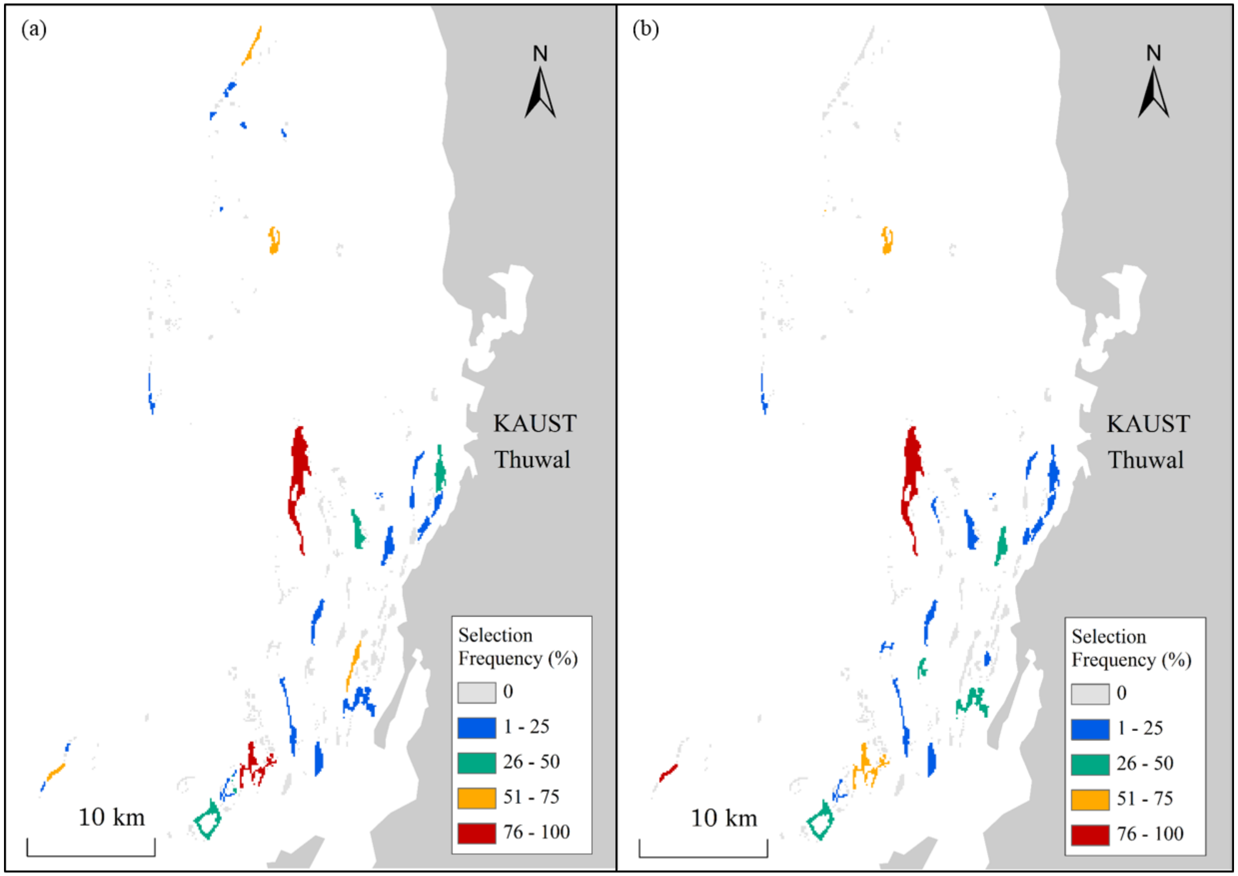


Figure 4.5: A visualization of the frequencies at which each reef in the study area (Thuwal, central Saudi Arabian Red Sea; total 355 reef patches) is selected for (a) fisheries, and (b) biodiversity scenario runs (total 10 fisheries and 12 biodiversity scenarios, listed in Table 4.2). The percent selection for each reef is color-coded as per the inset key. Each Marxan run performs 100 reptitions, producing 100 solutions. The selection frequency for each run is then provided in a summary file. The summary files for all runs were combined to create these visualizations in ArcMap. Dark gray indicates mainland.

4.4. Discussion

The spatial overlap between MPA solutions for fisheries and biodiversity found in this study, as well as the similarities in the patterns of selection frequency of reefs across the two scenario types (Figures 4.1 and 4.5), indicates that it may be possible to design an MPA network in Thuwal that could achieve both fisheries and biodiversity conservation goals simultaneously. This, in turn, indicates that efficient use of resources to manage a local MPA while allowing regulated fishing to continue may be feasible. This study presents the first application of a quantitative decision-making software tool such as Marxan in MPA design within the Red Sea, and it is also one of a small number of studies to include multiple species and consider multiple conservation goals. While there are a few limitations to the study that could be minimized by having a larger scientific dataset and access to socio-economic data, the findings address important practical considerations that can be immediately informative to managers or decision-makers.

Based on the results of Chapter 3, it was expected that FS solutions would be more spatially biased towards offshore reefs, while BS solutions would select more midshelf and inshore reefs. However, the results did not precisely follow this pattern. As best shown by the patterns in Figure 4.5, the general selection frequency was very spatially similar between FS and BS solutions. Although a higher number of offshore reefs tended to be selected in FS solutions, this seems to be due to the necessity of generating larger solutions in general in order to achieve FS targets. It is also important to note that the highest number of FS targets were missed when inshore reefs were locked out of reserve selection, which indicates that, at least for some commercial species, inshore habitat is important in this area. Thus, FS solutions were simply larger and more dispersed, but did not exhibit a higher selection frequency of offshore reefs than inshore reefs. However, the initial prediction was partly true for BS solutions, which did select a higher number of midshelf and inshore reefs. Nevertheless, one of the most frequently selected reefs in BS solutions (which can be seen at the bottom-left corner of Figure 4.5 b) was indeed an offshore reef, while the two most frequently selected reefs in FS solutions were midshelf reefs (Figure 4.5 a). Therefore, rather than showing a shift in spatial patterns of reserve selection, the comparison between FS and BS solutions highlights that FS targets were more challenging for the algorithm to achieve efficiently and may require more costly reserve networks in Thuwal.

The results also show that, although achieving FS targets was more costly, there was considerable spatial overlap between FS and BS solutions. This indicates that implementing a reserve network that focuses on the more limiting FS targets is likely to also meet many or most BS targets. This adds to the growing body of work from different parts of the world that suggests that it can be feasible to achieve multiple goals simultaneously while minimizing conflicts and opportunity costs (Lundquist and Granek 2005; Klein et al. 2008; Klein et al. 2009; Palumbi et al. 2009; Gaines et al. 2010; Schmiing et al. 2014).

Similar to Schmiing et al. (2014), the results also show that changing target levels had a strong impact on reserve selection patterns, the feasibility of solutions, and their ability to meet targets. Shifting from minimum to maximum target levels impacted the feasibility of FS solutions and their ability to meet targets more than it did BS targets. Even though BS solutions nearly doubled in size, they remained mostly within feasible limits and missed fewer targets.

This is likely a mere reflection of low variability in the spatial distribution of the densities of the commercial fish species included as conservation features in FSs. This low variability would “force” the algorithm to select more and more PUs into the reserve in order to reach the target, leading to larger and less feasible final solutions.

One of the interesting findings in this study is that inshore reefs (< 5 km from shore) appear to be of significant value to achieving conservation targets. This indicates that inshore reefs may have to be considered for reserve implementation despite their apparent vulnerability to stressors that are outside local control, such as thermal stress (Furby et al. 2013). Thus, decision-makers would have to assess the risk of allocating some management resources to areas that could be vulnerable “screen doors” in an otherwise protective reserve network (Jameson et al. 2002).

A general limitation of spatial planning in any location stems from the way in which conservation targets are set for marine ecosystems. The general guidelines and recommended target levels (e.g., World Parks Congress 2003; Convention on Biological Diversity 2010) are almost always percentage-based and do not rely on absolute values that were shown to enhance ecosystem health or were derived from empirical biological knowledge of life histories and environmental conditions (Flather et al. 2011). This is the case largely because, unlike for many terrestrial species, it is extremely challenging to obtain such knowledge (e.g., minimum viable population sizes) for marine species. Consequently, the widely applied solution to this problem was to resort to conserving a proportion of habitat and populations currently found in the environment, often without sufficient evidence as to whether these proportions would be adequate for enhancing or maintaining ecosystem health (Tear et al. 2005). The widely-applied ranges of 10 – 30% of habitat or populations are also partly derived from terrestrial conservation goals, the validity of which are questionable even within the field of terrestrial conservation (Rondinini and Chiozza 2010; Flather et al. 2011). This limitation is also magnified by shifting baselines and the lack of time-series data (Hughes et al. 2011). Thus, while it is generally agreed upon that clear goals and quantitative objectives are necessary for systematic conservation planning (Margules and Pressey 2000; Fernandes et al. 2005; Stelzenmüller et al. 2013), it remains challenging to set goals using objective and scientific methodologies (Tear et al. 2005). However, constant monitoring of ecosystems following the implementation of a reserve that was designed using the best available knowledge can indicate whether it is adequate and effective (e.g., Roberts et al. 2001; Gell and Roberts 2003), and whether its design should be adjusted to adapt to new information (Margules and Pressey 2000; Stelzenmüller et al. 2013).

The conservation features selected to achieve fisheries and biodiversity goals in this study are derived from the best available local knowledge. However, it is important to acknowledge that the biological data was obtained from a snapshot in time (Chapter 3), and that the species and benthic category abundance distributions were modeled using a purely distance-based spatial method that does not take into account any biological or biophysical environmental factors. This deficiency in the amount of data and accuracy of modeling is partly mitigated by using abundance classes (low, medium, and high) rather than absolute values. Nevertheless, future work on Thuwal reefs should include considerable expansion in the biological and environmental dataset and the incorporation of more sophisticated and validated techniques for modeling abundance distributions on reefs where data was not directly collected (e.g., general additive models used in Schmiing et al. (2014) or even more sophisticated species-specific models as applied in Costello et al. (2010)). The reserve selection technique presented in this study assumes that the protection of a proportion of the habitat of fisheries species, for instance, is sufficient to maintain or replenish their populations within reserves as well as the populations in adjacent fished areas (thus, benefiting fisheries). However, while protecting the habitat of fisheries species is indeed necessary (e.g., Pelc et al. 2010a; Bode et al. 2012) and has been shown to benefit fished areas via spillover (McClanahan and Mangi 2000; Kelly et al. 2002; Januchowski-Hartley et al. 2013), reserve effectiveness can be greatly improved by directly studying individual species' ontogenies (e.g., Sala et al. 2003; McMahon et al. in press), reproductive patterns and behaviors (e.g., Costello et al. 2010), and connectivity (e.g., Buston et al. 2012; Almany et al. 2013; D'Aloia et al. 2013). While much of this type of data is still largely missing in this study area (see DesRosiers 2011; Nanninga et al. 2015), the reserve solutions produced in this study should have high larval connectivity according to general guidelines (< 30 km distance between reserves) and current knowledge of larval dispersal in reef fishes (Almany et al. 2009; Jones et al. 2009; McCook et al. 2009).

This study would benefit from an improved assessment of the economic costs of reserves. The Marxan analysis was performed on the assumption that fishing pressure is more-or-less spatially homogeneous throughout the area. However, there is no data available for Thuwal regarding fishing effort, catch, or the revenue to fishermen. Since they are the primary stakeholders in this area, fishermen should be involved in both cost-assessment as well as implementation and management, as local involvement has repeatedly been shown to be highly effective in enhancing conservation (Mascia 2003; Borrini et al. 2004; Naughton-Treves et al. 2005; Green et al. 2009). Additionally, as mentioned in Section 4.2.4, the reefs provide economic and recreational benefits to local residents and business owners. This potential for long-term economic value (Angulo-Valdés and Hatcher 2010) could perhaps be used to argue for the promotion of alternative livelihoods for fishermen, such as operating boats and guiding trips for recreational businesses (Allison and Ellis 2001; Asiedu and Nunoo 2013), as well as for the necessity of implementing and enforcing management plans, as maintaining reef health would be essential for continued demand for recreational activities (Rees et al. 2010).

4.5. Conclusions

This study has shown that achieving multiple conservation goals such as biodiversity conservation and fisheries sustainability may be feasible on local scales within the Red Sea. While further expansion of biological data and the acquisition of socio-economic data could lower uncertainty, the analysis provides practical information that can be of immediate benefit to local decision-makers. Data deficiency is a common challenge in conservation planning; however, given the urgent need for immediate conservation action worldwide (Veron et al. 2009; Eakin et al. 2010), it is no longer a deterrent to initiating implementation effort and enlisting local support for MPAs (e.g., Giakoumi et al. 2011). Even purely opportunistic MPAs, while inefficient (Stewart et al. 2003), have been shown to be better than the alternative of no reserves at all (Roberts and Hawkins 2000). The Marxan approach applied here is objective, quantitative, transparent, flexible, and replicable, and it can be repeated to design, optimize, and even evaluate reserves as more information becomes available (Ball et al. 2009; Schmiing et al. 2014).

References

Allison EH, Ellis F (2001) The livelihoods approach and management of small-scale fisheries. Marine policy 25:377-388

Allison G, Lubchenco J, Carr M (1998) Marine reserves are necessary but not sufficient for marine conservation. Ecological Applications 8:S79-S92

Allnutt TF, McClanahan TR, Andréfouët S, Baker M, Lagabrielle E, McClennen C, Rakotomanjaka AJM, Tianarisoa TF, Watson R, Kremen C (2012) Comparison of marine spatial planning methods in Madagascar demonstrates value of alternative approaches. PLoS ONE 7:e28969

Almany G, Connolly S, Heath D, Hogan J, Jones G, McCook L, Mills M, Pressey R, Williamson D (2009) Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. Coral Reefs 28:339-351

Almany Glenn R, Hamilton Richard J, Bode M, Matawai M, Potuku T, Saenz-Agudelo P, Planes S, Berumen Michael L, Rhodes Kevin L, Thorrold Simon R, Russ Garry R, Jones Geoffrey P (2013) Dispersal of grouper larvae drives local resource sharing in a coral reef fishery. Current biology : CB 23:626-630

Angulo-Valdés JA, Hatcher BG (2010) A new typology of benefits derived from marine protected areas. Marine Policy 34:635-644

Asiedu B, Nunoo FK (2013) Alternative livelihoods: A tool for sustainable fisheries management in Ghana. Int J Fish Aquat Sci 2:21-28

Ball IR, Possingham HP, Watts M (2009) Marxan and relatives: software for spatial conservation prioritisation. In: Moilanen A, Wilson KA, Possingham HP (eds) Spatial conservation prioritisation: Quantitative methods and computational tools, Oxford University Press, Oxford, pp185–195

Barnes B, Sidhu H (2013) The impact of marine closed areas on fishing yield under a variety of management strategies and stock depletion levels. Ecological Modelling 269:113-125

Beger M, Jones GP, Munday PL (2003) Conservation of coral reef biodiversity: a comparison of reserve selection procedures for corals and fishes. Biological Conservation 111:53-62

Beger M, McKenna SA, Possingham HP (2007) Effectiveness of surrogate taxa in the design of coral reef reserve systems in the Indo-Pacific. Conservation Biology 21:1584-1593

Beger M, Linke S, Watts M, Game E, Treml E, Ball I, Possingham HP (2010) Incorporating asymmetric connectivity into spatial decision making for conservation. Conservation Letters 3:359-368

Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. Nature 429:827-833

Bode M, Armsworth P, Fox H, Bode L (2012) Surrogates for reef fish connectivity when designing marine protected area networks. Marine Ecology Progress Series 466:155-166

Borrini G, Kothari A, Oviedo G (2004) Indigenous and local communities and protected areas: Towards equity and enhanced conservation: Guidance on policy and practice for co-managed protected areas and community conserved areas. IUCN

Buston PM, Jones GP, Planes S, Thorrold SR (2012) Probability of successful larval dispersal declines fivefold over 1 km in a coral reef fish. Proceedings of the Royal Society of London B: Biological Sciences 279:1883-1888

Chong-Seng KM, Mannering TD, Pratchett MS, Bellwood DR, Graham NAJ (2012) The influence of coral reef benthic condition on associated fish assemblages. PLoS ONE 7:e42167

