ECOLOGY OF RECOVERING DEGRADED REEF COMMUNITIES WITHIN NO-TAKE MARINE RESERVES

by

JONATHAN ALBURO ANTICAMARA

B.Sc., University of the Philippines in the Visayas, 1994

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in

THE FACULTY OF GRADUATE STUDIES

(Resource Management and Environmental Studies)

THE UNIVERSITY OF BRITISH COLUMBIA

(Vancouver)

May 2009

Abstract

No-take marine reserves are a highly advocated tool to recover degraded marine ecosystems, but we have limited evidence as to how marine reserves facilitate recovery of marine communities. To address this limitation, we conducted monthly underwater visual censuses over three years on 423 reef fish species in eight sites where fishing had been excluded for different lengths of time. We then used our data to assess four impacts of protection within no-take marine reserves in the central Philippines: (1) magnitudes and rates of reef fish community recovery; (2) changes in reef fish diversity; (3) patterns of reef fish community succession; and (4) shifts in community interactions, based on distributions of pairwise correlations among reef fish species biomass. We found that total fish biomass increased with the duration of protection, but total fish abundance and species richness or diversity were both more influenced by site location than by reserve age. In addition, large-bodied herbivores drove the biomass recovery in older marine reserves, while small-bodied zoobenthivores and zooplanktivores influenced the higher abundance in offshore sites. Moreover, our results showed that ubiquitous large-bodied herbivore species (e.g. *Chlorurus bleekeri*) increased in biomass dominance in older reserves, whereas ubiquitous medium-bodied species (e.g. *Thalassoma lunare*) lost biomass dominance. Our non-metric multidimensional scaling (MDS) representation of reef fish community trajectories with duration of protection showed convergent trends in sites within similar locations relative to the mainland. Finally, the frequency distribution of pairwise correlation values among species biomass time-series within each site showed positive mean values regardless of protection-duration, as is typical of disturbed or high diversity systems. Indeed, less than ten percent of common species (those present in

≥50% of the 33 monthly surveys) within each site showed significant decline over time, while about 40 percent showed significant increase. In summary, our research provides comprehensive evidence on how marine reserves recover depleted reef fish communities. However, it also emphasizes that understanding of reef ecological processes could improve marine reserve site selection and design in order to meet specific conservation goals of marine reserve establishment.

Table of Contents

List of Tables

List of Figures

Acknowledgements

This thesis was conducted while I was a member of Project Seahorse at the Fisheries Centre of University of British Columbia. Many communities, co-workers, friends, organizations, and mentors have contributed to make this thesis possible – I owe you all a big and endless “THANK YOU”.

I would like to express my deepest gratitude to my main supervisor – Dr. Amanda Vincent. You gave me opportunities to pursue some of the questions that I find very interesting. Thank you for all your guidance and encouragement. Your vision of advancing marine conservation has inspired lots of people from around the world and certainly has been the inspiration for completing this thesis. I learned a lot from working with you – lessons that will be highly valuable as I continue my work in marine conservation.

My committee members have given me tremendous support and mentorship that helped me figure out a way to solve some of the seemingly daunting bits of this thesis and PhD student life. You all have opened your doors for me and given me time no matter how swamped you are with your work. I have enjoyed all the discussions I had with you. Dr. Dirk Zeller, your insights on marine ecology and reef system have saved me many times and pointed me to the right direction that made my thesis work. Dr. Jonathan Shurin, your cool approach of tackling some of my analytical and conceptual challenges has helped me a lot. You have given me plenty of ideas that helped me complete this thesis. Dr. Les Lavkulich, you have given me strength when I was weakest. Your insightful advice in

dealing with life's challenges will stay with me, always. Dr. Jessica Meeuwig, you have helped me set good directions for my work. You even flew all the way from Australia just to help me figure things out with my thesis. I will always value all your encouragement, guidance, and analytical insights. Thank you all for helping me achieve what I really needed. You are all a great inspiration!

To all my tireless and ever cheerful assistants, without your hard work and dedication this thesis will not happen. You all have braved typhoons and many months of swimming trough swarms of thimble and box jellies. You are all keen learners and have taught me your perspectives on things. To Marco Inocencio, you are a great leader and you have led our team amazingly! You always find ways to make things work when others say they won't work. I also remember you said how the Philippine reefs are screaming for help – I hope this thesis can help other people hear the reefs' cries, and can help find ways to save them from further destruction. To Manuel Abadiano, you have abandoned your fancy city life to work in the islands where you battled basic and poor island life, water that your stomach cannot agree, and still you manage to keep our team running well. To Jules Jason Asis, you came a long way from your home in Mindanao just to help my research. You have always kept the team spirit high even during the worst weather conditions. To all the local assistants who helped with the underwater surveys: Liguori Anabieza, Alvin Apostol, Vherwin Daan, Marlon Gutierrez, Jay Mejares, Renante Mejares, and Maximo Villas, your knowledge and familiarity of every single species that you've known growing-up with have made this research possible. You can spot distinct characters of species that I haven't. It is truly wonderful working with all of you. Lastly, to the two persons – Henry Socobos and Roger Pechoco who loved our boat so much, kept the engine in good running condition, and saved us from nasty weathers – I owe you a lot.

The local communities and government of the northwestern section of Danajon Bank, Bohol, Philippines – I thank you so much for all the support you gave me with my work. I really hope that this thesis and my future work can help you address some of the most pressing marine conservation issues that you are facing. My love for the ocean has gone deeper because of my interactions and fun conversations with many of you.

To all the Project Seahorse team members that I worked with in the Philippines, North America, and the UK, your commitment for advancing marine conservation is a source of inspiration. A huge part of who I am now is due to my interactions with you. I cannot thank you enough for all the care you have shown me. Your diverse backgrounds, rich stories, and great works in marine conservation have enriched my life in ways I have never imagined. I will always draw upon sweet memories of working with you and hope that we can keep the link no matter the distance in the future.

To my family and friends, thank you for being kind, patient, and supportive. To my parents: Jovito Anticamara and Evelyn Alburo, my brother and sister: Arnel and Haidee, thank you for your encouragement and love. My friends in Vancouver who helped me make my PhD journey so happy and full of great fun memories. Wai Lung Cheung and Vicky Lam, you are the most loving and cool friends I ever had, I am so happy to have found you. Shao-Lun Liu, you have been so kind to me especially when my life was upside down, thank you. Marivic Pajaro, you are my source of cool, and thanks for all your friendly advice. To Natalie Ban, Nicholas A.J. Graham, Dale Marsden, Jordan Rosenfeld, and Sara Lourie, thanks for your encouragement and for helping me proofread my thesis. To the many other friends that I made as I moved from places throughout my life, I cannot list all you names or they will fill pages and pages of this document, but I kept you all in my heart.

Finally, this thesis will not be possible without the main and generous financial support of John D. and Catherine T. MacArthur Foundation and the International Development Research Centre (IDRC) of Canada, through Project Seahorse and Principal Investigators Dr. Amanda Vincent (UBC), Dr. Jessica Meeuwig (University of Western Australia), Dr. Monica Mulrennan (Concordia University), and Dr. Colin Scott (McGill University). Additional supports came from John G. Shedd Aquarium of Chicago and Guylian Chocolates of Belgium through their partnerships in marine conservation with Project Seahorse. The Sea Around Us Project (SAUP) of UBC Fisheries Centre also helped me financially, through a Research Assistantship (RA) during the last portion of my degree. The UBC Centre for Intercultural Communications and Bamfield Marine Sciences gave me Teaching Assistantship (TA), which helped me survived financially during the last bits of my program. Similarly, Dr. James Tansey at UBC Sauder School of Business gave me RA work. Thank you all, I would not have done this thesis without your financial help.

Co-authorship Statement

The data chapters of this thesis (Chapters 3, 4, 5, and 6) were all prepared as stand-alone manuscripts for submission to peer-reviewed journals. I am the senior author of all these chapters. I was predominantly responsible for the conceptualization, design, data collection, data analyses, and writing of these chapters. Chapter 2, which is not a primary paper, benefited particularly from insights and assistance of Jessica Meeuwig and Dirk Zeller.

Amanda Vincent is a co-author on all chapters. Amanda, as the principal supervisor, worked with me to develop the basic hypotheses, and the sampling design and methods. She has also guided me throughout the development of the chapters and provided suggestions during the manuscript revisions.

The four data chapters all involved additional co-authors, whose contributions I now summarise. Chapter 3 was co-authored with Jessica Meeuwig and Amanda Vincent. Jessica Meeuwig guided me in setting the overall focus and direction of this chapter when there were many possible options, and provided suggestions during the manuscript revisions. Chapter 4 was co-authored with Dirk Zeller and Amanda Vincent. Dirk Zeller offered insight and ideas that helped improve this manuscript in terms of analyses, results interpretation, and writing. Chapter 5 was co-authored with Jessica Meeuwig and Amanda Vincent. Jessica Meeuwig provided me with suggestions in terms of the multivariate analyses that helped improve the application of the methods. Chapter 6 was co-authored with Jonathan Shurin and Amanda Vincent. Jonathan Shurin gave me many insights that helped improve this manuscript in terms of analyses, results interpretation, and writing.

1. Introduction

Theoretical framework

Disturbance and recovery of ecological systems

Understanding how ecosystems, communities, and populations recover from disturbances is important in ecology and conservation because it can provide guidance for the design and management of parks and reserves (Baker 1992, Wali 1999), and the restoration of damaged ecosystems (Cairns 1980, Sheley et al. 2006). In addition, research on ecosystem recovery after disturbance can help advance important ecological concepts such as ecosystem function (Abrams and Allison 1982, Kinzig and Pacala 2002), productivity (Stone et al. 1996, Schmitz 2004), stability (May 1973, Stone et al. 1996), and succession (Drury and Nisbet 1973, Walker and del Moral 2003).

For many years, ecologists have developed and tested hypotheses and theories to progress our understanding of ecosystem recovery (Drury and Nisbet 1973, Horn 1974, McIntosh 1980, McCook 1994, Wardle et al. 2004). However, most studies have focused on terrestrial ecosystems, with very limited and recent attention to aquatic ecosystems (Platt and Connell 2003, Hill et al. 2004, Hughes et al. 2005). More research is needed on the latter, particularly given how fundamentally they differ from terrestrial systems in physico-chemical properties and biological connectedness, *inter alia*. Also, a great understanding of recovery in freshwater and marine ecosystems could further inform terrestrial systems, by allowing comparisons and syntheses across different environments (Link 2002, Carr et al. 2003, Kinlan and Gaines 2003). In this thesis, we focus on recovery of exploited coral reefs, marine ecosystems of great evolutionary, ecological, and socioeconomic importance (Sale 1988, Crossland 1991, Wood 1998, Knowlton and

Jackson 2001, Cesar and van Beukering 2004).

The ability of ecosystems to recover from disturbance depends on the scale and nature of the disturbance (Berumen and Pratchett 2006), the structure of the ecosystems, and the interactions among its component species (Sutherland and Dickman 1999, Hoegh-Guldberg 2006). For example, ecosystems can often recover from natural disturbances such as volcano eruption (Tomascik et al. 1996), predator outbreaks (Colgan 1987), catastrophic storms (Walsh 1983), and forest fires (Clarkson 1997). In addition, disturbances that are not too frequent or too intense can help maintain diversity in many ecosystems (Connell 1997, Townsend et al. 1997, Molino and Sabatier 2001). In fact, some forms of disturbance (e.g. fire) are actually necessary for the maintenance of ecosystem dynamics (Attiwill 1994, Bergeron et al. 2002). In contrast, however, some ecosystems are unable to recover from disturbances, and instead undergo phase shifts (Hughes 1994, McManus et al. 2000, Folke et al. 2004, Mangel and Levin 2005). In particular, large-scale and long-term human-induced ecosystem disturbance (e.g. destructive overexploitation and climate change) has severely compromised the ability of ecosystems to recover, catalyzing regime shifts and even the extinction of species (Nystrom et al. 2000, Chazdon 2003, Dulvy et al. 2003, Schmitz 2004).

We use the term recovery throughout this thesis, defining it as the ability of ecosystems to increase in abundance, biomass, and diversity after the removal of the disturbance (Connell 1997, Jennings 2001). We believe that the indiscriminate use of many synonymous terms available to describe and test the ability of ecosystems to recover from disturbances can hamper understanding. Previous research on ecosystem disturbance has generated (1) descriptions of patterns of recovery (e.g. magnitudes and rates of recovery, changes in diversity, succession, and changes in community interactions), (2) explorations of factors influencing ecosystem recovery, and (3) general concepts, hypotheses, and theories to explain the processes and mechanisms involved in recovery. Recovery has been variably examined as fragility (Nilsson and Grelsson 1995), integrity (De Leo and Levin 1997), persistence (Ellner and Fussman 2003), resilience (Nystrom et al. 2000), resistance (Harrison 1979), stability (Connell and Sousa 1983), and variability (Ives et al. 1999). Although the terms sometimes refer to specific aspects of recovery (Stone et al. 1996), their ambiguity can potentially lead to debates rather than consolidation of findings (Loreau 2000).

No-take marine reserves: issues, theory, empirical evidence, and knowledge gaps

There is a great need to find effective ways to recover depleted and degraded marine ecosystems. Overexploitation (i.e. when removal of abundance, biomass, or species exceeds the ability of the ecosystem to replace it) is known to have significant detrimental consequences for marine ecosystems (Russ and Alcala 1989, Addessi 1994, Chou 1994, Hughes 1994, Brown 1997, Jackson 1997, Pauly et al. 1998, Tegner and Dayton 1999, White et al. 2000, Daan and Gislason 2005, Pauly et al. 2005). The main effects of prolonged and excessive human extraction on marine ecosystems are depletion of targeted communities or species (Myers and Worm 2003, Pandolfi et al. 2003, Baum and Myers 2004, Gewin 2004). In addition, human exploitative activities often destroy habitats associated with the target communities or species (Edinger et al. 1998, Thrush and Dayton 2002). The combination of resource extraction and habitat destruction can have cascading impacts on non-target community members (Pinnegar et al. 2002, Dulvy et al. 2004, Micheli et al. 2005). In this study, we examine the patterns of community recovery that are generated by protecting previously exploited marine ecosystems from further damage, as in the case of no-take marine reserves.

No-take marine reserves (also known as Marine Protected Areas or MPAs, no-take zones, or sanctuaries) are areas where human exploitation is prohibited and are currently highly advocated to help address marine depletion and ecosystem degradation (Ballantine 1995, Pauly et al. 2002, Norse et al. 2003, Russ and Zeller 2003, Mora et al. 2006). Global consensus statements and international endorsements for marine reserves have led many countries and conservation organizations to target an increase in the number and area of marine reserves (Kelleher 1996, Wells et al. 2007, Wood and Dragicevic 2007). However, the rate of establishment and sustained implementation of marine reserves globally, ultimately depends on how well marine reserves deliver their promise of recovering depleted and degraded marine ecosystems, thereby benefiting stakeholders and encourage favourable political will (Pomeroy et al. 1997, Agardy et al. 2003, Kaiser 2005, Sale et al. 2005).

Much remains to be learned about the magnitudes and rates of community recovery within marine reserves with duration of protection, specifically with regards to total abundance or biomass, which in our case included all the non-cryptic reef fishes. Empirical investigations suggest that top predator abundance and total community biomass recover slowly within reserves, with estimates of 40 years recovery time or more (Russ and Alcala 2004, Williamson et al. 2004, McClanahan et al. 2007). In addition, the magnitudes and rates of abundance or biomass recovery vary with community structure (i.e. species composition and relative abundance or biomass of those species) and among fish families (Côté et al. 2001). However, most published studies on magnitudes and rates of abundance or biomass recovery within reserves have depended on space-for-time substitution or meta-analyses of patchy data rather than on time-series data (Halpern 2003, Micheli et al. 2004b, Russ et al. 2005). Our study will provide the most data-intensive analyses so far of total community abundance or biomass recovery within marine reserves, using monthly time-series data over three years for 423 fish species found in six no-take marine reserves and two fished sites in the central Philippines.

Besides promoting recovery of fish abundance and biomass, marine reserves are also intended to preserve diversity (Botsford et al. 2003). However, the recovery of diversity has seldom been measured in the marine reserve literature as most studies deal with only few focal species (Côté et al. 2001, Halpern and Warner 2002, Micheli et al. 2004b). Empirical data, based on space-for-time substitution, suggest that diversity may recover more quickly than biomass within marine reserves (McClanahan and Graham 2005, McClanahan et al. 2007). One snapshot study showed a significantly higher diversity of targeted families in reserves than in unprotected areas (Jennings et al. 1995). The challenge, however, is to confirm these initial impressions, particularly since diversity measures are known to be sensitive to sampling effort (Peet 1975, Kolasa and Biesiadka 1984, Colwell and Coddington 1994). In this thesis, we will use three-year monthly time-series data within six marine reserves and two fished sites in the central Philippines to explore the recovery of diversity.

The recovery of abundance, biomass, and diversity of targeted or predatory species inside marine reserves may alter patterns of community succession (i.e. the sequential changes in community characteristics such as composition, dominance, trajectories, or turnover rates) (Drury and Nisbet 1973, Horn 1974, Walker and del Moral 2003). Studies on succession within marine reserves have often focused on trophic cascades (Pinnegar et al. 2002, Shears and Babcock 2003) or indirect effects of top predators on species at lower trophic levels. For example, the recovery of top predators within marine reserves may reduce herbivore populations, which can lead to sequential changes in algal communities within marine reserves (Pinnegar et al. 2002, Shears and Babcock 2003). However, the succession or sequential changes of fish communities or community characteristics within marine reserves has not yet been well investigated. One empirical study that used a space-for-time substitution found succession in the dominance of different fish families over time: parrotfishes (Scaridae) and wrasses (Labridae) showed rapid initial recovery and then declined, whereas triggerfishes (Balistidae) and surgeonfishes (Acanthuridae) increased more slowly but steadily (McClanahan et al. 2007). Meta-analyses of published data also found that communities showed succession trends in marine reserves over time (Micheli et al. 2004b). By evaluating changes in community composition, dominance, trajectories, and turnover rates, we will examine further the patterns of fish community succession within marine reserves (Wali 1999, Platt and Connell 2003, Walker and del Moral 2003).

The effects of halting exploitation raise questions about how community interactions change within marine reserves over time (Micheli et al. 2004b). Empirical studies have demonstrated strong negative population co-variations (negative interactions) between predatory species and their prey species within marine reserves (Shears and Babcock 2002, Graham et al. 2003). In addition, meta-analyses of published data also found significant negative interactions among species within marine reserves (Micheli et al. 2004a). However, our current understanding of interactions within marine reserves consists of limited data on a few sets of tightly linked predators and prey (Micheli et al. 2004a, Guidetti 2006, Langlois et al. 2006). The recovery of predators within marine reserves can have overall negative impacts on the prey communities if top-down control is pervasive, but otherwise most species will show an increase in population or biomass (Walters et al. 1999, Fanshawe et al. 2003, Halpern 2003, Micheli et al. 2004b). In this thesis, we will explore the changing distribution of community interactions through pairwise correlations (positive, neutral, and negative) of 423 species' biomass time-series data within marine reserves. We will also ask whether the prevalence of negative species population co-variations increased as exploited species recovered within marine reserves.

Thesis context

Coral reefs are important model systems in which to study recovery post-disturbance, both because they hold the greatest diversity of life on earth (Allen 2002, Carpenter and Springer 2005), and because they suffer from the combined effects of intense disturbances in the form of sedimentation (Rogers 1990, McClanahan and Obura 1997), bleaching due to temperature rise or climate changes (Brown et al. 2000, Marshall and Baird 2000), destructive fishing methods, and overexploitation (Pet-Soede et al. 1999, Fox and Erdmann 2000). The pressures are such that some coral reefs have exhibited regime shifts under intense and large-scale disturbances (Hughes 1994). Human impacts have already led to degradation of coral reef ecosystems globally (Jackson 1997, Nystrom et al. 2000, McClanahan 2002) and climate change is likely to further contribute to this degradation (Hughes et al. 2003, Baker et al. 2004). Throughout this thesis, we will focus on describing the patterns of reef fish community recovery in previously degraded coral reef areas after the removal of human exploitation, using no-take marine reserves.

The establishment of multiple small marine reserves in the northwest section of Danajon double barrier reef (also known as Danajon Bank) in the central Philippines offers opportunities to evaluate the impacts of marine reserves on previously exploited marine communities. In the last decade the number of no-take marine reserves within Danajon Bank (and the Philippines in general) has increased rapidly, partly in response to the encouraging success of early marine reserves in the Philippines – such as Apo Island and Sumilon (Alcala and Russ 2006) – and partly because the Philippines Republic Act 8550 Section 81 mandates the establishment of marine reserves or fish sanctuary to cover 15% of all municipal waters. At the moment, the location of new marine reserves in Danajon Bank (and the Philippines) is primarily based on societal preference with technical and policy inputs from conservation organizations and government agencies (personal observation) (Alcala and Russ 2006, Hansen et al. in prep.). Understanding the ecological impacts and implications of marine reserves could help the effective and sustained implementation of marine reserves in the Philippines as a strategy to conserve, manage, and recover highly depleted, but also highly diverse, coastal marine ecosystems.

Current ecological understanding of the dynamics of reef communities within Danajon Bank is very limited (Christie et al. 2006, Ban et al. in prep., Hansen et al. in prep.). Very few scientific reports have been published on the ecology of Danajon Bank even though it is considered to be one of only two well-defined double barrier reef system in the world (Pichon 1977, Rubec 1988, Christie et al. 2006). One accessible publication indicated that sedimentation from the mainland may explain why offshore Danajon Bank reefs have better-developed community structures than inshore reefs (Pichon 1977). Other publications showed that Danajon Bank is experiencing considerable habitat decline and is among the most degraded reef sites in the world (Christie et al. 2006, Marcus et al. 2007).

The implementation of marine reserves on Danajon Bank is proceeding in the absence of good ecological data, thanks to strong community engagement and political support. Assessment of the effectiveness of marine reserves in Danajon Bank demonstrated that some of the enforced marine reserves helped increase the abundance of a subset of families, particularly groupers (Serranidae), breams (Nemipteridae), and butterflyfishes (Chaetodontidae) (Samoilys et al. 2007), but did not reveal how Danajon Bank reserves affected total fish community abundance, biomass, diversity, succession, or community interactions. In addition, local fishing communities associated with the oldest reserve on

Danajon Bank expressed a more optimistic view of recovery than the existing limited underwater surveys revealed (Yasue et al. in prep.). This dearth of ecological data posed a challenge for designing networks of marine reserves or ecologically representative sites in this area (Ban et al. in prep., Hansen et al. in prep.).

This thesis examines the spatio-temporal dynamics of reef communities (abundance, biomass, diversity, succession, and community interactions) within marine reserves in Danajon Bank. Our work will add to the ecological knowledge of recovery in marine ecosystems in general, while specifically increasing our understanding of Danajon Bank, and how marine reserves might support its recovery.

Our research is part of a larger suite of research and conservation activities carried out by Project Seahorse, a marine conservation research and management team (**http://www.projectseahorse.org).** Project Seahorse has been active in the Philippines since 1994 and now works through a national non-governmental organisation, the Project Seahorse Foundation for Marine Conservation (PSF). This team of Filipino biologists and community organisers has supported the creation and implementation of 33 no-take marine reserves on Danajon Bank, and developed management teams and plans for most of them. It has also catalyzed the creation of many citizens' groups for managing the marine reserves, including a regional alliance of more than 1000 families of small-scale fishers.

Our research contributes to a larger research programme on the effectiveness of marine reserves on Danajon Bank. Since 1998, Project Seahorse biologists and volunteers have conducted bi-annual monitoring of fish recovery (at the family level) in Danajon Bank marine reserves, using a Before-After-Control-Impact (BACI) design. Our research takes a much more detailed and thorough look at reserve recovery, allowing deeper analyses than the rapid assessment approach of the in-country team. We have monthly time-series data over three years for 423 non-cryptic fish species in six reserves of different ages and in two fished sites. Our work complements the research by two other PhD students associated with Project Seahorse: Marivic Pajaro has been assessing the socio-economic indicators of marine reserve effectiveness across 10 sites on Danajon Bank (Pajaro 2009), and Eulalio Guieb has been determining the cultural basis for reserve effectiveness with anthropological research in two Danajon Bank communities with reserves (Guieb 2008).

Thesis development

Our main goal in this research is to provide accounts and analyses of recovery patterns of reef communities within a suite of no-take marine reserves with various duration of protection. Specifically, we want to provide intensive analyses of field data on the following aspects of reef community transitions within marine reserves: (1) magnitudes and rates of community recovery; (2) changes in diversity; (3) patterns of community succession; and (4) shifts in community interactions. Our approach is empirical, gathering data in which to seek patterns and address specific hypotheses.

This thesis comprises seven chapters, four of which are based on original data. We begin by introducing the rationale, objectives, and structure of the thesis (Chapter 1). We then outline the field sites, sampling protocols, and data treatments used as many are consistent across analyses (Chapter 2). In the first data chapter (Chapter 3), we ask how much and how quickly the abundance, biomass, and species richness of reef fish communities recovered within marine reserves. We then compare recovery of fish of different body size and trophic groups. In Chapter 4, we ask how various measures of reef fish diversity (e.g. richness, Shannon-Weiner diversity index, Pielou's evenness, and Abundance-Biomass Comparison (ABC) curves) changed within and across marine reserves. In Chapter 5, we ask if there was a pattern of reef fish community succession within marine reserves. Specifically, we want to understand how community characteristics such as composition, dominance, trajectories, and turnover rates varied within and across marine reserves over time. In Chapter 6, we ask how community interactions or population co-variations shifted within marine reserves over time. Specifically, we ask how frequency distributions of pairwise correlations of species' biomass time-series data can be used to infer changes in patterns of positive, neutral, and negative interactions among species within marine reserves over time. Finally, in Chapter 7, we summarize our research findings, discuss how they relate to the general field of ecosystem recovery, and identify important hypotheses that could be tested in future marine reserve researches. We comment on the strengths and weaknesses of our research findings and discussed their overall significance and applications.

References

Abrams, P. A., and T. D. Allison. 1982. Complexity, stability, and functional response. The American Naturalist **119**:240-249.

Addessi, L. 1994. Human disturbance and long-term changes on a rocky intertidal community. Ecological Applications **4**:786-797.

Agardy, T., P. Bridgewater, M. P. Crosby, J. Day, P. K. Dayton, R. Kenchington, D. Laffoley, P. McConney, P. A. Murray, J. E. Parks, and L. Peau. 2003. Dangerous targets? Unresolved issues and ideological clashes around marine protected areas. Aquatic Conservation: Marine and Freshwater Ecosystems **13**:353-367.

Alcala, A. C., and G. R. Russ. 2006. No-take marine reserves and reef fisheries management in the Philippines: a new people power revolution. AMBIO: A Journal of the Human Environment **35**:245-254.

Allen, G. R. 2002. Coral reef fish assessment in the 'coral triangle' of southeastern Asia. Environmental Biology of Fishes **65**:209-214.

Attiwill, P. M. 1994. The disturbance of forest ecosystems: the ecological bases for conservative management. Forest Ecology and Management **63**:247-300.

Baker, A. C., C. J. Starger, T. R. McClanahan, and P. W. Glynn. 2004. Corals' adaptive response to climate change. Nature **430**:741.

Baker, W. L. 1992. The landscape ecology of large disturbances in the design and management of nature reserves. Landscape Ecology **7**:181-194.

Ballantine, W. J., editor. 1995. Networks of "no-take" marine reserves are practical and necessary. Science and Management of Protected Areas Association, Wolfville, Nova Scotia, Canada.

Ban, N. C., G. J. A. Hansen, M. Jones, and A. C. J. Vincent. in prep. Systematic marine conservation planning in data-poor regions: socio-economic data is essential.

Baum, J. K., and R. A. Myers. 2004. Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. Ecology Letters **7**:135-145.

Bergeron, Y., A. Leduc, B. D. Harvey, and S. Gauthier. 2002. Natural fire regime: a guide for sustainable management of the Canadian boreal forest. SILVA FENNICA **36**:81-95.

Berumen, M. L., and M. S. Pratchett. 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.

Botsford, L. W., F. Micheli, and A. Hastings. 2003. Principles for the design of marine reserves. Ecological Applications **13**:S25-S31.

Brown, B. E. 1997. Disturbances to reefs in recent times. Pages 354-379 *in* C. Birkeland, editor. Life and death of coral reefs. Chapman & Hall, New York.

Brown, B. E., R. P. Dunne, M. S. Goodson, and A. E. Douglas. 2000. Bleaching patterns in reef corals. Nature **404**:142-143.

Cairns, J. J. 1980. Introduction. Pages 1-10 *in* J. J. Cairns, editor. The recovery process in damaged ecosystems. Ann Arbor Science Publishers, Inc., Ann Arbor, Michigan.

Carpenter, K. E., and V. G. Springer. 2005. The center of the center of marine shore fish biodiversity: the Philippine Islands. Environmental Biology of Fishes **72**:467-480.

Carr, M. H., J. E. Neigel, J. A. Estes, S. Andelman, R. R. Warner, and J. L. Largier. 2003. Comparing marine and terrestrial ecosystems: implications for the design of coastal marine reserves. Ecological Applications **13**:90-107.

Cesar, H. S. J., and P. J. H. van Beukering. 2004. Economic valuation of the coral reefs of Hawai'i. Pacific Science **58**:231-242.

Chazdon, R. L. 2003. Tropical forest recovery: legacies of human impact and natural disturbances. Perspectives in Plant Ecology, Evolution and Systematics **6**:51-71.

Chou, L. M. 1994. Marine environmental issues of Southeast Asia: state and development. Hydrobiologia **285**:139-150.

Christie, P., N. B. Armada, A. T. White, A. M. Gulayan, and H. H. Y. de Dios. 2006. Coastal environmental and fisheries profile of Danajon Bank, Bohol, Philippines. Fisheries Improved for Sustainable Harvest (FISH) Project, Cebu City, Philippines.

Clarkson, B. R. 1997. Vegetation recovery following fire in two Waikato peatlands at Whangamarino and Moanatuatua, New Zealand. New Zealand Journal of Botany **35**:167-179.

Colgan, M. W. 1987. Coral reef recovery on Guam (Micronesia) after catastrophic predation by *Acanthaster plancii*. Ecology **68**:1592-1605.

Colwell, R., and J. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society B **345**:101-118.

Connell, J. H. 1997. Disturbance and recovery of coral assemblages. Coral Reefs **16**:S101-113.

Connell, J. H., and W. P. Sousa. 1983. On evidence needed to judge ecological stability or persistence. The American Naturalist **121**:789-824.

Côté, I. M., I. Mosquera, and J. D. Reynolds. 2001. Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis. Journal of Fish Biology **59**:178-189.

Crossland, C. J. 1991. Role of coral reefs in global ocean production. Coral Reefs **10**:55-64.

Daan, N., and H. Gislason. 2005. Changes in the North Sea fish community: evidence of indirect effects of fishing? ICES Journal of Marine Science: Journal du Conseil **62**:177.

De Leo, G. A., and S. Levin. 1997. The multifaceted aspects of ecosystem integrity. Conservation Ecology **1**:3.

Drury, W. H., and C. T. Nisbet. 1973. Succession. The Arnold Arbor. J. **54**:331-368.

Dulvy, N. K., R. P. Freckleton, and N. V. C. Polunin. 2004. Coral reef cascades and the indirect effects of predator removal by exploitation. Ecology Letters **7**:410-416.

Dulvy, N. K., Y. Sadovy, and C. S. Reynolds. 2003. Extinction vulnerability in marine populations. Fish and Fisheries **4**:25-64.

Edinger, E. N., J. Jompa, G. V. Limmon, W. Widjatmoko, and M. J. Risk. 1998. Reef degradation and coral biodiversity in Indonesia: effects of land-based pollution, destructive fishing practices and changes over time. Marine Pollution Bulletin **36**:617-630.

Ellner, S. P., and G. Fussman. 2003. Effects of successional dynamics on metapopulation persistence. Ecology **84**:882-889.

Fanshawe, S., G. R. Vanblaricom, and A. A. Shelly. 2003. Restored top carnivores as detriments to the performance of marine protected areas intended for fishery sustainability: a case study with red abalones and sea otters. Conservation Biology **17**:273-283.

Folke, C., K. E. Carpenter, B. H. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology Evolution and Systematics **35**:557-581.

Fox, H. E., and M. V. Erdmann. 2000. Fish yields from blast fishing in Indonesia. Coral Reefs **19**:114.

Gewin, V. 2004. Troubled waters: the future of global fisheries. PLoS Biol **2**:e113.

Graham, N. A. J., R. D. Evans, and G. R. Russ. 2003. The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. Environmental Conservation **30**:200-208.

Guidetti, P. 2006. Marine reserves re-establish lost predatory interactions and cause community changes in rocky reefs. Ecological Applications **16**:963-976.

Guieb, E. R. 2008. Community, marine rights, and sea tenure: A political ecology of marine conservation in two Bohol villages in central Philippines. PhD Dissertation. McGill University, Montreal, Quebec, Canada.

Halpern, B. S. 2003. The impact of marine reserves: do reserves work and does reserve size matter? Ecological Applications **13**:S117-S137.

Halpern, B. S., and R. R. Warner. 2002. Marine reserves have rapid and lasting effects. Ecology Letters **5**:361-366.

Hansen, G. J., N. Ban, M. L. Jones, L. Kaufman, H. Panes, M. Yasue, and A. C. J. Vincent. in prep. Hindsight in marine protected area designation and planning: a comparison of community-driven and systematic approaches in Danajon Bank, Philippines.

Harrison, G. W. 1979. Stability, under environmental stress: resistance, resilience, persistence and variability. The American Naturalist **113**:659-669.

Hill, F., M., J. D. Witman, and H. Caswell. 2004. Markov chain analysis of succession in a rocky subtidal community. The American Naturalist **164**:E46-E60.

Hoegh-Guldberg, O. 2006. Complexities of coral reef recovery. Science **311**:42-43.

Horn, H. S. 1974. The ecology of secondary succession. Annual Review of Ecology and Systematics **5**:25-37.

Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science **265**:1547-1551.

Hughes, T. P., A. H. Baird, D. R. Belwood, M. Card, R. M. Connolly, C. Folke, R. Grosberg, O. Hoegh-Guldberg, J. B. C. Jackson, J. Kleypas, J. M. Lough, P. Marshall, M. Nystrom, S. Palumbi, R., J. M. Pandolfi, B. Rosen, and J. Roughgarden. 2003. Climate change, human impacts, and the resilience of coral reefs. Science **301**:929-933.

Hughes, T. P., D. R. Bellwood, C. Folke, R. S. Steneck, and J. Wilson. 2005. New paradigms for supporting the resilience of marine ecosystems. Trends in Ecology and Evolution **20**:380-386.

Ives, A. R., K. Gross, and J. L. Klug. 1999. Stability and variability in competitive communities. Science **286**:542-544.

Jackson, J. B. C. 1997. Reef since Columbus. Coral Reefs **16**:23-32.

Jennings, S. 2001. Patterns and prediction of population recovery in marine reserves. Reviews in Fish Biology and Fisheries **10**:209-231.

Jennings, S., E. M. Grandcourt, and N. V. C. Polunin. 1995. The effects of fishing on the diversity, biomass, and trophic structure of Seychelles' reef fish communities. Coral Reefs **14**:225-235.

Kaiser, M. J. 2005. Are marine protected areas a red herring or fisheries panacea? Canadian Journal of Fisheries and Aquatic Sciences **62**:1194-1199.