Clarke K, Gorley R (2006) PRIMER: User manual/Tutorial. PRIMER-E, Plymouth

Convention on Biological Diversity (2010) Decision X/2 — The strategic plan for biodiversity 2011–2020 and the Aichi biodiversity targets. Tenth Meeting of the Conference of the Parties to the Convention on Biological Diversity, Nagoya, Aichi Prefecture, Japan

Costello C, Rassweiler A, Siegel D, De Leo G, Micheli F, Rosenberg A (2010) The value of spatial information in MPA network design. Proceedings of the National Academy of Sciences 107:18294-18299

D'Aloia CC, Bogdanowicz SM, Majoris JE, Harrison RG, Buston PM (2013) Self-recruitment in a Caribbean reef fish: a method for approximating dispersal kernels accounting for seascape. Molecular Ecology 22:2563-2572

DesRosiers N (2011) Growth and maturation of Plectropomus spp. in the Saudi Arabian Red Sea. PhD Thesis. King Abdullah University of Science and Technology, Thuwal, Kingdom of Saudi Arabia

Eakin CM, Morgan JA, Heron SF, Smith TB, Liu G, Alvarez-Filip L, Baca B, Bartels E, Bastidas C, Bouchon C, Brandt M, Bruckner AW, Bunkley-Williams L, Cameron A, Causey BD, Chiappone M, Christensen TRL, Crabbe MJC, Day O, de la Guardia E, Diaz-Pulido G, DiResta D, Gil-Agudelo DL, Gilliam DS, Ginsburg RN, Gore S, Guzman HM, Hendee JC, Hernandez-Delgado EA, Husain E, Jeffrey CFG, Jones RJ, Jordan-Dahlgren E, Kaufman LS, Kline DI, Kramer PA, Lang JC, Lirman D, Mallela J, Manfrino C, Marechal J-P, Marks K, Mihaly J, Miller WJ, Mueller EM, Muller EM, Orozco Toro CA, Oxenford HA, Ponce-Taylor D, Quinn N, Ritchie KB, Rodriguez S, Rodriguez Ramirez A, Romano S, Samhouri JF, Sanchez JA, Schmahl GP, Shank BV, Skirving WJ, Steiner SCC, Villamizar E, Walsh SM, Walter C, Weil E, Williams EH, Roberson KW, Yusuf Y (2010) Caribbean corals in crisis: Record thermal stress, bleaching, and mortality in 2005. PLoS One 5

ESRI (2014) ArcGIS Desktop 10.2. Environmental Systems Research Institute, Redlands, CA

Faith D, Minchin P, Belbin L (1987) Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69:57-68

Fernandes L, Day JON, Lewis A, Slegers S, Kerrigan B, Breen DAN, Cameron D, Jago B, Hall J, Lowe D, Innes J, Tanzer J, Chadwick V, Thompson L, Gorman K, Simmons M, Barnett B, Sampson K, De'Ath G, Mapstone B, Marsh H, Possingham H, Ball IAN, Ward T, Dobbs K, Aumend J, Slater DEB, Stapleton K (2005) Establishing representative no-take areas in the Great Barrier Reef: Large-scale implementation of theory on marine protected areas. Conservation Biology 19:1733-1744

Flather CH, Hayward GD, Beissinger SR, Stephens PA (2011) Minimum viable populations: is there a magic number for conservation practitioners? Trends in ecology & evolution 26:307-316

Furby KA, Bouwmeester J, Berumen ML (2013) Susceptibility of central Red Sea corals during a major bleaching event. Coral Reefs 32:505-513

Gaines SD, White C, Carr MH, Palumbi SR (2010) Designing marine reserve networks for both conservation and fisheries management. Proceedings of the National Academy of Sciences 107:18286-18293

Game ET, Grantham HS (2008) Marxan user manual: For Marxan Version 1.8.10. University of Queensland, St. Lucia, Queensland, Australia, and Pacific Marine Analysis and Research Association, Vancouver, British Columbia, Canada. 127 pp.

Game ET, McDonald-Madden EVE, Puotinen ML, Possingham HP (2008) Should We Protect the Strong or the Weak? Risk, Resilience, and the Selection of Marine Protected Areas. Conservation Biology 22:1619-1629

Gell FR, Roberts CM (2003) Benefits beyond boundaries: the fishery effects of marine reserves. Trends in Ecology & Evolution 18:448-455

Giakoumi S, Grantham HS, Kokkoris GD, Possingham HP (2011) Designing a network of marine reserves in the Mediterranean Sea with limited socio-economic data. Biological Conservation 144:753-763

Green A, Smith SE, Lipsett-Moore G, Groves C, Peterson N, Sheppard S, Lokani P, Hamilton R, Almany J, Aitsi J, Bualia L (2009) Designing a resilient network of marine protected areas for Kimbe Bay, Papua New Guinea. Oryx 43:488-498

Green AL, Fernandes L, Almany G, Abesamis R, McLeod E, Aliño PM, White AT, Salm R, Tanzer J, Pressey RL (2014) Designing marine reserves for fisheries management, biodiversity conservation, and climate change adaptation. Coastal Management 42:143-159

Halpern BS (2003) The impact of marine reserves: Do reserves work and does reserve size matter? Ecological Applications 13:117-137

Halpern BS, Warner RR (2002) Marine reserves have rapid and lasting effects. Ecology Letters 5:361-366

Hastings A, Botsford LW (2003) Comparing designs of marine reserves for fisheries and for biodiversity. Ecological Applications 13:S65-S70

Hermoso V, Kennard MJ, Linke S (2012) Integrating multidirectional connectivity requirements in systematic conservation planning for freshwater systems. Diversity and Distributions 18:448-458

Hilborn R, Stokes K, Maguire J-J, Smith T, Botsford LW, Mangel M, Orensanz J, Parma A, Rice J, Bell J, Cochrane KL, Garcia S, Hall SJ, Kirkwood GP, Sainsbury K, Stefansson G, Walters C (2004) When can marine reserves improve fisheries management? Ocean & Coastal Management 47:197-205

Hughes T, Bellwood D, Baird A, Brodie J, Bruno J, Pandolfi J (2011) Shifting base-lines, declining coral cover, and the erosion of reef resilience: comment on Sweatman et al. (2011). Coral Reefs 30:653-660

Jameson SC, Tupper MH, Ridley JM (2002) The three screen doors: can marine “protected” areas be effective? Marine Pollution Bulletin 44:1177-1183

Januchowski-Hartley FA, Graham NAJ, Cinner JE, Russ GR (2013) Spillover of fish naivete from marine reserves. Ecology Letters 16:191-197

Jones GP, Almany GR, Russ GR, Sale PF, Steneck RS, van Oppen MJH, Willis BL (2009) Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. Coral Reefs 28:307-325

Kelly S, Scott D, MacDiarmid A (2002) The value of a spillover fishery for spiny lobsters around a marine reserve in northern New Zealand. Coast Manag 30:153

Klein CJ, Steinback C, Watts M, Scholz AJ, Possingham HP (2009) Spatial marine zoning for fisheries and conservation. Frontiers in Ecology and the Environment 8:349-353

Klein CJ, Chan A, Kircher L, Cundiff AJ, Gardner N, Hrovat Y, Scholz A, Kendall BE, AiramÉ S (2008) Striking a balance between biodiversity conservation and socioeconomic viability in the design of marine protected areas. Conservation Biology 22:691-700

Linke S, Watts M, Stewart R, Possingham HP (2011) Using multivariate analysis to deliver conservation planning products that align with practitioner needs. Ecography 34:203-207

Lomolino MV (1994) An evaluation of alternative strategies for building networks of nature reserves. Biological Conservation 69:243-249

Lundquist CJ, Granek EF (2005) Strategies for successful marine conservation: Integrating socioeconomic, political, and scientific factors. Conservation Biology 19:1771-1778

Margules CR, Pressey RL (2000) Systematic conservation planning. Nature 405:243-253

Mascia MB (2003) The human dimension of coral reef marine protected areas: recent social science research and its policy implications. Conservation biology:630-632

McClanahan T, Mangi S (2000) Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. Ecol Appl 10:1792

McCook L, Almany G, Berumen M, Day J, Green A, Jones G, Leis J, Planes S, Russ G, Sale P, Thorrold S (2009) Management under uncertainty: guide-lines for incorporating connectivity into the protection of coral reefs. Coral Reefs 28:353-366

McMahon K, Thorrold S, Houghton L, Berumen M (2015) Tracing carbon through coral reef food webs using a compound-specific stable isotope approach. Oecologia doi: 10.1007/s00442-015-3475-3

Nanninga GB, Saenz-Agudelo P, Zhan P, Hoteit I, Berumen ML (2015) Not finding Nemo: limited reef-scale retention in a coral reef fish. Coral Reefs:1-10

Naughton-Treves L, Holland MB, Brandon K (2005) The role of protected areas in conserving biodiversity and sustaining local livelihoods. Annu Rev Environ Resour 30:219-252

Palumbi SR, Sandifer PA, Allan JD, Beck MW, Fautin DG, Fogarty MJ, Halpern BS, Incze LS, Leong J-A, Norse E, Stachowicz JJ, Wall DH (2009) Managing for ocean biodiversity to sustain marine ecosystem services. Frontiers in Ecology and the Environment 7:204-211

Pelc RA, Warner RR, Gaines SD, Paris CB (2010a) Detecting larval export from marine reserves. Proceedings of the National Academy of Sciences of the United States of America 107:18266-18271

Pelc RA, Warner RR, Gaines SD, Paris CB (2010b) Detecting larval export from marine reserves. Proceedings of the National Academy of Sciences 107:18266-18271

Possingham H, Ball I, Andelman S (2000) Mathematical methods for identifying representative reserve networks In: Quantitative methods for conservation biology. Springer, pp291-306

Rees SE, Rodwell LD, Attrill MJ, Austen MC, Mangi SC (2010) The value of marine biodiversity to the leisure and recreation industry and its application to marine spatial planning. Marine Policy 34:868-875

Roberts CM, Hawkins JP (2000) Fully-protected marine reserves: a guide. WWF Endangered Seas Campaign, Washington, DC, USA and Environment Department, University of York, York, UK

Roberts CM, Bohnsack JA, Gell F, Hawkins JP, Goodridge R (2001) Effects of marine reserves on adjacent fisheries. Science 294:1920-1923

Rondinini C, Chiozza F (2010) Quantitative methods for defining percentage area targets for habitat types in conservation planning. Biological Conservation 143:1646-1653

Sala E, Aburto-Oropeza O, Paredes G, Thompson G (2003) Spawning aggregations and reproductive behavior of reef fishes in the Gulf of California. Bulletin of Marine Science 72:103-121

Schmiing M, Diogo H, Serrão Santos R, Afonso P (2014) Marine conservation of multispecies and multi-use areas with various conservation objectives and targets. ICES Journal of Marine Science: Journal du Conseil

Stelzenmüller V, Breen P, Stamford T, Thomsen F, Badalamenti F, Borja Á, Buhl-Mortensen L, Carlstöm J, D'Anna G, Dankers N, Degraer S, Dujin M, Fiorentino F, Galparsoro I, Giakoumi S, Gristina M, Johnson K, Jones PJS, Katsanevakis S, Knittweis L, Kyriazi Z, Pipitone C, Piwowarczyk J, Rabaut M, Sørensen TK, van Dalfsen J, Vassilopoulou V, Vega Fernández T, Vincx M, Vöge S, Weber A, Wijkmark N, Jak R, Qiu W, ter Hofstede R (2013) Monitoring and evaluation of spatially managed areas: A generic framework for implementation of ecosystem based marine management and its application. Marine Policy 37:149-164

Stewart RR, Noyce T, Possingham HP (2003) Opportunity cost of ad hoc marine reserve design decisions: an example from South Australia. Marine Ecology Progress Series 253:25-38

Tear TH, Kareiva P, Angermeier PL, Comer P, Czech B, Kautz R, Landon L, Mehlman D, Murphy K, Ruckelshaus M, Scott JM, Wilhere G (2005) How much is enough? The recurrent problem of setting measurable objectives in conservation. BioScience 55:835-849

Tewfik A, Bene C (2003) Effects of natural barriers on the spillover of a marine mollusc: implications for fisheries reserves. Aquat Conserv: Mar Freshw Ecosyst 13:473

Veron JEN, Hoegh-Guldberg O, Lenton TM, Lough JM, Obura DO, Pearce-Kelly P, Sheppard CRC, Spalding M, Stafford-Smith MG, Rogers AD (2009) The coral reef crisis: The critical importance of < 350 ppm CO(2). Marine Pollution Bulletin 58:1428-1436

World Parks Congress (2003) Recommendation V.22: building a global system of marine and coastal protected area networks. Vth IUCN World Parks Congress. IUCN, Durban, South Africa

Williamson DH, Russ GR, Ayling AM (2004) No-take marine reserves increase abundance and biomass of reef fish on inshore fringing reefs of the Great Barrier Reef. Environmental Conservation 31:149-159

Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, Halpern BS, Jackson JBC, Lotze HK, Micheli F, Palumbi SR, Sala E, Selkoe KA, Stachowicz JJ, Watson R (2006) Impacts of biodiversity loss on ocean ecosystem services. Science 314:787-790

CHAPTER 5: A NOTE ON THE HUMAN DIMENSIONS OF RED SEA CONSERVATION IN SAUDI ARABIA

5.1. Introduction

The aim of this dissertation was to explore the design of science-based marine protected areas (MPAs) in the Thuwal area of the Saudi Arabian Red Sea. This aim is quite different from creating a comprehensive resource management plan. The latter would be a larger and more multidisciplinary effort that must take into consideration socio-economics and politics as well as science. This chapter is a note on some of the main socio-economic challenges facing conservation in the Saudi Arabian Red Sea.

Some of the main goals of a management plan are to sustain ecosystem services (food, livelihoods, cultural, and aesthetic value, etc.) (Adams 2014) and, ultimately, from a more ethical perspective, to simply preserve biodiversity for the sake of biodiversity (McCauley 2006). Most management plans focus on preserving ecosystem services by regulating human activities in order to prevent the overexploitation of the environment (Worm et al. 2006; Palumbi et al. 2009; Kelble et al. 2013). Figure 5.1 shows a conceptual model of the main drivers in the Thuwal area that could eventually lead to the loss of ecosystem services and the pathway by which this loss could occur. Most of these stressors are local human activities (fishing, coastal development, recreational activities, wastewater, etc.), while others are outside immediate local control, such as climate change and extreme weather. MPAs may only reduce the impact of fishing and physical damage to the reefs inside them, and those benefits may “spill over” to non-reserve areas either through larval supply or the migration of adult fish (e.g., McClanahan and Mangi 2000; Ashworth and Ormond 2005; Forcada et al. 2009; Januchowski-Hartley et al. 2013; Emslie et al. 2015). Reserves may also improve the resilience of vulnerable reefs so that they can recover quickly from disturbances that are outside immediate local control, such as thermal stress (Bellwood et al. 2006; McCook et al. 2010; McGilliard et al. 2011).