Kelleher, G. 1996. A global representative system of marine protected areas. Ocean and Coastal Management **32**:123-126.

Kinlan, B. P., and S. D. Gaines. 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. Ecology **84**:2007-2020.

Kinzig, A. P., and S. W. Pacala. 2002. Successional biodiversity and ecosystem functioning. Pages 175-212 *in* A. P. Kinzig, S. W. Pacala, and D. Tilman, editors. The functional consequences of biodiversity. Princeton University Press, Princeton.

Knowlton, N., and J. B. Jackson. 2001. The ecology of coral reefs. Pages 395-422 *in* M. D. Bertness, S. D. Gaines, and M. E. Hay, editors. Marine community ecology. Sinauer Associates Inc., Sunderland.

Kolasa, J., and E. Biesiadka. 1984. Diversity concept in ecology. Acta Biotheoretica **33**:145-162.

Langlois, T. J., M. J. Anderson, R. C. Babcock, and S. Kato. 2006. Marine reserves demonstrate trophic interactions across habitats. Oecologia **147**:134-140.

Link, J. 2002. Does food web theory work for marine ecosystems? Marine Ecology Progress Series **230**:9.

Loreau, M. 2000. Biodiversity and ecosystem functioning: recent theoretical advances. Oikos **91**:3.

Mangel, M., and P. S. Levin. 2005. Regime, phase and paradigm shifts: making community ecology the basic science for fisheries. Philosophical Transactions of the Royal Society B **360**:95.

Marcus, J. E., M. A. Samoilys, J. J. Meeuwig, Z. A. D. Villongco, and A. C. J. Vincent. 2007. Benthic status of near-shore fishing grounds in the central Philippines and associated seahorse densities. Marine Pollution Bulletin **54**:1483-1494.

Marshall, P. A., and A. H. Baird. 2000. Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. Coral Reefs **19**:155-163.

May, R. 1973. Stability and complexity in model ecosystems. Princeton University Press, New Jersey.

McClanahan, T. R. 2002. The near future of coral reefs. Environmental Conservation **29**:460-483.

McClanahan, T. R., and N. A. J. Graham. 2005. Recovery trajectories of coral reef fish assemblages within Kenyan marine protected areas. Marine Ecology Progress Series **294**:241-248.

McClanahan, T. R., N. A. J. Graham, J. M. Calnan, and M. A. MacNeil. 2007. Towards pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. Ecological Applications **17**:1055-1067.

McClanahan, T. R., and D. Obura. 1997. Sedimentation effects on shallow coral communities in Kenya. Journal of Experimental Marine Biology and Ecology **209**:103-122.

McCook, L. J. 1994. Understanding ecological community succession: causal models and theories, a review. Plant Ecology **110**:115-147.

McIntosh, R. P. 1980. The relationship between succession and the recovery process in ecosystems. Pages 11-62 *in* J. J. Cairns, editor. The recovery process in damaged ecosystems. Ann Arbor Science Publishers, Inc., Ann Arbor, Michigan.

McManus, J. W., L. A. B. Menez, K. N. Kesner-Reyes, S. G. Vergara, and M. C. Ablan. 2000. Coral reef fishing and coral-algal phase shifts: implications for global reef status. ICES Journal of Marine Science: Journal du Conseil **57**:572.

Micheli, F., P. Amarasekare, J. Bascompte, and L. R. Gerber. 2004a. Including species interactions in the design and evaluation of marine reserves: some insights from a predator-prey model. Bulletin of Marine Science **74**:653-669.

Micheli, F., L. Benedetti-Cecchi, S. Gambaccini, I. Bertocci, C. Borsini, G. C. Osio, and F. Romano. 2005. Cascading human impacts, marine protected areas, and the structure of Mediterranean assemblages. Ecological Monographs **75**:81-102.

Micheli, F., B. S. Halpern, L. W. Botsford, and R. R. Warner. 2004b. Trajectories and correlates of community change in no-take marine reserves. Ecological Applications **14**:1709-1723.

Molino, J. F., and D. Sabatier. 2001. Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. Science **294**:1702-1704.

Mora, C., S. Andrefouet, M. J. Costello, C. Kranenburg, A. Rollo, J. Veron, K. J. Gaston, and R. Myers. 2006. Coral reefs and the global network of marine protected areas. Science **312**:1750-1751.

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

Nilsson, C., and G. Grelsson. 1995. The fragility of ecosystems: a review. Journal of Applied Ecology **32**:677-692.

Norse, E. A., C. B. Grimes, S. Ralston, R. Hilborn, J. C. Castilla, S. R. Palumbi, D. Fraser, and P. Kareiva. 2003. Marine reserves: the best option for our oceans. Frontiers in Ecology and the Environment **1**:495-502.

Nystrom, M., C. Folke, and F. Moberg. 2000. Coral reef disturbance and resilience in a human-dominated environment. Trends in Ecology and Evolution **15**:413-417.

Pajaro, M. G. 2009. The indicators of effectiveness in community-managed marine protected areas. PhD Dissertation. The University of British Columbia, Vancouver, British Columbia, Canada.

Pandolfi, J. M., H. Bradbury, E. Sala, T. P. Hughes, K. A. Bjorndal, R. G. Cooke, D. McArdle, L. McClenachan, M. J. H. Newman, G. Paredes, R. Warner, and J. B. C. Jackson. 2003. Global trajectories of the long-term decline of coral reef ecosystems. Science **301**:955-958.

Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres Jr. 1998. Fishing down marine food webs. Science **279**:860.

Pauly, D., V. Christensen, S. Guenette, T. J. Pitcher, U. R. Sumaila, C. J. Walters, R. Watson, and D. Zeller. 2002. Towards sustainability in world fisheries. Nature **418**:689-695.

Pauly, D., R. Watson, and J. Alder. 2005. Global trends in world fisheries: impacts on marine ecosystems and food security. Philosophical Transactions of the Royal Society B **360**:5-12.

Peet, R. K. 1975. Relative diversity indices. Ecology **56**:496-498.

Pet-Soede, C., H. S. J. Cesar, and J. S. Pet. 1999. An economic analysis of blast fishing on Indonesian coral reefs. Environmental Conservation **26**:83-93.

Pichon, M. 1977. Physiography, morphology, and ecology of the double barrier reef of North Bohol (Philippines). Pages 261-267 *in* Proceedings of the Third International Coral Reef Symposium, Miami, Florida.

Pinnegar, J. K., N. V. C. Polunin, P. Francour, F. Badalamenti, R. Chemello, M. L. Harmelin-Vivien, B. Hereu, M. Milazzo, M. Zabala, and G. D'Anna. 2002. Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. Environmental Conservation **27**:179-200.

Platt, W. J., and J. H. Connell. 2003. Natural disturbances and the directional replacement of species. Ecological Monographs **73**:507-522.

Pomeroy, R. S., R. B. Pollnac, B. M. Katon, and C. D. Predo. 1997. Evaluating factors contributing to the success of community-based coastal resource management: the central Visayas regional project - 1, Philippines. Ocean and Coastal Management **36**:97-120.

Rogers, C. S. 1990. Responses of coral reefs and reef organisms to sedimentation. Marine Ecology Progress Series **62**:185-202.

Rubec, P. J. 1988. The need for conservation and management of Philippine coral reefs. Environmental Biology of Fishes **23**:141-154.

Russ, G. R., and A. C. Alcala. 1989. Effects of intense fishing pressure on an assemblage of coral reef fishes. Marine Ecology Progress Series **56**:13-27.

Russ, G. R., and A. C. Alcala. 2004. Marine reserves: long-term protection is required for full recovery of predatory fish populations. Oecologia **138**:622-627.

Russ, G. R., B. Stockwell, and A. C. Alcala. 2005. Inferring versus measuring rates of recovery in no-take marine reserves. Marine Ecology Progress Series **292**:1-12.

Russ, G. R., and D. C. Zeller. 2003. From mare liberum to mare reservarum. Marine Policy **27**:75-78.

Sale, P. F. 1988. What coral reefs can teach us about ecology. Pages 19-27 *in* Proceedings of the Sixth International Coral Reef Symposium, Australia.

Sale, P. F., R. K. Cowen, B. S. Danilowics, G. P. Jones, J. P. Kritzer, K. C. Lindeman, S. Planes, N. V. C. Polunin, G. R. Russ, Y. J. Sadovy, and R. S. Steneck. 2005. Critical science gaps impede use of no-take fishery reserves. Trends in Ecology and Evolution **20**:74-80.

Samoilys, M. A., K. M. Martin-Smith, B. G. Giles, B. Cabrera, J. A. Anticamara, E. O. Brunio, and A. C. J. Vincent. 2007. Effectiveness of five small Philippines' coral reef reserves for fish populations depends on site-specific factors, particularly enforcement history. Biological Conservation **136**:584-601.

Schmitz, O. J. 2004. Perturbation and abrupt shift in trophic control of biodiversity and productivity. Ecology Letters **7**:403-409.

Shears, N. T., and R. C. Babcock. 2002. Marine reserves demonstrate top-down control of community structure on temperate reefs. Oecologia **132**:131-142.

Shears, N. T., and R. C. Babcock. 2003. Continuing trophic cascade effects after 25 years of no-take marine reserve protection. Marine Ecology Progress Series **246**:1-16.

Sheley, R. L., J. M. Mangold, and J. L. Anderson. 2006. Potential for successional theory to guide restoration of invasive-plant-dominated rangeland. Ecological Monographs **76**:365-379.

Stone, L., A. Gabric, and T. Berman. 1996. Ecosystem resilience, stability and productivity: seeking a relationship. The American Naturalist **148**:892-903.

Sutherland, E. F., and C. R. Dickman. 1999. Mechanisms of recovery after fire by rodents in the Australian environment: a review. Wildlife Research **26**:405-419.

Tegner, M. J., and P. K. Dayton. 1999. Ecosystem effects of fishing. Trends in Ecology and Evolution **14**:261-262.

Thrush, S. F., and P. K. Dayton. 2002. Disturbance to marine benthic habitats by trawling and dredging: implications for marine biodiversity. Annual Reviews in Ecology and Systematics **33**:449-473.

Tomascik, T., R. van Woesik, and A. J. Mah. 1996. Rapid coral colonization of a recent lava flow following a volcanic eruption, Banda Islands, Indonesia. Coral Reefs **15**:169-175.

Townsend, C. R., M. R. Scarsbrook, and S. Doledec. 1997. The intermediate disturbance hypothesis, refugia, and biodiversity in streams. Limnology and Oceanography **42**:938-949.

Wali, M. K. 1999. Ecological succession and the rehabilitation of disturbed terrestrial ecosystems. Plant and Soil **213**:195-220.

Walker, L. R., and R. del Moral. 2003. Primary succession and ecosystem rehabilitation. Cambridge University Press, Cambridge.

Walsh, W. J. 1983. Stability of a coral reef fish community following a catastrophic storm. Coral Reefs **2**:49-63.

Walters, C. J., D. Pauly, and V. Christensen. 1999. Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. Ecosystems **2**:539-554.

Wardle, D. A., L. R. Walker, and R. D. Bardgett. 2004. Ecosystem properties and forest decline in contrasting long-term chronosequences. Science **305**:509-513.

Wells, S., N. Burgess, and A. Ngusaru. 2007. Towards the 2012 marine protected area targets in Eastern Africa. Ocean and Coastal Management **50**:67-83.

White, A. T., H. P. Vogt, and T. Arin. 2000. Philippine coral reefs under threat: the economic losses caused by reef destruction. Marine Pollution Bulletin **40**:598-605.

Williamson, D. H., G. R. Russ, and A. M. Ayling. 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.

Wood, L. J., and S. Dragicevic. 2007. GIS-Based multi-criteria evaluation and fuzzy sets to identify priority sites for marine protection. Biodiversity and Conservation **16**:2539-2558.

Wood, R. 1998. The ecological evolution of reefs. Annual Review of Ecology and Systematics **29**:179-206.

Yasue, M., L. Kaufman, and A. C. J. Vincent. in prep. Assessing ecological changes in and around marine reserves using community perceptions and biological surveys.

2. General methods

The main goal of this research was to describe patterns of reef fish community change within no-take marine reserves that fell along categories of protection-duration and location relative to the mainland. Specifically, we investigated the following: (1) magnitudes and rates of community recovery; (2) changes in reef fish diversity, (3) patterns of reef fish community succession; and (4) shifts in reef fish species' net or overall community interactions. The latter were defined as the frequency distribution of all inter-species biomass time-series pairwise correlation *r* values (+, 0, -) within and across the study sites. Below we described the general methods that we used to estimate reef fish abundance, biomass, diversity, and reef benthic habitat cover within the eight reef study sites in Danajon Bank in the central Philippines (Figure 2.1). We also described the general analytical approaches used to test the influence of protection-duration and site location on the changes in reef fish communities within and across the study sites. All the field and analytical methods that we used throughout this research have been applied and tested in research on marine reserves, reef ecology, or general ecology, but we give references when appropriate. In addition, all the data chapters of this thesis were designed as stand-alone manuscripts focused on answering the four specific research objectives as stated above. However, since all the data chapters share the same study sites, data sets, and a common analytical framework, these common aspects are presented here in the general methods to prevent unnecessary repetition throughout the thesis. Where additional specific analyses were needed to answer a given chapter's question, these analyses are presented in the methods section of that data chapter.

Study sites

Danajon Bank has a number of features that make it a very interesting focal area for research on the changes in reef fish communities in response to the establishment of marine reserves: (1) the number of marine reserves in Danajon bank has been steadily increasing since 1995; (2) Danajon Bank is a rare reef formation, one of only two known double barrier reefs in the world (Pichon 1977), but not well-studied; and (3) Danajon Bank had been subjected to intense destructive fishing, and there is a great need to find effective ways for it to recover (Green et al. 2002). At the beginning of our research in 2002, there were six well-enforced no-take marine reserves in Danajon Bank with various periods of protection-duration and at varying distances from the mainland (Table 2.1). We selected these six marine reserves and two fished sites as our study sites (Figure 2.1). For analytical purposes, we classified the eight reef sites into protection-duration categories as fished (F; n=2), younger marine reserves (YMR; n=3), and older marine reserves (OMR: n=3), based on the length of time the sites had been protected at the beginning of the study (Table 2.1). We also classified the eight reef sites as inshore (In; n=5) and offshore (Off; n=3), based on their relative distance from the mainland of Bohol (Table 2.1; Figure 2.1). This location classification was based on earlier work in Danajon Bank (Pichon 1977), which demonstrated that the inshore reefs are heavily influenced by sedimentation from the mainland while the offshore reefs had clearer water and thereby were able to develop much larger reef areas and better-defined reef zones (e.g. reef flats, reef crests, and reef slopes) than the inshore reefs. The unbalanced and un-replicated design of our study is a consequence of logistic and sampling constraints married to the limited availability of well-enforced marine reserves in Danajon Bank during the period of our field work.

Our eight study sites were located in three different municipalities (Buenavista, Getafe, Tubigon) and were associated with communities with human populations ranging from approximately 850 to 3000 people (Table 2.2). The size of the marine reserves ranged from about 5 to 50 hectares, with the size of the fished sites not quantifiable or bounded (Table 2.2). In an ideal world, factors such as marine reserve size and human population would have been controlled in order to focus on the two main factors of protection-duration and site location, but we were working in the real world where the establishment of marine reserves is a function of local communities' decision-making, and therefore difficult to control (Ban et al. in prep., Hansen et al. in prep.). We interpreted and discussed the results of our analyses in full awareness of the lack of balanced design, site replication, and control for some confounding factors.

Benthic habitat survey

We characterized the benthic habitat using the line intercept transect (LIT) method (English et al. 1997). We conducted benthic surveys at each study site from July 2002 to December 2004 (Table 2.3). During each benthic survey, five to eight haphazardly located, replicate transects were measured for percentage cover of all sessile and attached benthos including hard corals (identified by their forms such as branching, digitate, encrusting, foliose, knobby, massive etc.), soft corals, other invertebrates (sponges, tunicates, sea fans etc.), and abiotic categories (dead corals, sand or silt) following benthic habitat categories and methods developed in the Great Barrier Reef (English et al. 1997).

Benthic habitat is known to influence the structure of reef fish assemblages (Friedlander and Parrish 1998, Ohman and Rajasuriya 1998, Aburto-Oropeza 2001), but benthic habitat and reef fish relationships vary, and can be site or species-specific (Tolimiere 1995, Chabanet et al. 1997, Nanami et al. 2005). Our aim, as in other marine reserve studies, was to choose similar habitat across our study sites in order to minimise its potential influence on the changes in fish communities (Graham et al. 2003, McClanahan and Graham 2005). Thus, we conducted all our fish UVC on or near the reef slopes in all study sites. Reef slopes often harbour the highest abundance, biomass, and richness of fish communities compared to the other reef zones (e.g. reef flats or reef crest) (Birkeland 1988, Williams 1991, Sorokin 1993).

As a background to the focal reef fish community analyses of this thesis, we assessed habitat changes within each site and differences in habitat across the eight sites. Analyses of Variance (ANOVA) did not detect a significant influence of protection-duration and site location on the percentage cover of benthic life forms across the study sites, using the final year of data sampled (Figure 2.2). Nor did ANOVA detect a significant influence of protection-duration and site location on the rates of changes of live coral cover across the study sites over the course of the study (Figure 2.3). The habitat measures, while coarse, were at levels (i.e. broader taxonomic groups and life form levels instead of specific taxa) that should have been sufficient to detect fish and habitat associations as commonly investigated in many coral reef studies (Friedlander and Parrish 1998, Garcia Charton and Perez Ruzafa 1998, Ohman and Rajasuriya 1998). The similar benthic habitat cover across the study sites means that the effects of protection-duration and site location on the changes in fish communities within and across the study sites can be assessed independent of habitat.

Fish Underwater Visual Census (UVC) and estimates of abundance, biomass, and species richness

We conducted monthly UVCs at each study site to identify fish species and to estimate their abundance (Samoilys and Carlos 2000). Specifically, we conducted monthly surveys within each study site from June 2002 to February 2005 (Table 2.4) along standardized 70 m long x 5 m wide belt transects. One day prior to the UVC, we laid eight transects haphazardly and parallel to the reef slope of each site. On the day of the UVC, two trained surveyors (see following section on standardization of surveyors' skills) swam on each side of the belt transect (2.5 m wide for each side) and identified all non-cryptic fish species, counted them, and estimated their lengths to the nearest cm. To minimize census bias, we enumerated fishes greater than 10 cm in total length (TL) in the first 50 m section of the transect, and then enumerated fishes between 1 cm and 10 cm in the last 20 m section of the transect, as recommended in other reef research (Bellwood and Alcala 1988, Jennings et al. 1996).

Based on the UVC of the eight haphazardly laid transects surveyed within each site each month, we determined a number of variables describing the reef fish community. We calculated the total species richness found across all eight transects surveyed within each site each month. We then did the same for the mean abundance of all species, calculated as number of individuals m^{-2}. The mean abundance of each species per month per site was calculated as the sum of the number of individuals m^{-2} from each transect section (i.e. first 50 meter section for individuals greater than 10 cm, and the last 20 m section for individuals between 1 and 10 cm). This approach assumes that the large and small size classes of each species are found at the similar densities on each sections of the transect on which they are not measured (Bellwood and Alcala 1988, Jennings et al. 1996). We also estimated the mean biomass for each species ($g \cdot m^{-2}$) based on the length estimates for all individual fish species encountered during the UVC (see following section for the methods used to convert fish length and abundance into biomass). We applied the same methods used for calculating the mean abundance of species found across the eight transects sampled within each site each month to calculate the mean biomass of all the species found within each site each month.

Conversion of fish length into biomass

We converted the fish length (cm) into weight (g) for each individual fish using published length-weight relationships (Weight = **a** x Length$^{\mathbf{b}}$) from FishBase (see Appendix A) (Froese and Pauly 2003). We found the parameters **a** and **b** for 227 out of the 423 total species in our study sites (see Appendix A). For the remaining 196 species, we used relationships from their closest congenerics of the same size and shape, or the average values for multiple congenerics of the same size and shape (see Appendix A) as has been done in other studies (Micheli et al. 2004, McClanahan and Graham 2005).

Categorization of fish species into body-size groups and trophic groups

We obtained the maximum total length for the 423 fish species belonging to 49 families observed during our study mainly from FishBase (see Table 2.5 and Appendix A) (Froese and Pauly 2003). We then used these maximum length estimates to group fish species within families according to the following body size categories: (a) extra large (greater than 60 cm maximum total length TL), (b) large (30.1-60 cm maximum TL), c) medium (10.1-30 cm maximum TL), and (d) small (1-10 cm maximum TL) (Table 2.5).

We obtained trophic information for all 423 fish species observed during our study from FishBase (Froese and Pauly 2003), fish identification guides (Allen et al. 1997, Randall et al. 1997, Lieske and Myers 2001), and other sources in the worldwide web (e.g. zipcodezoo.com and saltcorner.com; see Table 2.6 and Appendix A). The majority of the reef fishes in our study sites have varied diets and we therefore assigned the highest trophic group that they feed on to be a species' trophic category (e.g. a species that can feed on algae, detritus, and zoobenthos will be considered a zoobenthivore). We then used this trophic information to categorize species within families as (a) herbivores, (b) zoobenthivores, (c) zooplanktivores, (d) piscivores or (e) detrivores (Table 2.6).

Standardization of surveyors' skills

In order to standardize surveyor skills and maximize the consistency of observations among surveyors, training and testing were conducted with respect to fish species identification and fish length estimation. Surveyors were initially trained on land in fish identification for species known to occur in Danajon Bank using coloured photos from FishBase (Froese and Pauly 2003) and fish identification books (Allen et al. 1997, Randall et al. 1997, Lieske and Myers 2001). To facilitate easier identification of species and memorization of fish names, we used the common English fish names that appropriately described a distinguishing character of the species (e.g. six lined cardinalfish) (see Appendix A). In general, we found the common English fish names used in the guidebook "Marine Fishes of the Great Barrier Reef and Southeast Asia" very useful (Allen et al. 1997), and for species not found in this book we consulted other sources (Randall et al. 1997, Lieske and Myers 2001, Froese and Pauly 2003). Trained surveyors were subsequently tested quarterly to ensure consistency of identification. Whenever the surveyors misidentified particular species, their training was repeated, and testing continued until surveyors consistently identified the fish species correctly. This testing was repeated underwater where surveyors were asked to identify species. Similar to the land test, we repeatedly tested the surveyors for species that they misidentified until they consistently identified the fish species correctly. This ability was cross-checked quarterly.

We tested the trained surveyors' fish length estimation skills underwater by asking them to determine the individual length of a set of 30 cut-out aluminium fish models of known lengths ranging from 3 to 60 cm. The maximum length of 60 cm was established based on the biggest fish that was normally encountered in this region. We re-tested the trained surveyors' fish length estimation skill until the point that their errors were reduced to an average of ±5 cm, a method that has also been applied in other marine reserve research (Polunin and Roberts 1993, Roberts 1995).

General data analyses

Throughout this thesis, we are interested in knowing how attributes (e.g. abundance, biomass, species richness, diversity, abundance-biomass comparison curves) of the reef fish community changed with respect to protection-duration and location. We typically compared the absolute differences in study sites (i.e. magnitudes) as well as their rates of change over the 33 months of the study. With respect to the magnitude of changes in reef fish community characteristics, we used the mean values for the final year of the study with the individual months as replicates for each site (Table 2.4). Mean values from temporal replicates within sites to compare across sites have also been used in other marine reserve studies (Polunin and Roberts 1993, Roberts 1995). In our case, we considered the mean values of the final year as the maximum impact of protection for each site. In terms of rates of change, we plotted the monthly trends of reef fish community characteristics (e.g. abundance, biomass, and species richness) within each site as a function of time (monthly sampling), consistent with approaches used in estimating rates of community changes for the very limited research on marine reserves that used time-series data (Russ and Alcala 1996, McClanahan and Graham 2005).

The use of monthly time-series data as replicates may decrease the independence of the replicates (Pyper and Peterman 1998), but there is a great need to analyse changes in reef fish communities using successive temporal replicates within marine reserves or reef sites

(Sale 1991), the lack of which is currently considered a serious limitations in many marine reserve or coral reef ecology studies (Halpern 2003, Micheli et al. 2004, Russ et al. 2005). In fact, despite the potential issues of autocorrelation, analyses of temporal replicates from within reefs sites have been conducted in a diversity of marine reserve and reef ecology studies (Talbot et al. 1978, Polunin and Roberts 1993, Roberts 1995, Graham et al. 2003). The likely impact of using monthly time-series would be to decrease the variance around mean values or the influence of previous temporal values on the successive values (Breusch 1978, Turchin and Taylor 1992, Edgerton and Shukur 1999). However, we have somewhat mitigated the potential problems of autocorrelation in using time-series by surveying replicated and haphazardly-laid transects rather than fixed transects during each month within each site. We also used Durbin-Watson to test for autocorrelation in our data and in most cases our data passed the test (about 75% for total abundance and biomass analyses, but 37%-88% for the total species richness and other diversity indices data: see Appendix B). Our goal was to use one model – the linear model – in order to be able to compare across the study sites. Given the results of our data diagnostics in Appendix B, we did not correct for autocorrelation and are comfortable in using linear approaches (i.e. ANOVA and regression) in our analyses. In addition, given the relatively short time-frame of our study, over three years, linear assumptions for the temporal data trend should be acceptable. Our decision to use linear models and not to correct for autocorrelation is similar to that taken in other studies of marine reserve using time-series data (Russ and Alcala 2004, Williamson et al. 2004, McClanahan and Graham 2005). In fact, in some cases, eliminating autocorrelation can reduce the biological relevance of analyses (de Solla et al. 1999). Nonetheless, we advocate caution in interpreting our results based on the potential influence of temporal autocorrelation that could bias our outcomes.

We used two-way Analyses of Variance (ANOVA) to test the influence of protection-duration and site location on the magnitudes and rates of changes (i.e. slopes of the regression line) in fish community characteristics (e.g. abundance, biomass, and species richness) within and across study sites. Each time we present outputs of a two-way ANOVA throughout this thesis, we first evaluate the effects of protection-duration, and then the effects of location. The effects of the two main factors were tested statistically, but the interaction between these two factors was not tested because of the unbalanced and un-replicated design of our study. Typically in two-way ANOVA, it is important to evaluate the interactions before the main factors (Zar 1999). However, the limitations of our sampling design (e.g. a lack of balanced replication within main factors) prevent us from treating the two-way ANOVA analyses in more conventional ways. We cannot test interactions between the two factors and can only test the effects of the main factors with caution (Zar 1999). Nevertheless, we noted that in some instances there were strong interaction trends between protection-duration and site location in influencing the changes in reef fish communities within the study sites (e.g. in terms of abundance and species richness). Therefore, although we did not test for interactions, we still present the figure of the potential interactions between the two factors. We also presented comments regarding this potential main factor interaction in our results and discussions using the two-way ANOVA interaction models (Figure 2.4) (Zar 1999). Moreover, throughout this thesis, we only presented the *F*-values, degrees of freedom, and *P*-values of the significant tests, denoting non-significant tests with "NS".

In summary, our research apparently offers the best available data on recovery of reef fish community dynamics. We provided the most comprehensive analyses of the responses of 423 reef fish species to marine reserve protection-duration and location. Specifically, we conducted well replicated monthly sampling within eight study sites for three years to answer questions on reef fish community changes within marine reserves such as the following: (a) magnitudes and rates of community changes, (b) changes in reef fish diversity, (c) patterns of reef fish succession, and d) shifts in reef fish species' net or overall community interactions. These were defined as the frequency distribution of all pairwise correlation *r* values (+, 0, -) among species biomass time-series within reef sites of various protection-duration and location relative to the mainland.

Tables

Table 2.1 Study sites on Danajon Bank and their protection status and distance relative to the mainland of Bohol, Philippines. Upper case site codes indicate inshore sites and lower case site codes indicate offshore sites.

Site code	Starting year of enforcement by the community	Enforcement rating in 2004[§]	Protection-duration categories	Shortest distance from mainland of Bohol (km)	Location categories
A	Unprotected	-	Fished (F)	12	Inshore (In)
b	Unprotected	-	Fished (F)	30	Offshore (Off)
C	2002	19	Younger marine reserves (YMR)	5	Inshore (In)
D	2002	19	Younger marine reserves (YMR)	8	Inshore (In)
e	2002	12	Younger marine reserves (YMR)	30	Offshore (Off)
F	1999	25	Older marine reserves (OMR)	4	Inshore (In)
g	1999	28	Older marine reserves (OMR)	22	Offshore (Off)
H	1995	34	Older marine reserves (OMR)	10	Inshore (In)

[§] Coastal Conservation Education Foundation (CCEF) in the Philippines adopts a point rating for MPA enforcement (see http://www.coast.ph/). The total possible points that an MPA can earn in this rating is 38. The rating categories are as follows: 6 points = pass; 12 points = fair; 20 points = good; 25 points = very good; and 30+ = excellent.

Table 2.2 Geographic, social, and political information about the eight study sites located on Danajon Bank, Bohol, Philippines.

Site code	Name, Municipality[†]	Size (m^2)[‡]	Human population (individuals)[‡]	Distance to the municipality (km)[‡]
A	Putik, Getafe	-	-	13
b	Ubayon, Tubigon	-	-	31
C	Jandayan Sur, Getafe	50, 000	1, 657	6
D	Jandayan Norte, Getafe	250, 000	876	9
e	Pandanon, Getafe	200, 000	3, 000	31
F	Asinan, Buenavista	500, 000	886	5
g	Batasan, Tubigon	210, 000	954	23
H	Handumon, Getafe	500, 000	1, 100	11

[†] See Figure 2.1 for the location on the map.
[‡] Source: Project Seahorse Foundation Philippines (2004).

Table 2.3 Number of benthic line intercept transects completed within study sites (A-H) from 2002 to 2005. Benthic sampling in year 1 was variable as logistics and techniques were established.

Sample	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
Month[a]	6	7	8	9	10	11	12	1	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5	6	7	8	9	10	11	12	1	2
Year	2002							2003												2004												2005	
Yearcode	Year 1												Year 2												Year 3								
Season	Rain						Dry						Rain						Dry						Rain						Dry		
A															8		8		8			8				8			8		8		
b															8		8		8			8				8			8		8		
C		5								6		6			8		8		8			8				8			8		8		
D		6								6		6			8		8		8			8				8			8		8		
e										6		6		8			8		8			8				8			8		8		
F										5		6		8			8		8			8				8			8		8		
g										6		6			8		8		8							8			8		8		
H		6								4		6		8			8		8			8				8			8		8		

---

[a] Month codes: 1 = January to 12 = December

Table 2.4 Number of Underwater Visual Census (UVC) transects completed (numbers in bold and <8 indicate reduced number of transects due to typhoons) during each monthly sampling event within study sites (A-H) from 2002 to 2005. Blank cells indicate that no sampling was conducted either due to extreme weather conditions (e.g. typhoons during sampling in Sites F and g), problems with sampling permits (Site e), or difficulty in identifying reference fished sites (Sites A and b).

Sample	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
Month[a]	6	7	8	9	10	11	12	1	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5	6	7	8	9	10	11	12	1	2
Year	2002							2003												2004												2005	
Yearcode	Year 1												Year 2												Year 3								
Season	Rain						Dry						Rain						Dry						Rain						Dry		
A											8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	**5**	8	8	8	8	8	8
b											8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
C	8	8	8	8	8	8			8	8	8	**6**	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
D	8	8	8	8	8	8			8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	**7**	8	8	8	8	8	8
e				8	8	8			**7**	8	8	8	**7**	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
F	8		8	8	8	8			8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
g	8	8	8	8	8	8			8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8		8	8	8	8	8	8	8
H	8	8	8	8	8	8			8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8

---

[a] Month codes: 1 = January to 12 = December

Table 2.5 Distribution of body size groups across families.

Family	No. spp.	Extra large	Large	Medium	Small
Acanthuridae	10	2	3	5	-
Apogonidae	26	-	-	10	16
Atherinidae	1	-	-	-	1
Balistidae	3	1	-	2	-
Belonidae	1	1	-	-	-
Blenniidae	15	-	-	9	7
Bothidae	1	-	1	-	-
Caesionidae	6	-	5	1	-
Callionymidae	3	-	-	1	2
Carangidae	4	3	-	1	-
Centriscidae	1	-	-	1	-
Chaetodontidae	20	-	-	20	-
Cirrhitidae	3	-	-	1	2
Dasyatidae	2	1	-	1	-
Diodontidae	1	1	-	-	-
Ephippidae	3	1	1	1	-
Fistularidae	2	2	-	-	-
Gerreidae	1	-	-	1	-
Gobiesocidae	1	-	-	-	1
Gobiidae	21	-	-	6	15
Haemulidae	5	4	1	-	-
Holocentridae	4	-	2	2	-
Kyphosidae	1	-	1	-	-
Labridae	63	5	11	43	4
Lethrinidae	7	-	5	2	-
Lutjanidae	9	2	7	-	-
Malacanthidae	1	-	-	1	-
Monacanthidae	11	1	1	6	3
Mullidae	7	-	5	2	-
Muraenidae	3	3	-	-	-
Nemipteridae	10	-	2	8	-
Ostraciidae	3	-	1	2	-
Pinguipedidae	6	-	-	5	1
Platycephalidae	1	-	1	-	-
Plotosidae	1	-	1	-	-
Pomacanthidae	5	-	2	3	-
Pomacentridae	73	-	-	33	40
Pseudochromidae	5	-	1	2	2
Scaridae	26	5	17	4	-
Scombridae	1	-	1	-	-
Scorpaenidae	4	-	1	3	0
Serranidae	21	8	6	7	-
Siganidae	11	-	4	7	-
Soleidae	1	-	-	1	-
Sphyraenidae	3	2	1	-	-
Syngnathidae	2	-	-	2	-
Synodontidae	3	-	2	1	-
Tetraodontidae	10	2	3	3	2
Zanclidae	1	-	-	1	-
Total	**423**	**44**	**87**	**196**	**96**

Table 2.6 Distribution of trophic groups across families.