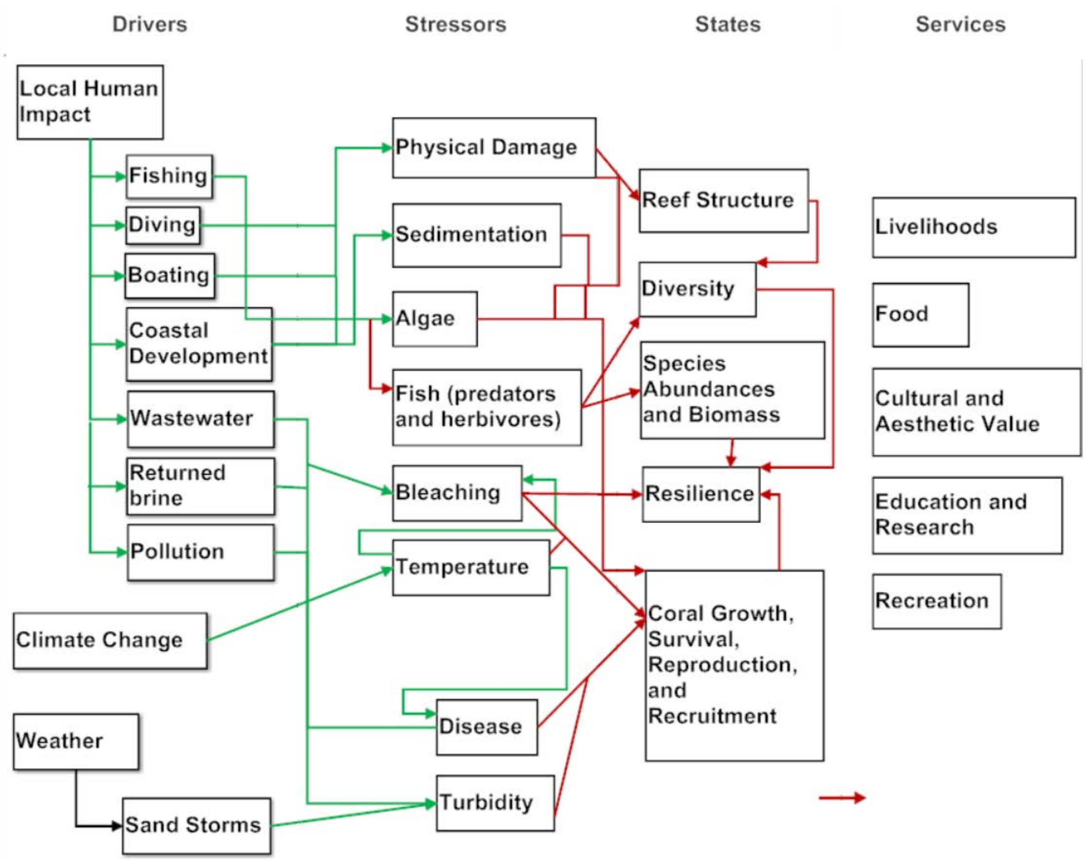


Figure 5.1: A conceptual diagram illustrating how driving forces (“drivers” listed on the left-hand side) cause “stressors” on the environment, which then alter the natural “state” or balance of the ecosystem, leading to the loss of “ecosystem services”. The “drivers” listed are thought to be the main ones acting in Thuwal in the central Saudi Arabian Red Sea, which is the main study area in this thesis. Green arrows indicate positive effects, while red arrows indicate negative effects.

However, for many reasons, simple spatial closure is not sufficient for preserving the environment and sustaining ecosystem services (Allison et al. 1998). For example, if fishing pressure is not brought down to sustainable levels everywhere in Saudi Arabia, spatial closure would merely lead to a displacement of fishing pressure, and no economic benefit to fisheries would be observed (Halpern et al. 2003, 2004; Jin et al. 2012). Similarly, marine organisms with home ranges that stretch well beyond the range of an MPA (e.g., marine mammals, sharks, and other large pelagic predators) must be protected by other means, such as well-enforced fishing regulations. Therefore, a local MPA network in Thuwal may produce benefit to fishermen and to the environment, but only if it is accompanied by both local and national regulations on the maximum number of fishing licenses issued and well-enforced species-specific regulations such as minimum and maximum catch size, limited quotas, and bans on fishing threatened species. While some fishing laws have indeed been issued in Saudi Arabia (e.g., a ban on shark fishing (Department of Fisheries 2008)), hardly any compliance with or enforcement of these laws seems to be taking place, and Saudi fisheries are currently thought to be operating well beyond sustainable levels (Jin et al. 2012; Spaet 2014; Spaet and Berumen 2015).

This highlights the importance of the human dimension to the success of conservation efforts in Saudi Arabia, which includes the socio-economic, cultural, and political aspects of conservation and is the focus of the next section.

5.2. The Human Dimension in Saudi Arabian Marine Conservation

Providing a scientific basis is one of the first steps in systematic conservation planning, which was the focus of this thesis; however, conservation is a multidisciplinary field that also requires socio-economic and political considerations to be taken into account (Margules and Pressey 2000; Tear et al. 2005; Stelzenmüller et al. 2013). Such socio-economic data are either missing or difficult to access in Saudi Arabia, but they would include information that covers all human uses of the marine environment, such as: 1) detailed information on fishing pressure, catch per unit effort, the fishers' income, the cultural importance of fishing, gear types, etc.; 2) information on the economic and social value of recreational marine activities, such as the income to dive operators, job opportunities created by the diving industry, etc.; and 3) an assessment of the financial cost of implementing and enforcing MPAs (both management and opportunity costs). Without such information, it is challenging to formulate a comprehensive management plan.

Equally important to the formulation of a comprehensive plan is the capacity to implement it. As mentioned earlier in the case of fishing laws, there seems to be a large and persistent gap between science and implementation or enforcement in conservation in Saudi Arabia. Although scientific data on the physical and biological aspects of the environment are limited in the Red Sea (Berumen et al. 2013), they are not completely absent, and science-based conservation efforts could have been initiated many years ago. Annual reports of large-scale patterns in biodiversity as well as recommendations for the placement of MPAs in Saudi Arabian waters have been and continue to be published, at least since the 1980s, by regional and international organizations (e.g., IUCN/UNEP 1988; PERSGA/GEF 2003). However, these recommendations were almost never followed or acted upon beyond the establishment of one or two “paper parks” (Chapter 1). Saudi Arabia possibly lacks the appropriate organizational structure that is capable of implementing and enforcing resource management plans. However, this structure would not be too challenging to assemble if sufficient political will were present.

Apart from the absence of political will and an appropriate organizational structure, there is also very little education or involvement of the local resource users, such as fishermen and recreational business owners, in conservation issues. This leads to an environment where: 1) the main resource users are not aware of how their activities (the “drivers” on the left-hand side in Figure 5.1) impact their own livelihoods (the “ecosystem services” on the right-hand side in Figure 5.1); 2) they seem to have little awareness of or trust in the benefits of any management regulations, and, therefore, are not willing to comply; and 3) many of them seem to have little sense of ownership, agency, or stewardship for the environment (possibly due to the top-down authoritative government system), and so, are unlikely to take initiative or be supportive of conservation effort. Indeed, the involvement of local resource users in the decision-making and implementation process has repeatedly been shown to play an important role in the success of community-based MPAs (Pollnac et al. 2001; Mascia 2003; Borrini et al. 2004; Naughton-Treves et al. 2005; Keane et al. 2008), and this was perhaps the main reason for the momentary success of the Farasan Islands protected area in the southern Saudi Arabian Red Sea (Gladstone 2000).

However, it is also important to acknowledge that the presence of the science-action gap, which is a worldwide phenomenon and not merely a local one, is also partly due to the detachment of researchers from the decision-makers, practitioners, and resource users (Knight et al. 2008). It has been argued that there are advantages to this detachment, as it allows scientists to explore the best possible courses of action for the sake of the environment without bias towards practically or politically favorable solutions, taking into account only natural processes and the requirements for sustaining them (Tear et al. 2005). However, much can be gained from sourcing some of the research questions pertaining to conservation from practitioners and resource users as well as from ensuring that academics have basic knowledge of implementation processes and local policy (Knight et al. 2008).

5.2.1. Unique Saudi Arabian Challenges: The Fishing Dilemma

In addition to the general challenges to the success of conservation effort mentioned above, Saudi Arabia faces its own unique socio-economic and political challenges, especially with regards to the regulation of fishing activities. Fisheries are in crisis all over the world (Pauly et al. 2002), and, while direct fishing data is needed to support this claim, it seems that Saudi Arabian Red Sea fisheries are no exception (Jin et al. 2012; Spaet and Berumen 2015). Jin et al. (2012) have shown that the fishing fleet in the Saudi Arabian Red Sea is, at minimum, three times larger than it should be in order to maximize economic benefit from fisheries, and this estimate is likely to be an underestimation. This presents a major problem of overcapacity that is thought to have been present since the mid-1990s (Jin et al. 2012).

Thus, it is clear that, at least for economic purposes, if not for environmental purposes, the volume of fishing pressure in the Saudi Arabian Red Sea needs to be drastically reduced. However, the challenge is further complicated by a possibly unique aspect of Saudi Arabian fisheries, which is that the majority of fishermen actively fishing the sea are not local Saudi fishermen, but, in fact, foreign laborers. For example, Thuwal is estimated to have around 200 fishing boats, which are mostly small, single-engine boats on which fishing is done mostly by hand-lining (R. Jahdali and H. Jahdali, pers. comm.). Only about 70 of these boats are owned and operated by local Saudi fishermen whose families had been fishing Thuwal waters for many generations. The remaining majority of the boats are run by foreign fishermen (mostly Egyptian and Bengali) who operate under the sponsorship of Saudi businessmen who provide the boats for a monthly rental fee (R. Jahdali and H. Jahdali, pers. comm.). The interests of those non-Saudi fishermen are only financial and short-term, and the long-term health of Red Sea fisheries is of little concern to them, as most of them eventually return to their home countries after saving sufficient funds. Thus, they cannot be expected to support a local MPA or to comply with fishing regulations unless strict enforcement is in place. In fact, Saudi fishermen in Thuwal seem to believe that the non-Saudi fishermen fish all year-round, fish indiscriminately, and use illegal methods (such as gill nets) far more frequently than they, the Saudi fishers, do (R. Jahdali and H. Jahdali, pers. comm.). While there is currently no direct evidence that the fishing behavior of Saudi and non-Saudi Thuwal fishermen is different, the challenge remains that it would be difficult to gain support for and compliance with fishing regulations or with an MPA in Thuwal. However, it may be possible to reduce the number of fishing boats over the coming years if Saudi authorities decline to renew fishing licenses or issue new licenses for non-Saudi fishers.

A commonly used and often successful approach for reducing fishing pressure in various parts of the world is the alternative livelihoods approach, where fishers are provided with opportunities to pursue alternative careers in the ecotourism industry or other industries (McManus 1997). However, alternative livelihood programs require initial assessments through interviews of the fishers’ acceptance of the idea (Asiedu and Nunoo 2013), an understanding of how important fishing is to well-being and to the local culture (Pollnac et al. 2006), as well as an understanding of the local culture (Allison and Ellis 2001). Alternative livelihoods in the diving tourism business or other water-based recreational businesses may potentially be a viable option for Saudi fishermen. However, the fact that tourism is highly restricted and limited in Saudi Arabia may severely limit its viability.

5.3. Conclusions

The need for conservation action in the Saudi Arabian Red Sea is urgent, and the currently available information is sufficient to initiate immediate action. The work presented in this thesis applies a modern and easily repeatable method for designing MPAs that would be manageable on the scale of one fishing village. It also shows that it is possible to achieve multiple conservation goals with one feasible MPA network. This method can also be easily adapted as larger datasets become available. However, the major challenges to marine conservation in Saudi Arabia remain socio-economic and political in nature. Political will and the education and involvement of locals are two of the major missing elements vital to the success of conservation efforts in the Arabian region, and, without them, scientific research will fail to benefit resource users as well as the natural environment itself. Nevertheless, researchers must also continue to increase knowledge of the environment and make an effort to communicate their findings to the relevant authorities and stakeholders.

References

Adams WM (2014) The value of valuing nature. Science 346:549-551

Allison EH, Ellis F (2001) The livelihoods approach and management of small-scale fisheries. Marine policy 25:377-388

Allison G, Lubchenco J, Carr M (1998) Marine reserves are necessary but not sufficient for marine conservation. Ecological Applications 8:S79-S92

Almany G, Connolly S, Heath D, Hogan J, Jones G, McCook L, Mills M, Pressey R, Williamson D (2009) Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. Coral Reefs 28:339-351

Ashworth JS, Ormond RFG (2005) Effects of fishing pressure and trophic group on abundance and spillover across boundaries of a no-take zone. Biological Conservation 121:333-344

Asiedu B, Nunoo FK (2013) Alternative livelihoods: A tool for sustainable fisheries management in Ghana. Int J Fish Aquat Sci 2:21-28

Bellwood DR, Hoey AS, Ackerman JL, Depczynski M (2006) Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. Global Change Biology 12:1587-1594

Borrini G, Kothari A, Oviedo G (2004) Indigenous and local communities and protected areas: Towards equity and enhanced conservation: Guidance on policy and practice for co-managed protected areas and community conserved areas. IUCN

Department of Fisheries MoA (2008) Protection of sharks. 50020000, Kingdom of Saudi Arabia

Emslie Michael J, Logan M, Williamson David H, Ayling Anthony M, MacNeil MA, Ceccarelli D, Cheal Alistair J, Evans Richard D, Johns Kerryn A, Jonker Michelle J, Miller Ian R, Osborne K, Russ Garry R, Sweatman Hugh PA (2015) Expectations and Outcomes of Reserve Network Performance following Re-zoning of the Great Barrier Reef Marine Park. Current Biology 25:983-992

Forcada A, Valle C, Bonhomme P, Criquet G, Cadiou G, Lenfant P, Sánchez-Lizaso J (2009) Effects of habitat on spillover from marine protected areas to artisanal fisheries. Marine Ecology Progress Series 379:197-211

Gladstone W (2000) The ecological and social basis for management of a Red Sea marine-protected area. Ocean & Coastal Management 43:1015-1032

Halpern BS, Gaines SD, Warner RR (2003) Export of production and the displacement of effort from marine reserves: effects on fisheries and monitoring programs. Oceans 2003 Celebrating the Past Teaming Toward the Future (IEEE Cat No03CH37492)

Halpern BS, Gaines SD, Warner RR (2004) Confounding effects of the export of production and the displacement of fishing effort from marine reserves. Ecological Applications 14:1248-1256

Januchowski-Hartley FA, Graham NAJ, Cinner JE, Russ GR (2013) Spillover of fish naivete from marine reserves. Ecology Letters 16:191-197

Jin D, Kite-Powell HL, Hoagland P, Solow AR (2012) A bioeconomic analysis of traditional fisheries in the Red Sea off the coast of the Kingdom of Saudi Arabia. Marine Resource Economics 27:137-148

Keane A, Jones JPG, Edwards-Jones G, Milner-Gulland EJ (2008) The sleeping policeman: understanding issues of enforcement and compliance in conservation. Animal Conservation 11:75-82

Kelble CR, Loomis DK, Lovelace S, Nuttle WK, Ortner PB, Fletcher P, Cook GS, Lorenz JJ, Boyer JN (2013) The EBM-DPSER conceptual model: Integrating ecosystem services into the DPSIR framework. PLoS ONE 8:e70766

Knight AT, Cowling RM, Rouget M, Balmford A, Lombard AT, Campbell BM (2008) Knowing but not doing: Selecting priority conservation areas and the research–implementation gap. Conservation Biology 22:610-617

Margules CR, Pressey RL (2000) Systematic conservation planning. Nature 405:243-253

Mascia MB (2003) The human dimension of coral reef marine protected areas: recent social science research and its policy implications. Conservation biology:630-632

McCauley DJ (2006) Selling out on nature. Nature 443:27-28

McClanahan T, Mangi S (2000) Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. Ecol Appl 10:1792

McCook LJ, Ayling T, Cappo M, Choat JH, Evans RD, De Freitas DM, Heupel M, Hughes TP, Jones GP, Mapstone B, Marsh H, Mills M, Molloy FJ, Pitcher CR, Pressey RL, Russ GR, Sutton S, Sweatman H, Tobin R, Wachenfeld DR, Williamson DH (2010) Adaptive management of the Great Barrier Reef: A globally significant demonstration of the benefits of networks of marine reserves. Proceedings of the National Academy of Sciences

McGilliard CR, Punt AE, Hilborn R (2011) Spatial structure induced by marine reserves shapes population responses to catastrophes in mathematical models. Ecological Applications 21:1399-1409

McManus JW (1997) Tropical marine fisheries and the future of coral reefs: a brief review with emphasis on Southeast Asia. Coral Reefs 16:S121-S127

Naughton-Treves L, Holland MB, Brandon K (2005) The role of protected areas in conserving biodiversity and sustaining local livelihoods. Annu Rev Environ Resour 30:219-252

Palumbi SR, Sandifer PA, Allan JD, Beck MW, Fautin DG, Fogarty MJ, Halpern BS, Incze LS, Leong J-A, Norse E, Stachowicz JJ, Wall DH (2009) Managing for ocean biodiversity to sustain marine ecosystem services. Frontiers in Ecology and the Environment 7:204-211

Pauly D, Christensen V, Guénette S, Pitcher TJ, Sumaila UR, Walters CJ, Watson R, Zeller D (2002) Towards sustainability in world fisheries. Nature 418:689-695

Pollnac RB, Crawford BR, Gorospe MLG (2001) Discovering factors that influence the success of community-based marine protected areas in the Visayas, Philippines. Ocean & Coastal Management 44:683-710

Pollnac RB, Abbott-Jamieson S, Smith C, Miller ML, Clay PM, Oles B (2006) Toward a model for fisheries social impact assessment. Marine Fisheries Review 68:1-18

Spaet JL (2014) Integrating fisheries dependent and independent approaches to assess fisheries, abundance, diversity, distribution and genetic connectivity of Red Sea elasmobranch populations. PhD Thesis. King Abdullah University of Science and Technology, Saudi Arabia,

Spaet JLY, Berumen ML (2015) Fish market surveys indicate unsustainable elasmobranch fisheries in the Saudi Arabian Red Sea. Fisheries Research 161:356-364

Stelzenmüller V, Breen P, Stamford T, Thomsen F, Badalamenti F, Borja Á, Buhl-Mortensen L, Carlstöm J, D'Anna G, Dankers N, Degraer S, Dujin M, Fiorentino F, Galparsoro I, Giakoumi S, Gristina M, Johnson K, Jones PJS, Katsanevakis S, Knittweis L, Kyriazi Z, Pipitone C, Piwowarczyk J, Rabaut M, Sørensen TK, van Dalfsen J, Vassilopoulou V, Vega Fernández T, Vincx M, Vöge S, Weber A, Wijkmark N, Jak R, Qiu W, ter Hofstede R (2013) Monitoring and evaluation of spatially managed areas: A generic framework for implementation of ecosystem based marine management and its application. Marine Policy 37:149-164

Tear TH, Kareiva P, Angermeier PL, Comer P, Czech B, Kautz R, Landon L, Mehlman D, Murphy K, Ruckelshaus M, Scott JM, Wilhere G (2005) How much is enough? The recurrent problem of setting measurable objectives in conservation. BioScience 55:835-849

Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, Halpern BS, Jackson JBC, Lotze HK, Micheli F, Palumbi SR, Sala E, Selkoe KA, Stachowicz JJ, Watson R (2006) Impacts of biodiversity loss on ocean ecosystem services. Science 314:787-790

CHAPTER 6: GENERAL DISCUSSION AND CONCLUSIONS

The work presented in this thesis explored and analyzed the potential for systematic conservation planning in the Saudi Arabian Red Sea using modern methods as well as to provide some of the basic scientific data required to design local marine protected areas (MPAs) in Thuwal. Chapter 2 considered the use of spatial habitat distribution features for designing MPAs that could be well-connected with larval supply; Chapter 3 provided basic biological knowledge of the local reef communities in Thuwal; and Chapter 4 produced and analyzed designs of various potential local MPAs to achieve multiple conservation goals. None of these questions had been addressed using current methods on a small, locally-manageable, scale within the context of the Red Sea prior to this thesis, which makes it a valuable contribution to marine ecology and conservation literature both locally and globally.