Family	No spp.	Detrivore	Herbivore	Piscivore	Zoobenthivore	Zooplanktivore
Acanthuridae	10	-	9	-	1	-
Apogonidae	26	-	-	4	21	1
Atherinidae	1	-	-	-	-	1
Balistidae	3	-	-	-	3	-
Belonidae	1	-	-	1	-	-
Blenniidae	15	1	7	1	2	4
Bothidae	1	-	-	-	1	-
Caesionidae	6	-	-	-	1	5
Callionymidae	3	-	-	-	3	-
Carangidae	4	-	-	3	1	-
Centriscidae	1	-	-	-	-	1
Chaetodontidae	20	-	-	-	20	-
Cirrhitidae	3	-	-	3	-	-
Dasyatidae	2	-	-	-	2	-
Diodontidae	1	-	-	1	-	-
Ephippidae	3	-	2	-	1	-
Fistularidae	2	-	-	2	-	-
Gerreidae	1	-	-	-	1	-
Gobiesocidae	1	-	-	-	1	-
Gobiidae	21	1	-	-	20	-
Haemulidae	5	-	-	-	5	-
Holocentridae	4	-	-	2	2	-
Kyphosidae	1	-	1	-	-	-
Labridae	63	-	-	11	48	4
Lethrinidae	7	-	-	2	5	-
Lutjanidae	9	-	-	9	-	-
Malacanthidae	1	-	-	1	-	-
Monacanthidae	11	-	-	-	11	-
Mullidae	7	-	-	-	7	-
Muraenidae	3	-	-	2	1	-
Nemipteridae	10	-	-	-	10	-
Ostraciidae	3	-	-	-	3	-
Pinguipedidae	6	-	-	1	5	-
Platycephalidae	1	-	-	-	1	-
Plotosidae	1	-	-	1	-	-
Pomacanthidae	5	-	1	-	4	-
Pomacentridae	73	-	6	2	27	38
Pseudochromidae	5	-	-	2	3	-
Scaridae	26	-	24	-	2	-
Scombridae	1	-	-	1	-	-
Scorpaenidae	4	-	-	2	2	-
Serranidae	21	-	-	15	4	2
Siganidae	11	-	8	-	2	1
Soleidae	1	-	-	-	1	-
Sphyraenidae	3	-	-	3	-	-
Syngnathidae	2	-	-	-	2	-
Synodontidae	3	-	-	3	-	-
Tetraodontidae	9	-	1	-	9	-
Zanclidae	1	-	-	-	1	-
Total	**423**	**2**	**59**	**73**	**232**	**57**

Figures

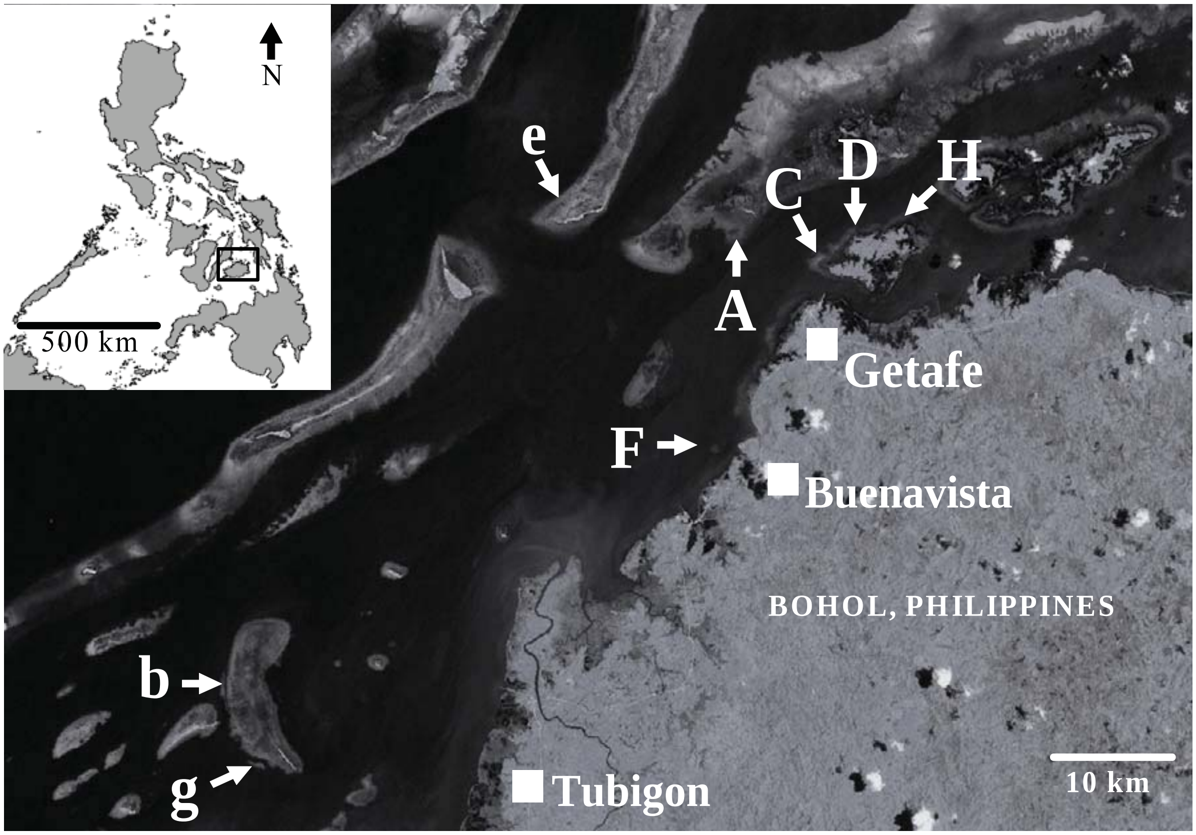


Figure 2.1 Location of the study sites on Danajon Bank, off the northwest coast of Bohol in the central Philippines. Upper case site codes indicate inshore sites and lower case site codes indicate offshore locations.

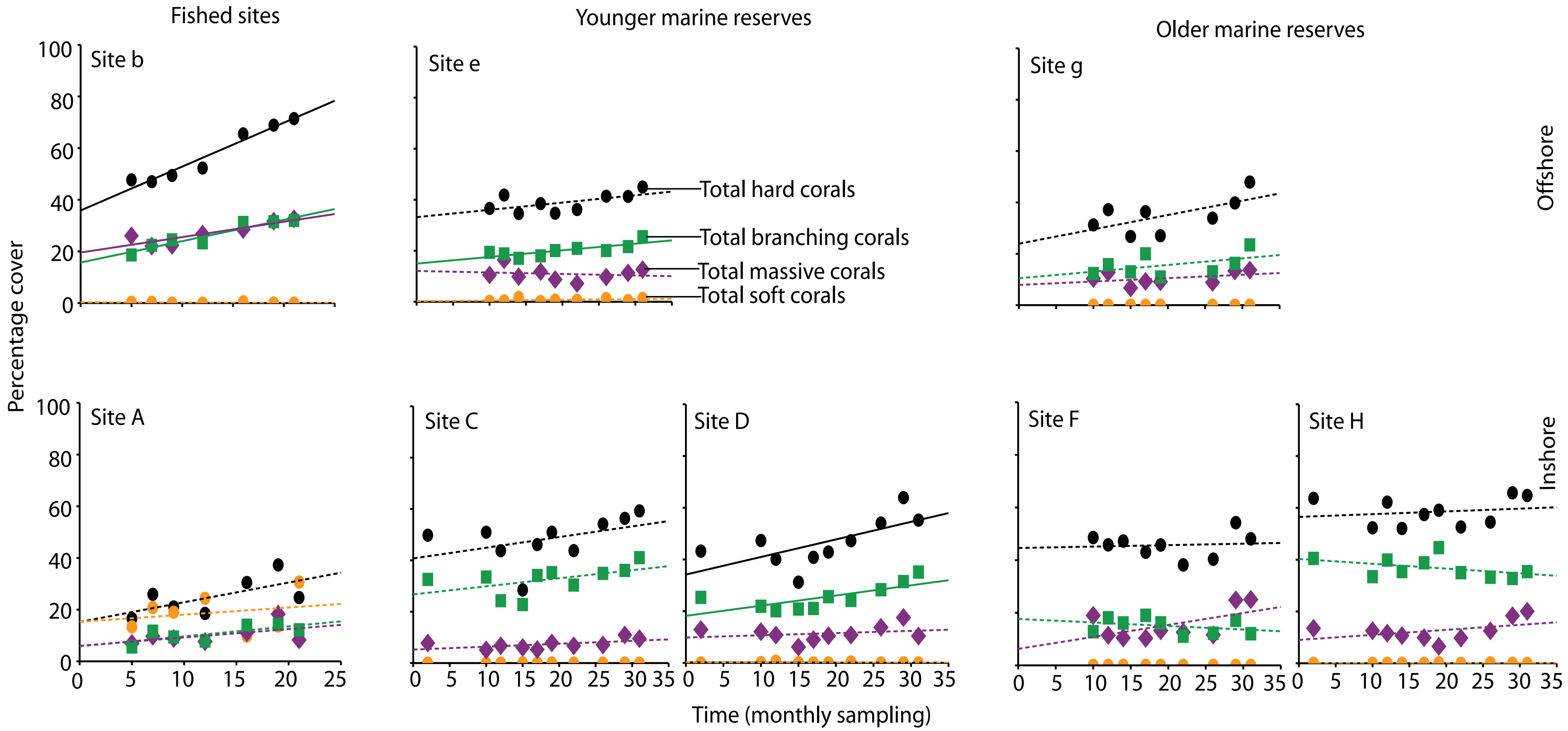


Figure 2.2 Regression of percentage cover of live benthic habitat against sampling time (monthly sampling interval from 2002-2005). Legends: black circles and lines (total hard corals), green squares and lines (branching corals), purple diamonds and lines (massive corals), and orange circles and lines (soft corals). Other coral life forms (e.g. foliose, knobby, columnar, digitate etc.) and other living benthic organisms (e.g. algae, sponges, tunicates etc.) comprised a small proportion of the total benthic cover and are not presented. Solid lines are significant regression lines and dashed lines are non-significant regression lines within sites. Because of the variability in the significance of these slopes Two-way ANOVA on the effects of protection-duration and site location was not tested.

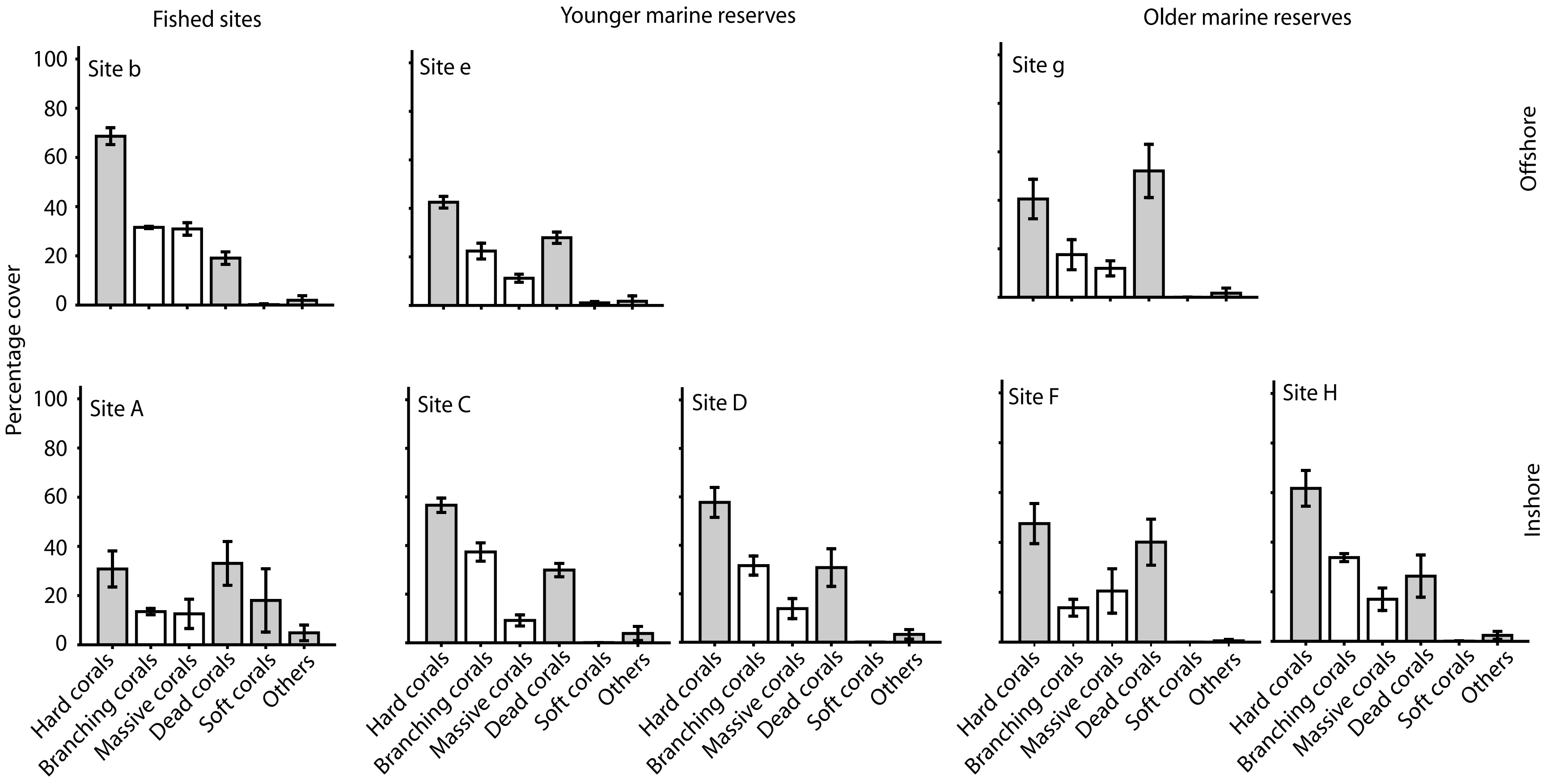


Figure 2.3 Mean percentage benthic cover (± SE) within sites during the last year of sampling. White bars (branching and massive corals) indicate dominant subset of hard coral life forms.

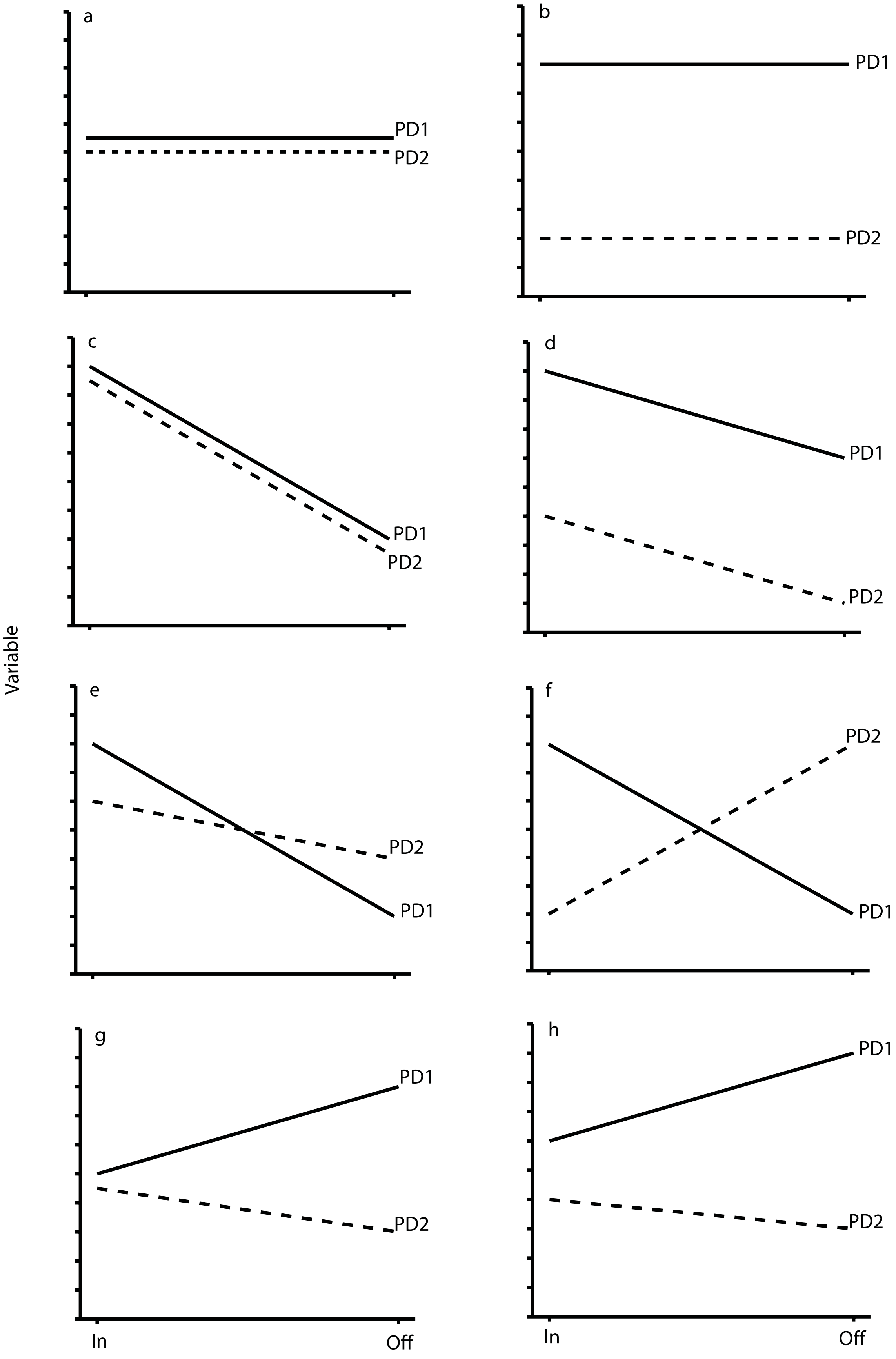

Variable
a
PD1
PD2
b
PD1
PD2
c
PD1
PD2
d
PD1
PD2
e
PD2
PD1
f
PD2
PD1
g
PD1
PD2
h
PD1
PD2
In
Off
In
Off

Figure 2.4 Hypothetical outputs of two-way ANOVA testing the effects of two main factors: Protection-duration (PD1 and PD2) and Location (Inshore (In) and Offshore (Off)), and the interaction trends of the two main factors: (a) no effect of Location, small effect of Protection-duration, and no interaction main factors; (b) no effect of Location, large effect of Protection-duration, and no interaction of main factors; (c) large effect of Location, small effect of Protection-duration, and no interaction of main factors; (d) large effect of Location, large effect of Protection-duration, and no interaction of main factors; (e) large effect of location, no effect of Protection-duration, and slight interaction of main factors; (f) no effect of location, no effect of Protection-duration, but interaction between main factors; (g) no effect of location, large effect of Protection-duration, and large interaction between main factors; (h) effect of location, large effect of Protection-duration, and large interaction between main factors (adapted from Zar 1999).

References

Aburto-Oropeza, O. 2001. Community structure of reef fish in several habitats of a rocky reef in the Gulf of California. Marine Ecology **22**:283-305.

Allen, G. R., R. Swainston, and J. Ruse. 1997. Marine fishes of the Great Barrier Reef and South-east Asia. Western Australian Museum, Perth, Western Australia.

Ban, N. C., G. J. A. Hansen, M. Jones, and A. C. J. Vincent. in prep. Systematic marine conservation planning in data-poor regions: socio-economic data is essential.

Bellwood, D. R., and A. C. Alcala. 1988. The effect of a minimum length specification on visual estimates of density and biomass of coral reef fishes. Coral Reefs **7**:23-27.

Birkeland, C. 1988. Geographic comparisons of coral-reef community processes. Pages 211-219 *in* Proceedings of the Sixth International Coral Reef Symposium, Australia.

Breusch, T. S. 1978. Testing for autocorrelation in dynamic linear models. Australian Economic Papers **17**:334-355.

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

de Solla, S. R., R. Bonduriansky, and R. J. Brooks. 1999. Eliminating autocorrelation reduces biological relevance of home range estimates. Journal of Animal Ecology **68**:221-234.

Edgerton, D., and G. Shukur. 1999. Testing autocorrelation in a system perspective testing autocorrelation. Econometric Reviews **18**:343-386.

English, S., C. R. Wilkinson, and V. Baker. 1997. Survey manual for tropical marine resources. Australian Institute of Marine Science, Townsville, Australia.

Friedlander, A. M., and J. D. Parrish. 1998. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. Journal of Experimental Marine Biology and Ecology **224**:1-30.

Froese, R., and D. Pauly. 2003. Fish Base 2000: concepts, design and data sources. International Center for Living Aquatic Resources Management, Makati City, Philippines.

Garcia Charton, J. A., and A. Perez Ruzafa. 1998. Correlation between habitat structure and a rocky reef fish assemblages in the Southwest Mediterranean. P.S.Z.N.: Marine Ecology **19**:111-128.

Graham, N. A. J., R. D. Evans, and G. R. Russ. 2003. The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. Environmental Conservation **30**:200-208.

Green, S. J., R. D. Alexander, A. M. Gulayan, C. C. Migriño III, J. Jarantilla-Paler, and C. A. Courtney. 2002. Bohol Island: its coastal environment profile. Bohol Environment Management Office and Coastal Resource Management Project, Cebu.

Halpern, B. S. 2003. The impact of marine reserves: do reserves work and does reserve size matter? Ecological Applications **13**:S117-S137.

Hansen, G. J., N. Ban, M. L. Jones, L. Kaufman, H. Panes, M. Yasue, and A. C. J. Vincent. in prep. Hindsight in marine protected area designation and planning: a comparison of community-driven and systematic approaches in Danajon Bank, Philippines.

Jennings, S., S. S. Marshall, and N. V. C. Polunin. 1996. Seychelles' marine protected areas: comparative structure and status of reef communities. Biological Conservation **75**:201-209.

Lieske, E., and R. Myers. 2001. Coral reef fishes: Indo-Pacific and Caribbean. Princeton University Press, New Jersey.

McClanahan, T. R., and N. A. J. Graham. 2005. Recovery trajectories of coral reef fish assemblages within Kenyan marine protected areas. Marine Ecology Progress Series **294**:241-248.

Micheli, F., B. S. Halpern, L. W. Botsford, and R. R. Warner. 2004. Trajectories and correlates of community change in no-take marine reserves. Ecological Applications **14**:1709-1723.

Nanami, A., M. Nishihira, T. Suzuki, and H. Yokochi. 2005. Species-specific habitat distribution of coral reef fish assemblages in relation to habitat characteristics in an Okinawan coral reef. Environmental Biology of Fishes **72**:55-65.

Ohman, M. C., and A. Rajasuriya. 1998. Relationships between habitat structure and fish communities on coral and sandstone reefs. Environmental Biology of Fishes **53**:19-31.

Pichon, M. 1977. Physiography, morphology, and ecology of the double barrier reef of North Bohol (Philippines). Pages 261-267 *in* Proceedings of the Third International Coral Reef Symposium, Miami, Florida.

Polunin, N., and C. Roberts. 1993. Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. Marine Ecology Progress Series **100**:167-176.

Pyper, B. J., and R. M. Peterman. 1998. Comparison of methods to account for autocorrelation in correlation analyses of fish data. Canadian Journal of Fisheries and Aquatic Sciences **55**:2127-2140.

Randall, J. E., G. R. Allen, and R. C. Steene. 1997. Fishes of the Great Barrier Reef and Coral Sea. University of Hawaii Press, Honolulu, Hawaii.

Roberts, C. M. 1995. Rapid build-up of fish biomass in a Carribean marine reserve. Conservation Biology **9**:815-826.

Russ, G. R., and A. C. Alcala. 1996. Marine reserves: rates and patterns of recovery and decline of large predatory fish. Ecological Applications **6**:947-961.

Russ, G. R., and A. C. Alcala. 2004. Marine reserves: long-term protection is required for full recovery of predatory fish populations. Oecologia **138**:622-627.

Russ, G. R., B. Stockwell, and A. C. Alcala. 2005. Inferring versus measuring rates of recovery in no-take marine reserves. Marine Ecology Progress Series **292**:1-12.

Sale, P. F. 1991. Reef fish communities: open non-equilibrial systems. Pages 564-598 *in* P. F. Sale, editor. The ecology of fishes on coral reefs. Academic Press, London.

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

Sorokin, Y. 1993. Coral reef ecology. Springer Verlag, Berlin Heidelberg.

Talbot, F. H., B. C. Russell, and G. R. V. Anderson. 1978. Coral reef fish communities: unstable, high-diversity systems? Ecological Monographs **48**:425-440.

Tolimiere, N. 1995. Effects of microhabitat characteristics on the settlement and recruitment of a coral reef fish at two spatial scales. Oecologia **102**:52-63.

Turchin, P., and A. D. Taylor. 1992. Complex dynamics in ecological time series. Ecology **73**:289-305.

Williams, D. M. 1991. Patterns and processes in the distribution of coral reef fishes. Pages 437-474 *in* P. F. Sale, editor. The ecology of fishes on coral reefs. Academic Press, Inc., London.

Williamson, D. H., G. R. Russ, and A. M. Ayling. 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.

Zar, J. H. 1999. Biostatistical analyses, 4th edition. Prentice-Hall, Inc., New Jersey.

3. How much and how quickly can reef fish communities recover within no-take marine reserves? [*]

---

[*] A version of this chapter has been submitted for publication. Anticamara, J.A., J. J. Meeuwig, and A.C.J. Vincent. How much and how quickly can reef fish communities recover within no-take marine reserves?

Introduction

Marine ecosystems are experiencing severe degradation as a result of overexploitation and other human disturbances. Wide-scale damage is evident in the decline of marine fisheries production (Hutchings 2000, Dulvy et al. 2003, Pauly et al. 2005) as well as the gross destruction of habitat (Hodgson et al. 1994, Hughes 1994). Both large-scale overexploitation and habitat destruction can lead to diversity loss and catastrophic shifts in marine ecosystem functioning (Scheffer et al. 2001, Symstad and Tilman 2001). Moreover, the destruction of marine ecosystems has adverse consequences for world economies and food security (Moberg and Folke 1999). There is, therefore, a great need to develop effective ways to facilitate the recovery of degraded marine ecosystems.

No-take marine reserves are strongly advocated for recovery of degraded marine ecosystems (Roberts and Polunin 1991, Russ 2002, Lubchenco et al. 2003). Current predictions and available empirical evidence summarised through meta-analyses have argued that marine reserves can facilitate fast (within a three-year period) and long-term recovery of degraded marine ecosystems, regardless of site characteristics (Halpern and Warner 2002, Halpern 2003). However, results from other marine reserve studies have found recovery within marine reserves to be slow and variable depending on the life history of study species, families, or functional groups of fish (Russ and Alcala 2004, McClanahan and Graham 2005). In addition, the potential for community interactions within marine reserves may result in diverse recovery trajectories of various community components (Graham et al. 2003, Micheli et al. 2004), and spatial heterogeneity in environmental conditions has also led to different rates of recovery amongst different marine reserves (Benedetti-Cecchi et al. 2003). In light of these variable results, the establishment of marine reserves creates opportunities to improve our understanding of how degraded marine ecosystems can recover.

In the last decade, many field studies have been published on the effects of marine reserves on reef fish communities. However, knowledge gaps on marine reserve effects still abound (Russ 2002, Sale et al. 2005). Many of these marine reserve field studies have been confined to a few study sites, limited sampling periods, and focal species or functional groups (Côté et al. 2001, Micheli et al. 2004). Consequently, our understanding of the magnitudes and rates of fish community recovery within marine reserves also remains constrained (Russ et al. 2005). Additionally, actual rates of recovery using time-series data within marine reserves have seldom been explored; instead, recovery rates have been inferred from snapshot data and the age of the marine reserves. Also, there is a need to further investigate how location influences patterns and aspects of community recovery within marine reserves, considering the spatially heterogeneous nature of many ecosystems (Stewart et al. 1999, Benedetti-Cecchi et al. 2003). Finally, there remains a need to assess how a wider range of taxa and functional groups respond to protection-duration and how they interact within marine reserves (Walters et al. 1999, Micheli et al. 2004). Filling current gaps in our knowledge about marine reserves will not only advance our ecological understanding of marine ecosystems but also improve our use of marine reserves as tools to help recover degraded marine areas (Sale et al. 2005).

Here, we present a comprehensive analysis of the magnitudes and rates of fish community recovery within marine reserves. The analysis is based on monthly time-series data over three years from eight sites representing protection-durations ranging from no enforcement to ten years of enforcement – perhaps the most intensive data for marine reserves so far. The eight study sites also represent two spatial regions relative to the mainland (i.e. inshore and offshore). For the three younger marine reserve sites, the start of their sampling coincided with their establishment. All non-cryptic fish species were included in the monthly underwater visual censuses. The main objective of the study was to test the influence of protection-duration and site location on the magnitudes and rates of community recovery within marine reserves while considering fish biomass, abundance, and species richness of the whole assemblage and within defined body size classes and trophic groups.

Methods

Study sites, field sampling protocol, data treatment, and general analytical approach

The study sites, field sampling protocol, data treatment, and general analytical approach were similar for the four data chapters of this thesis (Chapters 3, 4, 5, and 6), and described in details in the general methods (Chapter 2) to prevent repetition throughout the thesis. The methods and analyses specific to this chapter were described below.

Data analyses

The monthly estimates of mean fish biomass (g · m^{-2}), abundance (m^{-2}), and species richness (see Chapter 2: Table 2.4) were analyzed at three levels: (a) whole assemblage, (b) body size classes (see Chapter 2: Table 2.5), and (c) trophic groups (see Chapter 2: Table 2.6). As the data passed the test of normality, autocorrelation, and constant variance in most cases (about 63%-100% of the cases tested for total abundance and biomass, but only 37%-100% for the species richness: see Chapter 2; Appendix B), we used untransformed data in all analyses.

We were mainly interested in two responses among the sites: magnitudes and rates of reef fish community change. Magnitudes of change were defined as the mean monthly values for biomass, abundance, and species richness in the third year of the study (see Chapter 2: Table 2.4). We then tested differences in the magnitudes of biomass, abundance, and species richness using a two-way Analyses of Variance (ANOVA) with protection-duration (i.e. fished (F; n=2), younger marine reserves (YMR; n=3), and older marine reserves (OMR; n=3)) and site location (i.e. inshore (In; n=5) and offshore (Off; n=3)) as main factors, and the interaction term evaluated but not tested (see Chapter 2). Monthly mean values from the third year of the study were used as replicates because temporal autocorrelation was not detected among monthly samples, and because the third year data represent the time to maximum change within sites (see Chapter 2; Appendix B).

We defined rates as the change in biomass, abundance, and species richness per month, measured over the 33 months of the study (see Chapter 2: Table 2.4). We calculated the rates of change in fish biomass, abundance, and species richness by regressing monthly means against month over the 33 months of the study. We treated the slopes of these regressions as estimates of the mean rate of change per month. Where the regressions were not significant, the slopes were defined as zero. We then tested the differences in the rates of fish community recovery as a function of protection-duration and location using two-way ANOVA as with the magnitudes analysis.

Results

Whole assemblage

Of the three whole assemblage metrics, only total fish biomass showed increasing magnitudes and rates of increase (albeit non-significant) with protection-duration, whereas total fish abundance and species richness did not show a significant change in either magnitudes or rates of increase with protection-duration (Figure 3.1 a.1-b.1). There was no interaction between protection-duration and site location, which suggested higher mean biomass in older marine reserves than younger marine reserves and fished sites in both inshore and offshore sites (Figure 3.1 a.3). However, we noted interactions between protection-duration and site location, which indicated that older marine reserves had higher rates of increase in biomass than younger marine reserves and fished sites in inshore sites, but not in offshore sites (Figure 3.1 b.3).

In contrast, total fish abundance and its rates of increase were greater in offshore than inshore sites (ANOVA: $F_{1,2} = 164$, $P = 0.006$; $F_{1,2} = 378$, $P = 0.003$, respectively) (Figures 3.1 a.2 and b.2). In addition, we noted interactions between protection-duration and site location, which suggested that older marine reserves had higher magnitudes and rates of increases in fish abundance than younger marine reserves and fished sites in inshore sites, but not in offshore sites (Figures 3.1 a.3 and b.3).

The magnitudes and rates of increase in species richness were higher in offshore than inshore sites (ANOVA: $F_{1,2} = 638$, $P = 0.002$; $F_{1,2} = 26$, $P = 0.04$, respectively) (Figures 3.1 a.2 and b.2). The interaction between protection-duration and site location was also apparent for both the magnitudes and rates of increase in total species richness, which hinted that older marine reserves had higher magnitudes and rates of increase in species richness than younger marine reserves and fished sites in inshore sites, but not in offshore sites (Figures 3.1 a.3 and b.3).

Body size classes

When total fish biomass was partitioned into four size classes (see Chapter 2), only extra-large and large-bodied species showed higher mean total biomass with protection-duration, and significantly so for the latter (ANOVA: $F_{2,2} = 190$, $P = 0.005$) (Figures 3.2 a.1-d.1). On the other hand, mean total biomass of large, medium and small-bodied fish species were higher in offshore than inshore sites, and significantly so for large and small fish (ANOVA: $F_{1,2} = 29$, $P = 0.03$; $F_{1,2} = 109$, $P = 0.009$, respectively) (Figures 3.2 a.2-d.2). There was no interaction between protection-duration and site location as factors influencing the differences in mean total biomass of the extra-large, large, and medium body size groups, but there was an interaction for the small body size groups, such that older marine reserves had higher mean biomass than younger marine reserves and fished sites in inshore sites, but not in offshore sites (Figures 3.2 a.3-d.3). None of the body size groups showed significant differences in rates of increase in biomass with protection-duration (Figures 3.3 a.1-d.1). However, the rates of increase in biomass of small-bodied species were significantly higher in offshore than inshore sites, but not for the three other body size groups (ANOVA: $F_{1,2} = 96$, $P = 0.01$) (Figures 3.3 a.2-d.2). We noted interactions between protection-duration and site location for rates of increase in biomass of all body size groups, which suggested that older marine reserves showed higher or equal rates of increase in biomass compared with younger marine reserves and fished sites in inshore sites, but not in offshore sites (Figures 3.3 a.3-d.3).

None of the four body size groups showed clear differences in total abundance with protection-duration, although ANOVA detected significant differences for medium-bodied species (ANOVA: $F_{2,2} = 18$, $P = 0.05$) (Figures 3.2 a.1-d.1). However, the total abundances of large, medium, and small-bodied species (but not extra large-bodied species) were significantly higher in offshore sites than inshore sites (ANOVA: $F_{1,2} = 47$, $P = 0.02$; $F_{1,2} = 130$, $P = 0.008$; $F_{1,2} = 214$, $P = 0.008$, respectively) (Figures 3.2 a.2-d.2). We noted interactions for magnitudes of abundance of large, medium, and small body size groups – but not for extra large-bodied group – which suggested that older marine reserve showed higher or equal magnitudes of abundance than younger marine reserves and fished sites in inshore sites, but not in offshore sites (Figures 3.2 a.3-d.3). None of the body size groups showed clear differences in rates of increases in abundance with protection-duration, although ANOVA detected significant differences for small-bodied species (ANOVA: $F_{2,2} = 21$, $P = 0.04$) (Figures 3.3 a.1-d.1). In addition, the medium and small-bodied species showed higher rates of increase in abundance in offshore than inshore sites (ANOVA: $F_{1,2} = 30$, $P = 0.03$; $F_{1,2} = 353$, $P = 0.003$, respectively) (Figures 3.3 a.2-d.2). Moreover, we noted interactions for rates of increase in abundance of medium and small body size groups (but not for extra large and large body size groups, which showed no significant increase), which suggested that older marine reserves showed higher rates of increase than younger marine reserves and fished sites in inshore sites, but not in offshore sites (Figures 3.3 a.3-d.3).

Mean species richness was greater in older marine reserves than younger marine reserves and fished sites, but only for large-bodied species (ANOVA: $F_{2,2} = 611$, $P = 0.002$) (Figures 3.2 a.1-d.1). However, the mean species richness of large-bodied and medium-bodied species were significantly higher in offshore than inshore sites (ANOVA: $F_{1,2} = 3694$, $P < 0.001$; $F_{1,2} = 63$, $P = 0.015$, respectively) (Figures 3.2 a.2-d.2). We noted interactions between protection-duration and site location on the mean species richness of body size groups (except for large-bodied species), which showed that older marine reserves had greater species richness than younger reserves and fished sites in inshore sites, but not in offshore sites (Figures 3.2 a.3-d.3). There were no clear differences in the rates of change in species richness of the four body size groups with protection-duration, although ANOVA detected significant differences for large-bodied species (ANOVA: $F_{2,2} = 23$, $P = 0.04$) (Figures 3.3 a.1-d.1). The rates of increase in species richness of large-bodied species (but not the other body size groups) were significantly higher in offshore than inshore sites (ANOVA: $F_{1,2} = 978$, $P = 0.01$) (Figures 3.3 a.2-d.2). We noted interactions between protection-duration and site location for the rates of increase in species richness of extra large, large, and medium-bodied groups (but not small-bodied species), which suggested that older marine reserves had higher rates on increase in species richness than younger marine reserves and fished sites in inshore sites, but not in offshore sites (Figure 3.3 a.3-d.3).