The current absence of MPAs in the Saudi Arabian Red Sea presented an opportunity to “start fresh” by developing hypotheses and obtaining data to design effective MPAs based on modern scientific principles. These principles include connectivity (which could be larval, adult, ontogenetic, or other), adequacy (which requires obtaining detailed data on reef communities in order to capture key ecological processes within MPAs), representativeness (of key habitats and species), efficiency (minimizing costs), and flexibility (providing multiple options to managers and using adaptable methods) (Margules and Pressey 2000; Tear et al. 2005). Chapter 2 of this thesis addressed aspects of the connectivity principle; Chapter 3 provided information required to achieve adequacy and representativeness; and Chapter 4 addressed, to varying extents, adequacy, representativeness, efficiency, and flexibility. As a whole, the thesis presents a model for designing small-scale MPAs in the Red Sea that are science-based and feasible. Finally, Chapter 5 addressed the socio-economic and political challenges facing conservation efforts in Saudi Arabia. This chapter discusses some of the contributions of this work to the local and global scientific literature and identifies some of its limitations and recommended future work.

6.1. Contribution to Incorporating Connectivity in MPA Design

There is a growing body of literature discussing the incorporation of larval connectivity into conservation planning, ranging from proposing general guidelines (e.g., Almany et al. 2009; McCook et al. 2009), to validating the connectedness of existing MPAs (e.g., Harrison et al. 2012; Almany et al. 2013), to using dispersal models to inform management decisions (e.g., Kininmonth et al. 2011; Beger et al. 2015), to simply attempting to improve the current understanding of larval dispersal patterns of model species (e.g., Berumen et al. 2012; Almany et al. 2013). Also, due to the difficulties and high costs of studying connectivity, some surrogates of connectivity were tested that could allow managers to cheaply incorporate connectivity into MPA design (e.g., Bode et al. 2012). However, the effect of small-scale spatial configuration (or patchiness) of reefs on local dispersal patterns remains poorly understood, although the need to improve the understanding of this effect is recognized (D’Aloia et al. 2013).

Chapter 2 of this thesis attempted to advance the understanding of how patchiness may affect real dispersal patterns of reef organisms, and showed that increased habitat patchiness may be correlated with the occurrence of longer maximum dispersal distances. This implies that it may be possible to design more widely spaced (less dense) MPAs in patchier habitats while maintaining larval connectivity. The chapter also proposed using a comparative method to continue exploring this relationship between patchiness and dispersal as more empirical dispersal data becomes available. This method also proposes a relatively cheap solution that could be applicable in areas where obtaining empirical dispersal data or creating sophisticated dispersal models are not possible, as a comparative evaluation of the degree of habitat patchiness may be sufficient to guide MPA placement. However, due to the paucity of empirical dispersal data and the failure to acquire fully empirically-validated dispersal information from within the Red Sea, this contribution is currently more valuable to theoretical ecology and conservation until further testing of the hypothesis can be done. Acquiring more empirical dispersal data from different locations, for different species, and different time periods could take the conclusions of this work from the realm of theory to that of specific practical instructions and guidelines.

Besides the need for more empirical dispersal data, there is also a need for detailed habitat maps. In the patchiness analysis in Chapter 2, it was assumed that whole reefs were equally viable habitat patches for dispersing larvae, which, while simpler to analyze and easier to obtain from satellite imagery and web-based GIS databases, is not ecologically accurate. Habitat patches could be redefined in each studied location based on the niche of the species whose dispersal patterns are being considered. For example, in Manus Island, where the grouper *Plectropomus areolatus* was studied, habitat patches could be redefined to only include sheltered lagoons where grouper larvae are most likely to recruit (Almany et al. 2013). Similarly, for clownfish species, habitat patches could be redefined to only include areas where there are high densities of anemones (Nanninga 2013). However, while it is important to recognize the limitations of this assumption, it is also important to note that incorporating this level of detail into the analysis would defeat the purpose of eventually proposing a cheap and fairly simple method for incorporating larval connectivity into MPA design, as it would require extensive mapping efforts.

6.2. Contribution to Coral Reef Ecology

The data presented in Chapter 3 is mostly descriptive and provides a snapshot of the spatial variation and cross-shore trends of local reef communities near Thuwal. Most of the data available for the Saudi Arabian Red Sea prior to this work is conducted on a much larger spatial scale and at lower spatial resolution (e.g., Roberts 1992; PERSGA/GEF 2003; Roberts et al. 2015). The small scale and level of detail of the surveys described in Chapter 3 provides information that has more practical value to local decision-makers. Specifically, by highlighting the most important biological and ecological characteristics of inshore and offshore reef communities, the data presented in Chapter 3 made it possible to identify the locations where key ecological processes (e.g., spawning and recruitment) may be captured if included within a local MPA, thus making it possible to later fulfill some aspects of the adequacy principle recommended for effective MPAs. It also made it possible to make a preliminary assessment of the relative health of inshore and offshore reefs. This information is essential, as systematic conservation planning is ultimately a spatial exercise (Margules and Pressey 2000), and so, requires spatially-explicit information to be provided on an appropriate scale. The data also identifies species that are representative of different local communities and habitats, thus making it possible to also fulfill aspects of the representativeness principle.

It is important to note, however, that a single snapshot in time is not adequate for making permanent prioritization decisions. Reef community assemblages may vary seasonally due to the recruitment or migration patterns of different species or due to climate, and, thus, future work should include more surveys through time. Future work could also include surveys of other supporting habitats besides coral reefs, such as sea grass beds and mangroves, as well as attempt to locate local spawning aggregations of commercially important species.

6.3. Contribution to Conservation Science

It is rare for initial conservation efforts to be based on knowledge of the abundances of such a large number of species as those surveyed in Chapter 3, and, currently, many MPAs still fail due to opportunistic rather than science-based placement (Roberts and Hawkins 2000; Stewart et al. 2003). Therefore, Chapter 3 not only contributes to the growing body of much-needed knowledge of Red Sea reefs (Berumen et al. 2013), but also serves as an example of good practice for accumulating as much scientific knowledge as possible prior to spatial prioritization.

The spatial prioritization exercise that is detailed in Chapter 4 (based on the data collected in Chapter 3) and used to propose multiple designs of MPAs in Thuwal is the first of its kind to be done in the Red Sea. It follows the relevant principles of systematic conservation planning by: 1) identifying conservation goals, 2) setting quantitative targets, 3) using the best available science, 4) identifying priority areas, and 5) providing multiple alternatives (Margules and Pressey 2000; Tear et al. 2005). It is also, to the best of my knowledge at the time of writing, the first conservation planning exercise in the Red Sea to use a powerful decision-making software tool such as Marxan to optimize MPA design, and to do so on a scale that is locally-manageable. On a more global scale, the results of this analysis add to the literature debating the feasibility of designing MPAs that can achieve multiple, and often contrasting, goals simultaneously and efficiently (Hastings and Botsford 2003; Green et al. 2014). The results add to the literature showing that achieving a balance between fisheries and biodiversity conservation goals is possible at least in some circumstances (e.g., Schmiing et al 2014).

It is important, however, to acknowledge the main limitations of this analysis. First, the species abundances were modeled throughout the study area using a splining function rather than an ecological model that is based on environmental variables. A more sophisticated modeling technique may lead to different abundance maps, and therefore, different spatial prioritization results. However, the splining method has the advantage of being easy and quick to implement with access to any GIS software, and its accuracy can be improved by having a larger number of spatial replicates. Second, abundances per 100 m^2 were scaled up to entire reefs using a simple area-weighted sum, which could also be made more accurate using more sophisticated conversion formulas. However, area-weighted sums allow taking into consideration the sizes of individual reefs when conducting Marxan analyses with irregular reef-shapes as planning units. Finally, the socio-economic costs (e.g., losses to fishermen) of selecting individual reefs into MPAs could not be considered in this analysis due to the difficulty of obtaining or accessing socio-economic information in Saudi Arabia. It was assumed that costs would be more-or-less equal for all reefs, which may not be accurate. One of the strongest advantages of using a tool like Marxan is its ability to find the cheapest and most efficient MPA solutions. Therefore, incorporating economic costs, or at least a surrogate of such costs, would allow a user to make much better use of Marxan's power and make more effective decisions. Thus, future work should include more accurate ecological models and relevant socio-economic data.

6.4. Conclusions

This thesis applied theoretical, investigative/descriptive, and analytical approaches to address the question of how science-based MPAs could be designed using modern techniques in a data-poor region of the world. While the acquisition of larger datasets and more sophisticated modeling techniques could improve various parts of this work, the findings are sufficient to guide the initiation of conservation planning in the Thuwal area as well as provide a model for other parts of the Red Sea. The methods applied here are also relatively quick and cheap to employ, which would allow for quick decision-making with room for future adaptation as more data becomes available.

References

Almany Glenn R, Hamilton Richard J, Bode M, Matawai M, Potuku T, Saenz-Agudelo P, Planes S, Berumen Michael L, Rhodes Kevin L, Thorrold Simon R, Russ Garry R, Jones Geoffrey P (2013) Dispersal of grouper larvae drives local resource sharing in a coral reef fishery. Current biology : CB 23:626-630

Almany G, Connolly S, Heath D, Hogan J, Jones G, McCook L, Mills M, Pressey R, Williamson D (2009) Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. Coral Reefs 28:339-351

Beger M, McGowan J, Treml EA, Green AL, White AT, Wolff NH, Klein CJ, Mumby PJ, Possingham HP (2015) Integrating regional conservation priorities for multiple objectives into national policy. Nat Commun 6

Berumen M, Almany G, Planes S, Jones G, Thorrold S (2012) Persistence of self-recruitment and patterns of larval connectivity in a marine protected area network. Ecology and Evolution 2:444-452

Berumen ML, Hoey AS, Bass WH, Bouwmeester J, Catania D, Cochran JEM, Khalil MT, Miyake S, Mughal MR, Spaet JLY, Saenz-Agudelo P (2013) The status of coral reef ecology research in the Red Sea. Coral Reefs 32:737-748

Bode M, Armsworth P, Fox H, Bode L (2012) Surrogates for reef fish connectivity when designing marine protected area networks. Marine Ecology Progress Series 466:155-166

Green AL, Fernandes L, Almany G, Abesamis R, McLeod E, Aliño PM, White AT, Salm R, Tanzer J, Pressey RL (2014) Designing marine reserves for fisheries management, biodiversity conservation, and climate change adaptation. Coastal Management 42:143-159

Harrison Hugo B, Williamson David H, Evans Richard D, Almany Glenn R, Thorrold Simon R, Russ Garry R, Feldheim Kevin A, van Herwerden L, Planes S, Srinivasan M, Berumen Michael L, Jones Geoffrey P (2012) Larval Export from Marine Reserves and the Recruitment Benefit for Fish and Fisheries. Current biology : CB 22:1023-1028

Hastings A, Botsford LW (2003) Comparing designs of marine reserves for fisheries and for biodiversity. Ecological Applications 13:S65-S70

International Union for the Conservation of Nature (IUCN)/United Nations Environmental Program (UNEP) (1988) Coral reefs of the world: Volume 2: Indian Ocea, Red Sea and Gulf. UNEP/IUCN, Gland, Switzerland and Cambridge UK/UNEP, Nairobi, Kenya

Kininmonth S, Beger M, Bode M, Peterson E, Adams VM, Dorfman D, Brumbaugh DR, Possingham HP (2011) Dispersal connectivity and reserve selection for marine conservation. Ecological Modelling 222:1272-1282

Margules CR, Pressey RL (2000) Systematic conservation planning. Nature 405:243-253

McCook L, Almany G, Berumen M, Day J, Green A, Jones G, Leis J, Planes S, Russ G, Sale P, Thorrold S (2009) Management under uncertainty: guide-lines for incorporating connectivity into the protection of coral reefs. Coral Reefs 28:353-366

Nanninga GB (2013) Merging approaches to explore connectivity in the Anemonefish, Amphiprion bicinctus, along the Saudi Arabian Coast of the Red Sea. King Abdullah University of Science and Technology, p186

PERSGA/GEF (2003) Coral reefs in the Red Sea and Gulf of Aden: Surveys 1990 to 2000: Summary and recommendations PERSGA Technical Series No 7. PERSGA, Jeddah

Roberts CM, Alexander RDS, Ormond RFG (1992) Large-Scale Variation in Assemblage Structure of Red Sea Butterflyfishes and Angelfishes. Journal of Biogeography 19:239-250

Roberts CM, Hawkins JP (2000) Fully-protected marine reserves: a guide. WWF Endangered Seas Campaign, Washington, DC, USA and Environment Department, University of York, York, UK

Schmiing M, Diogo H, Serrão Santos R, Afonso P (2014) Marine conservation of multispecies and multi-use areas with various conservation objectives and targets. ICES Journal of Marine Science: Journal du Conseil

Stewart RR, Noyce T, Possingham HP (2003) Opportunity cost of ad hoc marine reserve design decisions: an example from South Australia. Marine Ecology Progress Series 253:25-38

Tear TH, Kareiva P, Angermeier PL, Comer P, Czech B, Kautz R, Landon L, Mehlman D, Murphy K, Ruckelshaus M, Scott JM, Wilhere G (2005) How much is enough? The recurrent problem of setting measurable objectives in conservation. BioScience 55:835-849

APPENDIX 1: USING LARVAL DISPERSAL MODELS TO EVALUATE THE USE OF HABITAT SPATIAL PROXIMITY ANALYSIS IN RESERVE NETWORK DESIGN IN THE CENTRAL SAUDI ARABIAN RED SEA

This material was presented as a poster at the International Marine Conservation Congress (IMCC) in August, 2014, at Glasgow, Scotland.

Authors: Maha Khalil[1], Peng Zhen[1], Gerrit Nanninga[1], Marc Genton[1], Rebecca Weeks[2], Robert Pressey[2], and Michael Berumen[1]

Affiliations:

[1]King Abdullah University of Science and Technology, Saudi Arabia

[2]James Cook University, Australia

Introduction

There is considerable debate over how to optimize marine protected area (MPA) networks to meet various ecological goals. With regards to larval connectivity, priority is usually placed on reefs which are presumed sources rather than sinks of larvae in a given region of interest, as source reefs have the capacity to replenish other locations under different scenarios of disturbance (Almany et al. 2009; McCook et al. 2009).

An analysis of habitat spatial distribution in an area of interest could in some cases be the simplest and most accessible type of information available for decision makers (Costello et al. 2010), especially in areas where larval dispersal patterns are highly variable and where other types of data are scarce. Here, we use a larval dispersal model to evaluate if spatial habitat proximity may be a good indicator for potential source reefs in data-deficient locations.

Research Questions:

- Using a biophysical connectivity model, which of 7 representative reefs in the Thuwal region of the central Saudi Arabian Red Sea are important sources of larvae to other reefs during the main spawning season of *Amphiprion bicinctus* (the Red Sea anemonefish)*?*
- Can proximity to other reefs serve as an indicator of a given reef's predicted successful larval output within the network?

Methods:

Study Site

Patchy reef habitat along 70 km of the central Saudi Arabian Red Sea coast near KAUST and Thuwal (Figure 1).

Model

Physical features of the dispersal model are based on a 3-dimensional, small-domain, high-resolution Massachusetts Institute of Technology (MIT) general circulation model, ranging from 22.1 to 22.8°N and 38.5 to 39.2°E. The physical current data provides the background hydrodynamics of the Connectivity Modeling System (CMS) (Paris et al. 2013), which calculates Lagrangian particle trajectories. The model organism used for this study is the Red Sea anemonefish, *Amphiprion bicinctus,* which produces eggs in January. Biological attributes (e.g. settlement competency) were estimated from the literature (Nanninga 2013). Table 1 shows model parameters.

Table A1.1: List of model parameters.

Parameter	Value
Pelagic larval duration	12 days
Settlement competency	6 days
Assumed range for larvae to detect settlement habitat	2 km
Mortality	6 days
Number of larvae released	9000/reef
Release dates	January 5 - 6, 2012

Spatial Proximity Analysis

The number of reefs occurring within a defined radius of the 7 modeled source reefs was counted in ArcGIS. The search radius was standardized to 14 km (20% of the length of the study area) for simplicity, and the results were summarized in the form of histograms.

Results:

- Three reefs – Offshore 2, Midshelf 2, and Inshore 3 – may have successfully supplied larvae to other reefs in the winter spawning season of the Red Sea anemonefish in 2012 (Table 2).
- Two reefs – Midshelf 2 and Inshore 3 – had the highest numbers of reefs distributed within 14 km of them. Offshore 2 has one of the lowest proximity rates in all reefs examined.
- Rates of local retention were very low for all reefs (Table 2).

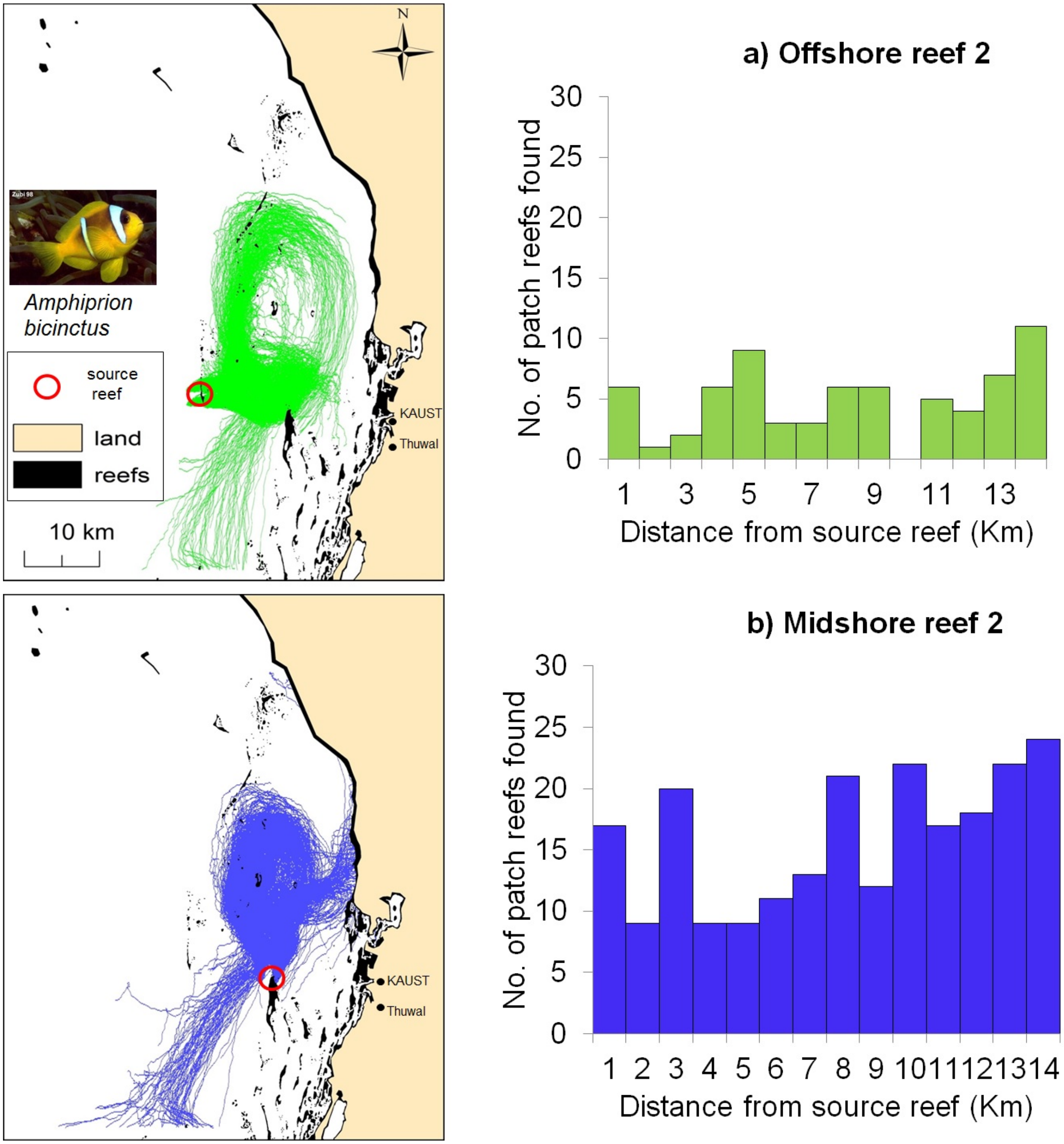


Figure A1: Left panel shows simulated anemonefish larval trajectories for January, 2012, in the Thuwal region of the Saudi Red Sea originating from 2 of the most successful source reefs identified by the model a) Offshore 2, and b) Midshelf 2. The right panel shows habitat proximity histograms for the same reefs.

Table A1.2: Summary of local retention and larval supply as per the model.

Source reef	Percent local retention (%)	No. of receiving patch reefs (no. of larvae supplied)
Offshore 1	0	3 (9)
Offshore 2	0.13	19 (180)
Midshelf 1	0	2 (17)
Midshelf 2	0.39	14 (162)
Inshore 1	0.03	10 (37)
Inshore 2	0.1	7 (98)
Inshore 3	0.08	10 (144)

Discussion and Future Work:

- Two out of three potentially valuable source reefs also had relatively high spatial proximity rates which indicates that analysis of proximity may be a useful tool to use in regions where data is scarce.
- Future work may show high temporal variability in dispersal patterns, in which case proximity analysis may be even more useful.
- Future genetic analyses could validate whether the source reefs identified by the model are actually functioning as sources.
- Very low rates of local retention suggest little to no self-recruitment on Thuwal reefs, as was also shown empirically for one reef by Nanninga (2013) using parentage analysis. This, as well as the highly fragmented nature of the habitat, suggests that, for Thuwal, a network of many, small reserves may be more effective in conserving populations than fewer, larger reserves.

References:

Almany G, Connolly S, Heath D, Hogan J, Jones G, McCook L, Mills M, Pressey R, Williamson D (2009) Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. Coral Reefs 28:339-351

Costello C, Rassweiler A, Siegel D, De Leo G, Micheli F, Rosenberg A (2010) The value of spatial information in MPA network design. Proceedings of the National Academy of Sciences 107:18294-18299

McCook L, Almany G, Berumen M, Day J, Green A, Jones G, Leis J, Planes S, Russ G, Sale P, Thorrold S (2009) Management under uncertainty: guide-lines for incorporating connectivity into the protection of coral reefs. Coral Reefs 28:353-366

Nanninga GB (2013) Merging approaches to explore connectivity in the Anemonefish, Amphiprion bicinctus, along the Saudi Arabian Coast of the Red Sea. King Abdullah University of Science and Technology, p186

Paris C, Helgers J, Van Sebille E, Srinivasan A (2013) Connectivity Modeling System: A probabilistic modeling tool for the multi-scale tracking of biotic and abiotic variability in the ocean. Environmental Modelling & Software 42:47-54

APPENDIX 2: RUGOSITY PATTERNS AND CORRELATIONS ON THUWAL REEFS

Justification

Previous studies have shown some positive correlations between the structural complexity (rugosity) of reef habitat and ecological variables such as benthic and fish diversity (e.g., Wilson et al. 2007; Chong-Seng et al. 2012; Graham and Nash 2013), while other studies showed no correlation (e.g., Roberts and Ormond 1987) and questioned the use of habitat measures in general as proxies for biodiversity (Beger et al. 2007; Lindsay et al. 2008). As an exploratory investigation, rugosity measurements were collected from Thuwal reefs to examine whether structural complexity may be a good predictor of biomass or diversity indices on this local scale. This was done in order to search for a potentially simple local proxy of diversity that could then be used in spatial prioritization for conservation.

Materials and Methods

In May 2014, the structural complexity of the same 9 reefs on which visual surveys were conducted (Chapter 3) was estimated digitally using the same method as Dustan et al. (2013). Fine-scale pressure measurements were taken using the HOBO U20 Titanium Water Level Logger U20-001-02-Ti (Onset Computer Company #U20-001-02-Ti, http://www.onsetcomp.com/products/data-loggers/u20-001-02-ti) which operates within a range of 0 – 30 meters of depth with a resolution of 0.41 cm and an accuracy of +/– 1.5 cm. The logger was set to record pressure every second once initialized. Pressure measurements were then mathematically converted to depth using the formula: depth (meters) = pressure (decibars) x 1.019716. Rugosity was then characterized as the standard deviation of the set of depth measurements (Dustan et al. 2013). Measurements were taken along 3 replicate transects per reef. Each transect was 25 meters long, and all were at a depth of 10 meters. Transects were laid out at the same GPS locations on the reefs where the fish surveys were conducted (Chapter 3).

A Kruskal-Wallis test was performed to identify differences between reefs, and simple linear regressions were performed to investigate the relationship between reef rugosity and distance from shore as well as reef rugosity and biological variables: fish biomass, fish species richness, coral cover, and coral genus richness.

Results

Average rugosity per reef ranged from 0.16 ±0.01 on the inshore reef ASR to 0.73 ±0.11 on the offshore reef AMR (Table A2.1 and Figure A2). No statistical significance was found in the differences between reefs ($p_{Kruskal\text{-}Wallis} = 0.047$). Pearson's Correlation test also showed no significant correlation between mean reef rugosity and distance from shore ($R = 0.558$, $R^2 =$

0.312, p = 0.153). Mean reef rugosity was also found to be a poor predictor of fish species biomass, fish species richness, mean percent coral cover, and coral genus richness (regression coefficients are shown in Table A2.2).

Discussion and Conclusions

The results above are similar to one previous study conducted in the Red Sea on a different scale, using different methods for measuring rugosity (Roberts and Ormond 1987), which also found habitat complexity to be a poor predictor of reef biodiversity.

It is possible that the sample size in this study and the number of replicates are inadequate for revealing spatial patterns in rugosity on the scale of Thuwal reefs or for revealing relationships between rugosity and biodiversity. It would also be more appropriate to collect rugosity measurements at the same time as the fish and benthic data and on the same transects. Moreover, it is possible that the relationship between rugosity and biodiversity may be more complex and require more in-depth analysis. For example, rugosity may be related only to the abundances of small fishes (Wilson et al. 2007), which cannot be observed in this preliminary analysis.

It is also important to note that the method employed here for measuring rugosity electronically, while high in resolution, is somewhat difficult to employ. Most reefs in this area have nearly vertical walls and shallow, flat, tops, and structural complexity at 10 m depth occurs mostly in the form of crevices and outcrops that are perpendicular to the reef walls. On the other hand, measuring rugosity using a pressure logger (or even using the traditional chain method) is a vertical process that can only record complexity in one dimension (up and down) that, on a steep wall, is not the dimension in which most of the structural variation in complexity occurs. Therefore, this method is more suitable for measuring habitat complexity on “flat” reef structures, while other methods, such as counting holes and crevices or visually categorizing complexity (see McCormick (1994) for a review of methods), may be more appropriate for steep reefs such as Thuwal reefs.

Table A2.1: Mean rugosity and standard error of 3 offshore, 3 midshelf, and 3 inshore reefs in Thuwal, central Saudi Arabian Red Sea. Data were collected from the same locations from which biological data were collected. Rugosity was characterized as the standard deviation of fine-scale pressure measurements collected by a HOBO pressure logger. For a list of full reef names, see the List of Abbreviations and Chapter 3.

Location	Reef name	Mean rugosity	Standard error
Offshore	RR	0.51	0.01
	NR	0.64	0.12
	AMR	0.73	0.11
Midshelf	FR	0.40	0.04
	TWR	0.34	0.08

	AHR	0.44	0.07
Inshore	ASR	0.16	0.01
	TR	0.62	0.13
	EFR	0.511	0.18

Table A2.2: A summary of results of regression analyses, showing a list of the dependent biological variables, Pearson's coefficients (R values), the R^2 values, and the significance values. The independent variable was mean reef rugosity, which was calculated for each of 9 reefs from 3 transect replicates per reef at 10 m depth. Results show no significant correlation between rugosity and the listed biological variables.

Dependent variable	R	R^2	Significance*
Mean fish biomass per reef (kg/100m2)	0.449	0.201	0.226
Total fish species richness per reef	0.067	0.004	0.865
Mean hard coral cover per reef (%)	0.353	0.125	0.351
Total hard coral genus richness per reef	0.413	0.17	0.27

* Alpha value = 0.005

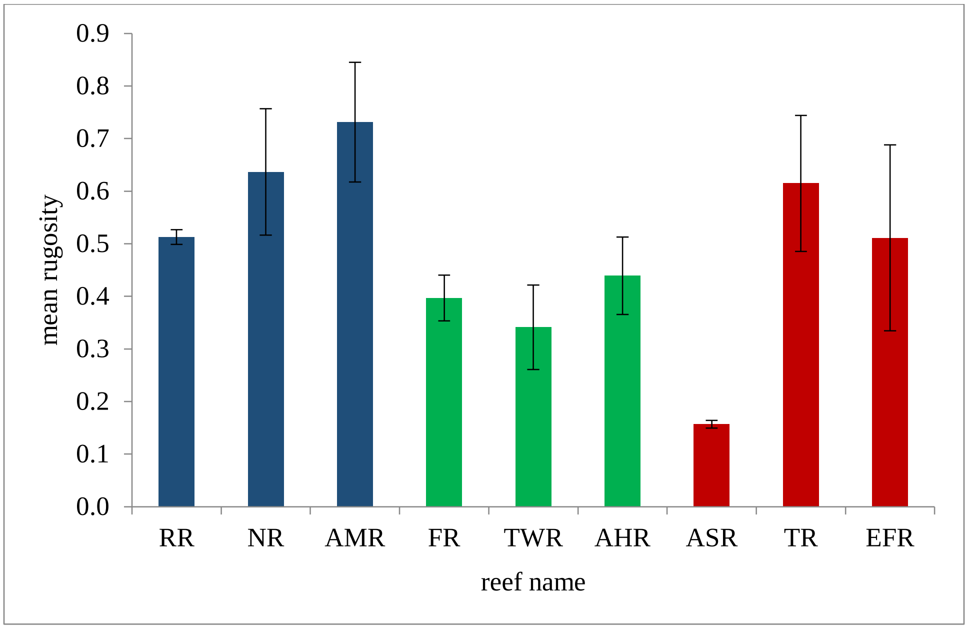


Figure A2: Mean rugosity on 9 reefs in Thuwal, central Saudi Arabian Red Sea. Bars show standard error of the mean. Red bars indicate inshore reefs, green bars indicate midshelf reefs, and blue bars show offshore reefs. The x-axis shows abbreviated reef names. Mean rugosity was calculated from 3 replicates per reef at 10 m depth. Rugosity was characterized as the standard deviation in fine-scale pressure measurements collected using a HOBO pressure logger.