Trophic groups

All four trophic groups (see Chapter 2 for species categorization into trophic groups) showed an increasing trend in total biomass with protection-duration, but none of these were statistically significant (Figures 3.4 a.1-d.1). Similarly, ANOVA did not detect a significant difference in total biomass of the four trophic groups in inshore and offshore sites (Figures 3.4 a.2-d.2). There was no interaction between protection duration and site location for the magnitudes of biomass of the four trophic groups, which suggested that older marine reserves had higher biomass than younger marine reserve and fished sites in both inshore and offshore sites. The rates of increase in biomass of herbivores, zooplanktivores, and piscivores (but not zoobenthivores) suggested increasing trends with protection-duration, although ANOVA did not detect these as significant (Figures 3.5 a.1-d.1). ANOVA also did not detect any significant differences in the rates of changes in biomass of the four trophic groups in inshore and offshore sites (Figures 3.5 a.2-d.2). We noted interactions between protection-duration and site location for the rates of increase of the trophic groups (except for zooplanktivores), which suggested that older reserves had higher rates of increase than younger marine reserves and fished sites in inshore sites, but not in offshore sites (Figure 3.5 a.3-d.3).

There was no significant difference in the total abundance of the four trophic groups with protection-duration (Figures 3.4 a.1-d.1). However, all the four trophic groups showed higher abundance in offshore sites than inshore sites and significantly so for zoobenthivores and zooplanktivores (ANOVA: $F_{1,2} = 466$, $P = 0.002$; $F_{1,2} = 27$, $P = 0.03$, respectively) (Figures 3.4 a.2-d.2). We noted interactions between protection-duration and site location for the magnitudes of abundance of the trophic groups (except for herbivores), which indicated that older marine reserves showed higher abundance than younger marine reserves and fished sites in inshore sites, but not in offshore sites (Figures 3.4 a.3-d.3). ANOVA also did not detect a significant influence of protection-duration on the rates of changes in total abundance of the four trophic groups across the study sites (Figures 3.5 a.1-d.1). However, the rates of increase in the abundance of zoobenthivores and zooplanktivores (but not of herbivores and piscivores) over time were higher in offshore sites than inshore sites (ANOVA: $F_{1,2} = 82$, $P = 0.01$; $F_{1,2} = 27$, $P = 0.03$, respectively) (Figures 3.5 a.2-d.2). We noted interactions between protection-duration and site location for the rates of increase in abundance of trophic groups, which indicated that older marine reserves had higher or equal rates of increase in abundance than younger marine reserves and fished sites in inshore sites, but not in offshore sites (Figures 3.5 a.3-d.3).

ANOVA detected a significantly higher species richness of herbivores and piscivores (but not zoobenthivores and zooplanktivores) in older marine reserves relative to younger marine reserves and fished sites (ANOVA: $F_{2,2} = 47$, $P = 0.02$; $F_{2,2} = 21$, $P = 0.04$, respectively) (Figures 3.4 a.1-d.1). In addition, all herbivores, zoobenthivores, zooplanktivores, and piscivores showed higher species richness in offshore than inshore sites (ANOVA: $F_{1,2} = 213$, $P = 0.005$; $F_{1,2} = 136$, $P = 0.007$, $F_{1,2} = 65$, $P = 0.015$, $F_{1,2} = 172$, $P = 0.006$, respectively) (Figures 3.4 a.2-d.2). We noted interactions between protection-duration and site location for the magnitudes of species richness of trophic groups (except zooplanktivores), which suggested that older marine reserves had higher species richness than younger marine reserves and fished sites in inshore sites, but not in offshore sites (Figures 3.4 a.3-d.3). There was no significant influence of protection-duration on the rates of changes in species richness of the four trophic groups across the study sites (Figures 3.5 a.1-d.1). However, all four trophic groups showed higher rates of increase in species richness in offshore sites than inshore sites and significantly so for herbivores (ANOVA: $F_{1,2} = 71$, $P = 0.01$) (Figures 3.5 a.2-d.2). We noted interactions between protection-duration and site location for the rates of increase in species richness of the trophic groups (except for zooplanktivores), which hinted that older marine reserves had higher rates of increase in species richness than younger marine reserves and fished sites in inshore sites, but not in offshore sites (Figures 3.5 a.3-d.3).

Discussion

The influence of protection-duration on fish communities

Marine reserves are generally observed to increase biomass, abundance and species richness relative to reference sites and to do so in relatively short periods of time (Halpern and Warner 2002), although there remains a great deal of variability with respect to specific trophic groups and locations (Côté et al. 2001, McClanahan and Graham 2005). Our results did not totally agree with the patterns suggested by meta-analyses, especially in terms of abundance and species richness, and support the observations of variable responses. Total biomass trended upwards with protection-duration while total abundance and species richness were relatively insensitive to protection-duration. When size classes and trophic groups were considered, responses were highly variable. Potential, but untested explanations for this relatively weak response to protection may reflect the general high level of habitat degradation in Danajon Bank (although our sites had similar live habitat cover) (Marcus *et al.* 2007), high rates of exploitation that existed prior to marine reserve establishment (Vincent et al. 2007), variable levels of enforcement (Samoilys et al. 2007), high rates of fishing on the reserve boundaries (Samoilys et al. 2007, Yasue et al. in prep.), the relatively small size of the marine reserves, and their relative 'youth'.

A key issue in considering recovery within marine reserves in the Philippines is the absolute magnitude of recovery given the role of marine reserves in rehabilitating fisheries and food security. The biomass increase (42% for the younger marine reserves and 300% for the older marine reserves relative to the fished sites – average of 171%) observed in this study is comparable to that reported for other marine reserves (192% average biomass increase relative to reference sites) (Halpern and Warner 2002). However, the absolute level of biomass supported by the younger (1-3 years old) and older (6-10 years old) marine reserves is approximately 28 $g \cdot m^{-2}$ and 68 $g \cdot m^{-2}$ respectively. These results are on average less than half of the 120 $g \cdot m^{-2}$ biomass estimates from marine reserves in Kenya observed following 37 years of protection (McClanahan et al. 2007). Like the departure of these reserves from general patterns, the relatively low levels of biomass observed in the study sites may again reflect the small size of these marine reserves, the high level of previous exploitation, or perhaps the relatively recent establishment of these marine reserves in comparison to the Kenyan ones. Combined, these results demonstrate that while proportional changes may be both significant and similar to those generally observed in other areas, the increases in the absolute levels of biomass may require longer periods, particularly with respect to marine reserves that started in highly depleted conditions such as observed on Danajon Bank (Russ and Alcala 2004, McClanahan et al. 2007).

Recovery with respect to increased biomass within marine reserves may result from immigration as well as growth of individuals within the marine reserves (Holland and Brazee 1996, Kramer and Chapman 1999, Jennings 2001). Recovery rates are typically inferred by comparing snapshot data from marine reserves of different ages (Côté et al. 2001, Halpern and Warner 2002, McClanahan and Graham 2005) or through sequential seasonal or annual sampling of a given marine reserve (Russ and Alcala 2004, Williamson et al. 2004). Such comparisons may make it difficult to observe how fish communities respond over finer temporal scales. Although not significant, there was some suggestion that the mean rate of biomass accumulation was higher in older marine reserves as compared to younger marine reserves and fished sites. Additionally, although not statistically significant, there was also some indication of increasing abundance of large and extra large-bodied species with protection-duration even though there was no evidence of increase in abundance of any of the four trophic groups with protection-duration. Combined, these results suggest that the observed increases in total biomass and biomass of some body size groups with protection-duration were driven by the larger body size of individual fish in older marine reserves rather than greater numbers of those fish. Such observations suggest that recovery in younger reserves is primarily a function of immigration while older reserves reflect both immigration and growth of individuals (Polunin and Roberts 1993, Kramer and Chapman 1999, Jennings 2001).

Previous marine reserve studies in both tropical and temperate systems demonstrated that only those species and size classes that were targeted by fishing showed significant increase in biomass or abundance (Edgar and Barrett 1999, Côté et al. 2001, Micheli et al. 2004). Additionally, species recovery varied due to differential impacts of exploitation preference as a function of life history group (Jennings et al. 1999). Our results showed that biomass responses for size and trophic groups were variable and a function of life history and not simply a response to previous fishing exploitation. Specifically, in the reserves that we studied, protection-duration resulted in a significant increase in biomass and rate of increase for large-bodied species only. In addition, though not significant, an upward trend was also observed in the absolute biomass of the extra large-bodied species category, which are highly favoured by fishers, suggesting that this group responded positively to protection-duration, but they did so more slowly than the large-bodied species. However, the recovery in the biomass of large species corresponded only with the significant recovery of the biomass of herbivores, many of which are large-bodied (Hoegh-Guldberg 2006). This suggests that similar sized piscivores, although previously highly targeted by fisheries, have difficulty recovering in marine reserves as compared to herbivores, presumably due to their inherent life history characteristics.

Further evidence of influences of life-history traits on the response to marine reserves were provided by the medium-bodied species, for which no effect of protection-duration on biomass was observed, despite the fact that many of these were targeted by subsistence fishers on Danajon Bank (personal observation). This result is consistent with other studies indicating that medium-bodied species are more resilient to fishing pressure because of their faster life histories and their ability to maintain biomass in fished sites similar to that in protected areas (Côté et al. 2001, Micheli et al. 2004). Alternatively, the medium-bodied and small-bodied species in the older marine reserves may be negatively impacted by recovering larger species (Shears and Babcock 2002, Langlois et al. 2006). However, there was no evidence of negative effects of recovering large species, which are mainly herbivores, on the absolute magnitudes and rates of change in the biomass of medium and small-bodied species that was observed. Thus, as with other studies (Graham et al. 2003, Willis and Anderson 2003, Micheli et al. 2004), our study supports the position that community responses to marine reserves will likely vary according to community composition.

That absolute species richness was similar across sites indicates that species richness is perhaps a relatively insensitive index to changes in fish community with protection-duration, at least at the scale of protection-duration and size of marine reserves observed here. There is some suggestion that a more rapid increase in species richness occurred in the younger marine reserves relative to the older marine reserves and fished sites. This trend may reflect a process by which there is a relative burst of recovery with respect to species richness in the first few years of protection-duration that may slow-down as marine reserves get older and the pool of available "new" species declines (Halpern and Warner 2002, McClanahan et al. 2007).

The influence of location on fish communities

Empirical studies at regional scales indicate strong effects of spatial heterogeneity on community recovery across marine reserves (Benedetti-Cecchi et al. 2003). In addition, predictions of spatial heterogeneity or natural inequality of community distribution across various ecosystems are prevalent (Hastings 1990, Stewart et al. 1999). Our study revealed strong effects of spatial heterogeneity on abundance and species richness, but not on biomass. The lack of difference in total fish biomass between inshore and offshore sites was surprising as the offshore sites generally have much larger and better developed reef zones than the inshore sites, and therefore can be expected to have higher carrying capacities than the inshore sites in terms of biomass and abundance or on a per m^2 basis (Thresher 1991, Sorokin 1993). This lack of difference in biomass between the inshore and offshore sites is perhaps a reflection of the severe depletion in these sites prior to protection and the slow recovery of species that were previously heavily targeted by fisheries across all the study sites.

Total fish abundance consistently showed significantly higher magnitudes and rates of increase in the offshore sites compared to the inshore sites. Combined with the lack of difference in biomass, this means that offshore site assemblages were composed of smaller individuals than the assemblages associated with the inshore sites. Indeed, when total fish biomass and abundance were partitioned amongst body size classes, it was clear that medium and small-bodied species drove the higher biomass and abundance values observed in the offshore sites as opposed to the inshore sites. In fact, the rates of increase in abundance of smaller fish species were also significantly higher in the offshore than in the inshore sites.

Species richness was also significantly greater in the offshore sites as compared to the inshore sites, and this result was consistent across most size classes and trophic groups. This pattern may, again, be a function of the greater reef development in the offshore areas that thus provide a greater "pool" of species for accumulation within the offshore marine reserves (Birkeland 1988, Sorokin 1993, Birkeland 1997). The development of larger reef areas in the offshore sites is partly determined by the clarity of water as these are distant from river mouths and other sources of sedimentation (Pichon 1977), and reef development in general is limited by availability of light (Veron 1986). Thus, further recovery of fish assemblages across these study sites, particularly in terms of species richness, will likely vary depending on site location on a regional scale. Alternatively, it is tempting to think that distance from mainland may equate to lower human pressure and could potentially explain the inshore-offshore gradients in fish species richness and abundance. However, the offshore sites actually had higher populations of fishers than inshore sites, and they were also further from police patrol bases, which were mainly stationed in the municipality in the mainland of Bohol (see Chapter 2: Table 2.2; Figure 2.1). Both factors mean that they tended to have experienced high levels of illegal fishing activities such as dynamite fishing and trawling prior to their enforcement as marine reserves (Marcus et al. 2007, Samoilys et al. 2007).

Interactions between the effects of protection-duration and site location

In general, total biomass and biomass of most body size and trophic groups did not show interactions between protection-duration and site location, which suggested that magnitudes (but not rates of increase) of fish biomass were higher in the older marine reserves than the younger marine reserves and fished sites in both the inshore and offshore sites. This further supported our conclusion that the main effect of marine reserves lay in allowing both the growth and immigration of large-bodied species and individuals, thus boosting the total biomass consistently, regardless of site location. In contrast, in terms of total abundance and species richness of most body size and trophic groups, there were interactions between protection-duration and site location, which suggested that the older marine reserves showed higher magnitudes and rates of increase than the younger marine reserves and fished sites in the inshore sites, but not in the offshore sites. Such results further supported our conclusion that the effects of marine reserve on both abundance and species richness were site-specific and that local processes in our offshore sites favoured higher carrying capacity and species diversity than the inshore sites.

Implications for conservation and management

Overall, this study demonstrated a number of patterns that are important in clarifying current expectations of community recovery within marine reserves as well as improving criteria for the design of networks of marine reserves. If the goal of marine reserve establishment is to recover biomass of previously depleted large-bodied species, then perhaps a relatively wide range of sites can facilitate recovery. Our results showed that the main function of marine reserves is to allow large-bodied fish species to settle and grow undisturbed within marine reserve boundaries. However, if the main objective of setting marine reserves is to enhance and maintain species richness, then careful consideration of the spatially heterogeneous patterns and processes of diversity distribution across a certain region is necessary. Our study showed that the offshore sites contained more species diversity than inshore sites regardless of protection-duration. Thus, protecting the offshore sites is important in enhancing and maintaining regional diversity (but see Chapter 4 for the analyses of the effects of marine reserves on the quantity and quality of reef fish diversity).

Variable recovery patterns of different life-history groups should be taken into account in the management of associated multi-species fisheries. This study demonstrated that piscivores showed slower recovery than herbivores within these marine reserves, and would require a much longer time-frame or larger area to recover than the 10 years to date, or the 5 to 50 ha of the present marine reserves. Where fisheries target extra-large and large-bodied piscivores, the exploitation of these groups must be carefully regulated if the species are to be subjected to future sustainable exploitation (Dulvy et al. 2003). In contrast, the fact that the herbivores showed much higher recovery capacity than the piscivores indicates that these groups can perhaps endure relatively higher exploitation pressure than the piscivores, and is consistent with previous studies (Jennings et al. 1999).

Although statistically significant recovery in terms of total fish biomass and biomass of large-bodied fish and herbivores was observed, the actual magnitudes and rates of recovery appeared to be low, particularly given the requirements for food and income of the rapidly growing human population surrounding the study sites. These results suggest that small marine reserves that are less than ten years old likely make little contribution to the actual food and income security of fishers surrounding the marine reserve boundaries, although we recognise that the change in catch rates around the marine reserves remains unknown. Interestingly, fishers tend to perceive higher benefits from marine reserves than the measured recovery, which suggest that stability of catch rates, though in small quantity, may be an important fisheries benefit of marine reserves from the perspective of the fishers (Russ et al. 2004, Yasue et al. in prep.). Further research is needed to clarify (1) how much marine reserve area is required to meet the food and income needs of people surrounding the marine reserves, (2) how much time is needed to recover various reef fish taxa, and (3) which taxa can recover depending on marine reserve size. Ongoing assessment of the changes in biomass and abundance of various life history groups as our study sites continue to recover should also provide valuable insights into the differential effects of spatial heterogeneity on the recovery of biomass of various life history groups (Benedetti-Cecchi et al. 2003, Micheli et al. 2004). Overall, such information can help ensure that fishers have a clear understanding of what productivity they can expect from marine reserves and marine systems, and may thus help to focus management.

This study provided a comprehensive analysis of community recovery within marine reserves based on 423 species and monthly sampling over three years within and across eight study sites of various protection-duration and location relative to the mainland. The focus has been on presenting and discussing the differential recovery observed in terms of the overall assemblage, body size groups, and trophic groups, and on interpreting the observed patterns both in statistical and ecological terms. While the limitations of our design must be acknowledged – the lack of replication across locations and with respect to fished and protected sites may have biased the results and likely reduced the power to detect effects – controlled experimental design may be an exception rather than a rule in the case of marine reserves, especially given that current establishment is still mainly based on socio-economic needs rather than scientific knowledge (Guidetti 2002, Russ 2002, Ban et al. in prep., Hansen et al. in prep.). Our study demonstrated differential recovery patterns in fish communities within and across marine reserves. As such, it provides the foundation for further exploration of the ecological processes of community recovery within and across marine reserves. In this way, marine reserves serve us well as a tool to recover degraded marine systems, but also help advance our ecological understanding of marine community dynamics.

Figures

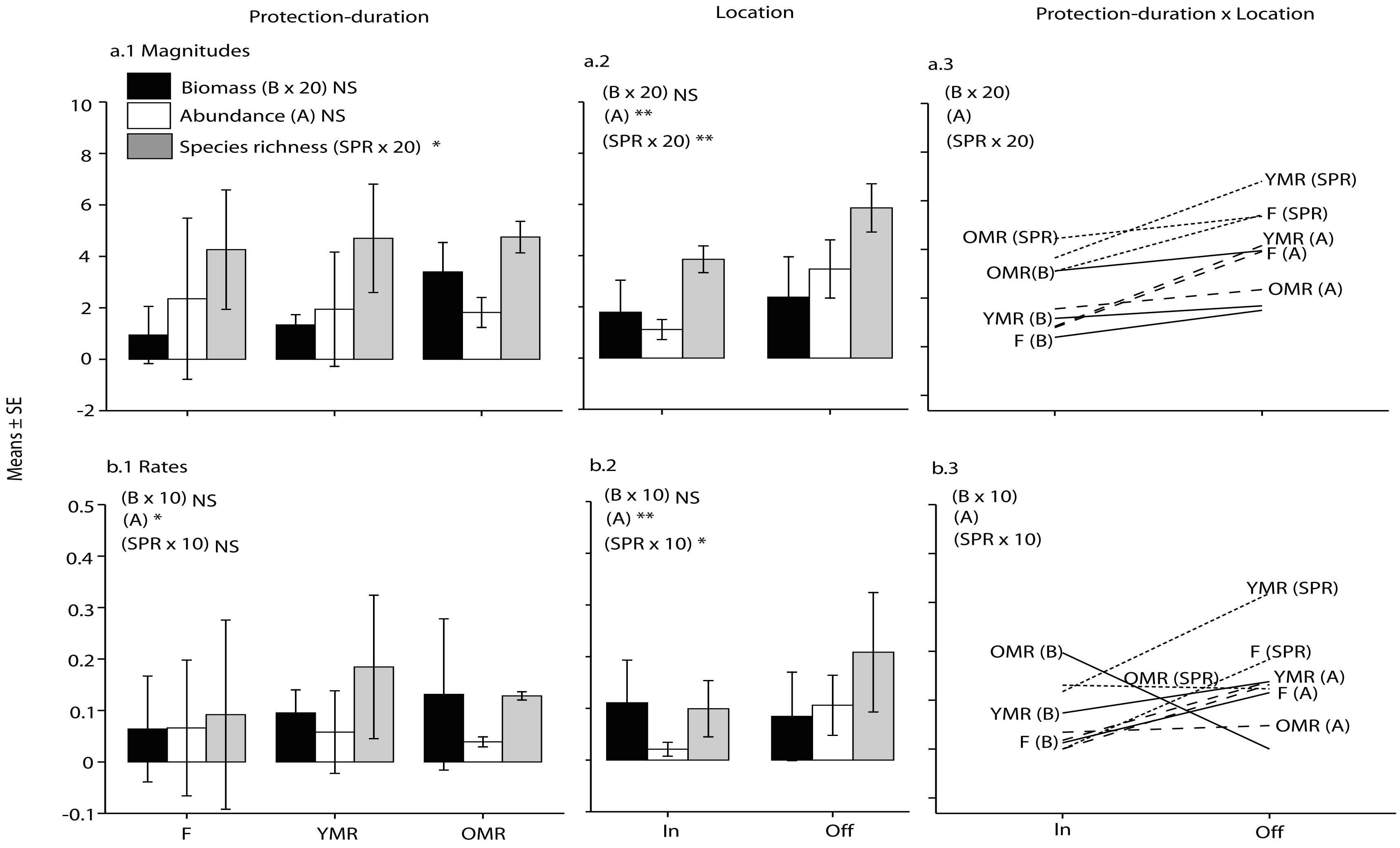

Protection-duration
Location
Protection-duration x Location
a.1 Magnitudes
Biomass (B x 20) NS
Abundance (A) NS
Species richness (SPR x 20) *
a.2
(B x 20) NS
(A) **
(SPR x 20) **
a.3
(B x 20)
(A)
(SPR x 20)
YMR (SPR)
F (SPR)
OMR (SPR)
YMR (A)
F (A)
OMR(B)
OMR (A)
YMR (B)
F (B)
10
8
6
4
2
0
-2
Means ± SE
b.1 Rates
(B x 10) NS
(A) *
(SPR x 10) NS
b.2
(B x 10) NS
(A) **
(SPR x 10) *
b.3
(B x 10)
(A)
(SPR x 10)
YMR (SPR)
OMR (B)
F (SPR)
OMR (SPR)
YMR (A)
F (A)
YMR (B)
OMR (A)
F (B)
0.5
0.4
0.3
0.2
0.1
0
-0.1
F
YMR
OMR
In
Off
In
Off

Figure 3.1 ANOVA on (a) the magnitudes of mean monthly values (± SE) and (b) the rates of change within sites of the three fish assemblage metrics: (1) total biomass ($g \cdot m^{-2}$), (2) total abundance (m^{-2}), and (3) total species richness. The magnitudes analyse were based on the third year samples from each site. The rates of change analyses were based on regression slopes of all mean monthly values of the fish assemblage metrics over the three-years sampling period. For comparison purposes, the actual values were re-scaled using multipliers as presented beside the legends for each metric tested. The two factors tested were protection-duration (F=fished sites, YMR = younger marine reserves/3-years old, and OMR = older marine reserves/6-10 years old) and site location (In = inshore and Off = offshore sites). The interaction patterns between protection-duration and site location are presented, but not tested (see Chapter 2). Also presented are the *P*-value symbols (* = 0.05, ** = 0.01, * <0.0001, NS = non-significant).**

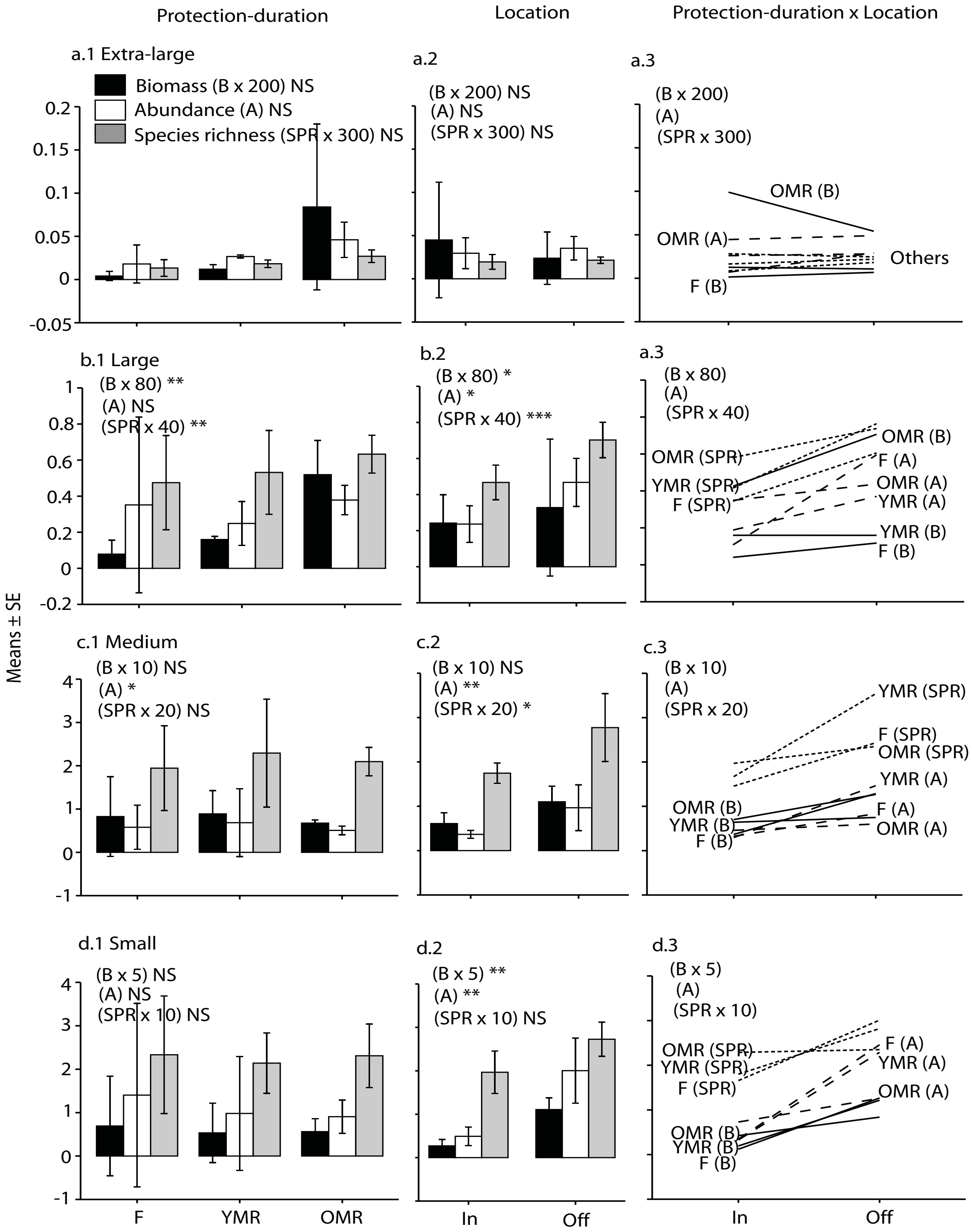


Figure 3.2 ANOVA on the magnitudes of mean monthly values m^{-2} of the four fish body size classes (a-d) and the three metrics: (1) total biomass ($g \cdot m^{-2}$), (2) total abundance (m^{-2}), and (3) total species richness. Magnitudes calculation $month^{-1}$ $site^{-1}$ was the same as Figure 3.1. Data presentation, treatments (e.g. re-scaling), factors tested, and ANOVA outputs presented were the same as Figure 3.1.

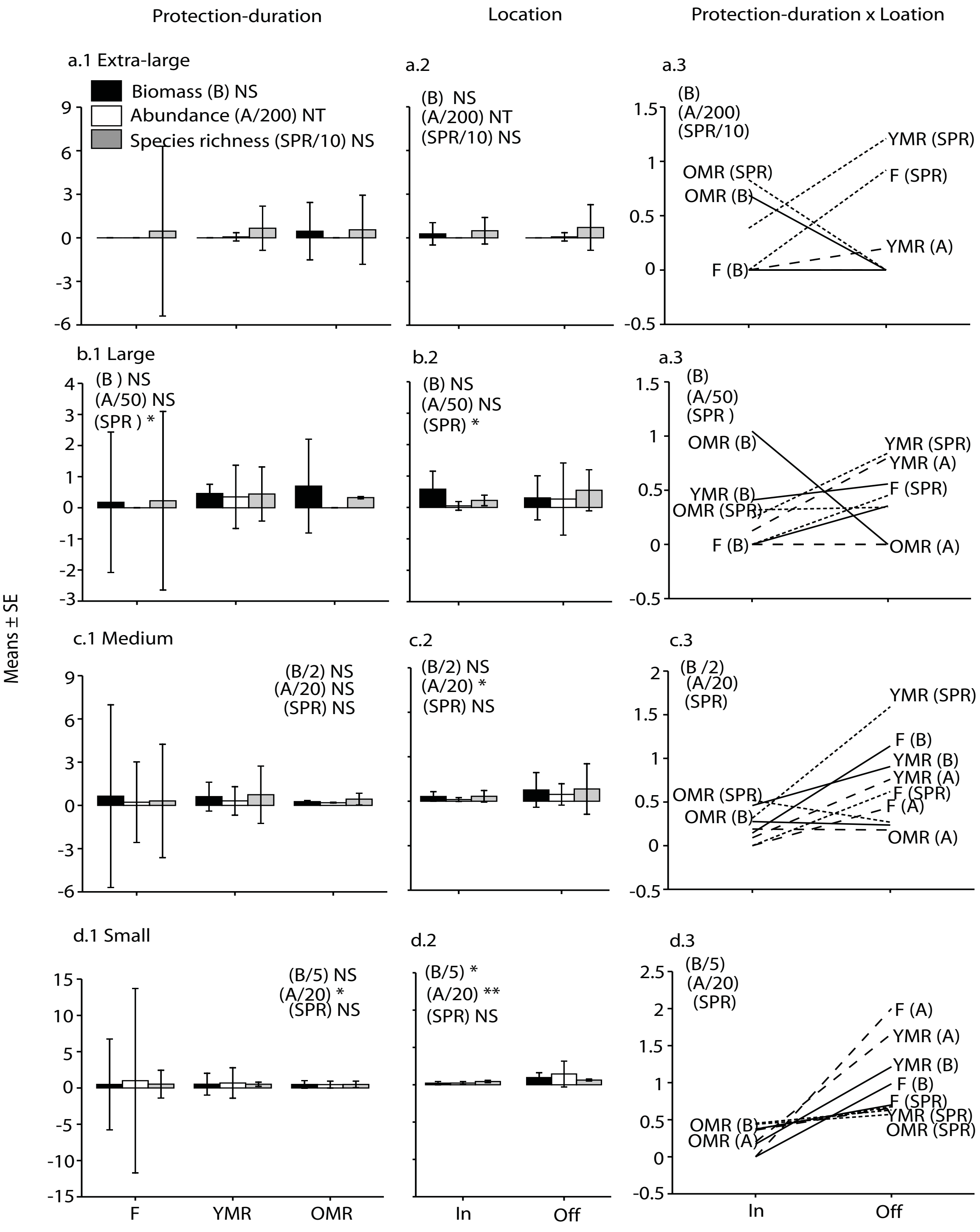


Figure 3.3 ANOVA on the regression slope values or the rates of change of the four fish body size classes (a-d) and the three metrics within study sites: (1) total biomass (g · m^{-2}), (2) total abundance (m^{-2}), and (3) total species richness. Calculation of the rates of change of the four body size classes and the three metrics within study sites was the same as Figure 3.1. Data presentation, treatments (e.g. re-scaling), factors tested, and ANOVA outputs presented were the same as Figure 3.1. NT = not tested/not enough data for ANOVA test.

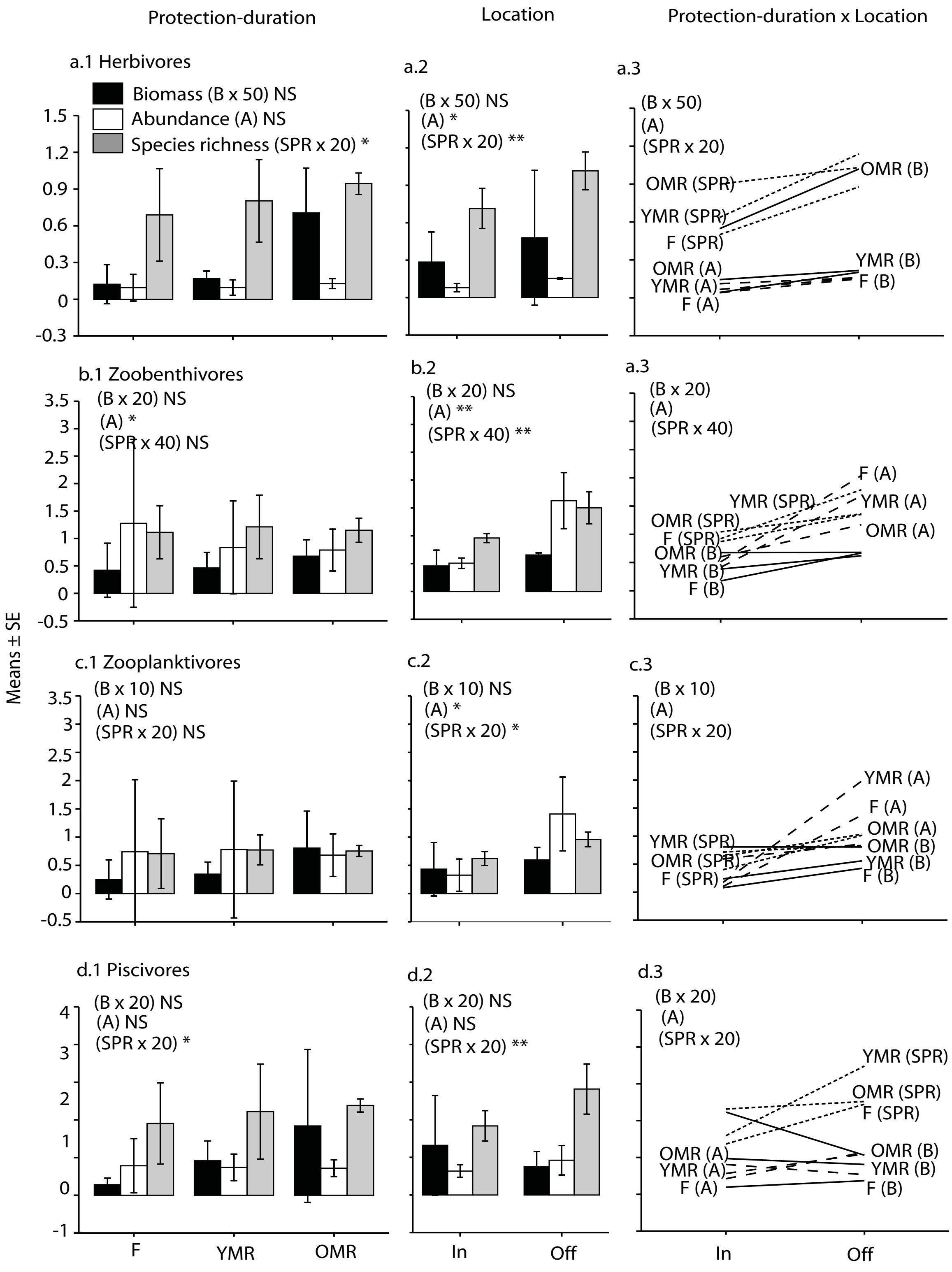


Figure 3.4 ANOVA on the magnitudes of mean monthly values of the four fish trophic groups (a-d) and the three metrics: (1) total biomass (g · m^{-2}), (2) total abundance (m^{-2}), and (3) total species richness. Magnitudes calculation month^{-1} site^{-1} was the same as Figure 3.1. Data presentation, treatments (e.g. re-scaling), factors tested, and ANOVA outputs presented were the same as Figure 3.1.