References

Beger M, McKenna SA, Possingham HP (2007) Effectiveness of surrogate taxa in the design of coral reef reserve systems in the Indo-Pacific. Conservation Biology 21:1584-1593

Chong-Seng KM, Mannering TD, Pratchett MS, Bellwood DR, Graham NAJ (2012) The influence of coral reef benthic condition on associated fish assemblages. Plos One 7

Dustan P, Doherty O, Pardede S (2013) Digital Reef Rugosity Estimates Coral Reef Habitat Complexity. PLoS ONE 8:e57386

Graham NAJ, Nash KL (2013) The importance of structural complexity in coral reef ecosystems. Coral Reefs 32:315-326

Lindsay M, Patterson H, Swearer S (2008) Habitat as a surrogate measure of reef fish diversity in the zoning of the Lord Howe Island Marine Park, Australia. Marine Ecology Progress Series 353:265-273

McCormick MI (1994) Comparison of field methods for measuring surface topography and their associations with a tropical reef fish assemblage Marine Ecology Progress Series 112:87-96

Roberts CM, Ormond RFG (1987) Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. Marine Ecology Progress Series 41:1-8

Wilson SK, Graham NAJ, Polunin NVC (2007) Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. Marine Biology 151:1069-1076

APPENDIX 3: SUMMER SEA SURFACE TEMPERATURES

Monthly average sea surface temperatures (SSTs) obtained via remote sensing were summarized for the years 2000 – 2009, covering most of the Thuwal area. The data was and made available by the National Oceanic and Atmospheric Administration's (NOAA) National Oceanographic Data Center (NODC) (Kilpatrick et al. 2001; NOAA 2013). The spatial resolution of the satellite data was 4 km and temperatures were recorded twice daily. Overall temperature patterns were visualized, and then summer temperatures were analyzed separately.

After preliminary visualization (Figure A3.1), SSTs in Thuwal were found to be highest during the month of August. Accordingly, average August SSTs from 2000 – 2009 were compared for inshore and offshore Thuwal waters to explore whether inshore reefs experienced significantly higher SSTs, thus revealing a potential explanation for their higher vulnerability to thermal stress (Furby et al. 2013). However, a t-test showed no significant difference between inshore and offshore average August SSTs ($t = 0.040$, $p = 0.969$) (Figure A3.2).

Surface temperatures may not be the important variable causing inshore reefs to be more susceptible to thermal stress, but rather deeper temperatures and overall water turnover.

Figure A3.1: Average monthly SSTs obtained via satellites in the Thuwal area (E 38.78° – 39.05, N 22.04° – 22.17°) averaged over the years 2000 – 2009. Data were obtained from NOAA (2013) at www.ncdc.noaa.gov.

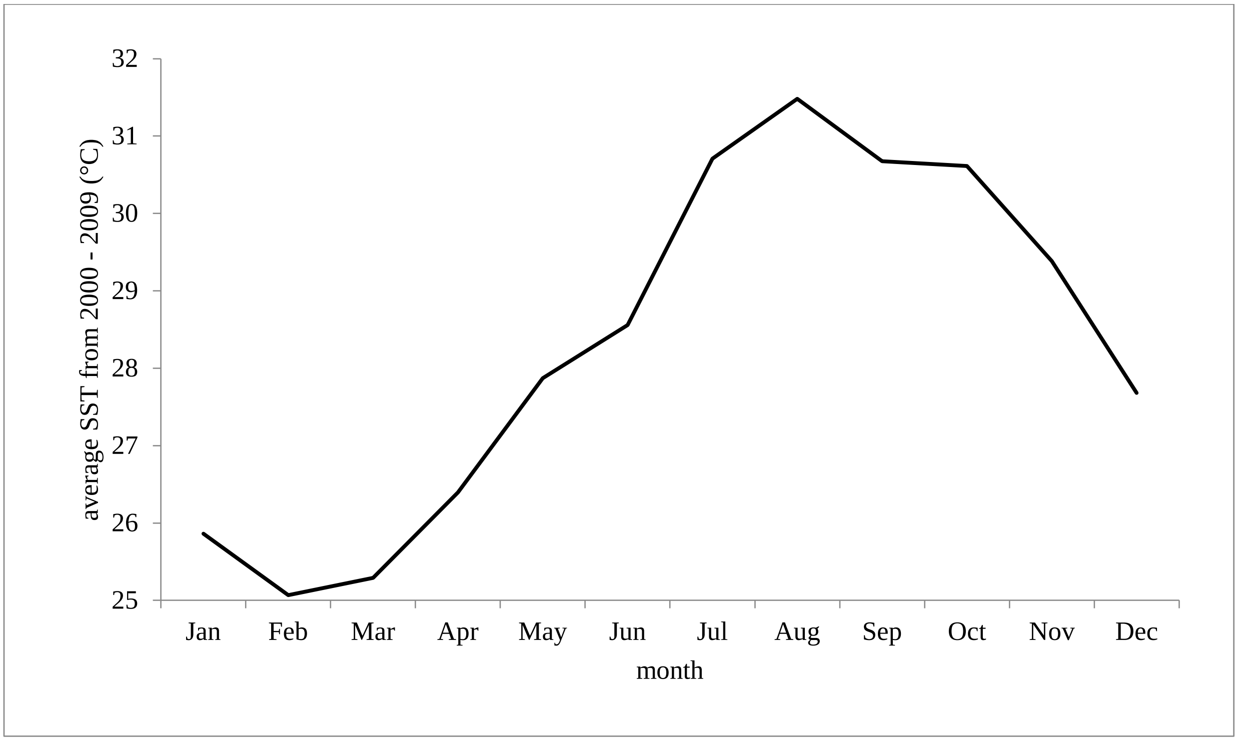


Figure A3.2: Average August SSTs obtained via satellites in Thuwal waters from 2000 – 2009 for inshore (< 5 km from shore, red line) and offshore (about 20 km from shore, black line). Data were obtained from NOAA (2013) at www.ncdc.noaa.gov.

References:

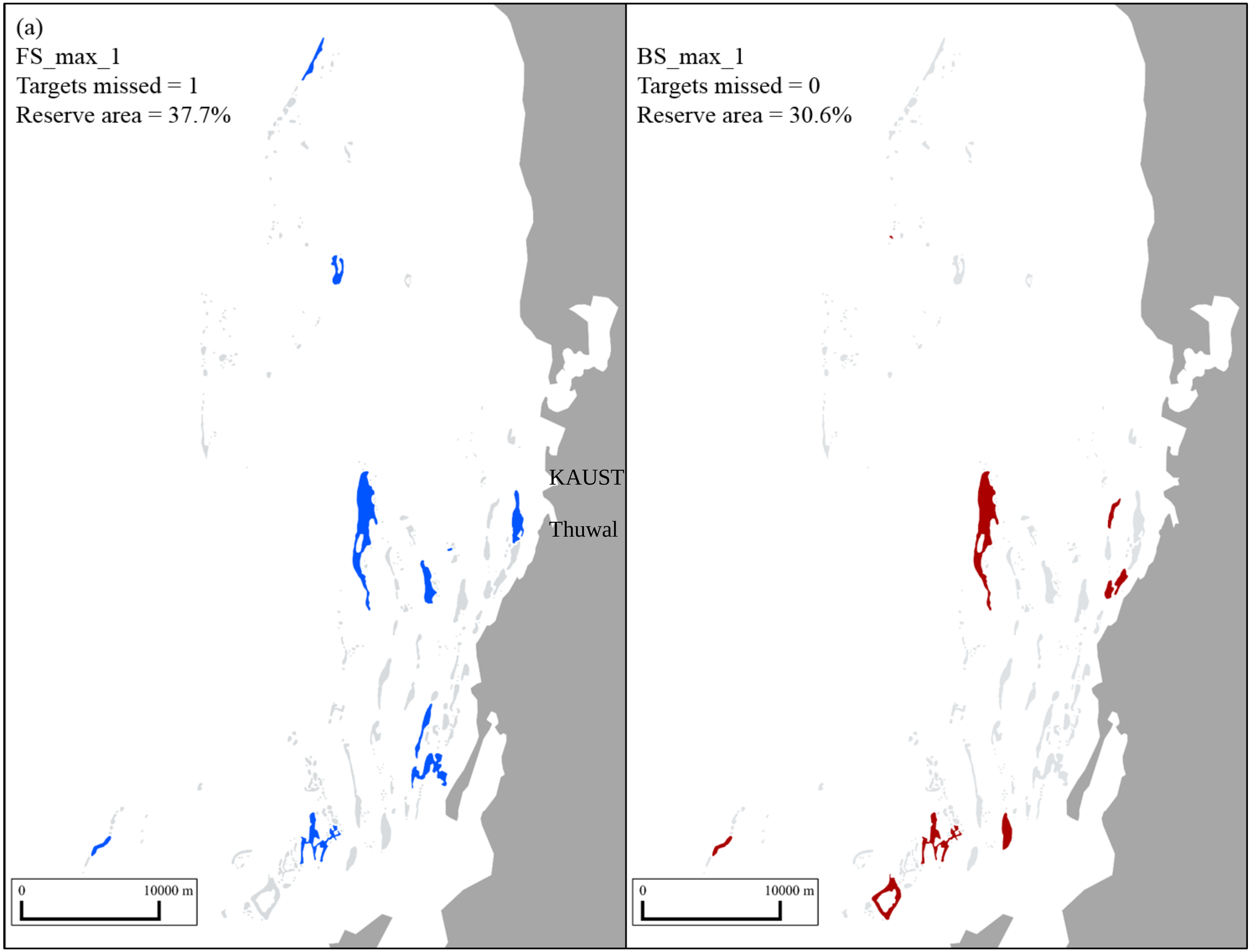
Furby KA, Bouwmeester J, Berumen ML (2013) Susceptibility of central Red Sea corals during a major bleaching event. Coral Reefs 32:505-513

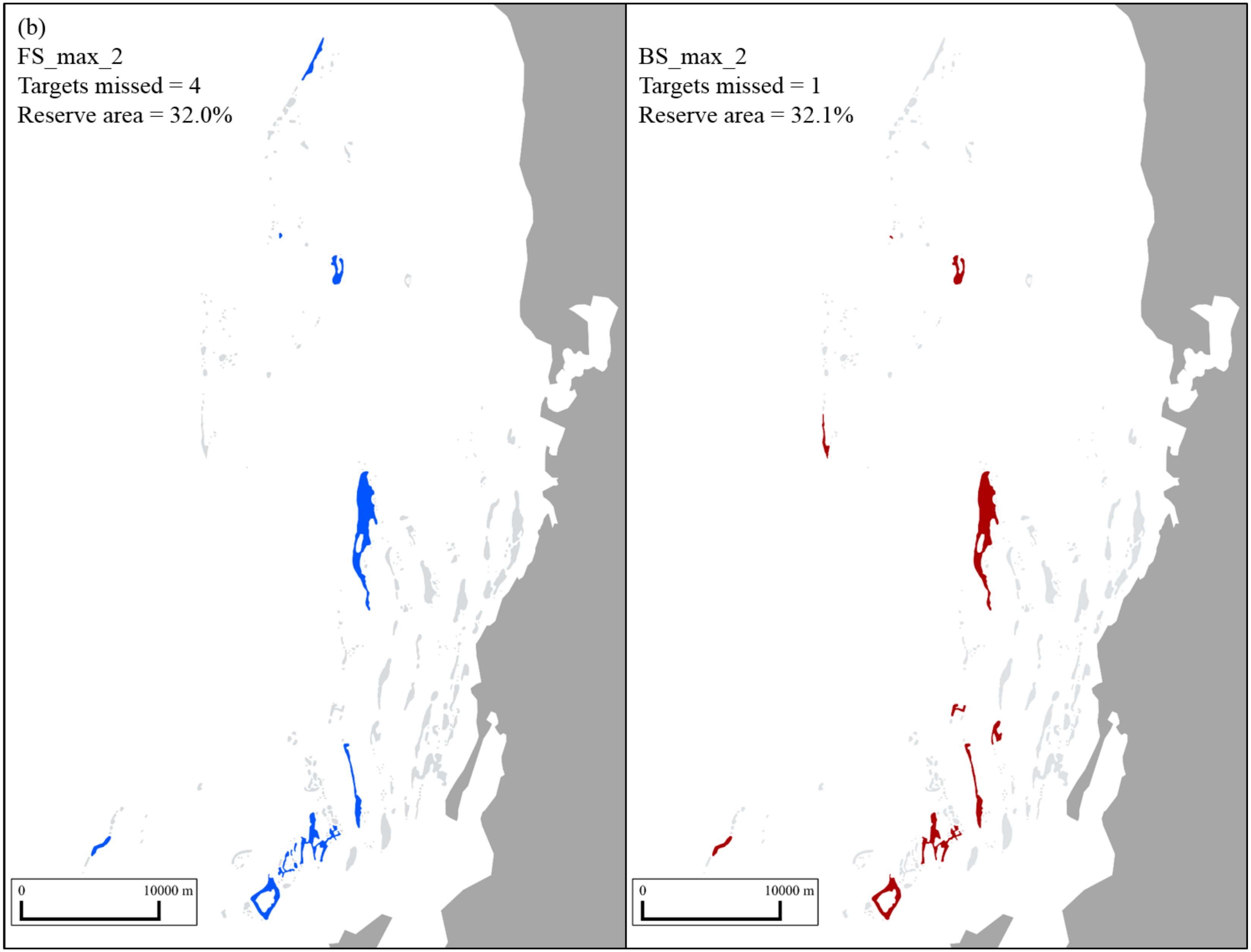
Kilpatrick KA, Podesta GP, Evans R (2001) Overview of the NOAA/NASA Advanced Very High Resolution Radiometer Pathfinder algorithm for sea surface temperature and associated matchup database. Journal of Geophysical Research-Oceans, 106 (C5): 9179-9197

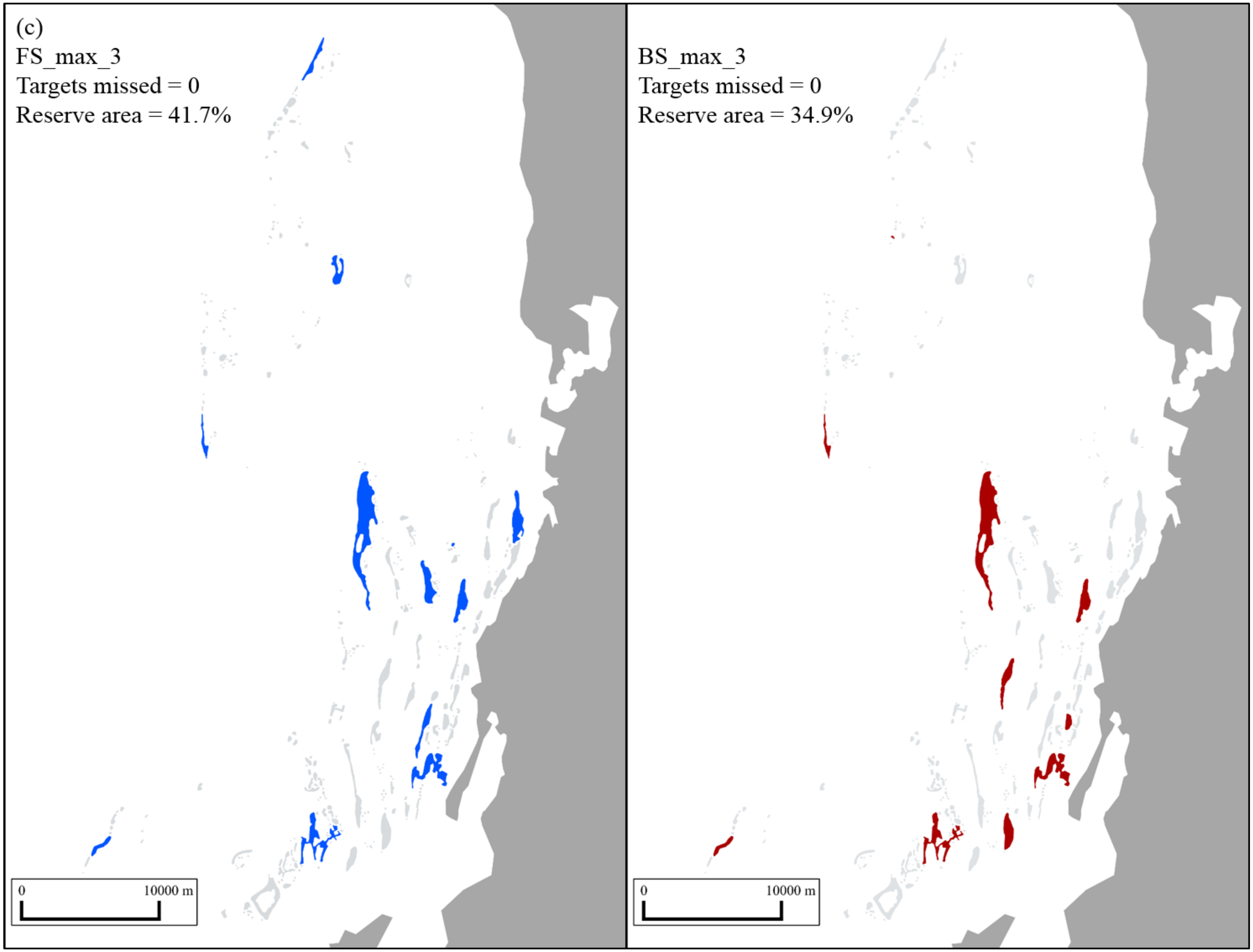
NOAA (2013) 4 km pathfinder version 5 user guide. http://www.nodc.noaa.gov/SatelliteData/pathfinder4km/userguide.html