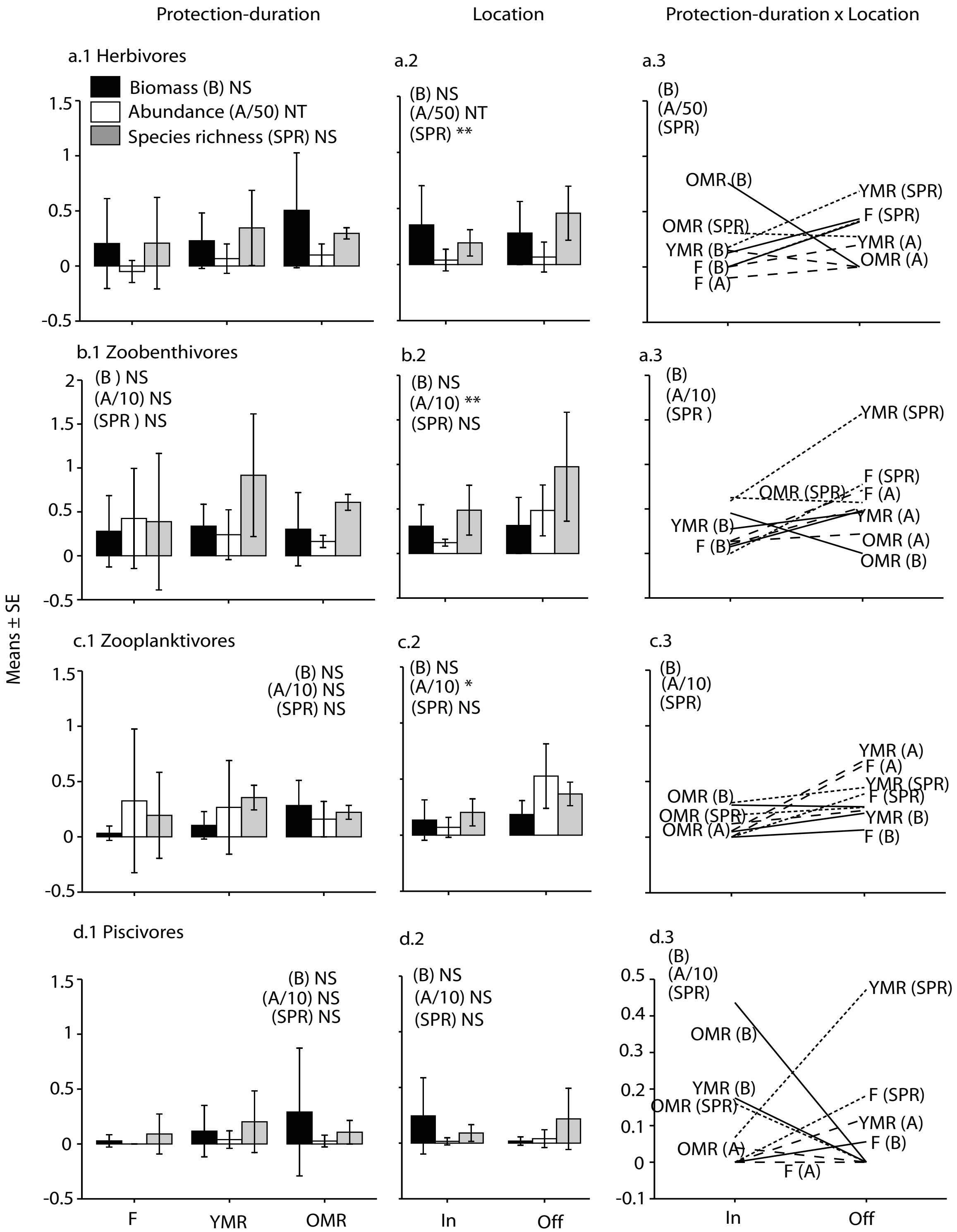


Figure 3.5 ANOVA on the regression slope values or the rates of change of the four fish trophic groups (a-d) and the three metrics within study sites: (1) total biomass (g · m^{-2}), (2) total abundance (m^{-2}), and (3) total species richness. Calculation of the rates of change of the four trophic groups and the three metrics within study sites was the same as Figure 3.1. Data presentation, treatments (e.g. re-scaling), factors tested, and ANOVA outputs presented were the same as Figure 3.1.

References

Ban, N. C., G. J. A. Hansen, M. Jones, and A. C. J. Vincent. in prep. Systematic marine conservation planning in data-poor regions: socio-economic data is essential.

Benedetti-Cecchi, L., I. Bertocci, F. Micheli, E. Maggi, E. Fosella, and S. Vaselli. 2003. Implications of spatial heterogeneity for management of marine protected areas (MPAs): examples from assemblages of rocky coasts in the northwest Mediterranean. Marine Environmental Research **55**:429-458.

Birkeland, C. 1988. Geographic comparisons of coral-reef community processes. Pages 211-219 *in* Proceedings of the Sixth International Coral Reef Symposium, Australia.

Birkeland, C. 1997. Geographic differences in ecological processes on coral reefs. Pages 273-287 *in* C. Birkeland, editor. Life and Death of Coral Reefs. Chapman & Hall, New York.

Côté, I. M., I. Mosquera, and J. D. Reynolds. 2001. Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis. Journal of Fish Biology **59**:178-189.

Dulvy, N. K., Y. Sadovy, and C. S. Reynolds. 2003. Extinction vulnerability in marine populations. Fish and Fisheries **4**:25-64.

Edgar, G. J., and N. S. Barrett. 1999. Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. Journal of Experimental Marine Biology and Ecology **242**:107-144.

Graham, N. A. J., R. D. Evans, and G. R. Russ. 2003. The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. Environmental Conservation **30**:200-208.

Guidetti, P. 2002. The importance of experimental design in detecting the effects of protection measures on fish in Mediterranean MPAs. Aquatic Conservation: Marine and Freshwater Ecosystems **12**:619-634.

Halpern, B. S. 2003. The impact of marine reserves: do reserves work and does reserve size matter? Ecological Applications **13**:S117-S137.

Halpern, B. S., and R. R. Warner. 2002. Marine reserves have rapid and lasting effects. Ecology Letters **5**:361-366.

Hansen, G. J., N. Ban, M. L. Jones, L. Kaufman, H. Panes, M. Yasue, and A. C. J. Vincent. in prep. Hindsight in marine protected area designation and planning: a comparison of community-driven and systematic approaches in Danajon Bank, Philippines.

Hastings, A. 1990. Spatial heterogeneity and ecological models. Ecology **71**:426-428.

Hodgson, G., J. C. Ogden, and T. P. Hughes. 1994. Coral reef catastrophe. Science **266**:1930-1933.

Hoegh-Guldberg, O. 2006. Complexities of coral reef recovery. Science **311**:42-43.

Holland, D. S., and R. J. Brazee. 1996. Marine reserves for fisheries management. Marine Resource Economics **11**:157-172.

Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science **265**:1547-1551.

Hutchings, J. A. 2000. Collapse and recovery of marine fishes. Nature **406**:882-885.

Jennings, S. 2001. Patterns and prediction of population recovery in marine reserves. Reviews in Fish Biology and Fisheries **10**:209-231.

Jennings, S., J. D. Reynolds, and N. V. C. Polunin. 1999. Predicting the vulnerability of tropical reef fishes to exploitation with phylogenies and life histories. Conservation Biology **13**:1466-1475.

Kramer, D. L., and M. R. Chapman. 1999. Implications of fish home range size and relocation for marine reserve function. Environmental Biology of Fishes **55**:65-79.

Langlois, T. J., M. J. Anderson, R. C. Babcock, and S. Kato. 2006. Marine reserves demonstrate trophic interactions across habitats. Oecologia **147**:134-140.

Lubchenco, J., S. R. Palumbi, S. D. Gaines, and S. Andelman. 2003. Plugging a hole in the ocean: the emerging science of marine reserves. Ecological Applications **13**:S3-S7.

Marcus, J. E., M. A. Samoilys, J. J. Meeuwig, Z. A. D. Villongco, and A. C. J. Vincent. 2007. Benthic status of near-shore fishing grounds in the central Philippines and associated seahorse densities. Marine Pollution Bulletin **54**:1483-1494.

McClanahan, T. R., and N. A. J. Graham. 2005. Recovery trajectories of coral reef fish assemblages within Kenyan marine protected areas. Marine Ecology Progress Series **294**:241-248.

McClanahan, T. R., N. A. J. Graham, J. M. Calnan, and M. A. MacNeil. 2007. Towards pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. Ecological Applications **17**:1055-1067.

Micheli, F., B. S. Halpern, L. W. Botsford, and R. R. Warner. 2004. Trajectories and correlates of community change in no-take marine reserves. Ecological Applications **14**:1709-1723.

Moberg, F., and C. Folke. 1999. Ecological goods and services of coral reef ecosystems. Ecological Economics **29**:215-233.

Pauly, D., R. Watson, and J. Alder. 2005. Global trends in world fisheries: impacts on marine ecosystems and food security. Philosophical Transactions of the Royal Society B **360**:5-12.

Pichon, M. 1977. Physiography, morphology, and ecology of the double barrier reef of North Bohol (Philippines). Pages 261-267 *in* Proceedings of the Third International Coral Reef Symposium, Miami, Florida.

Polunin, N., and C. Roberts. 1993. Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. Marine Ecology Progress Series **100**:167-176.

Roberts, C. M., and N. V. C. Polunin. 1991. Are marine reserves effective in management of reef fisheries? Reviews in Fish Biology and Fisheries **1**:65-91.

Russ, G. R. 2002. Yet another review of marine reserves as reef fishery management tools. *in* P. F. Sale, editor. Coral Reef Fishes Dynamics and Diversity in a Complex Ecosystem. Academic Press, San Diego, California.

Russ, G. R., and A. C. Alcala. 2004. Marine reserves: long-term protection is required for full recovery of predatory fish populations. Oecologia **138**:622-627.

Russ, G. R., A. C. Alcala, A. P. Maypa, H. P. Calumpong, and A. T. White. 2004. Marine reserve benefits local fisheries. Ecological Applications **14**:597-606.

Russ, G. R., B. Stockwell, and A. C. Alcala. 2005. Inferring versus measuring rates of recovery in no-take marine reserves. Marine Ecology Progress Series **292**:1-12.

Sale, P. F., R. K. Cowen, B. S. Danilowics, G. P. Jones, J. P. Kritzer, K. C. Lindeman, S. Planes, N. V. C. Polunin, G. R. Russ, Y. J. Sadovy, and R. S. Steneck. 2005. Critical science gaps impede use of no-take fishery reserves. Trends in Ecology and Evolution **20**:74-80.

Samoilys, M. A., K. M. Martin-Smith, B. G. Giles, B. Cabrera, J. A. Anticamara, E. O. Brunio, and A. C. J. Vincent. 2007. Effectiveness of five small Philippines' coral reef reserves for fish populations depends on site-specific factors, particularly enforcement history. Biological Conservation **136**:584-601.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. H. Walker. 2001. Catastrophic shifts in ecosystems. Nature **413**:591-596.

Shears, N. T., and R. C. Babcock. 2002. Marine reserves demonstrate top-down control of community structure on temperate reefs. Oecologia **132**:131-142.

Sorokin, Y. 1993. Coral reef ecology. Springer Verlag, Berlin Heidelberg.

Stewart, A. J. A., A. E. John, and M. J. Hutchings. 1999. The world is heterogeneous: ecological consequences of living in a patchy environment. Pages 1-8 *in* M. J. Hutchings, E. A. John, and A. J. A. Stewart, editors. The 40th symposium of the British Ecological Society. Blackwell Science, University of Sussex.

Symstad, A. J., and D. Tilman. 2001. Diversity loss, recruitment limitation, and ecosystem functioning: lessons learned from a removal experiment. Oikos **92**:424-435.

Thresher, R. E. 1991. Geographic variability in the ecology of coral reef fishes: evidence, evolution and possible implications. Pages 401-435 *in* P. F. Sale, editor. The ecology of fishes on coral reefs. Academic Press, Inc., London.

Veron, J. E. N. 1986. Corals of Australia and the Indo-pacific. Angus and Robertson Publishers, Australia.

Vincent, A. C. J., J. J. Meeuwig, M. G. Pajaro, and N. C. Perante. 2007. Characterizing a small-scale, data-poor, artisanal fishery: seahorses in the central Philippines. Fisheries Research **86**:207-215.

Walters, C. J., D. Pauly, and V. Christensen. 1999. Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. Ecosystems **2**:539-554.

Williamson, D. H., G. R. Russ, and A. M. Ayling. 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.

Willis, T. J., and M. J. Anderson. 2003. Structure of cryptic reef fish assemblages: relationships with habitat characteristics and predator density. Marine Ecology Progress Series **257**:209-221.

Yasue, M., L. Kaufman, and A. C. J. Vincent. in prep. Assessing ecological changes in and around marine reserves using community perceptions and biological surveys.

4. Quantity versus quality: spatio-temporal variation in reef fish diversity within no-take marine reserves[*]

---

[*] A version of this chapter will be submitted for publication. Anticamara, J.A., D. Zeller, and A.C.J. Vincent. Quantity versus quality: spatio-temporal variation in reef fish diversity within no-take marine reserves.

Introduction

Understanding spatio-temporal variation in diversity is important for developing effective biodiversity conservation strategies (Roberts and Gilliam 1995). For example, knowledge of spatio-temporal variations has led to the identification of diversity engines, centres, or sources (Moritz 2002, Briggs 2005, Carpenter and Springer 2005). Understanding the spatio-temporal distributions of threats to diversity is equally important for prioritizing diversity conservation efforts (Jackson 1997, McClanahan 2002, Brooks et al. 2006). Moreover, assessing the effectiveness of different strategies is necessary for diversity conservation to progress and achieve its goals (Kremen et al. 1998, Stem et al. 2005, Ferraro and Pattanayak 2006).

Advances in diversity research have produced knowledge that can aid diversity conservation efforts and assess their impacts. Importantly, diversity is strongly scale-dependent (Roberts and Gilliam 1995, He et al. 1996). At a global scale, studies suggest that the higher diversity observed in tropical regions is primarily related to warmer temperature, which enhanced organisms' metabolic rates and consequently accelerated genetic divergence and speciation (Allen and Gillooly 2006, Allen et al. 2006, Briggs 2007). On a regional scale, diversity research often focuses on processes such as dispersal and speciation, which is related to local diversity processes such as species interactions, adaptation, and local extinction (Ricklefs 1987, Cornell and Lawton 1992, Caley and Schluter 1997).

The variety of conceptualizations of diversity patterns and processes that have emerged are mirrored by a proliferation of metrics and indices to quantify diversity over the last 50+ years (MacArthur 1955, McIntosh 1967, Zahl 1977, Kempton 1979, Keylock 2005). Careful evaluation and selection from the plethora of diversity metrics that are currently available is generally advocated (Hurlbert 1971, Alatalo 1981, Gotelli and Colwell 2001, Sounding 2003). For simplicity, we can assign species diversity metrics to the following categories:

1) Measures of species accumulation sampled across space or over time (Willott 2001, Thompson and Withers 2003, Colwell et al. 2004);
2) Measures of richness, diversity, and evenness (McIntosh 1967, Zahl 1977, Kempton 1979); and
3) Measures of dominance in terms of species Abundance-Biomass Comparison (ABC) curves (Meire and Dereu 1990, Warwick and Clarke 1994, Clarke and Gorley 2006).

Although there has been debate on the problems associated with many diversity measures and the difficulty of their interpretation (Hurlbert 1971, Alatalo 1981), these remain the most common metrics to quantify diversity or assess community stability and spatial heterogeneity (Hill 1973, Clarke and Warwick 2001).

Coral reefs are highly diverse ecosystems ideally suited for advancing our understanding of diversity processes, testing diversity conservation strategies, and assessing the effectiveness of conservation measures. The centre of coral reef diversity is the Western

Pacific Coral Triangle (Birkeland 1997, Paulay 1997, Bellwood et al. 2005, Briggs 2005, Carpenter and Springer 2005). Habitat attributes and processes that are thought to contribute to high diversity in coral reefs include dispersal (Mora et al. 2003), habitat complexity (Roberts and Ormond 1987), lottery competition for habitable space (Sale 1977), niche partitioning (Knowlton and Jackson 1994), and total reef area (Galzin et al. 1994). In addition to these natural processes, reef communities are impacted by human-induced disturbances such as fishing (Jennings and Polunin 1997, Pauly et al. 2002) and global warming (Jones et al. 2004) that reduce reef diversity in many parts of the world and threaten reef survival (Brown 1997, McClanahan 2002). Variation in the combination and intensity of factors and processes that influence local and regional reef diversity likely contribute to the observed spatio-temporal heterogeneity in reef community dynamics (Gladfelter et al. 1980, Sale 1991, Nanami and Nishihira 2003).

Marine reserves are highly advocated tools to protect and recover reef diversity (Hastings and Botsford 2003, Lubchenco et al. 2003), but our current understanding of how diversity patterns change within reserves remains limited (Sale et al. 2005). Meta-analyses suggested that marine reserves rapidly restore reef diversity (Halpern and Warner 2002), but empirical studies based on long-term temporal data suggest that the recovery of reef fish diversity may take longer depending on life history dynamics (Russ and Alcala 2004, McClanahan et al. 2007). In addition, the heterogeneous nature of reef communities may cause pronounced spatial variation in diversity recovery trends (Benedetti-Cecchi et al. 2003). Thus, the current increase in marine reserve establishment in the Philippines and worldwide offers opportunities to understand the spatio-temporal dynamics of reef fish diversity in relation to protection-duration and spatial factors (Kelleher 1996, Alcala and Russ 2006, Wood and Dragicevic 2007).

Here, we present the results of a three-year study, where we tracked the changes in reef fish diversity at eight coral reef sites that fell along categories of protection-duration and site location (distance relative to the mainland of Bohol, Philippines). The main objectives of our research were (1) to describe the patterns of spatio-temporal variation in reef fish diversity – i.e. diversity accumulation, diversity indices, and dominance or the distribution of abundance and biomass across species – and (2) to investigate the potential influence of protection-duration and location (distance from shore) on the observed reef fish diversity patterns.

Methods

Study sites, field sampling protocol, data treatment, and general analytical approach

The study sites, field sampling protocol, data treatment, and general analytical approach were similar for the four data chapters of this thesis (Chapters 3, 4, 5, and 6), and described in details in the general methods (Chapter 2) to prevent repetition throughout the thesis. The methods and analyses specific to this chapter were described below.

Species accumulation curves

We plotted the species accumulation curve for each of the eight sites based on the mean monthly count of species recorded at each site during the three year sampling period, using permutation methods in Primer v.6 (Clarke and Gorley 2006). We then fitted logarithmic and power models to the species accumulation data for each site. We used a two-way Analysis of Variance (ANOVA) to test for an effect of protection-duration and site location on the slopes of the logarithmic and power models within each site (see Chapter 2).

Species diversity indices

We calculated a total of 12 diversity indices (species richness which is presented in Chapter 3 but not here, Hill's N_1, N_2, $N_{infinity}$, N_{10}, N_{21}, N_{10}, N_{21}, Pielou's J, Shannon-Weiner ln(H'), Simpson's 1-lambda, lambda,) based on the mean monthly abundance estimates of every species encountered at each site during the three year period (Clarke and Gorley 2006). However, all diversity indices correlated positively with each other (except Simpson's 1-lambda, which was negatively correlated with the other indices). Thus, we present only the results for the four indices most commonly used – namely: Hill's N_1, Pielou's J, Shannon-Weiner's ln(H'), and Simpson's 1-lambda, which are all measures of evenness (i.e. lower values of these indices means higher dominance of some species) (Peet 1974, Clarke and Warwick 2001), but see detailed analyses of species richness in Chapter 3.

We chose to present these four indices, instead of only one, as various studies showed differing preferences and we wanted to assess whether these indices perform differently. For instance, although Shannon-Weiner's ln(H') is the most common diversity index in the literature, it is often criticized for its very narrow range of values, usually between

1.5-3.5 (Peet 1974, Gotelli and Colwell 2001). To address this problem, Hill introduced the index N_1, which is the exp(ln(H')) in order to expand its values (Clarke and Warwick 2001). On the other hand, Pielou's J is simply the ratio of Shannon-Weiner ln(H') and its maximum value if all the species were equally abundant (Clarke and Warwick 2001). Lastly, Simpson's index – 1-lambda is advocated because it represents the probability that any two individuals chosen randomly from a sample will be the same species, and because it is not sensitive to sample size, in contrast to the other three indices (Clarke and Warwick 2001).

We used linear regression to examine if there were significant changes in these four diversity indices within sites over time. In addition, we used a two-way ANOVA to test for an effect of protection-duration and site location on (1) the mean values of the indices during the last year of sampling, and (2) the slope of the regression line for the indices within sites (see Chapter 2).

Abundance-Biomass Comparison (ABC) curves

We plotted the ABC curves for each site based on mean monthly abundance and biomass estimates of all species found at each site during the last year of the study (Warwick and Clarke 1994, Clarke and Gorley 2006). The general prediction was that in protected areas, large-bodied species would dominate the community and therefore, the cumulative biomass curves (i.e. the species rank on the x-axis and the cumulative contribution of species abundance or biomass on the y-axis) would be higher than the cumulative species abundance curves (Meire and Dereu 1990, Warwick and Clarke 1994, Clarke and Gorley

2006). The *W*-statistic associated with ABC curves measures the distance between the abundance and biomass curves i.e. a +1 *W*-statistic for higher biomass to abundance curve case or complete biomass dominance and an even abundance distribution across all species, and a -1 *W*-statistic for the reverse case (Meire and Dereu 1990, Warwick and Clarke 1994, Clarke and Gorley 2006). We used a two-way ANOVA to test for a relationship between protection-duration and site location on the *W*-statistics of the ABC curves for each study site (see Chapter 2).

Results

Species accumulation curves

The cumulative number of species per site recorded over the three-year period fitted both logarithmic and power models equally well, and species accumulation in the data approached asymptotic levels at approximately 200 species for fished sites and between approximately 250 and 300 species for marine reserves (Figure 4.1). The power model suggested a higher rate or slope of species accumulation than the logarithmic model across all sites (Figure 4.1). There was a trend towards higher species accumulation in young and older marine reserves than in fished sites (Figure 4.1). However, ANOVA did not detect a significant influence of protection-duration and site location on the rate of species accumulation within study sites, as measured by the slopes of the logarithmic and power models.

Species diversity indices

Of the twelve diversity indices that we analyzed, only species richness showed a consistent significant increase within sites over time, except for the fished site A (see Chapter 3 for detailed analyses of species richness). The temporal trends for the other four commonly used diversity indices – Hill's N_1, Pielou's J, Shannon-Weiner's ln(H'), and Simpson's 1-Lambda – demonstrated some site-specific changes over time, with fished sites displayed mainly downward temporal trends, whereas the younger and older marine reserves showed some increasing trends (Figure 4.2). However, ANOVA did not detect a significant effect of either protection-duration or site location on the rates of changes of these four indices within and across the study sites (Figure 4.2). In addition, there was a trend of higher third year mean values of the four diversity indices in the younger and older marine reserves than the fished sites (Figure 4.3). However, again, ANOVA did not detect significant influences of either protection-duration or site location on third year values of Hill's N_1, Pielou's J, Shannon-Weiner's ln(H'), and Simpson's 1-Lambda within study sites (Figure 4.3). In addition, there was an apparent interaction between protection-duration and site location for the third year values of the four indices, such that the younger marine reserves showed different trends at inshore and offshore sites, while the older marine reserves and fished sites maintained their differences in the inshore and offshore sites (Figure 4.3).

Abundance-Biomass Comparison (ABC) curves

The ABC curves for each site showed clear patterns of higher cumulative abundance than biomass curves in fished sites, and higher biomass than abundance curves in the majority of protected sites (except site e; Figure 4.4). This trend indicated that most of the protected sites (except site e) were dominated by large-bodied species (i.e. higher cumulative biomass curves than abundance curves, positive *W*-statistic) compared with the fished sites, which were dominated by highly abundant small-bodied fishes (negative *W*-statistic; Figure 4.4).

Discussion

Our analyses of spatio-temporal patterns in reef fish diversity within and across sites indicated that offshore sites maintained higher species richness than inshore sites regardless of protection-duration. These results support previously documented patterns in inshore-offshore comparisons from other locations, such as Australia's Great Barrier Reef (Williams 1982, Williams and Hatcher 1983, Williams 1991). In general, species richness has been related to available reef area (MacArthur 1972, Knowlton 2001). As previous studies have illustrated, the offshore reefs on Danajon Bank have larger and better developed reef areas compared to inshore reefs, and higher sedimentation in inshore areas has been suggested as an additional factor lowering the habitat quality of inshore reefs (Pichon 1977, Cornell and Karlson 2000). Overall, our data support the current understanding of patterns of reef diversity in relation to distance from shore, and this pattern was consistent, regardless of protection-duration at each site.

In contrast to the strong influence of location, we found that protection-duration had a relatively weak influence on the spatio-temporal trends of reef fish diversity in general, within and across our study sites. We should note, however, the interaction trends between location and protection-duration as factors influencing reef fish diversity across our study sites. Our data suggest that diversity in the fished sites may not have been quantitatively affected by fishing, since it did not differ greatly from older marine reserves. Our results are consistent with an empirical study that tracked changes in fish species richness in an intensely and destructively fished site (Sumilon Island, a re-opened marine reserve) and three other fished sites where fishing intensity was more or less constant, which showed that species richness only declined in the former (Russ and Alcala 1989, 1998). Similarly, a study in Kenya did not detect a significant difference in species diversity between protected and fished site (Watson et al. 1996). The authors suggested that fishing had a weaker influence on reef diversity in Kenya compared to other ecological processes such as larval/adult imports and predator-prey interactions (Watson et al. 1996). These studies support our findings that reef fish species richness in our sites are relatively stable and not detectably depleted at fished sites (i.e., considering similar diversity across the study sites regardless of protection-duration).

The rapid changes in species accumulation over the first ten months of sampling occurred across all sites and were clearly a sampling effect, given the fact that the rate of accumulation was similar across all sites regardless of protection-duration. This implies that for high diversity systems such as coral reefs, it may require intensive sampling over time to establish baseline data for the detection of potential diversity changes. Hence, conclusions on diversity recovery based on few, especially short-term data sets with limited sampling (Halpern and Warner 2002, McClanahan et al. 2007) may be biased for high diversity systems.

Although we did not detect a statistically significant change in diversity indices with protection-duration, we did observe a change in the quality or characteristics of fish diversity with age of protection in terms of the following: (1) diversity indices were slightly higher, in younger and older marine reserves than in fished sites, although such differences were not significant, and (2) the relative proportion of biomass-dominant or large-bodied species increased more in the younger and older marine reserves than in the fished sites.

The changes in the quality of diversity were apparent in the shifting of the ABC dominance curves between fished sites (higher abundance than biomass curves) and nearly all protected areas (higher biomass than abundance curves) for both inshore and offshore sites. Our results suggested that the primary effect of protection-duration on diversity patterns, in the absence of fishing-induced habitat destruction, may relate more to the quality of diversity (i.e. the increase in body-size of species comprising the community) rather than to direct changes in diversity indices. Hence, protection-duration permitted populations to grow undisturbed by fishing. This, in turn can potentially influence surrounding unprotected areas through adult spillover and potential recruitment-effects (Zeller et al. 2003, Russ et al. 2004, Abesamis and Russ 2005, Tetreault and Ambrose 2007).

Two main caveats are worth discussing in relation to their potential effects on our results. First, the lack of any observed relationship between fish diversity and habitat measures (see Chapter 2) may be attributable to the bias in sampling design and the relatively coarse methods employed for sampling habitat attributes. We sampled the benthic habitat in the first 20 m of each transect using a line transect intercept method with broad habitat types, whereas we sampled small fishes (<10 cm TL) that are potentially more responsive to habitat attributes in the last 20 m of the transect. The fact that we did not detect a relationship between fish and habitat using this approach suggests that a more focused and species-specific study design may be required to demonstrate fish-habitat relationships. Second, as explained in chapter 2, we lacked replicate sites for both offshore and fished sites.

In summary, we did not find distinct quantitative differences in diversity patterns for sites whose protection-duration period ranged from 0-10 years, despite intensive sampling over three years. However, our data do confirm the previously demonstrated inshore-offshore patterns in diversity for coral reef fish communities (Williams 1982, Williams and Hatcher 1983, Williams 1991). Thus, one could conclude that at the levels of fishing intensity occurring in the Danajon Bank area, basic diversity patterns (such as species richness and other diversity indices) appear to be unaffected by exploitation. A caveat to this relates clearly to the very large reef fish and highly mobile reef-associated species that are likely to have been heavily depleted in the highly exploited Philippine reef systems (see Chapter 3, 5, and 6).

The findings that we presented here demonstrate that diversity is unequally distributed across space as indicated by the higher species richness (see Chapter 3), and that four additional diversity indices had lower values (i.e. higher dominance) in our offshore sites than in our inshore sites, regardless of protection-duration. Hence, accounting for spatial heterogeneity matters if we are to optimize the design of marine reserves for the protection and maintenance of biodiversity as well as biomass. Future studies should examine how recovery of biomass in protected areas affects diversity patterns and trends over time, through trophic cascades or greater dispersal of large mobile individuals outside of reserves (see Chapter 6). This will require experimental approaches with high analytical power, and the controlled creation of multiple reserves on a spatial scale such as those are now emerging on Danajon Bank (see Chapter 6).

If they are to fulfill biological criteria relating to increased diversity, then the design and selection of networks of reserves must take into account prior knowledge of spatio-temporal diversity patterns and processes as much as possible, rather than proceeding with a simple ad-hoc site selection as is currently used for MPA establishment in Danajon Bank and the Philippines in general (Moritz 2002, Hastings and Botsford 2003, Tognelli et al. 2005). At present, our study offers the best available information on the patterns of spatio-temporal changes in reef diversity within Danajon marine reserves, but not the processes driving such inshore-offshore diversity patterns. Our findings on the strong inshore-offshore patterns of diversity distribution will be useful in considerations of marine reserve network design for Danajon Bank and in other locations that exhibit strong heterogeneous diversity patterns across space.

Figures

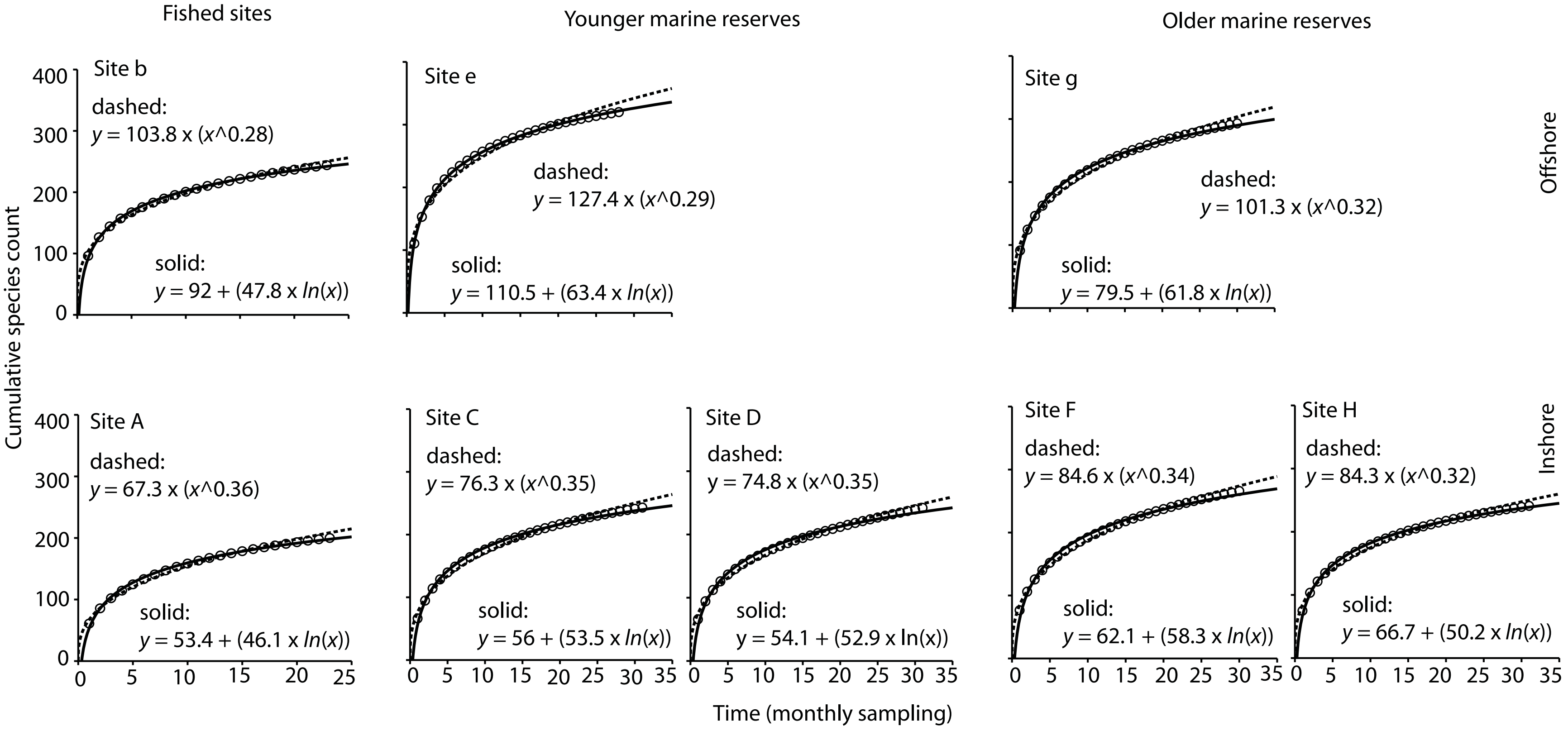


Figure 4.1 Power (dashed lines) and logarithmic (solid lines) curves fitted to the cumulative species count based on the mean monthly abundance estimates of species found within study sites during the three year sampling period. Also presented are the models of each curve. All curves had an $r^2 = 0.9$ and *P*-values <0.0001.