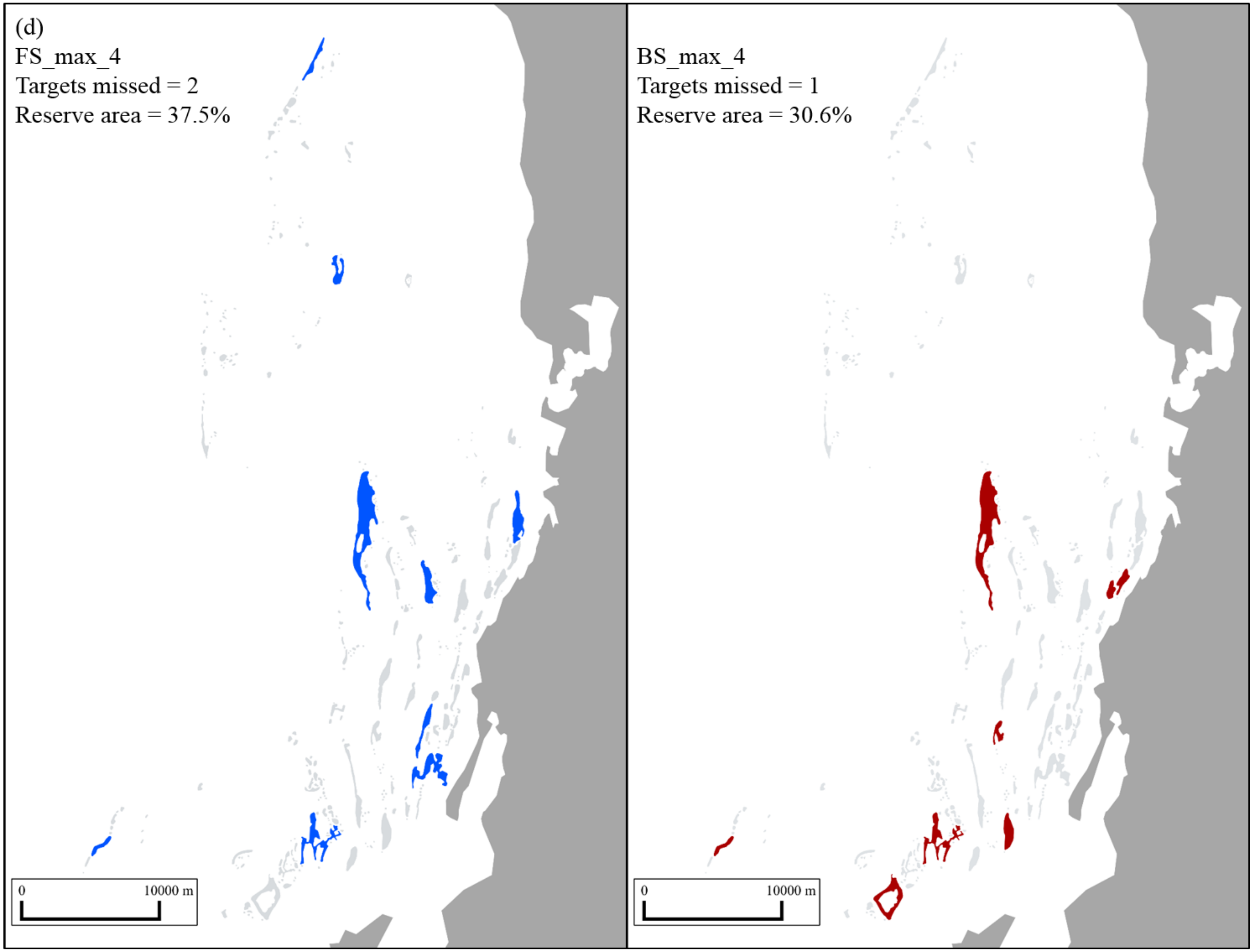
APPENDIX 4: MARXAN SOLUTIONS

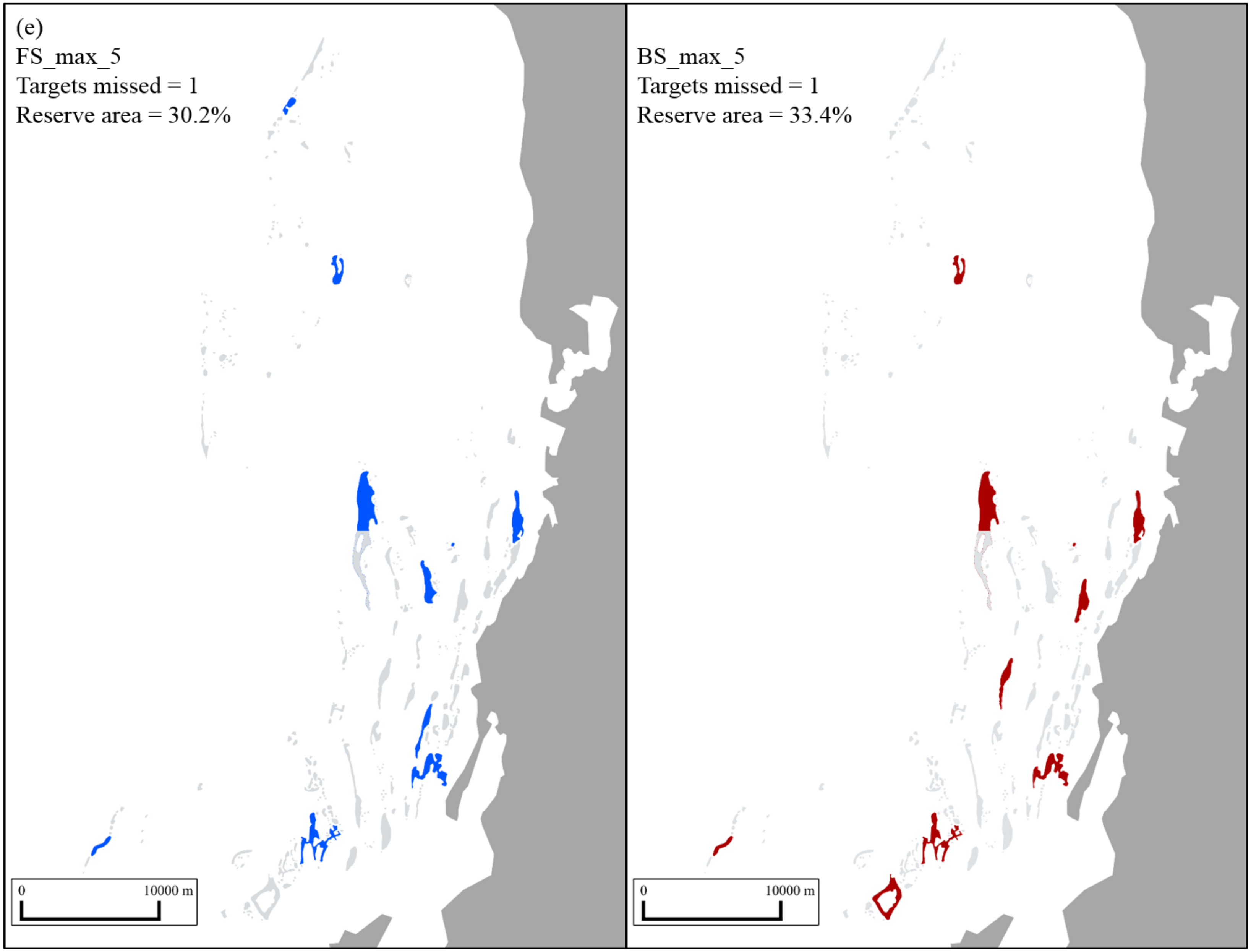
Figure A4: Marxan best solutions for 20 scenarios run on the reefs near Thuwal, central Saudi Arabian Red Sea: 10 fisheries scenarios (FS), and 10 biodiversity scenarios (BS). Panels (a) – (e) show best solutions for scenarios with maximum targets (max). The left panels are FS solutions showing selected reefs shown in blue, and the right panels show BS solutions with selected reefs shown in red. Panels (f) – (j) show best solutions for scenarios with minimum (min) target levels. Unselected reefs are shown in pale gray, and mainland coast is shown in dark grey. All panels are labeled as follows: scenario type (FS or BS)_target level (max or min)_iteration number. Iteration numbers can be interpreted as follows (see also Table 2 in Chapter 4): 1 = control runs, no reefs locked in or out; 2 = inshore reefs (< 5 km from shore locked out), 3 = research monitoring sites locked in; 4 = patches smaller than 0.1 km^2 locked out; 5 = half of the largest reef in the area is locked out. The number of targets missed by each solution and the percent reef area included in the reserve are also indicated on the panels. Cost and boundary length modifier were equal to 1 for all planning units and all scenarios.

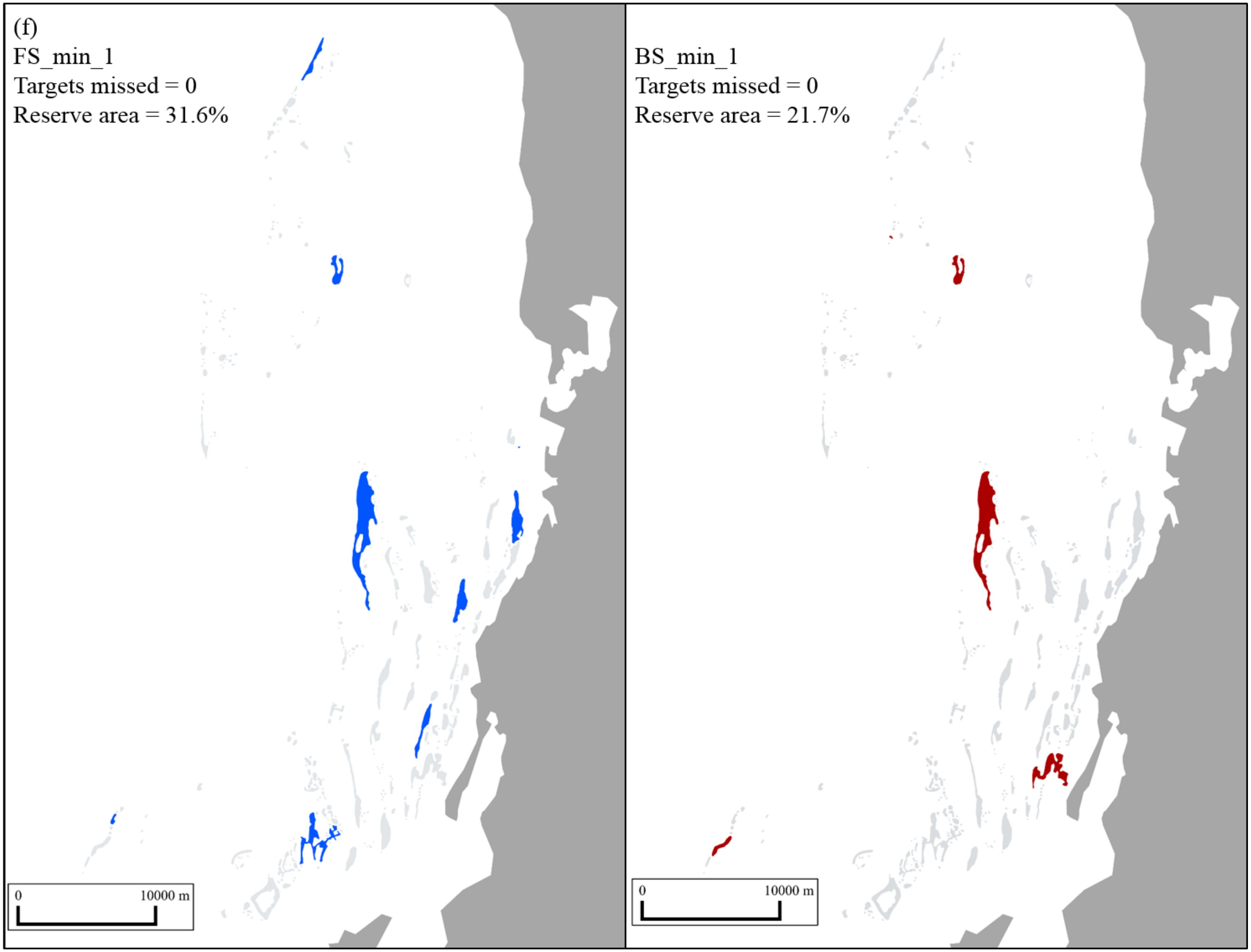

(a)
FS_max_1
Targets missed = 1
Reserve area = 37.7%
KAUST
Thuwal
0
10000 m
BS_max_1
Targets missed = 0
Reserve area = 30.6%
0
10000 m

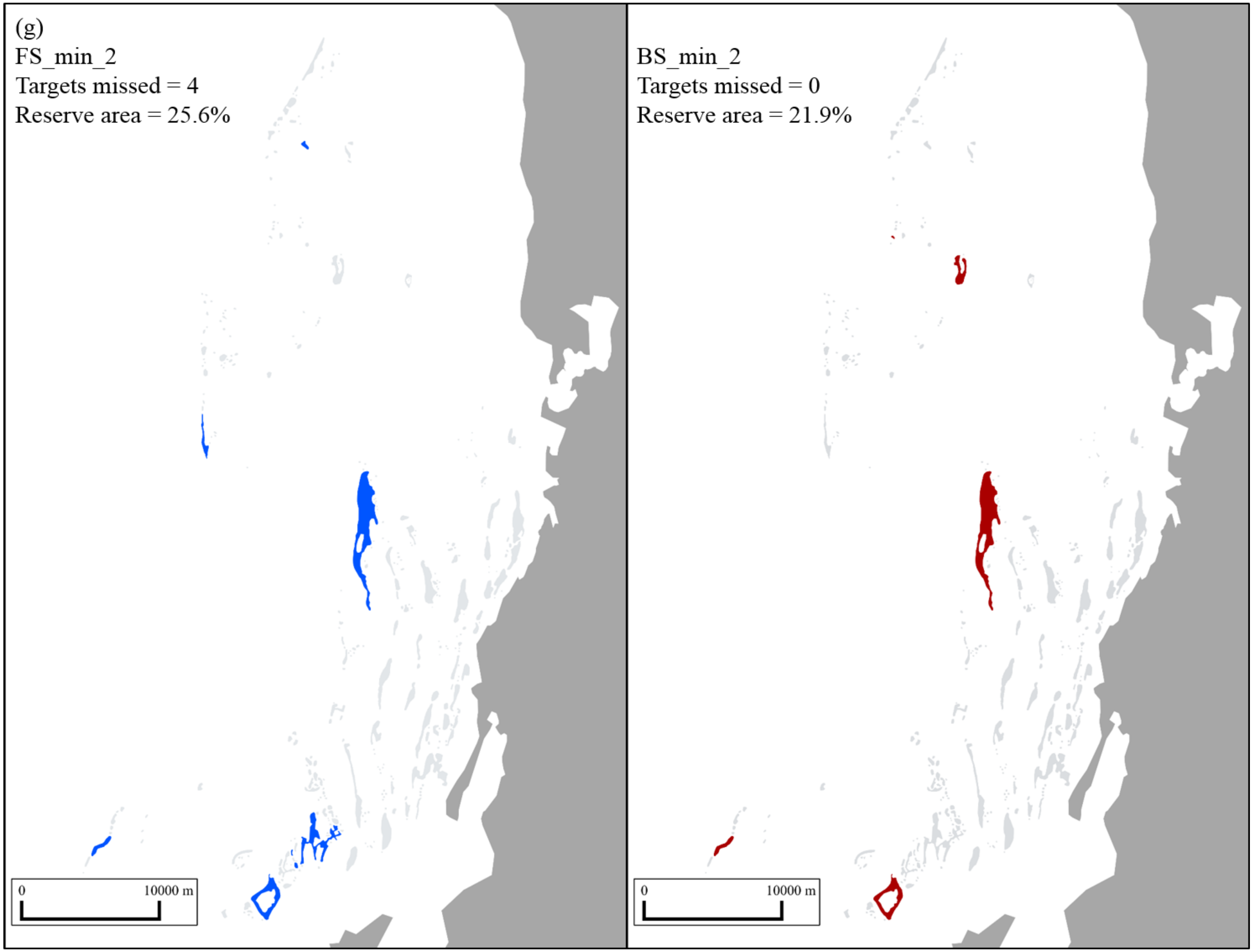

(b)
FS_max_2
Targets missed = 4
Reserve area = 32.0%
0
10000 m
BS_max_2
Targets missed = 1
Reserve area = 32.1%
0
10000 m

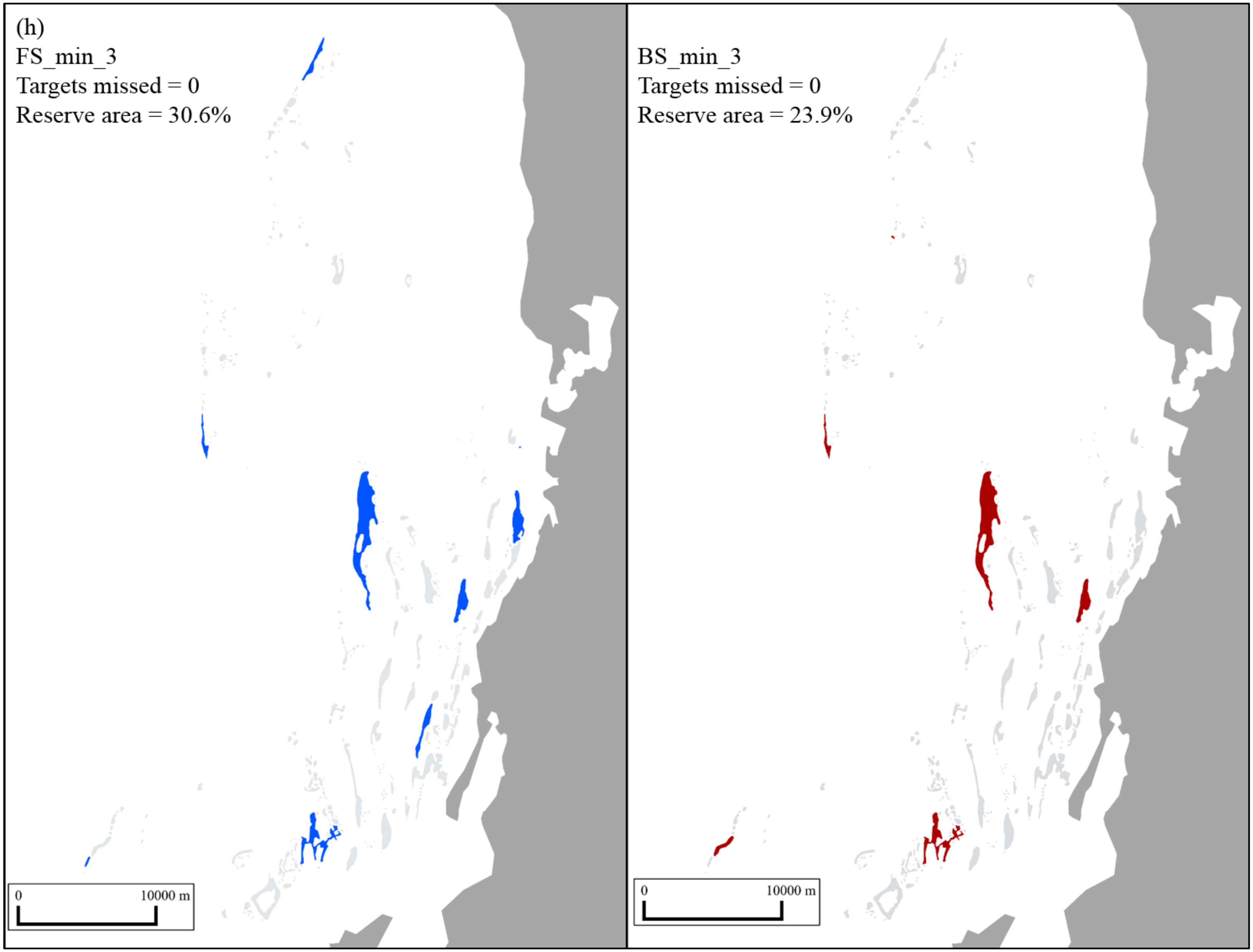

(c)
FS_max_3
Targets missed = 0
Reserve area = 41.7%
0
10000 m
BS_max_3
Targets missed = 0
Reserve area = 34.9%
0
10000 m

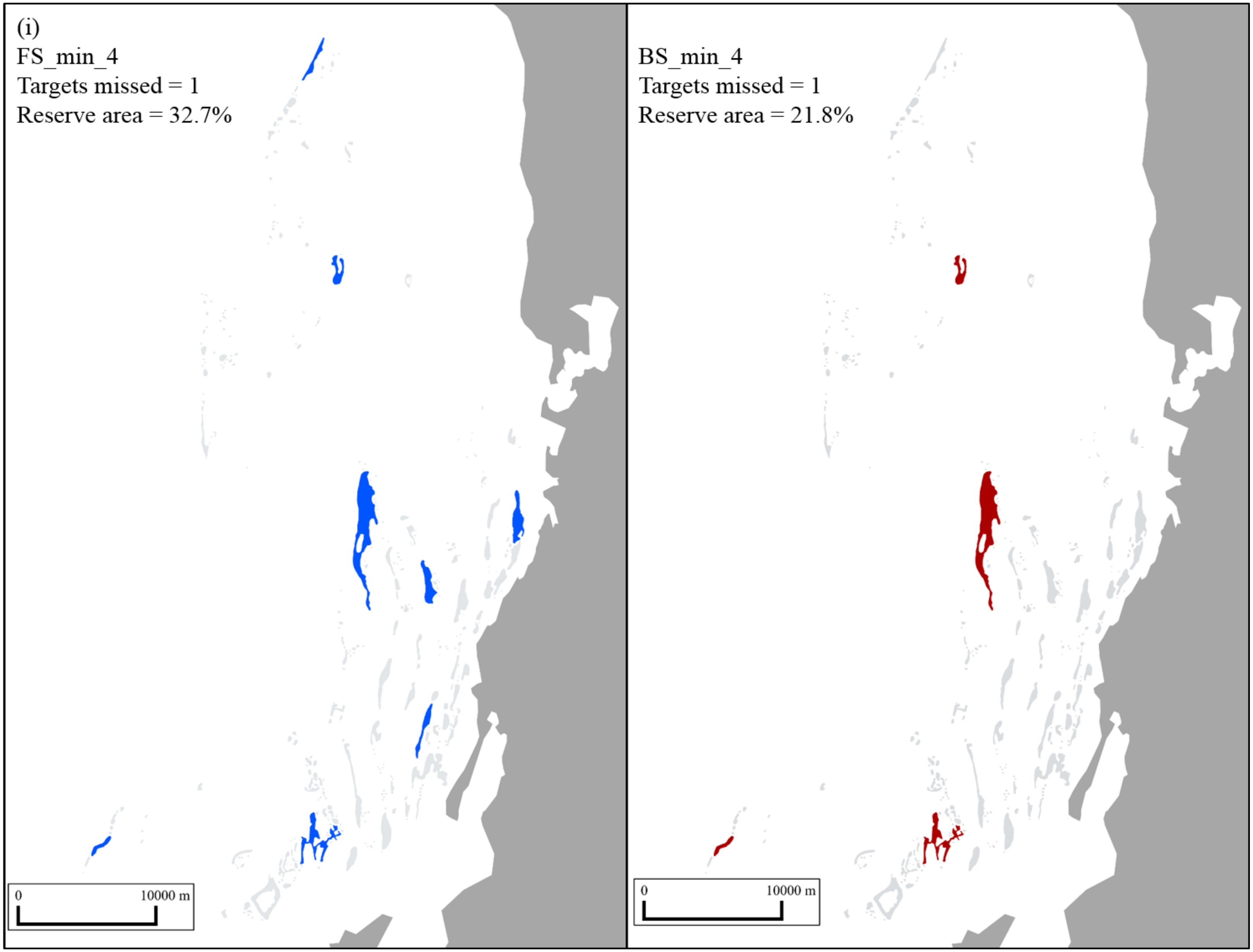

(d)
FS_max_4
Targets missed = 2
Reserve area = 37.5%
0
10000 m
BS_max_4
Targets missed = 1
Reserve area = 30.6%
0
10000 m

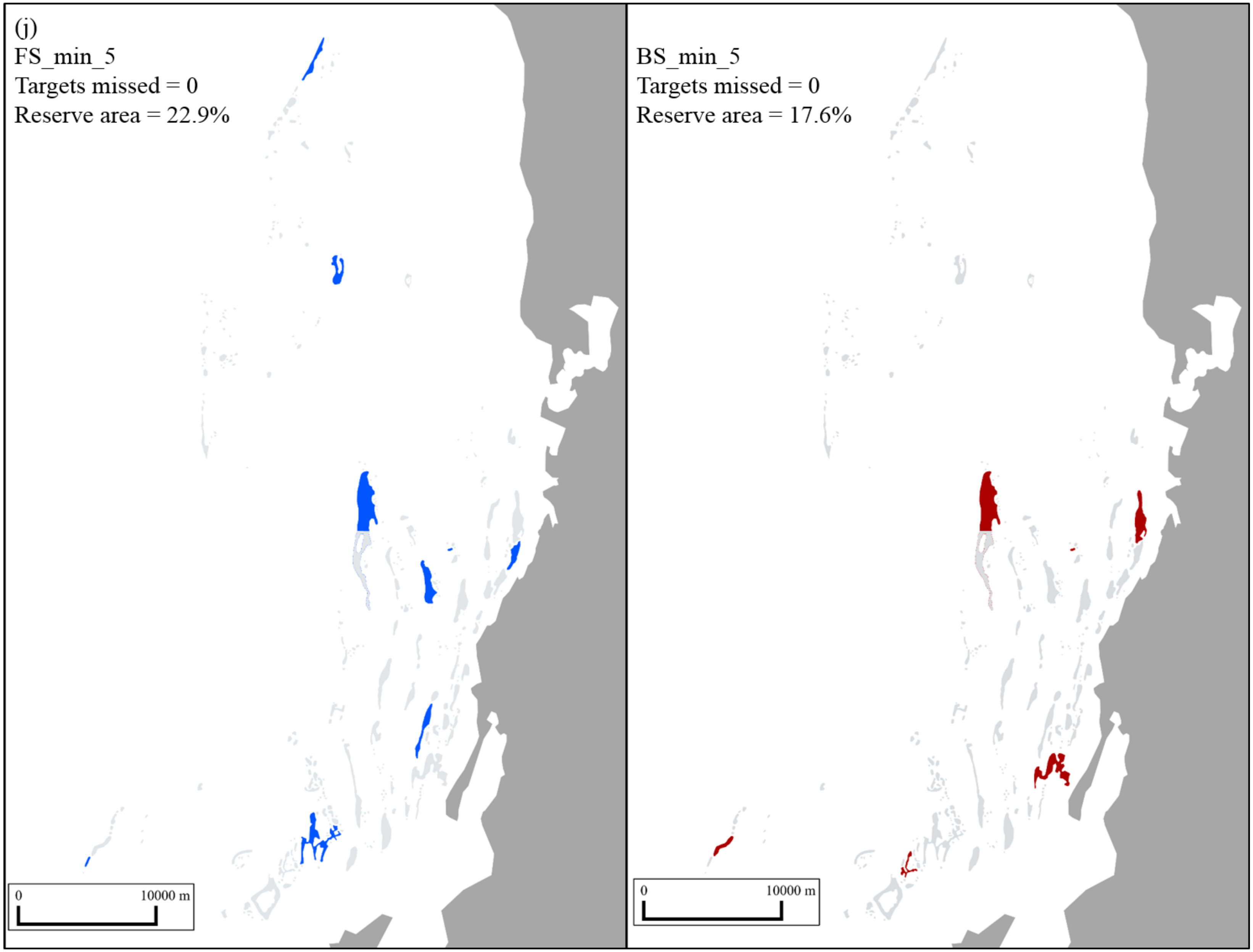

(e)
FS_max_5
Targets missed = 1
Reserve area = 30.2%
0
10000 m
BS_max_5
Targets missed = 1
Reserve area = 33.4%
0
10000 m


(f)
FS_min_1
Targets missed = 0
Reserve area = 31.6%
0
10000 m
BS_min_1
Targets missed = 0
Reserve area = 21.7%
0
10000 m


(g)
FS_min_2
Targets missed = 4
Reserve area = 25.6%
0
10000 m
BS_min_2
Targets missed = 0
Reserve area = 21.9%
0
10000 m


(h)
FS_min_3
Targets missed = 0
Reserve area = 30.6%
0
10000 m
BS_min_3
Targets missed = 0
Reserve area = 23.9%
0
10000 m


(i)
FS_min_4
Targets missed = 1
Reserve area = 32.7%
0
10000 m
BS_min_4
Targets missed = 1
Reserve area = 21.8%
0
10000 m


(j)
FS_min_5
Targets missed = 0
Reserve area = 22.9%
0
10000 m
BS_min_5
Targets missed = 0
Reserve area = 17.6%
0
10000 m

APPENDIX 5: LIST OF PUBLICATIONS BY THE AUTHOR

Publications directly arising from this dissertation:

In preparation:

Khalil M, Almany G, Beger M, Genton M, Berumen M (in prep) Can spatial habitat distribution predict larval dispersal distances and inform MPA design? Targeted journals: Ecology Letters, Conservation Letters, Biological Conservation

Khalil M, Bouwmeester J, Berumen M (in prep). Spatial variation in coral reef fish and benthic communities in the central Saudi Arabian Red Sea. Targeted journal: PeerJ

Khalil M, Beger M, Berumen M (in prep) Exploring spatial MPA priority sites for multiple conservation goals in the Saudi Arabian Red Sea. Targeted journal: Ocean and Coastal Management

Khalil M (in prep) Unique challenges to coral reef conservation in the Red Sea: The Saudi Arabian case. Opinion piece. Targeted journal: Oryx

Other publications:

Khalil M, Cochran JM, Berumen M (2013) The abundance of herbivorous fish on an inshore Red Sea reef following a mass coral bleaching event. Environmental Biology of Fishes 96:1065-1072

Berumen ML, Hoey AS, Bass WH, Bouwmeester J, Catania D, Cochran JEM, **Khalil MT**, Miyake S, Mughal MR, Spaet JLY, Saenz-Agudelo P (2013) The status of coral reef ecology research in the Red Sea. Coral Reefs 32:737-748

Bouwmeester J, **Khalil MT**, De La Torre P, Berumen ML (2011) Synchronous spawning of Acropora in the Red Sea. Coral Reefs 30:1011-1011

DiBattista JD, Roberts M, Bouwmeester J, Bowen BW, Coker DF, Lozano-Cortés DF, Choat JH, Gaither MR, Hobbs JP, **Khalil M**, Kochzius M, Myers R, Paulay G, Robitzc V, Saenz-Agudelo P, Salas E, Sinclair-Taylor TH, Toone RJ, Westneat M, Williams S, and Berumen ML (2015) A review of contemporary patterns of endemism for shallow water reef fauna in the Red Sea. Journal of Biogeography. doi: 10.1111/jbi.12649