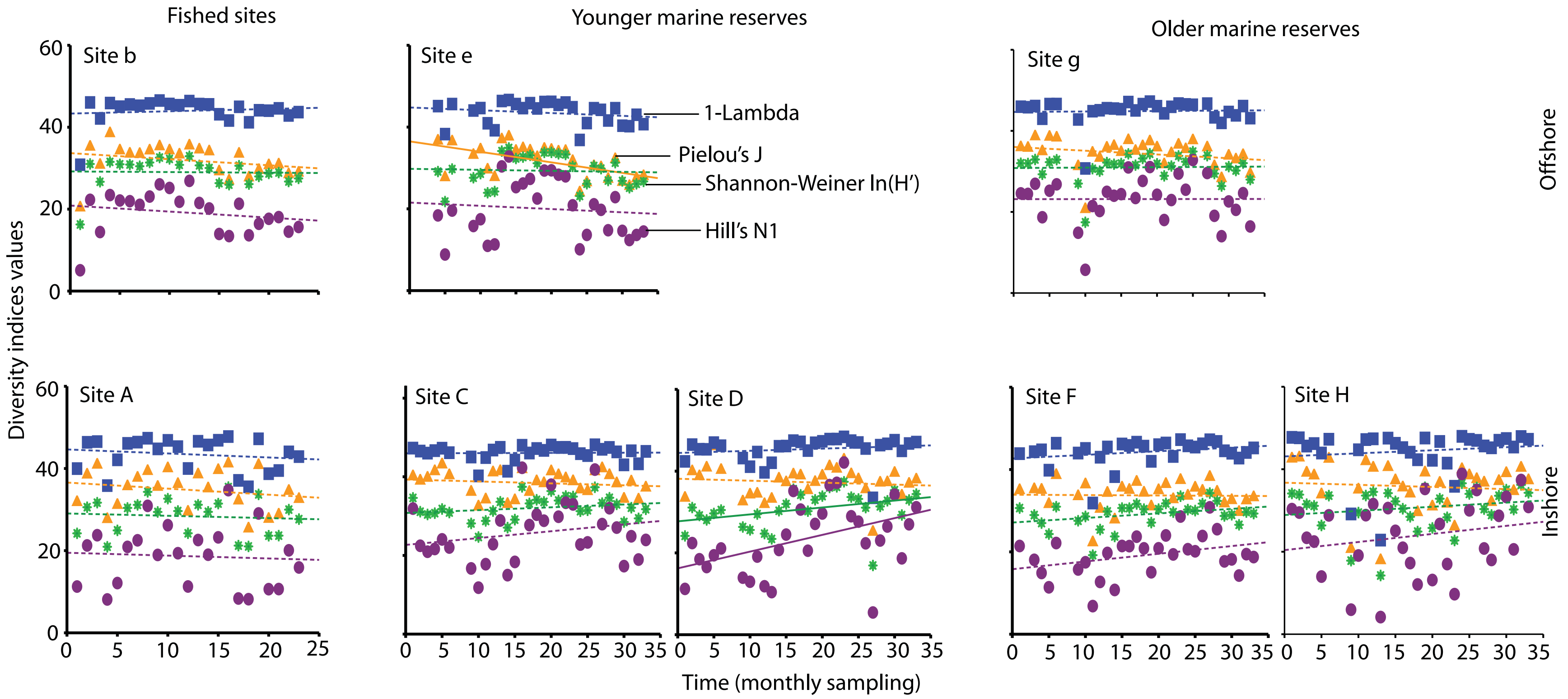


Figure 4.2 Regression of the four most commonly used diversity indices against sampling time (monthly sampling 2002-2005). Legends: blue squares and lines (Simpson's 1-lambda x 50), orange triangles and lines (Pielous's J x 50), green asterisks and lines (Shannon-Weiner ln(H') x 10, and purple circles and lines (Hill's N1). Solid lines are significant regression lines and dashed lines are non-significant regression lines.

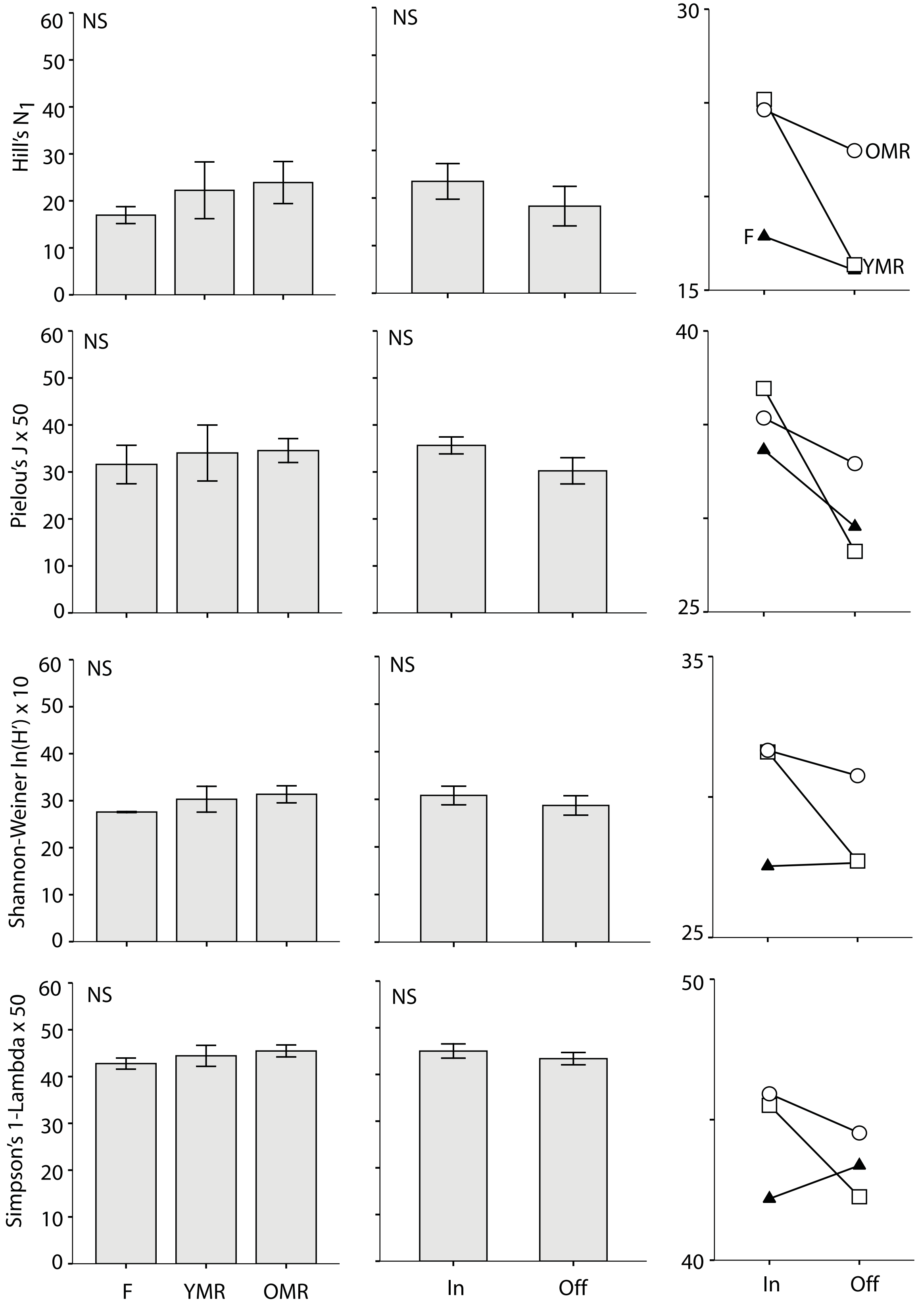

Hill's N_1
Pielou's J x 50
Shannon-Weiner ln(H') x 10
Simpson's 1-Lambda x 50
NS
0
10
20
30
40
50
60
15
25
35
40
50
F
YMR
OMR
In
Off

Figure 4.3 ANOVA on the magnitudes or third year mean values (± SE) of four diversity indices. The two factors tested were protection-duration (F=fished sites, YMR = younger marine reserves/3-years old, and OMR = older marine reserves/6-10 years old) and site location (In = inshore and Off = offshore sites). The main factors (protection-duration and site location) did not have a significant effect and indicated as non-significant or NS. Interaction patterns were not tested (see Chapter 2), but were noted in the text.

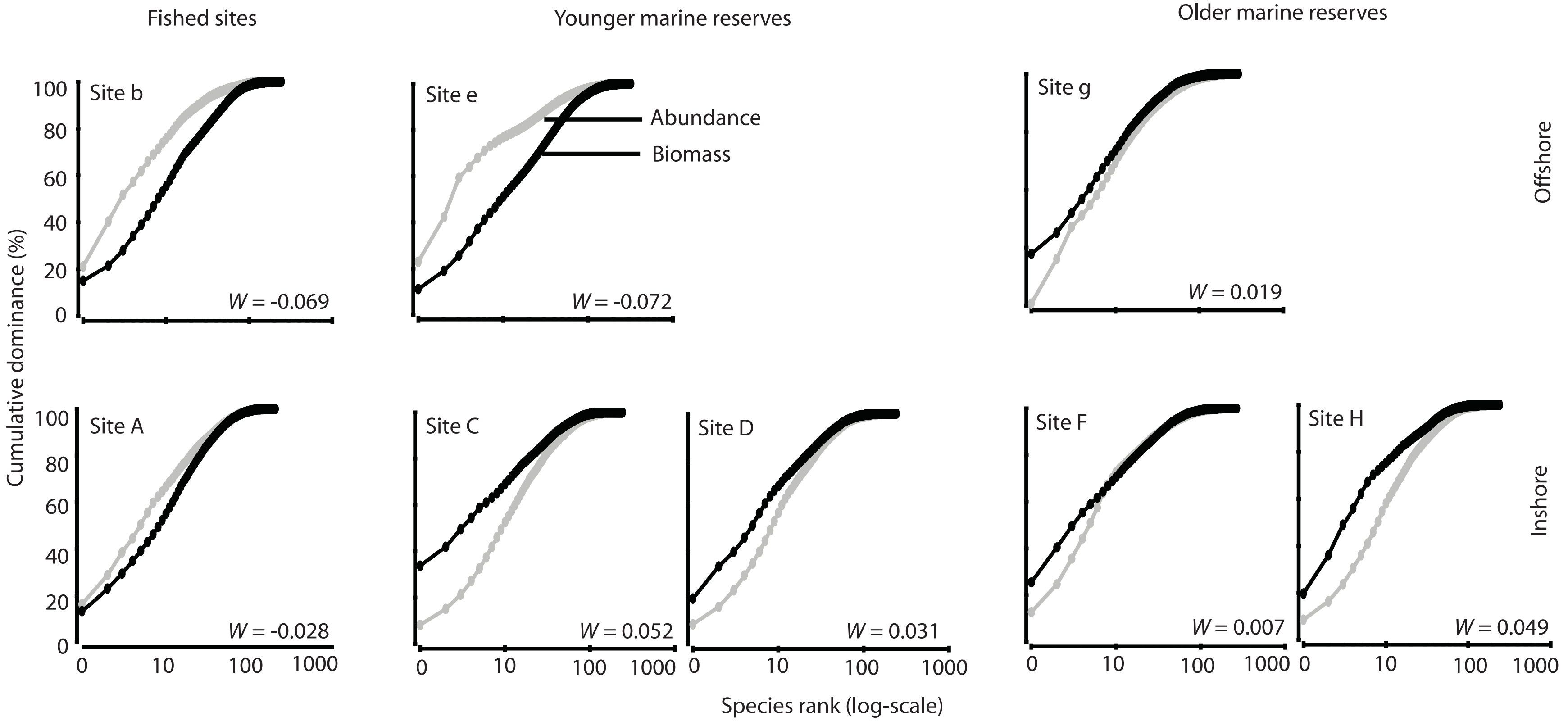


Figure 4.4 Abundance-Biomass Comparison (ABC) curves based on the mean monthly abundance of all fish species found within each site during the third year of sampling (see Chapter 2). Also presented are the *W*-statistics, a measure of the closeness of each pair of curves.

References

Abesamis, R. A., and G. R. Russ. 2005. Density-dependent spill-over from a marine reserve: long-term evidence. Ecological Applications **15**:1798-1812.

Alatalo, R. V. 1981. Problems in the measurement of evenness in ecology. Oikos **37**:199-204.

Alcala, A. C., and G. R. Russ. 2006. No-take marine reserves and reef fisheries management in the Philippines: a new people power revolution. AMBIO: A Journal of the Human Environment **35**:245-254.

Allen, A. P., and J. F. Gillooly. 2006. Assessing latitudinal gradients in speciation rates and biodiversity at the global scale. Ecology Letters **9**:947-954.

Allen, A. P., J. F. Gillooly, V. M. Savage, and J. H. Brown. 2006. Kinetic effects of temperature on rates of genetic divergence and speciation. Proceedings of the National Academy of Sciences **103**:9130-9135.

Bellwood, D. R., R. N. Hughes, R. M. Connolly, and J. E. Tanner. 2005. Environmental and geometric constraints on Indo-Pacific coral reef biodiversity. Ecology Letters **8**:643-651.

Benedetti-Cecchi, L., I. Bertocci, F. Micheli, E. Maggi, E. Fosella, and S. Vaselli. 2003. Implications of spatial heterogeneity for management of marine protected areas (MPAs): examples from assemblages of rocky coasts in the northwest Mediterranean. Marine Environmental Research **55**:429-458.

Birkeland, C. 1997. Geographic differences in ecological processes on coral reefs. Pages 273-287 *in* C. Birkeland, editor. Life and Death of Coral Reefs. Chapman & Hall, New York.

Briggs, J. C. 2005. Coral reefs: conserving the evolutionary sources. Biological Conservation **126**:297-305.

Briggs, J. C. 2007. Marine longitudinal biodiversity: causes and conservation. Diversity & Distributions **13**:544-555.

Brooks, T. M., R. A. Mittermeier, G. A. B. da Fonseca, J. Gerlach, M. Hoffmann, J. F. Lamoreux, C. G. Mittermeier, J. D. Pilgrim, and A. S. L. Rodrigues. 2006. Global biodiversity conservation priorities. Science **313**:58-61.

Brown, B. E. 1997. Disturbances to reefs in recent times. Pages 354-379 *in* C. Birkeland, editor. Life and death of coral reefs. Chapman & Hall, New York.

Caley, M. J., and D. Schluter. 1997. The relationship between local and regional diversity. Ecology **78**:70-80.

Carpenter, K. E., and V. G. Springer. 2005. The center of the center of marine shore fish biodiversity: the Philippine Islands. Environmental Biology of Fishes **72**:467-480.

Clarke, K. R., and R. N. Gorley. 2006. PRIMER v6: User manual/tutorial. PRIMER-E Ltd, Plymouth, UK.

Clarke, K. R., and R. M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretations, 2nd edition. *in*. PRIMER-E Ltd, Plymouth, UK.

Colwell, R. K., C. X. Mao, and J. Chang. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology **85**:2717-2727.

Cornell, H. V., and R. H. Karlson. 2000. Coral species richness: ecological versus biogeographical influences. Coral Reefs **19**:37-49.

Cornell, H. V., and J. H. Lawton. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. The Journal of Animal Ecology **61**:1-12.

Ferraro, P. J., and S. K. Pattanayak. 2006. Money for nothing? A call for empirical evaluation of biodiversity conservation investments. PLoS Biology **4**:e105.

Galzin, R., S. Planes, V. Dufour, and B. Salvat. 1994. Variation in diversity of coral reef fish between French Polynesian atolls. Coral Reefs **13**:175-180.

Gladfelter, W. B., J. C. Ogden, and E. H. Gladfelter. 1980. Similarity and diversity among coral reef fish communities: a comparison between tropical western Atlantic (Virgin Islands) and tropical central Pacific (Marshall Islands) patch reefs. Ecology **61**:1156-1168.

Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters **4**:379-391.

Halpern, B. S., and R. R. Warner. 2002. Marine reserves have rapid and lasting effects. Ecology Letters **5**:361-366.

Hastings, A., and L. W. Botsford. 2003. Comparing designs of marine reserves for fisheries and for biodiversity. Ecological Applications **13**:S65-S70.

He, F., P. Legendre, and J. V. LaFrankie. 1996. Spatial pattern of diversity in a tropical rain forest in Malaysia. Journal of Biogeography **23**:57-74.

Hill, M. 1973. Diversity and evenness: a unifying notation and its consequences. Ecology **54**:427-432.

Hurlbert, S. 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology **52**:577-586.

Jackson, J. B. C. 1997. Reef since Columbus. Coral Reefs **16**:23-32.

Jennings, S., and N. V. C. Polunin. 1997. Impacts of predator depletion by fishing on the biomass and diversity of non-target reef fish communities. Coral Reefs **16**:71-82.

Jones, G. P., M. I. McCormick, M. Srinivasan, and J. V. Eagle. 2004. Coral decline threatens fish biodiversity in marine reserves. Proceedings of the National Academy of Sciences **101**:8251-8253.

Kelleher, G. 1996. A global representative system of marine protected areas. Ocean and Coastal Management **32**:123-126.

Kempton, R. A. 1979. The structure of species abundance and measurement of diversity. Biometrics **35**:307-321.

Keylock, C. J. 2005. Simpson diversity and the Shannon-Wiener index as special cases of a generalized entropy. Oikos **109**:203-207.

Knowlton, N. 2001. Coral reef biodiversity-habitat size matters. Science **292**:1493-1495.

Knowlton, N., and J. B. C. Jackson. 1994. New taxonomy and niche partitioning on coral reefs: jack of all trades or master of some? Trends in Ecology and Evolution **9**:7-9.

Kremen, C., I. Raymond, and K. Lance. 1998. An interdisciplinary tool for monitoring conservation impacts in Madagascar. Conservation Biology **12**:549-563.

Lubchenco, J., S. R. Palumbi, S. D. Gaines, and S. Andelman. 2003. Plugging a hole in the ocean: the emerging science of marine reserves. Ecological Applications **13**:S3-S7.

MacArthur, R. 1955. Fluctuations of animal populations, and measure of community stability. Ecology **36**:533-536.

MacArthur, R. H. 1972. Geographical ecology. Princeton University Press, Princeton.

McClanahan, T. R. 2002. The near future of coral reefs. Environmental Conservation **29**:460-483.

McClanahan, T. R., N. A. J. Graham, J. M. Calnan, and M. A. MacNeil. 2007. Towards pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. Ecological Applications **17**:1055-1067.

McIntosh, R. P. 1967. An index of diversity and the relation of certain concepts to diversity. Ecology **48**:392-404.

Meire, P. M., and J. Dereu. 1990. Use of the abundance/biomass comparison method for detecting environmental stress: some considerations based on intertidal macrozoobenthos and bird communities. The Journal of Applied Ecology **27**:210-223.

Mora, C., P. M. Chittaro, P. F. Sale, J. P. Kritzer, and S. A. Ludsin. 2003. Patterns and processes in reef fish diversity. Nature **421**:933-936.

Moritz, C. 2002. Strategies to protect biological diversity and the evolutionary processes that sustain it. Systematic Biology **51**:238-254.

Nanami, A., and M. Nishihira. 2003. Population dynamics and spatial distribution of coral reef fishes: comparison between continuous and isolated habitats. Environmental Biology of Fishes **68**:101-112.

Paulay, G. 1997. Diversity and distribution of reef organism. Pages 298-353 *in* C. Birkeland, editor. Life and Death of Coral Reefs. Chapman & Hall, New York.

Pauly, D., V. Christensen, S. Guenette, T. J. Pitcher, U. R. Sumaila, C. J. Walters, R. Watson, and D. Zeller. 2002. Towards sustainability in world fisheries. Nature **418**:689-695.

Peet, R. K. 1974. The measurement of species diversity. Annual Reviews in Ecology and Systematics **5**:285-307.

Pichon, M. 1977. Physiography, morphology, and ecology of the double barrier reef of North Bohol (Philippines). Pages 261-267 *in* Proceedings of the Third International Coral Reef Symposium, Miami, Florida.

Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. Science **235**:167.

Roberts, C. M., and R. F. G. Ormond. 1987. Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. Marine Ecology Progress Series **41**:1-8.

Roberts, M. R., and F. S. Gilliam. 1995. Patterns and mechanisms of plant diversity in forested ecosystems: implications for forest management. Ecological Applications **5**:969-977.

Russ, G. R., and A. C. Alcala. 1989. Effects of intense fishing pressure on an assemblage of coral reef fishes. Marine Ecology Progress Series **56**:13-27.

Russ, G. R., and A. C. Alcala. 1998. Natural fishing experiments in marine reserves 1983-1993: roles of life history and fishing intensity in family responses. Coral Reefs **17**:399-416.

Russ, G. R., and A. C. Alcala. 2004. Marine reserves: long-term protection is required for full recovery of predatory fish populations. Oecologia **138**:622-627.

Russ, G. R., A. C. Alcala, A. P. Maypa, H. P. Calumpong, and A. T. White. 2004. Marine reserve benefits local fisheries. Ecological Applications **14**:597-606.

Sale, P. F. 1977. Maintenance of high diversity in coral reef fish communities. The American Naturalist **111**:337-359.

Sale, P. F. 1991. Reef fish communities: open non-equilibrial systems. Pages 564-598 *in* P. F. Sale, editor. The ecology of fishes on coral reefs. Academic Press, London.

Sale, P. F., R. K. Cowen, B. S. Danilowics, G. P. Jones, J. P. Kritzer, K. C. Lindeman, S. Planes, N. V. C. Polunin, G. R. Russ, Y. J. Sadovy, and R. S. Steneck. 2005. Critical science gaps impede use of no-take fishery reserves. Trends in Ecology and Evolution **20**:74-80.

Sounding, E. 2003. A tribute to Claude Shannon (1916–2001) and a plea for more rigorous use of species richness, species diversity and the 'Shannon–Wiener' index. Global Ecology and Biogeography **12**:177-179.

Stem, C., R. Margoluis, N. Salafsky, and M. Brown. 2005. Monitoring and evaluation in conservation: a review of trends and approaches. Conservation Biology **19**:295-309.

Tetreault, I., and R. F. Ambrose. 2007. Temperate marine reserves enhance targeted but not untargeted fishes in multiple no-take MPAs. Ecological Applications **17**:2251-2267.

Thompson, G. G., and P. C. Withers. 2003. Effect of species richness and relative abundance on the shape of the species accumulation curve. Austral Ecology **28**:355-360.

Tognelli, M. F., C. Silva-Garci´a, F. A. Labra, and P. A. Marquet. 2005. Priority areas for the conservation of coastal marine vertebrates in Chile. Biological Conservation **126**:420-428.

Warwick, R. M., and K. R. Clarke. 1994. Relearning the ABC: taxonomic changes and abundance/biomass relationships in disturbed benthic communities. Marine Biology **118**:739-744.

Watson, M., D. Righton, T. Austin, and R. F. G. Ormond. 1996. The effects of fishing on coral reef fish abundance and diversity. Journal of Marine Biological Association of the United Kingdom **76**:229-233.

Williams, D. M. 1982. Patterns in the distribution of fish communities across the central Great Barrier Reef. Coral Reefs **1**:35-43.

Williams, D. M. 1991. Patterns and processes in the distribution of coral reef fishes. Pages 437-474 *in* P. F. Sale, editor. The ecology of fishes on coral reefs. Academic Press, Inc., London.

Williams, D. M., and A. L. Hatcher. 1983. Structure of fish communities on outer slopes of inshore, mid-shelf and outer shelf reefs of the Great Barrier Reef. Marine Ecology Progress Series **10**:239-250.

Willott, S. J. 2001. Species accumulation curves and the measure of sampling effort. Journal of Applied Ecology **38**:484-486.

Wood, L. J., and S. Dragicevic. 2007. GIS-Based multi-criteria evaluation and fuzzy sets to identify priority sites for marine protection. Biodiversity and Conservation **16**:2539-2558.

Zahl, S. 1977. Jackknifing an index of diversity. Ecology **58**:907-913.

Zeller, D., S. L. Stoute, and G. R. Russ. 2003. Movements of reef fishes across marine reserve boundaries: effects of manipulating a density gradient. Marine Ecology Progress Series **254**:269-280.

5. Patterns of reef fish succession within no-take marine reserves[*]

---

[*] A version of this chapter will be submitted for publication. Anticamara, J.A., J.J. Meeuwig and A.C.J. Vincent. Patterns of reef fish succession within no-take marine reserves.

Introduction

Overexploitation of marine ecosystems leads to the depletion of many marine populations and communities (Pandolfi et al. 2003, Micheli et al. 2005, Pauly et al. 2005). The sequential depletion of preferred or targeted species over time – i.e. targeting high trophic, often large-bodied groups first, and lower trophic groups thereafter – is a well established trend in human exploitation impacts on ecosystems (Pauly et al. 1998). In addition, the use of destructive fishing methods has resulted in gross alterations of marine habitats, often rendering them less productive (Pet-Soede et al. 1999, Turner et al. 1999, Fox and Erdmann 2000). Marine ecosystems such as coral reefs have clearly been experiencing declines over long periods, largely because of human exploitation (Jackson 1997). However, documenting and accounting for local extirpations and global extinctions of marine populations needs further research (Jennings et al. 1999, Dulvy et al. 2003).

No-take marine reserves are highly advocated tools to recover depleted marine communities (Kelleher 1996, Lubchenco et al. 2003, Wood and Dragicevic 2007), but our current understanding of their effectiveness is limited to a few sites and few species or species groups (Russ 2002, Sale et al. 2005). A number of studies have focused on community-wide changes within marine reserves (Jennings et al. 1996, Micheli et al. 2004, McClanahan and Graham 2005, Guidetti 2006). Many of these considered the effects of marine reserves on total community abundance, biomass, and species richness (Jennings 2001, Halpern and Warner 2002, Russ 2002, McClanahan et al. 2007). A few empirical studies using time-series data have demonstrated that marine reserves can facilitate recovery of top predator species and species previously exploited by fishing (Russ and Alcala 2004, Williamson et al. 2004, McClanahan et al. 2007). In addition, other studies have established that marine reserves can restore top-down trophic interactions that had been affected by fishing (Shears and Babcock 2002, Graham et al. 2003). With respect to succession, changes in family dominance over time have been demonstrated in marine reserves in Africa (McClanahan et al. 2007). However, there remains a need to explore further the changes in community structure, dynamics, and composition within marine reserves.

Succession, the pattern of changes in community structure (e.g. abundance, biomass, diversity), dynamics (e.g. productivity, stability, trajectory, and turnover rate), and composition after the removal of disturbance, has been well investigated in terrestrial systems (Drury and Nisbet 1973, Horn 1974, Horn 1976, Christensen and Peet 1984, Rejmanek and Rosen 1992, Wali 1999, Walker and del Moral 2003). Succession has typically referred to a directional trajectory or change in community following cessation of the disturbance, and reflects the theory of community stability or equilibrium, which argues that disturbed communities can return to a pre-disturbance state (Christensen and Peet 1984, Halpern 1989), although this is changing with the development of non-equilibrium theory of community dynamics (Wiens 1984). More recently, succession has also referred to a range of community trajectories including convergence, cyclic, divergence, parallel, and network, following cessation of the disturbance (Platt and Connell 2003, Walker and del Moral 2003). The degree to which succession processes are stable or unstable may depend on the spatial and temporal scale being investigated (Whittaker 2000).

Knowledge of succession in marine ecosystem is well-developed for benthic systems such as intertidal algal communities and subtidal communities (Foster et al. 2003, Hill et al. 2004). For example, algal communities show increasing abundance, biomass and diversity during early to mid-succession stages that then stabilize in late succession stages (Dean and Connell 1987). In terms of community composition, intertidal algal communities exhibit patterns similar to succession trends in terrestrial forest systems, wherein early colonizing species are later replaced by long-lived and late succession-dominating species with the communities reaching a climax or state of less change (Foster 1975, Murray and Littler 1978, Sousa 1979, Foster et al. 2003).

The mechanisms and time-frames of succession in intertidal algal communities differ from those of terrestrial systems because early colonizing species in intertidal communities tend to inhibit rather that facilitate the invasion or establishment of late succession-dominating species (Sousa 1979, Kim 1997). It is only because early succession species tend to be more susceptible to dislodgement by herbivores and desiccation that late succession-dominating species are able to invade, establish, and dominate (Lubchenco 1978, Sousa 1979, Robles and Cubit 1981). Moreover, the whole process of succession in intertidal communities can be achieved within a ten year period or less as compared to succession processes in terrestrial and forest systems that often require hundreds of years or more to complete (Sousa 1979, Chapman and Underwood 1998).

In contrast to intertidal algal communities, relatively few studies have explored the patterns and mechanisms of reef fish succession post-disturbance, and debate continues as to whether or not reef fish communities are stable. Previously, reef fish community structure with respect to abundance, biomass, and diversity was considered to be highly unstable, fluctuating greatly in values, and essentially in a non-equilibrium state, at least at the scale of patch reefs (Talbot et al. 1978, Sale 1991), although some patch reefs showed stability in reef fish community structure (Brock et al. 1979). More recently, a number of studies have indicated increased stability in fish communities associated with contiguous reefs (Nanami and Nishihira 2002). Reef fish communities showed rapid recovery of community structure after a catastrophic storm (Walsh 1983) or even persistence after a manipulative destruction of habitat (Syms and Jones 2000). Discussions on the stability or instability of reef fish communities have generally focused on turnover rates or changes in similarities of species composition and relative abundances between samples collected over time, post-disturbance (Bohnsack 1983, Sale 1991, Nanami and Nishihira 2002). There is a great need to expand our current understanding of reef fish succession using analytical approaches applied in terrestrial or intertidal communities, considering for example, changes in species dominance and trajectories of community development, post-disturbance.

Over the past decade, the number of no-take marine reserves on the Danajon Bank in the central Philippines has been increasing. This trend presents a valuable opportunity to document and understand the patterns of reef fish succession within previously exploited reef communities across varying periods of protection and location. Philippine reefs provide an excellent opportunity to study community succession given that these systems are highly diverse, form part of the Coral Triangle, the world centre of marine biodiversity, but are also among the most degraded marine ecosystems in the world (Gomez 1997, White et al. 2000, Carpenter and Springer 2005).

The main goal of this study was to document the patterns of succession in reef fish community structure and composition within a suite of coral reef sites that represent three categories of protection-duration time: fished, younger marine reserves (1-3 years old), and older marine reserves (6-10 years old). These sites also represent two categories of location: inshore and offshore. The specific objectives of this research are to (1) characterize trajectories of reef fish communities, (2) quantify the turnover rates of reef fish communities, and (3) evaluate the changing patterns of species composition and dominance.

Methods

Study sites, field sampling protocol, data treatment, and general analytical approach

The study sites, field sampling protocol, data treatment, and general analytical approach were similar for the four data chapters of this thesis (Chapters 3, 4, 5, and 6), and described in details in the general methods (Chapter 2) to prevent repetition throughout the thesis. The methods and analyses specific to this chapter were described below.

Community trajectories

We characterized the community trajectories at each site, over the 33-month period of the study, using non-metric Multi Dimensional Scaling (MDS) analysis (Clarke and Gorley 2006). Biomass estimates (g · m^{-2}) for each species found at each site and each month were transformed by square-root. We chose the square-root transformation transformation in order to increase the influence of rare species while still maintaining that of dominant species (Clarke and Warwick 2001, Clarke and Gorley 2006). We then used Bray-Curtis similarity coefficient to quantify similarity amongst monthly samples within sites as a measure of turnover rates (Beals 1984, Clarke and Warwick 2001, Micheli et al. 2004, Clarke and Gorley 2006). The Bray-Curtis similarity coefficient has the following advantages: (1) it can take the value of zero for samples that have no common species whereas other coefficients usually cannot; (2) its value is not affected by the inclusion or exclusion of species that are jointly absent in compared samples; and (3) it is robust in reconstructing non-linear responses (Clarke and Warwick 2001, Clarke and Gorley 2006).

We used non-metric Multi-Dimensional Scaling (MDS) analysis plots to demonstrate the changing trajectories of fish communities within sites (Clarke and Warwick 2001, Clarke and Gorley 2006). These plots are interpreted such that months with greatest similarity in terms of assemblage composition lie closer in the two-dimensional space than months with relatively more distinct assemblages (Clarke 1993, Clarke and Warwick 2001, Clarke and Gorley 2006).

We tested the degree to which community trajectories across sites converged using second-stage MDS analyses (Clarke 1993, Clarke and Warwick 2001, Wong et al. 2003, Clarke and Gorley 2006, Clarke et al. 2006, Wellington 2006). However, the large number of monthly samples across all sites made the MDS visually chaotic and difficult to interpret. Thus, we instead calculated the annual mean biomass of each species based on the monthly samples from each site. We then used these annual mean values of species biomass for each site to display the comparative average community trajectory within and across the study on MDS space over the three-year sampling period. As with monthly biomass values, we used a square-root transformation of the annual mean species biomass estimates and applied the Bray-Curtis coefficient to measure similarities between annual mean biomass values. The relative position of each study site on the subsequent second-stage MDS space represents the similarity of species composition and the relative biomass of those species within the study sites over time and across the study sites (Clarke 1993, Clarke and Gorley 2006).

Community turnover

We estimated the community turnover as the change in the similarity of species composition and relative species biomass between monthly samples (Bohnsack 1983, Sale and Douglas 1984, Nanami and Nishihira 2003). Specifically, we used the Bray-Curtis coefficient to calculate the similarities of species composition and relative biomass between successive monthly samples within sites over time (Clarke 1993, Clarke and Gorley 2006). We then regressed the calculated Bray-Curtis similarity values between successive monthly samples against the ordinal time of the sample pair over the three-year sampling period (Clarke and Warwick 2001, Nanami and Nishihira 2002, Rodríguez et al. 2003, Clarke and Gorley 2006). We also used two-way ANOVA to test effects of protection-duration (i.e. fished (F; n=2), younger marine reserves (YMR; n=3), and older marine reserves (OMR; n=3)) and site location (i.e. inshore (In; n=5), and offshore (Off; n=3)) (see Chapter 2; Table 2.1) on the mean Bray-Curtis similarity of successive monthly samples during the third year of the sampling period. We used the third year since it represents the maximum values of the changes in Bray-Curtis similarity of successive monthly samples over the three-year sampling period (see Chapter 2).

Community dominance

We demonstrated the changing patterns of species dominance across time and within sites using dominance curves and by determining the key species that characterized sites by month (Peet 1974, Lambshead et al. 1983, Clarke 1993, Kaiser et al. 2000, Clarke and Warwick 2001, Clarke and Gorley 2006). For the dominance curves, we estimated the annual mean biomass of each species within each site during each monthly sampling over the three-year study period. We then plotted the relative dominance (i.e. percentage contribution of each species to the total annual mean biomass of each site) against the species rank (Clarke 1993, Clarke and Warwick 2001, Clarke and Gorley 2006).

We used Similarity of Percentage Contribution (SIMPER) analysis to determine the species that most characterized sites within a given year (Clarke and Warwick 2001, Clarke and Gorley 2006). Here we assigned the monthly biomass samples into annual groupings (see Chapter 2; Table 2.4). We used SIMPER to calculate the average contribution of individual species on the similarity of all the square-root transformed monthly samples within annual groups for each site. We also used SIMPER to rank species based on their average similarity contributions to the similarities of monthly biomass samples, grouped by year, from within each site. We then presented the five species that made the largest contribution to the similarities of monthly samples, grouped by year, using bar charts to present both actual and percentage values. We decided to present only the top five species as these five typically dominated the sites, contributing to at least 50% of the similarity between monthly samples within sites.

Results

Community trajectories

Non-metric Multidimensional Scaling (MDS) plots showed high variability of reef fish community trajectories within each site over time (Figure 5.1). For four sites of different protection-duration and site location (sites b, D, e and g), the fish communities exhibited less variability towards the end of the three-year sampling period, while the other sites showed high variations in community trajectories over the course of the three-year study (Figure 5.1). In all the study sites, the reef fish communities in the initial months of the study differed from those in the last months of the study (Figure 5.1).

When we plotted the MDS trajectories of reef fish communities using the annual mean of the monthly biomass samples for each site, we found trends suggesting community convergence with protection-duration, with the three older marine reserves located closer to each other on MDS space than the rest of the study sites, including the offshore older marine reserve (Figure 5.2 a). The remaining offshore sites showed similar trajectories relative to each other and were clearly distinct from the other six sites (Figure 5.2 a) However, the second-stage MDS suggested the influence of both protection-duration and site location on the community trajectories (Figure 5.2 b). For example, in terms of protection-duration, the oldest marine reserve, Handumon (H) showed different community trajectories from the rest of the study sites (Figure 5.2 b). Two of the inshore marine reserves, one older and one younger, were similar as were the offshore younger and older marine reserves (Figure 5.2 b). However, the fished sites were different in their trajectories from each other as well as from the marine reserves (Figure 5.2 b).

Community turnover

We observed high turnover rates in reef fish community composition and relative biomass of fish species comprising each successive monthly sample in each study site (Figure 5.3). Bray-Curtis similarity measured between successive monthly samples from each site ranged from about 25-80% (Figure 5.3). There were general upward trends in Bray-Curtis with time suggesting that, in general, the successive monthly fish species composition and their relative biomass became increasingly more similar over time. However, while these upward trends were all statistically significant for the offshore sites, only two of the inshore sites (D and H) showed significant upward trends, with the remaining inshore sites showing no significant change over time. There was also no significant effect of protection-duration on the mean Bray-Curtis values of the third year mean values (Figure 5.4 a). However, the offshore sites showed significantly higher mean Bray-Curtis similarity values than the inshore sites (Figure 5.4 b). In addition, we noted interactions between protection-duration and site location, which indicated that older marine reserves showed higher turnover rates than their corresponding younger marine reserves and fished sites in the inshore sites, but not for the offshore sites (Figure 5.4 c).

Community dominance

All the study sites were dominated by a few reef fish species in terms of the biomass of each species relative to the total biomass estimated for each site during each monthly sampling over the course of the three-year study (Figure 5.5). The actual biomass dominance values of top ranking species were lower and more annually variable in the fished sites, younger marine reserves and even the inshore and older marine reserve site F, than in the two older marine reserve sites g and H (Figure 5.5).

A total of 37 species out of a total of 423 species were identified as within the top five dominant species of a given site over the three-year study period (Table 5.1). The majority of these 37 dominant species showed site and year-specific dominance, with only two species (*Chlorurus bleekeri* and *Thalassoma lunare*) showing a relatively consistent dominance within sites over time and across sites (Table 5.2). Most of the large-bodied species were only dominant in the younger and older protected marine reserves; however, there were also cases where a few a large-bodied species were dominant in the fished sites (Table 5.2). Similarly, medium and small-bodied species were also dominant in the fished sites, younger marine reserves, and older marine reserves with no clear pattern associated with protection-duration (Table 5.2).

The mean biomass of top ranking species that contributed to the similarity of monthly samples from within sites each year of the three-year study showed increasing trends within sites over time (for most study sites) and with protection-duration (Figure 5.6). The top five species that contributed to the similarity of monthly samples from within each site for each year constituted about 20-45% of the total biomass (Figure 5.7). The large-bodied and ubiquitous herbivore *Chlorurus bleekeri* showed increasing mean biomass and percentage biomass contribution with protection-duration (Figures 5.6 and 5.7). In contrast, the other ubiquitous but medium-bodied species, *Thalassoma lunare*, showed declining dominance with protection-duration (Figures 5.6 and 5.7).

Discussion

No-take marine reserves are considered important approaches in the recovery of communities that have been depleted by exploitation (Shears and Babcock 2003, Guidetti and Sala 2007). Recent research has indicated patterns of succession in terms of changing dominance within marine reserves at the level of families (McClanahan et al. 2007). Our analyses of community changes within and across marine reserves at the species level demonstrated that changing reef fish communities within no-take marine reserves also exhibited patterns of succession in the form of changing biomass-dominance patterns over protection-duration. However, the complexity of processes that drive patterns in reef fish communities (e.g. spatial heterogeneity of species recruitment, growth, interaction, immigration, and emigration strengths or rates) influences the actual direction and characteristics of reef fish succession within marine reserves (Williams 1982, Garcia Charton and Perez-Ruzafa 1999). Meta-analyses of community changes within marine reserves also suggest that patterns of community succession within marine reserves may exhibit transient patterns (Micheli et al. 2004). It also seems that longer time-frames may be required for full recovery of some expected late succession dominant fish species within marine reserves such as top predators (Russ and Alcala 2004). Community studies like ours may offer only short-term windows on succession within marine reserves.

The application of multivariate techniques – used to study succession in terrestrial environments (Walker and del Moral 2003) and marine pollution studies (Clarke and Warwick 2001) – to reef fish communities and marine reserves has provided important insights into how these communities may change over time. Community trajectories within and across the study sites have shown that, while trajectories of reef fish communities may appear chaotic at a fine monthly temporal scales, trends can be discerned at coarser, annual temporal scales. For instance, based on the annual averages of species biomass, we found that reef fish communities within marine reserves may exhibit patterns suggestive of some degree of community convergence over time. This potential for community convergence is suggested by the close location of older marine reserve sites to each other on the MDS space over the three-year period. However, only a longer-term study can explore whether this convergence would ever occur, especially given the inshore-offshore community trends that are also apparent on the MDS trajectory of our study communities. If the reef fish communities show some directional trends with protection duration, but also maintain their inshore-offshore differences, then the community trajectories across our study sites over time might be considered "parallel trajectories" as identified in terrestrial succession studies (Walker and del Moral 2003).

Coral reef fish communities are known for their high turnover rates, which is the fundamental basis for considering reef fish communities to be non-equilibrium systems. At the level of patch reefs, the similarity is reported to be approximately 56% between successive assemblage samples and thus argued to be unstable (Sale and Douglas 1984). However, other researchers working in contiguous reef systems have argued that reef fish communities can be relatively stable, reporting levels of 50-80% similarity amongst community samples over time (Nanami and Nishihira 2004) – a conclusion that illustrates the subjectivity of interpreting similarity valuesOur results are within the range of turnover rates predicted for contiguous reefs with mean similarity between successive reef fish samples of about 58-70% depending on site location. We did not see a clear effect of protection-duration on the changes in community turnover rates within and across our study sites, but instead we detected a significant effect of site location with the offshore sites showing greater similarity in composition between successive samples; this may well reflect the greater reef development associated with the offshore sites (Pichon 1977).

An aspect of reef fish succession that is strongly influenced by protection-duration lies in the changing patterns of species dominance in terms of biomass. At the spatio-temporal scale that we observed, large-bodied and ubiquitous species such as *Chlorurus bleekeri* are the ones to gain the most consistent dominance with protection-duration. Other species that are ubiquitous, but small or medium-bodied such as *Thalassoma lunare* may show biomass dominance initially in younger marine reserves, but may lose this dominance to large-bodied species over protection-duration. In addition, our results showed that the majority of species that may gain dominance with protection-duration are probably site-specific. The actual mechanisms driving the site-specific dominance of species need exploration in future research.

Our current presentation of patterns of reef fish community succession within marine reserves is the most sampling-intensive and species-comprehensive study on this topic to date. The intensive monthly sampling within each site means that we have captured the relatively short-term temporal variations in community changes within each site and are therefore confident of the succession trends that are illustrated. In addition, the coverage of multiple marine reserves that fell along ordinal categories of protection-duration (spanning 0-10 years) and site location (relative distance from the mainland) means that we have captured spatio-temporal variability that is relevant to heterogeneity of reef fish organization. However, based on our results, it is apparent that longer-term studies of reef fish succession within marine reserves will be needed to confirm the patterns that we observed such as parallel community trajectories of inshore-offshore reef fish communities or the convergence of inshore or inshore reef fish communities with protection-duration.

Overall, we found that the establishment of no-take marine reserves led to succession in reef fish communities depleted by past intensive fishing activities. Marine reserves allowed large-bodied species not exploited by fishing to grow or reside within reserves, undisturbed by further exploitation. However, the exact mechanisms of biomass recovery of species within reserves (e.g. the relative influence of population growth of post-settlement individuals versus immigration of adults) still need further investigation. In addition, the reef fish succession patterns that we observed indicated that large-bodied herbivores, zoobenthivores, and zooplanktivores are the most likely to recover first within highly depleted no-take reserves such as our study sites. The piscivore species may require longer time frames or larger marine reserve areas given their life-history strategy as we presented and discussed in Chapter 3 (Russ and Alcala 2004, McClanahan et al. 2007). The patterns of reef fish succession that we have presented are useful in clarifying current expectations of marine reserve effects and may have implications for improving future marine reserve studies and understanding of reef fish ecology and succession.

Tables

Table 5.1 Scientific, common, and family names of the 37 species that comprised the top five species contributing to the total biomass in a given site and year over the three-year study period.

Species Code	Scientific name	Common name	Family name
1	*Amblyglyphidodon curacao*	Staghorn damselfish	Pomacentridae
2	*Caesio cuning*	Red bellied fusilier	Caesionidae
3	*Cheilidopetrus qunquilineatus*	Five lined cardinalfish	Apogonidae
4	*Chelmon rostratus*	Beaked butterflyfish	Chaetodontidae
5	*Chlorurus bleekeri*	Bleeker's parrotfish	Scaridae
6	*Chlorurus bowersi*	Bower's parrotfish	Scaridae
7	*Chlorurus japanensis*	Red tail parrotfish	Scaridae
8	*Chlorurus sordidus*	Bullethead parrotfish	Scaridae
9	*Choerodon anchorago*	Anchor tusk fish	Labridae
10	*Chromis atripectoralis*	Black axil chromis	Pomacentridae
11	*Chromis viridis*	Blue green chromis	Pomacentridae
12	*Cirrhilabrus cyanopleura*	Blue side wrasse	Labridae
13	*Exyrias belissimus*	Beautiful goby	Gobiidae
14	*Gerres argyreus*	Common mojarra	Gerreidae
15	*Halichoeres scapularis*	Zigzag wrasse	Labridae
16	*Hemigymnus melapterus*	Black eye thick lip	Labridae
17	*Lutjanus argentimaculatus*	Mangrove jack	Lutjanidae
18	*Lutjanus decussatus*	Checkered snapper	Lutjanidae
19	*Lutjanus fulvus*	Yellow margined snapper	Lutjanidae
20	*Parapercis cylindrica*	Sharp nose sand perch	Pinguipedidae
21	*Parupeneus barberinoides*	Bicolor goatfish	Mullidae
22	*Pentapodus bifasciatus*	White shoulder bream	Nemipteridae
23	*Plectroglyphidodon lacrymatus*	Jewel damselfish	Pomacentridae
24	*Pomacentrus burroughi*	Burrough's damselfish	Pomacentridae
25	*Pomacentrus moluccensis*	Lemon damselfish	Pomacentridae
26	*Scarus chameleon*	Chameleon parrotfish	Scaridae
27	*Scarus flavipectoralis*	Yellow fin parrotfish	Scaridae
28	*Scarus ghobban*	Blue barred parrotfish	Scaridae
29	*Scarus niger*	Swarthy parrotfish	Scaridae
30	*Scarus psittacus*	Pale nose parrotfish	Scaridae
31	*Scarus quoyi*	Quoy's parrotfish	Scaridae
32	*Scarus rivulatus*	Surf's parrotfish	Scaridae
33	*Scolopsis bilineata*	Bridled monocle bream	Nemipteridae
34	*Scolopsis trilineata*	Three lined monocle bream	Nemipteridae
35	*Thalassoma hardwicke*	Six bar wrasse	Labridae
36	*Thalassoma lunare*	Moon wrasse	Labridae
37	*Upeneus tragula*	Freckled goatfish	Mullidae

Table 5.2 Outputs from SIMPER analyses showing the patterns of dominance (indicated by + sign) of the top five species (see Table 5.1 for complete species names) within sites every year over the three year sampling period. Also indicated are the body size class (XL = extra-large/60+ cm total length TL, L = large/30.1-60 cm TL, M = medium/ 10.1-30 cm TL, and SM = small/1-10 cm TL) and trophic categories of each species (D = detrivores, H = herbivores, ZB = zoobenthivores, ZP = zooplanktivores, and P = piscivores).

Spp. Code	Body Category	Trophic Category	A			b			C			D			E			F			g			H		
			1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
1	M	ZB					+	+																		
2	L	ZP											+					+	+	+						
3	M	P												+												
4	M	ZB									+		+													
5	L	H			+				+	+	+	+	+	+		+	+		+	+	+	+	+	+	+	+
6	L	H																			+					
7	L	H								+			+								+			+		
8	L	H					+	+																		
9	L	P	+	+					+									+						+		
10	M	ZB					+																			
11	SM	ZP													+	+	+									
12	M	ZP															+									
13	M	D		+	+																					
14	M	ZB												+												
15	M	ZB													+											
16	XL	P							+	+	+	+	+	+				+			+			+	+	+
17	XL	P																							+	+
18	L	P																+								
19	L	P																								+
20	M	ZB		+	+																					
21	M	ZB		+	+																					
22	M	ZB																	+							
23	SM	ZB				+																				
24	SM	ZP					+																			
25	SM	ZP				+	+	+							+	+	+					+				
26	L	H	+																							
27	L	H	+																							
28	XL	H								+		+								+	+			+		
29	L	H																					+			
30	M	H	+																							
31	L	H								+	+								+	+		+	+		+	+
32	L	H																				+	+			
33	M	ZB						+																		
34	M	ZB				+																				
35	M	ZP													+	+										
36	M	ZB	+	+	+				+	+	+	+	+	+	+	+	+	+	+	+		+			+	
37	M	ZB				+	+	+																		

Figures

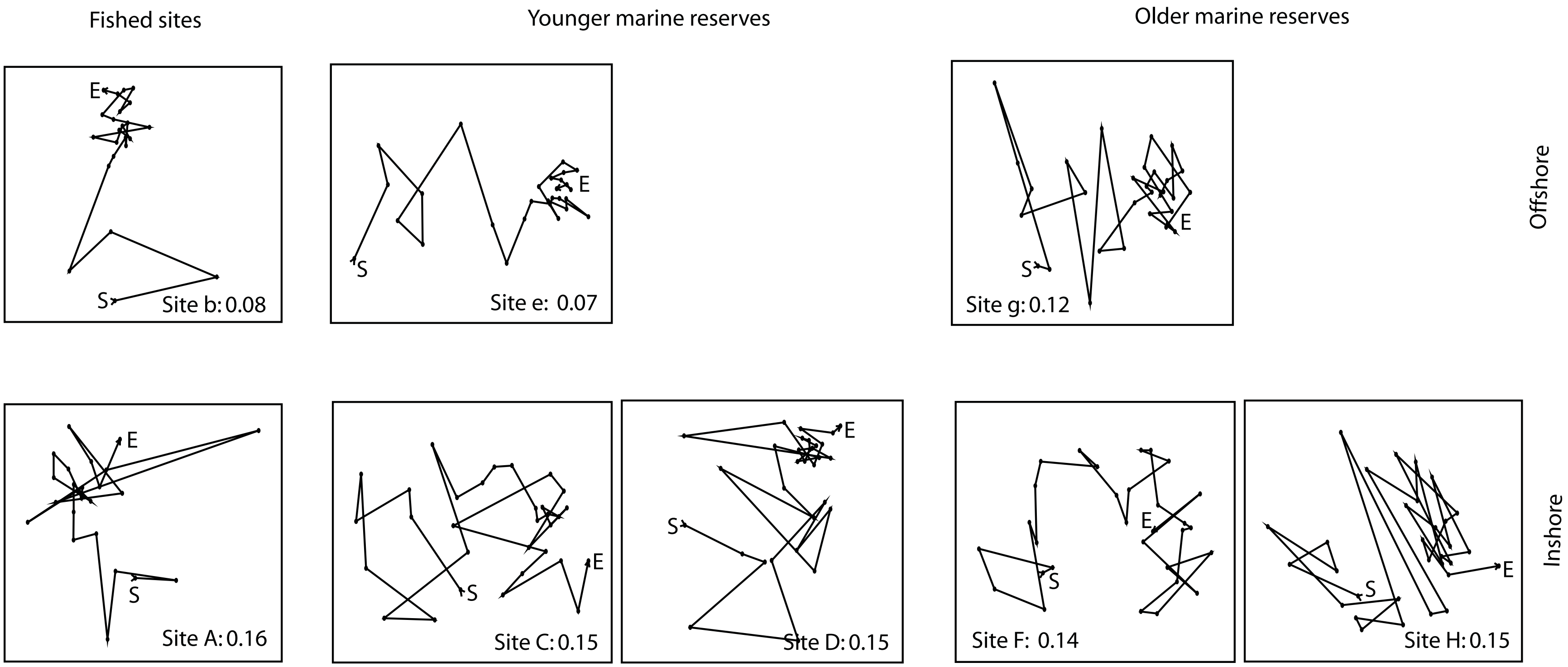


Figure 5.1 Non-metric Multidimensional Scaling (MDS) plots showing the trajectories of reef fish communities within sites over the course of three year monthly sampling time (2002-2005). The relative distance of each point (monthly samples) on MDS space is a measure of similarity (based on Bray-Curtis similarity) of species composition and relative biomass of those species between those monthly samples. Also presented are the site codes (see Table 2.1) and the stress of the MDS beside each site code. S = start of the sampling months and E = end of the sampling months.

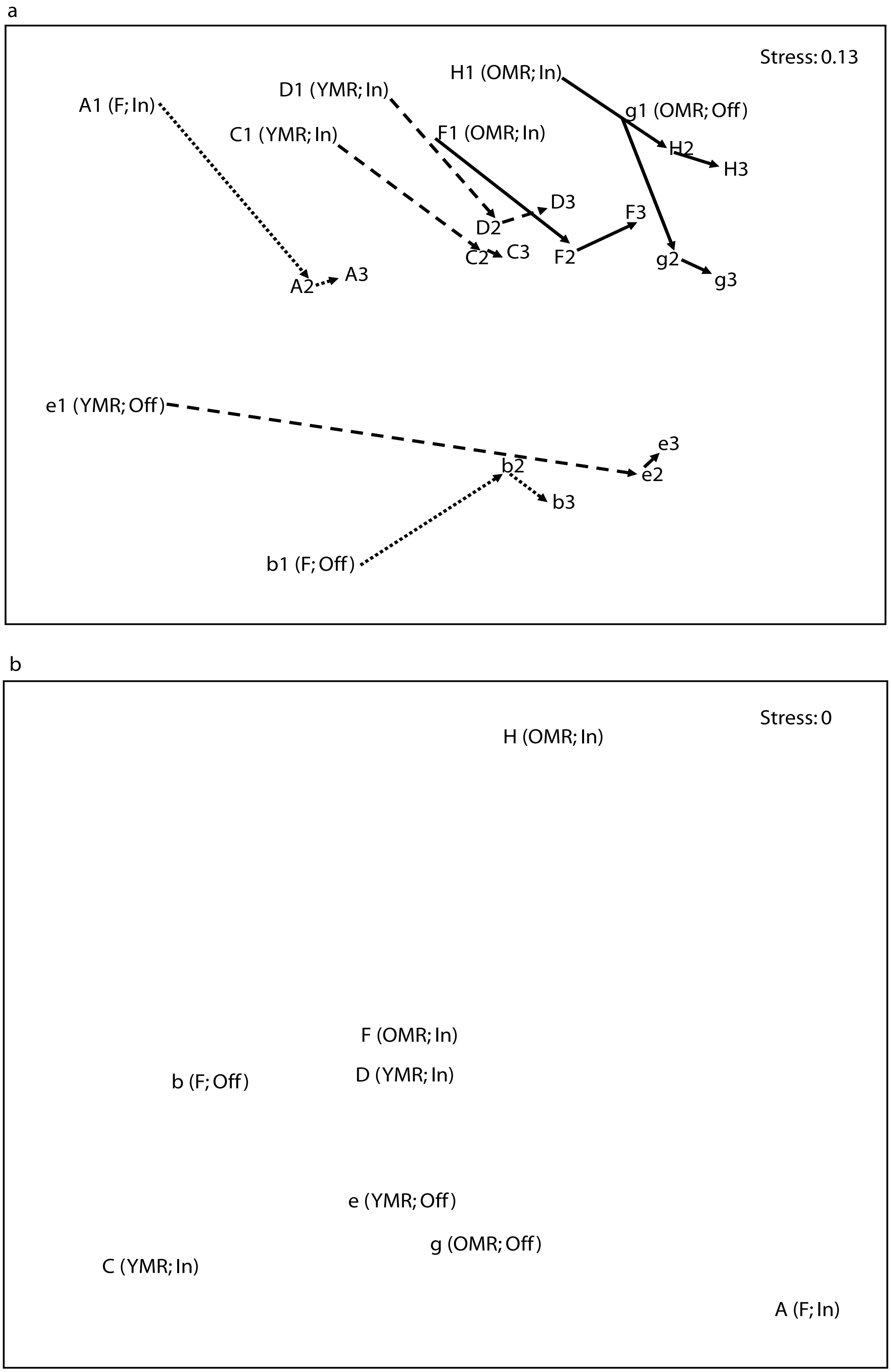

a
Stress: 0.13
A1 (F; In)
D1 (YMR; In)
H1 (OMR; In)
g1 (OMR; Off)
C1 (YMR; In)
F1 (OMR; In)
H2
H3
D3
F3
D2
C2
C3
F2
g2
g3
A2
A3
e1 (YMR; Off)
e3
b2
e2
b3
b1 (F; Off)
b
Stress: 0
H (OMR; In)
F (OMR; In)
b (F; Off)
D (YMR; In)
e (YMR; Off)
g (OMR; Off)
C (YMR; In)
A (F; In)

Figure 5.2 (a) Non-metric Multidimensional Scaling (MDS) plots showing the trajectories of reef fish communities within sites over the course of three year monthly sampling time (2002-2005). The relative distance of each point on MDS space is a measure of similarity (based on Bray-Curtis similarity) of species composition and relative annual mean biomass of those species between the three year study period. Also presented are the site codes (see Table 2.1) and the stress of the MDS beside each site code; (b) Second-stage MDS representing a measure of similarities in annual trajectories of reef fish communities within and across sites.

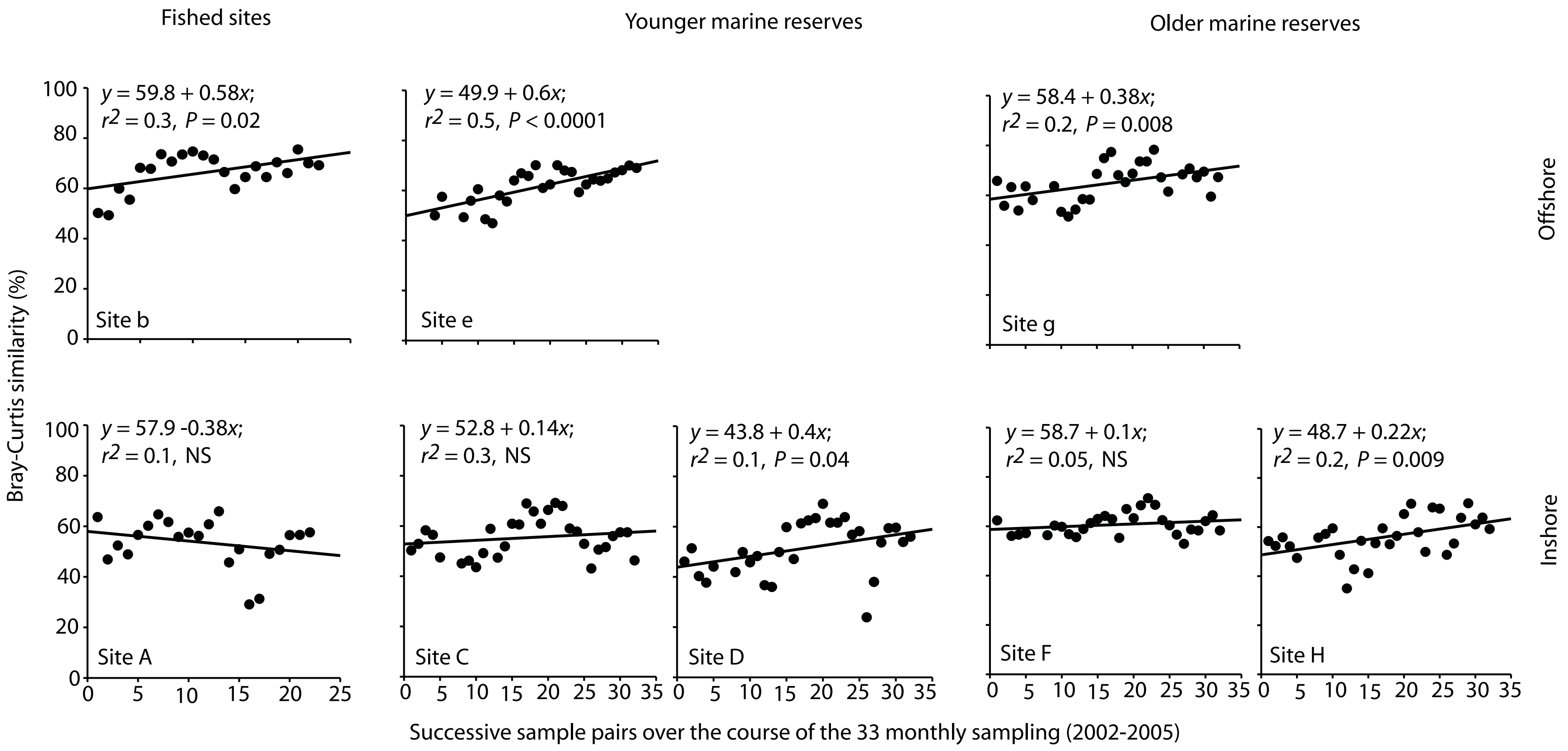


Figure 5.3 Regression of Bray-Curtis similarity values between successive monthly samples from within each site against ordinal sample pair time. Also presented are the regression models, r^2, and the *P*-values. NS means not significant.

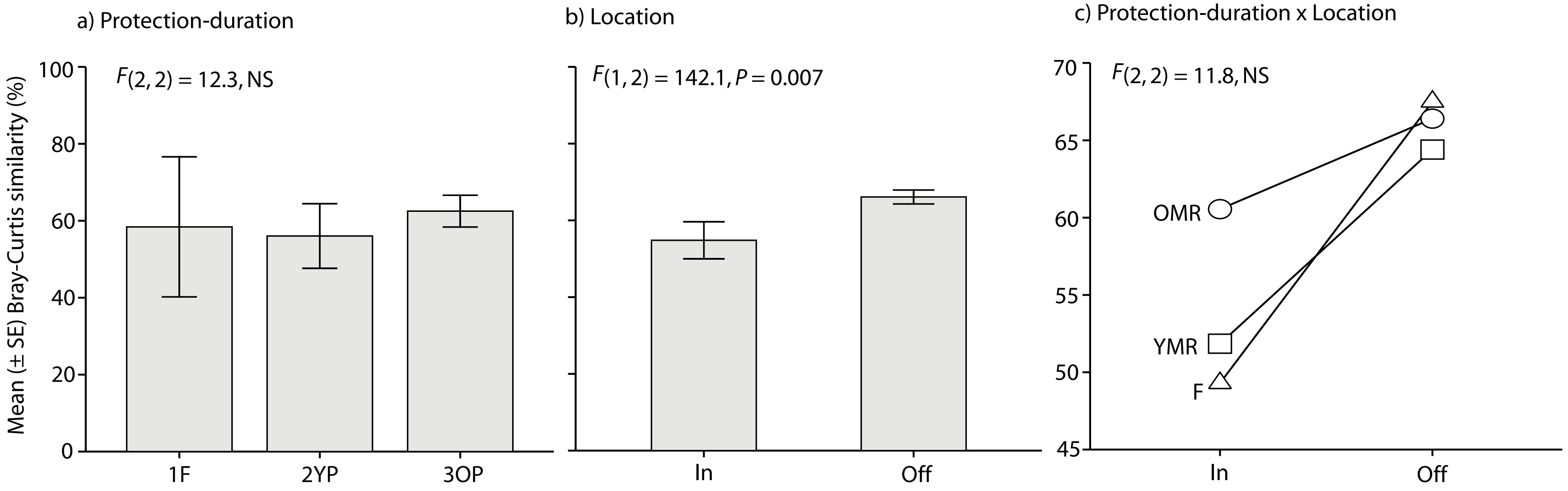


Figure 5.4 Outputs of the two-way ANOVA testing the influence of protection-duration and site location on the mean Bray-Curtis similarity of successive sample pairs within site during the third year of the sampling period. Also presented are the *F* and *P*-values of the main effects and the interaction of the two main factors.

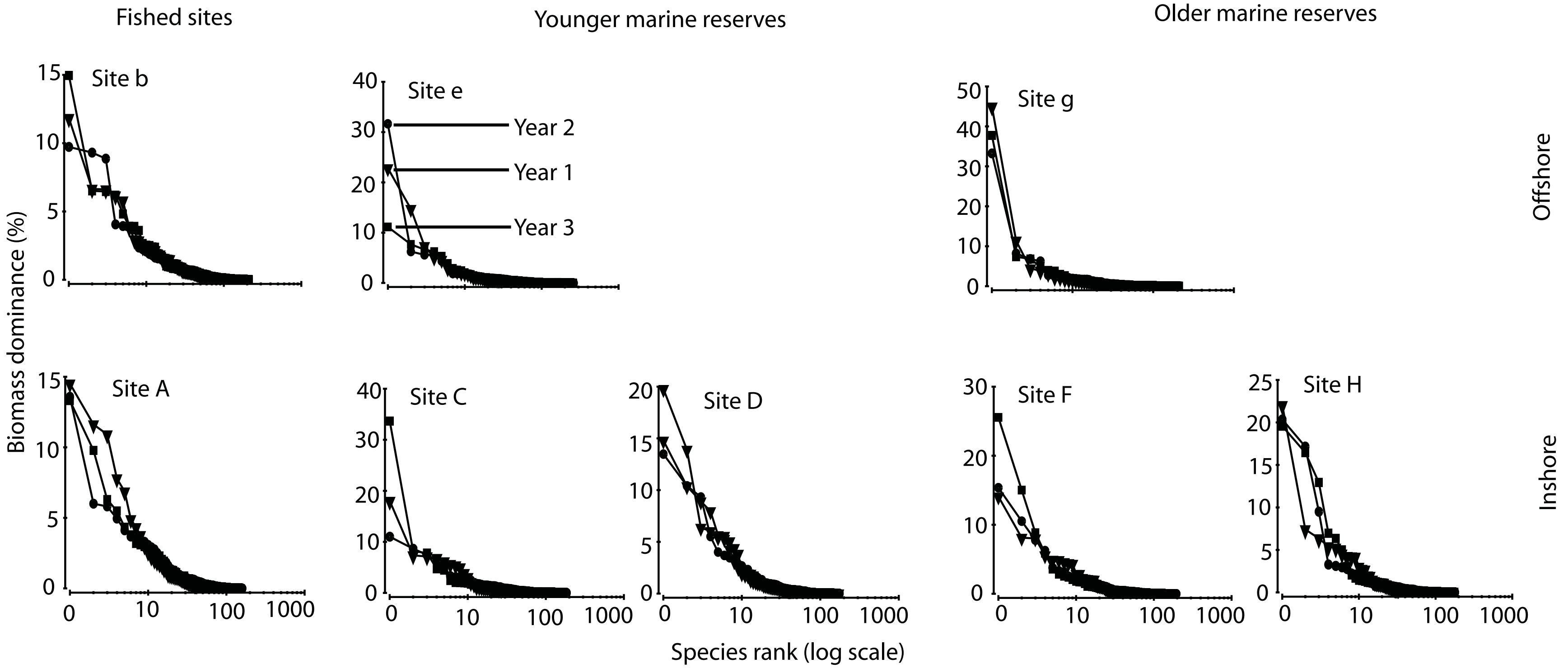


Figure 5.5 Dominance curves showing the ranking (x-axis) of reef fish species based on their contribution (percentage biomass dominance; y-axis) to the total annual mean of the monthly fish biomass estimates for each site.

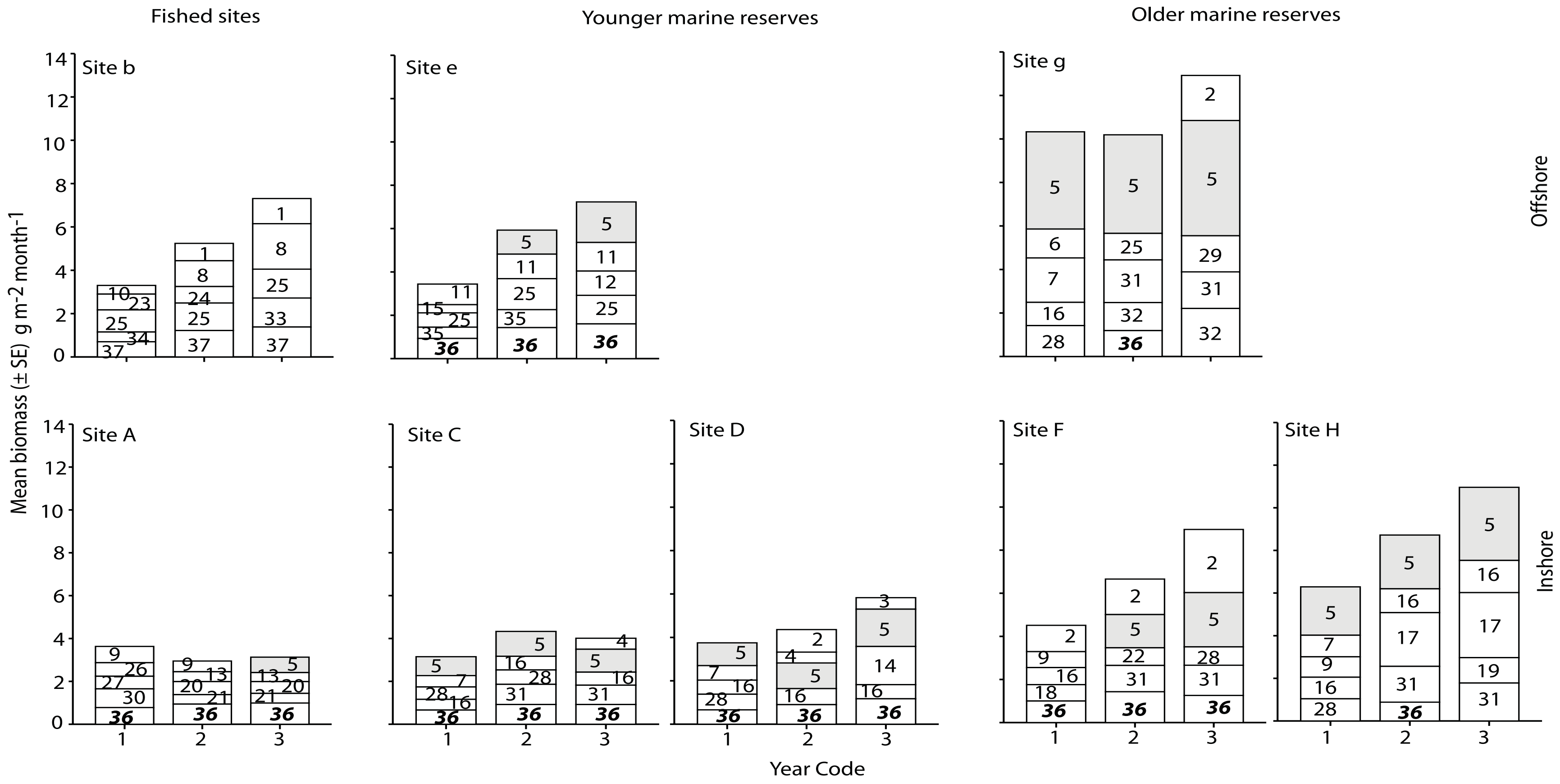


Figure 5.6 Outputs from SIMPER analyses showing the mean biomass of the top five species (species codes shown on the stack bar) contributing to the similarities reef fish communities (i.e. species composition and relative biomass of those species) between monthly samples of the three-year period sampling for each site. See Table 5.1 for the scientific, common, and family names associated with the species codes. Highlighted (1) in grey is *Chlorurus bleekeri(5)*, which showed increasing dominance with increasing protection-duration, and (2) in bold and italics is *Thalassoma lunare(36)*, which lost dominance with increasing protection-duration.

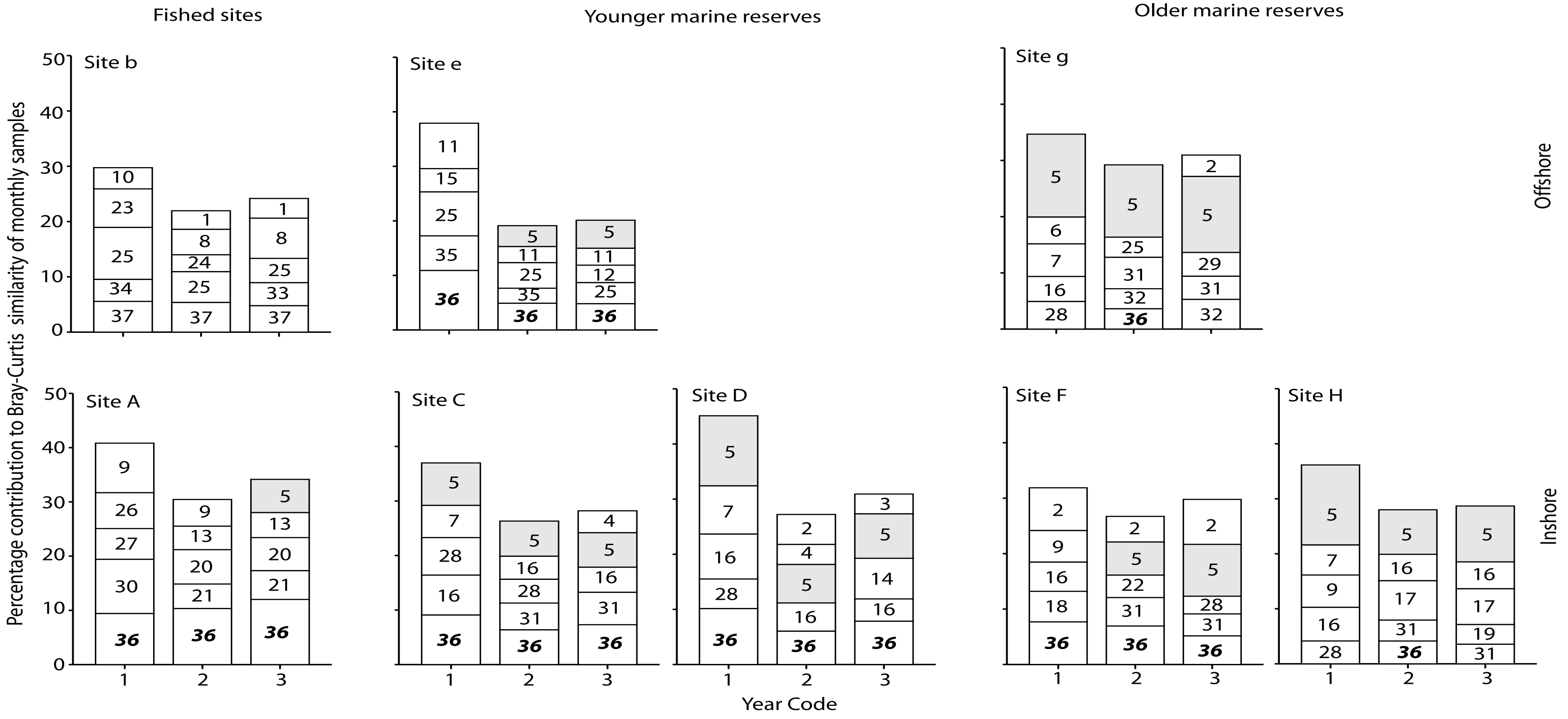


Figure 5.7 Outputs from SIMPER analyses showing the percentage contribution of the top five species (species codes shown on the stack bar) to the similarities reef fish communities (i.e. species composition and relative biomass of those species) between monthly samples of the three-year period sampling for each site. See Table 5.1 for the scientific, common, and family names associated with the species codes. Highlighted (1) in grey is *Chlorurus bleekeri(5)*, which showed increasing dominance with increasing protection-duration, and (2) in bold and italics is *Thalassoma lunare(36)*, which lost dominance with increasing protection-duration.

References

Beals, E. W. 1984. Bray-curtis ordination: an effective strategy for analysis of multivariate ecological data. Advances in Ecological Research **14**:1-55.

Bohnsack, J. A. 1983. Species turnover and the order versus chaos controversy concerning reef fish community structure. Coral Reefs **1**:223-228.

Brock, R. E., C. Lewis, and R. C. Wass. 1979. Stability and structure of a fish community on a coral patch reef. Marine Biology **54**:281-292.

Carpenter, K. E., and V. G. Springer. 2005. The center of the center of marine shore fish biodiversity: the Philippine Islands. Environmental Biology of Fishes **72**:467-480.

Chapman, M. G., and A. J. Underwood. 1998. Inconsistency and variation in the development of rocky intertidal algal assemblages. Journal of Experimental Marine Biology and Ecology **224**:265-289.

Christensen, N. L., and R. K. Peet. 1984. Convergence during secondary forest succession. Journal of Ecology **72**:25-36.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology **18**:117-143.

Clarke, K. R., and R. N. Gorley. 2006. PRIMER v6: User manual/tutorial. PRIMER-E Ltd, Plymouth, UK.

Clarke, K. R., P. J. Somerfield, L. Airoldi, and R. M. Warwick. 2006. Exploring interactions by second-stage community analyses. Journal of Experimental Marine Biology and Ecology **338**:179-192.

Clarke, K. R., and R. M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretations, 2nd edition. *in*. PRIMER-E Ltd, Plymouth, UK.

Dean, R. L., and J. H. Connell. 1987. Marine invertebrates in an algal succession. II: tests of hypotheses to explain changes in diversity with succession. Journal of Experimental Marine Biology and Ecology **109**:217-247.

Drury, W. H., and C. T. Nisbet. 1973. Succession. The Arnold Arbor. J. **54**:331-368.

Dulvy, N. K., Y. Sadovy, and C. S. Reynolds. 2003. Extinction vulnerability in marine populations. Fish and Fisheries **4**:25-64.

Foster, M. S. 1975. Algal succession in a *Macrocystis pyrifera* forest. Marine Biology **32**:313-329.

Foster, M. S., E. W. Nigg, L. M. Kiguchi, D. D. Hardin, and J. S. Pearse. 2003. Temporal variation and succession in an algal-dominated high intertidal assemblage. Journal of Experimental Marine Biology and Ecology **289**:15-39.

Fox, H. E., and M. V. Erdmann. 2000. Fish yields from blast fishing in Indonesia. Coral Reefs **19**:114.

Garcia Charton, J. A., and A. Perez-Ruzafa. 1999. Ecological heterogeneity and the evaluation of the effects of marine reserves. Fisheries Research **42**:1-20.

Gomez, E. D. 1997. Reef management in developing countries: a case study in the Philippines. Coral Reefs **16**:S3-S8.

Graham, N. A. J., R. D. Evans, and G. R. Russ. 2003. The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. Environmental Conservation **30**:200-208.

Guidetti, P. 2006. Potential of marine reserves to cause community-wide changes beyond their boundaries. Conservation Biology **21**:540-545.

Guidetti, P., and E. Sala. 2007. Community-wide effects of marine reserves in the Mediterranean Sea. Marine Ecology Progress Series **335**:43-56.

Halpern, B. S., and R. R. Warner. 2002. Marine reserves have rapid and lasting effects. Ecology Letters **5**:361-366.

Halpern, C. B. 1989. Early successional patterns of forest species: interactions of life history traits and disturbance. Ecology **70**:704-720.

Hill, F., M., J. D. Witman, and H. Caswell. 2004. Markov chain analysis of succession in a rocky subtidal community. The American Naturalist **164**:E46-E60.

Horn, H. 1976. Sucession. Pages 197-204 *in* R. May, editor. Theoritical ecology - Principles and applications. W.B. Saunders, Philadelphia, Toronto.

Horn, H. S. 1974. The ecology of secondary succession. Annual Review of Ecology and Systematics **5**:25-37.

Jackson, J. B. C. 1997. Reef since Columbus. Coral Reefs **16**:23-32.

Jennings, S. 2001. Patterns and prediction of population recovery in marine reserves. Reviews in Fish Biology and Fisheries **10**:209-231.

Jennings, S., S. S. Marshall, and N. V. C. Polunin. 1996. Seychelles' marine protected areas: comparative structure and status of reef communities. Biological Conservation **75**:201-209.

Jennings, S., J. D. Reynolds, and N. V. C. Polunin. 1999. Predicting the vulnerability of tropical reef fishes to exploitation with phylogenies and life histories. Conservation Biology **13**:1466-1475.

Kaiser, M. J., K. Ramsay, C. A. Richardson, F. E. Spence, and A. R. Brand. 2000. Chronic fishing disturbance has changed shelf sea benthic community structure. Journal of Animal Ecology **69**:494-503.

Kelleher, G. 1996. A global representative system of marine protected areas. Ocean and Coastal Management **32**:123-126.

Kim, J. H. 1997. The role of herbivory, and direct and indirect interactions, in algal succession. Journal of Experimental Marine Biology and Ecology **217**:119-135.

Lambshead, P. J. D., H. M. Platt, and K. M. Shaw. 1983. The detection of differences among assemblages of marine benthic species based on an assessment of dominance and diversity. Journal of Natural History **17**:859-874.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. The American Naturalist **112**:23.

Lubchenco, J., S. R. Palumbi, S. D. Gaines, and S. Andelman. 2003. Plugging a hole in the ocean: the emerging science of marine reserves. Ecological Applications **13**:S3-S7.

McClanahan, T. R., and N. A. J. Graham. 2005. Recovery trajectories of coral reef fish assemblages within Kenyan marine protected areas. Marine Ecology Progress Series **294**:241-248.

McClanahan, T. R., N. A. J. Graham, J. M. Calnan, and M. A. MacNeil. 2007. Towards pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. Ecological Applications **17**:1055-1067.

Micheli, F., L. Benedetti-Cecchi, S. Gambaccini, I. Bertocci, C. Borsini, G. C. Osio, and F. Romano. 2005. Cascading human impacts, marine protected areas, and the structure of Mediterranean assemblages. Ecological Monographs **75**:81-102.

Micheli, F., B. S. Halpern, L. W. Botsford, and R. R. Warner. 2004. Trajectories and correlates of community change in no-take marine reserves. Ecological Applications **14**:1709-1723.

Murray, S. N., and M. M. Littler. 1978. Patterns of algal succession in a perturbated marine intertidal community. Journal of Phycology **14**:506-512.

Nanami, A., and M. Nishihira. 2002. The structures and dynamics of fish communities in an Okinawan coral reef: effects of coral-based habitat structures at sites with rocky and sandy sea bottoms. Environmental Biology of Fishes **63**:353-372.

Nanami, A., and M. Nishihira. 2003. Population dynamics and spatial distribution of coral reef fishes: comparison between continuous and isolated habitats. Environmental Biology of Fishes **68**:101-112.

Nanami, A., and M. Nishihira. 2004. Microhabitat association and temporal stability in reef fish assemblages on massive Porites microatolls. Ichthyological Society of Japan **51**:165-171.

Pandolfi, J. M., H. Bradbury, E. Sala, T. P. Hughes, K. A. Bjorndal, R. G. Cooke, D. McArdle, L. McClenachan, M. J. H. Newman, G. Paredes, R. Warner, and J. B. C. Jackson. 2003. Global trajectories of the long-term decline of coral reef ecosystems. Science **301**:955-958.

Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres Jr. 1998. Fishing down marine food webs. Science **279**:860.

Pauly, D., R. Watson, and J. Alder. 2005. Global trends in world fisheries: impacts on marine ecosystems and food security. Philosophical Transactions of the Royal Society B **360**:5-12.

Peet, R. K. 1974. The measurement of species diversity. Annual Reviews in Ecology and Systematics **5**:285-307.

Pet-Soede, C., H. S. J. Cesar, and J. S. Pet. 1999. An economic analysis of blast fishing on Indonesian coral reefs. Environmental Conservation **26**:83-93.

Pichon, M. 1977. Physiography, morphology, and ecology of the double barrier reef of North Bohol (Philippines). Pages 261-267 *in* Proceedings of the Third International Coral Reef Symposium, Miami, Florida.

Platt, W. J., and J. H. Connell. 2003. Natural disturbances and the directional replacement of species. Ecological Monographs **73**:507-522.

Rejmanek, M., and E. Rosen. 1992. Cycles of heterogeneity during succession: a premature generalization? Ecology **73**:2329-2331.

Robles, C. D., and J. Cubit. 1981. Influence of biotic factors in an upper intertidal community: dipteran larvae grazing on algae. Ecology **62**:1536-1547.

Rodríguez, C., E. Leoni, F. Lezama, and A. Altesor. 2003. Temporal trends in species composition and plant traits in natural grasslands of Uruguay. Journal of Vegetation Science **14**:433-440.

Russ, G. R. 2002. Yet another review of marine reserves as reef fishery management tools. *in* P. F. Sale, editor. Coral Reef Fishes Dynamics and Diversity in a Complex Ecosystem. Academic Press, San Diego, California.

Russ, G. R., and A. C. Alcala. 2004. Marine reserves: long-term protection is required for full recovery of predatory fish populations. Oecologia **138**:622-627.

Sale, P. F. 1991. Reef fish communities: open non-equilibrial systems. Pages 564-598 *in* P. F. Sale, editor. The ecology of fishes on coral reefs. Academic Press, London.

Sale, P. F., R. K. Cowen, B. S. Danilowics, G. P. Jones, J. P. Kritzer, K. C. Lindeman, S. Planes, N. V. C. Polunin, G. R. Russ, Y. J. Sadovy, and R. S. Steneck. 2005. Critical science gaps impede use of no-take fishery reserves. Trends in Ecology and Evolution **20**:74-80.

Sale, P. F., and W. A. Douglas. 1984. Temporal variability in the community structure of fish on coral patch reefs and the relation of community structure to reef structure to reef structure. Ecology **65**:409-422.

Shears, N. T., and R. C. Babcock. 2002. Marine reserves demonstrate top-down control of community structure on temperate reefs. Oecologia **132**:131-142.

Shears, N. T., and R. C. Babcock. 2003. Continuing trophic cascade effects after 25 years of no-take marine reserve protection. Marine Ecology Progress Series **246**:1-16.

Sousa, W. P. 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecological Monographs **49**:227-254.

Syms, C., and G. P. Jones. 2000. Disturbance, habitat structure, and the dynamics of a coral-reef fish community. Ecology **81**:2714-2729.

Talbot, F., B. Russell, and G. Anderson. 1978. Coral reef fish communities: unstable, high-diversity systems? Ecological Monographs **48**:425-440.

Turner, S. J., S. F. Thrush, J. E. Hewitt, V. J. Cummings, and G. Funnell. 1999. Fishing impacts and the degradation or loss of habitat structure. Fisheries Management & Ecology **6**:401-420.

Wali, M. K. 1999. Ecological succession and the rehabilitation of disturbed terrestrial ecosystems. Plant and Soil **213**:195-220.

Walker, L. R., and R. del Moral. 2003. Primary succession and ecosystem rehabilitation. Cambridge University Press, Cambridge.

Walsh, W. J. 1983. Stability of a coral reef fish community following a catastrophic storm. Coral Reefs **2**:49-63.

Wellington, Z. 2006. Changes in subtidal macroinvertebrate community structure in Wellington Harbour (New Zealand) following a large-scale natural die-off. New Zealand Journal of Marine and Freshwater Research **40**:29-42.

White, A. T., H. P. Vogt, and T. Arin. 2000. Philippine coral reefs under threat: the economic losses caused by reef destruction. Marine Pollution Bulletin **40**:598-605.

Whittaker, R. J. 2000. Scale, succession and complexity in island biogeography: are we asking the right questions? Global Ecology and Biogeography **9**:75-85.

Wiens, J. A. 1984. Understanding a non-equilibrium world: myth and reality in community process. Pages 399-457 *in* D. R. J. Strong, D. Simberloff, L. Abele, and A. B. Thistle, editors. Ecological communities - Conceptual issues and evidence. Princeton University Press, Princeton.

Williams, D. M. 1982. Patterns in the distribution of fish communities across the central Great Barrier Reef. Coral Reefs **1**:35-43.

Williamson, D. H., G. R. Russ, and A. M. Ayling. 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.

Wong, D. C. L., D. Whittle, L. Maltby, and P. Warren. 2003. Multivariate analyses of invertebrate community responses to a C12–15AE-3S anionic surfactant in stream mesocosms. Aquatic Toxicology **62**:105-117.

Wood, L. J., and S. Dragicevic. 2007. GIS-Based multi-criteria evaluation and fuzzy sets to identify priority sites for marine protection. Biodiversity and Conservation **16**:2539-2558.

6. Positive reef fish population co-variations in up to ten years old marine reserves in the Philippines[*]

---

[*] A version of this chapter has been submitted for publication. Anticamara, J.A., J. Shurin, and A.C.J. Vincent. Positive reef fish population co-variations in up to ten years old marine reserves in the Philippines.

Introduction

The relative importance of various types of species interactions in shaping ecological communities is becoming an increasingly important question in ecological research (Menge 2000, Bruno et al. 2003, Maestre et al. 2003, Pennings et al. 2003). In the past, ecological research mainly focused on the role of negative interactions in driving community patterns (Connell 1972, Allen 1975, Katz 1985, Chase et al. 2002, Johnson and Agrawal 2003). In addition, the majority of previous studies on ecological interactions were focused on very few subsets of species within communities or tightly linked trophic groups (Tscharnke and Hawkins 2002). However, empirical and modelling studies have demonstrated that net positive community interaction is a very important feature, especially for disturbed or stressed habitats (Bertness and Leonard 1997), and can make important contributions to the maintenance of diversity (Hacker and Gaines 1997). In fact, an ecological modelling study has argued that species interactions when viewed at the whole system level tend to be more positive than negative; this is termed a network synergism or mutualism (Fath and Patten 1998). There is a great need to verify the relative importance of positive, neutral, and negative interactions in real ecosystems beyond those of the only ecosystem currently well documented – the intertidal marshland (Bertness and Leonard 1997, Menge 2000).

The challenge with quantifying net species interactions at the community level relates to the complexity of the actual processes associated with direct (e.g. commensalism, competition, mutualism, predation etc.) and indirect interactions (e.g. mediated interactions and trophic cascades) (Berlow 1999, Wootton and Emmerson 2005), and the difficulty of actually manipulating multiple species, especially in highly diverse systems (Freckleton and Watkinson 2001). As a starting point, ecologists have recommended the use of non-manipulative approaches or correlation of species population time-series data (i.e. +, 0, and – correlations as index of net effects of species interactions on the interacting species populations) to infer patterns of multiple species interactions within a community, especially in systems where there is a lack of prior knowledge (Underwood et al. 2000, Worm and Myers 2003, Zhang 2007). Applying these approaches to understanding the changes or differences in net community interactions in highly diverse habitats (e.g. coral reefs) with various levels of disturbances or protection (e.g. no-take marine reserves) can help clarify the relative importance of various types of species interactions in maintaining community dynamics.

Recent meta-analyses, empirical, and theoretical studies of community recovery within no-take marine reserves have all highlighted the effects of marine reserves in re-establishing community interactions (e.g. predator-prey) that were absent in most areas that are still subject to fishing (Walters et al. 1999, Shears and Babcock 2002, Graham et al. 2003, Micheli et al. 2004a, McClanahan et al. 2007). Fisheries management has shifted in recent years from approaches aimed at particular target species to an ecosystem-based perspective that aims to maintain the diverse processes and community interactions that maintain populations of exploited species (Pikitch et al. 2004). However, strategies aimed at biodiversity preservation versus resource management may be in conflict with one another as the design that exports the most exploited fish will also protect the fewest species (Hastings and Botsford 2003). Targeted species are often large predators that exert strong top-down control over entire communities (Worm and Myers 2003), therefore recovery of exploited species (e.g. predators or large-bodied species) may restructure marine ecosystems through increased predation or competition (i.e. negative interactions).

The proportion and relative importance of positive and negative community interactions within marine reserves are poorly understood. For instance, meta-analyses of community recovery within marine reserves indicated that about 19% of species showed population declines under protection presumably due to predation effects, while the other species showed population recovery trends (Micheli et al. 2004b). In addition, work in Australian marine reserves highlighted the different responses of various prey species to predation as well the preference of predators for different prey (Graham et al. 2003). Moreover, it appeared some individuals of potential prey could grow fast enough to escape predation by the recovering predators in a marine reserve (Hoegh-Guldberg 2006). The increase of potential prey populations within marine reserves can have implications for the effectiveness of marine reserves in maintaining diversity and restoring previously exploited fish populations or for species indirectly affected by exploitation through trophic cascades.

For community recovery, it is also important to probe factors that influence the dynamics of community interactions, and the stability of populations and ecosystem processes. For instance, ecological modelling has demonstrated that large and wide-ranging predators require large marine reserves in order to recover and therefore, may be replaced by small and sedentary predators in smaller reserves (Walters et al. 1999, Micheli et al. 2005). In addition, large predators require longer time-frame to recover from exploitation (Russ and Alcala 2004). Furthermore, predators can often have strong effects on lower trophic levels and ecosystem processes (Shurin et al. 2002) and may destabilize prey population dynamics (Borer et al. 2005). Thus, it is important to assess how well small marine reserves can recover trophic relationships that were affected by past fishing activities and how community interactions change with protection-duration.

In this paper, we report the temporal trends of all non-cryptic reef fish species in no-take marine reserves in the central Philippines that had been protected for 1-10 years during the three year period of the study. The two main objectives of our research were (1) to quantify the number of species showing significant population increases or declines (using monthly biomass time-series estimates) within reserves of different protection-durations, and (2) to assess and infer the net community interaction or population co-variation trends of all non-cryptic fish species by correlating monthly biomass time-series estimates within reserves with different protection–duration. Our goal was to evaluate the potential role of indirect effects in ecosystem recovery under protection, and to determine whether protection influences the types (i.e. positive, neutral, or negative interactions) or magnitudes of community interactions.

Methods

Study sites, field sampling protocol, data treatment, and general analytical approach

The study sites, field sampling protocol, data treatment, and general analytical approach were similar for the four data chapters of this thesis (Chapters 3, 4, 5, and 6), and described in details in the general methods (Chapter 2) to prevent repetition throughout the thesis. The methods and analyses specific to this chapter were described below.

Data analyses

We calculated the mean population biomass ($g \cdot m^{-2}$) of every non-cryptic fish species encountered in the eight random belt transects in each site every month (see Chapter 2). We then described the overall fish community structure across the study sites using total species richness, number of families, and number of species belonging to the five trophic categories and four body size categories (Chapter 2). We used two-way ANOVAs to test the influence of protection-duration (i.e. fished (F; n=2), younger marine reserves (YMR; n=3), and older marine reserves (OMR; n=3)) and site location (i.e. inshore (In; n=5) and offshore (Off; n=3)) on the fish community structure across the study sites.

We used linear regression to test for increases or decreases in biomass ($\log_{10}$ transformed $g \cdot m^{-2}$) of each species found in at least 50% of the 33 monthly samples for each study site. A low number of samples can weaken the power of a regression test so using only species with more than 15 estimates of biomass improved the regression results. We then used two-way ANOVA to test the differences in (1) the number of species found in at least 50% of the 33 monthly samples in sites, and (2) the number of species that showed significant biomass increase or decrease in sites over time, with protection-duration and site location as the two factors.

Correlated changes in population size may indicate the strength and direction of species interactions (Worm and Myers 2003). We examined the distribution of population co-variances among species with protection-duration and the inshore-offshore gradients. To do this, we used Pearson correlation to test the pairwise relationships between the mean monthly biomass ($g \cdot m^{-2}$) time series trends of every species that was found in at least 50% of the 33 monthly samples for each site, a method that has been recommended and applied in other community interaction studies, especially in areas with limited prior knowledge about patterns of community interaction (Connell 1983, Schoener 1983, Underwood et al. 2000, Zhang 2007). Conventionally, community interactions are measured using controlled and manipulated experiments limited to a few species (Connell 1972). However, the difficulty of manipulating multiple species in highly diverse communities means that recent studies have proposed the use of similarity, correlation, or regression approaches to measure and infer community interactions, employing population time-series data for non-manipulative experimental designs (Underwood et al. 2000, Freckleton and Watkinson 2001, Zhang 2007). We therefore plotted the distribution of the Pearson *r* correlation values between species within a site. We used two-way ANOVA to test the influence of protection-duration and site location on the main characteristic of the Pearson *r* correlation values distribution across the study sites (i.e. mean, number of unique interspecies correlations, skewness, and kurtosis).

Where interactions became stronger, or predominantly more negative or positive as fish communities recover from exploitation within marine reserves, we expect to see trends in the frequency distribution of correlation values.

Results

Significant species biomass changes within sites over time

The number of species that were found in at least 50% of the 33 monthly sampling showed an increasing trend with protection-duration for the inshore study sites, but a decline over time among offshore sites (Figure 6.1 a.1-a.3). However, the offshore sites showed a higher number of species found in 50% of the 33 monthly samplings than the inshore sites (Figure 6.1 a.2-a.3).

More species increased with protection-duration than decreased (Figure 6.1 b.1-b.3; 6.2 c.1-c.3). The number of species that showed a significant linear increase in biomass with 33 monthly sampling time was higher in the older and the younger marine reserves than in the fished sites, and also higher in the offshore sites than the inshore sites, but this trend was not significant (Figure 6.1 b.1-b.3). Fewer species showed significant declines in biomass with 33 monthly sampling time than increased (Figure 6.1 b.1-b.3; 5.2 c.1-c.3). In addition, more species showed significant declines in biomass during the 33 monthly sampling with protection-duration in the offshore sites. However, the opposite trend was observed in the inshore sites, making the main effects signal non-significant or weak (Figure 6.1 c.1-c.3).

The species that showed signs of recovery were highly variable among the six marine reserves (Figure 6.2 a-c). For instance, only 13 of the 90 species (14%) that showed significant changes in biomass over time within sites showed significant changes in at least four of the eight study sites, and the rest only showed significant changes in one to three of the eight study sites (Figure 6.2 a-c). Of the 90 species that showed significant changes, 46 were zoobenthivores (52%), 19 were herbivores (21%), 14 were zooplanktivores (15%), and 11 were piscivores (12%). In addition, of the 90 species that showed significant changes in biomass over time within sites, 39 were medium bodied (43%), 23 were small (26%), 21 were large (23%) and 7 were extra-large bodied (8%) (Figure 6.2 a-c). There was no significant influence of protection-duration and site location on the rate of changes in species biomass within sites.

Correlating species biomass time series data

The Pearson *r* correlations values of all species within each study site showed an overall normal and net positive distribution patterns (Figure 6.3). There was no significant influence of protection-duration or site location on the overall mean, skewness, or kurtosis of the correlation coefficient distribution within sites (Figure 6.4 a.1-a.3, c.1-c.3, and d.1-d.3). However, the offshore sites showed a significantly higher number of potentially interacting species (i.e. species with sufficient time series data for correlations analyses in their biomass) than the inshore sites, with more potentially interacting species found in the offshore and younger MPA site (Figure 6.4 b.1-b.3).

Discussion

Our results showed mostly positive or increasing temporal population trends of all non-cryptic species within the study sites regardless of protection-duration. This trend was apparent in the greater number of species showing significant biomass increases than declines over time, as well as in the slightly overall positive mean values of Pearson *r* correlation values within all the study sites. These results offered some evidence of the importance of non-negative interactions in relatively younger reserves and are consistent with the findings from meta-analyses that showed fewer negative than positive interactions within reserves (Micheli et al. 2004b). In addition, our results indicated that the effects of reduced fishing mortality outweighed predation effects, especially considering the fact that piscivore species hardly showed recovery in these sites yet. Also, our results are consistent with the findings and predictions from other marine reserve studies that re-establishment of negative community interactions takes longer because predators take longer to recover in marine reserves (Russ and Alcala 2004, McClanahan et al. 2007). We suggest that the negative or trophic cascade effects of recovery of exploited species, if they eventually occur, require more time to become apparent than the population recovery effects of reduced fishing mortality. Thus, our results indicated that after ten years of protection, these marine reserves are still in the earliest stages of recovery. An alternative view is that perhaps the positive net or overall community interaction that we observed in our study sites was a characteristic that helped maintain high diversity of reef system and may therefore always be slightly positive regardless of protection-duration (Fath and Patten 1998). These competing interpretations of our results can be explored in future experimental, longer term, and larger scale studies on community recovery within degraded areas that are turned into marine reserves.

In addition, the general lack of recovery among piscivores or extra-large species, and the strong recovery of herbivores, zoobenthivores, and zooplanktivores (small to large species**)** across our study sites, suggested a pattern of succession within marine reserves that is strongly influenced by life history strategies (see Chapters 3 and 5). Other studies on community recovery within marine reserves have also noted the different responses of species and life history groups (Mosquera et al. 2000, Côté et al. 2001, Micheli et al. 2004b, McClanahan et al. 2007). However, many of these studies have emphasized that targeted species by the fisheries showed the strongest signs of recovery. In our study system, fishers tended to catch any fish that could be eaten or sold in the market (including in the aquarium trade), making it difficult to distinguish target from non-target species, although there was still a general preference for large-bodied species that commanded higher market price. If we consider body size as the main determinant of fishers' preference, then our data show that recovery was not mainly a function of being previously targeted by fishers; the majority of the species that showed recovery in our sites were small to medium-bodied species, fewer were large and even fewer were extra large-bodied species. Therefore, we argue that life history strategies are perhaps a more important driver of recovery in our study sites. This result is consistent with other marine reserve findings that showed a relatively quicker recovery of herbivore species that were able to escape predation by growing large enough to achieve refuge as a function of their size (Hoegh-Guldberg 2006).

Although we found general trends in the recovery of life history groups across our study sites, our species level analyses showed a strong indication of site-specific recovery (Figure 6.2) (see Chapters 3, 4 and 5). This could mean that site specific conditions were important in determining recovery processes within marine reserves. The relative importance of site heterogeneity in the recovery processes has been highlighted in a regional study of a group of marine reserved in the Mediterranean region (Benedetti-Cecchi et al. 2003). However, marine reserve studies within any given region have generally been limited to a few sites, making it difficult to compare site differences in recovery. In the Philippines, the most thorough documentation of recovery inside two marine reserves (Apo and Sumilon Island) also suggests the effects of site heterogeneity wherein Sumilon tended to show greater fish biomass and abundance values than Apo despite the longer protection for the latter (Russ and Alcala 1996, 1999).

Overall, our results offered a comprehensive account of the temporal changes in all non-cryptic fish species within a suite of marine reserves in the central Philippines. Our main findings indicated more positive than negative population correlations across our study sites at this stage. These results hinted that, at this stage, more species were showing synchronous recovery or population trends across our study sites, and that top-down predation, if it occurred, was still relatively weak. Also, our results showed that young marine reserves such as our study sites offered opportunities for small to large-bodied herbivores, zoobenthivores, and zooplanktivores, but not as many for large to extra large-bodied species that may require longer time frame and larger areas to recover fully (Russ and Alcala 2004, McClanahan et al. 2007). Moreover, our results demonstrated that community recovery with marine reserves might be site-specific and could be a consequence of the spatial heterogeneity of factors and processes operating across various sites, although this still needs further exploration (Benedetti-Cecchi et al. 2003). These results illustrated that small marine reserves can help recover reef communities that have been depleted by previous overexploitation. However, the recovery of top predator species and the restoration of negative or predator-prey trophic interactions will require longer than the 3-10 years protection-duration of our study sites.

Figures

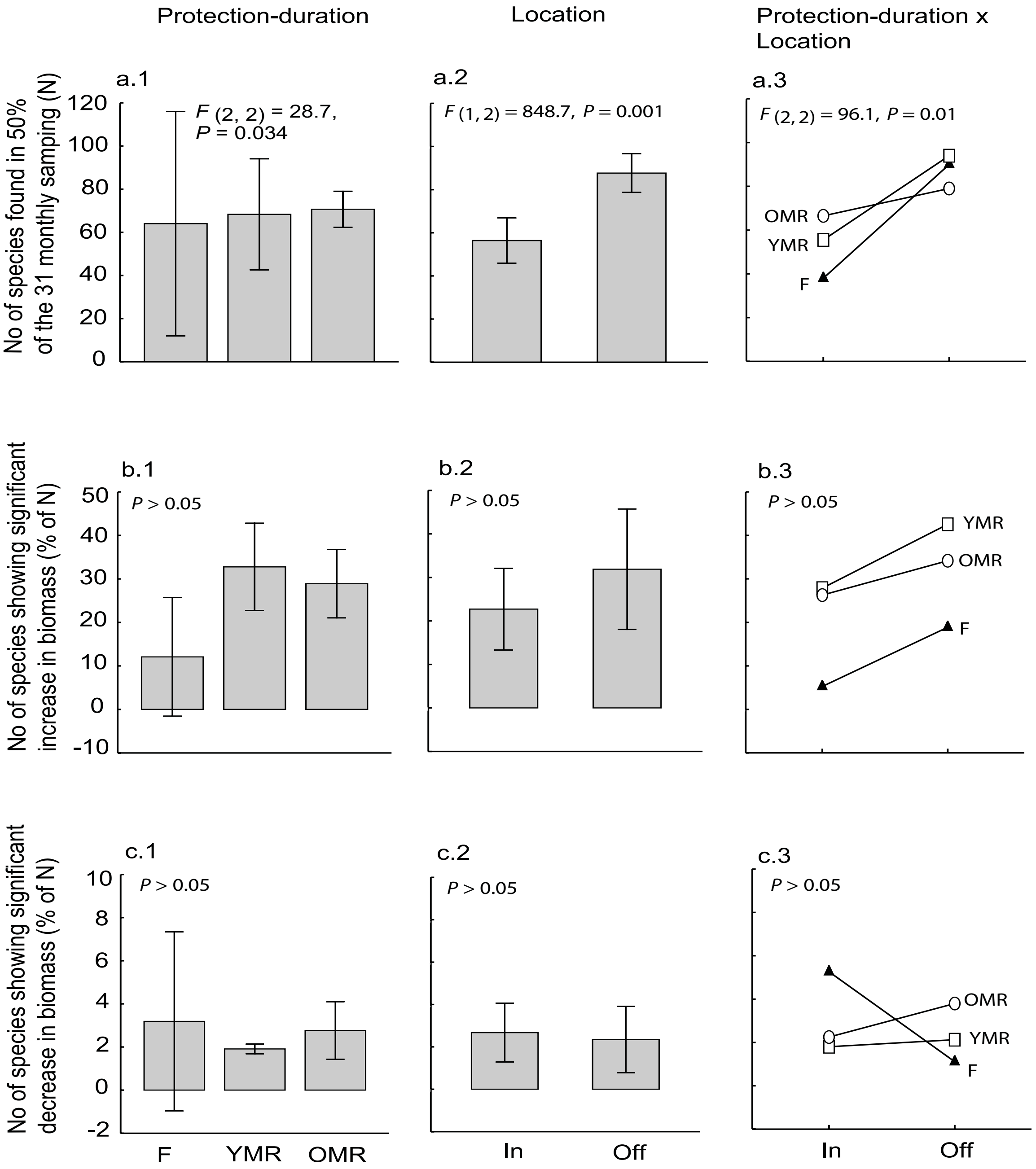
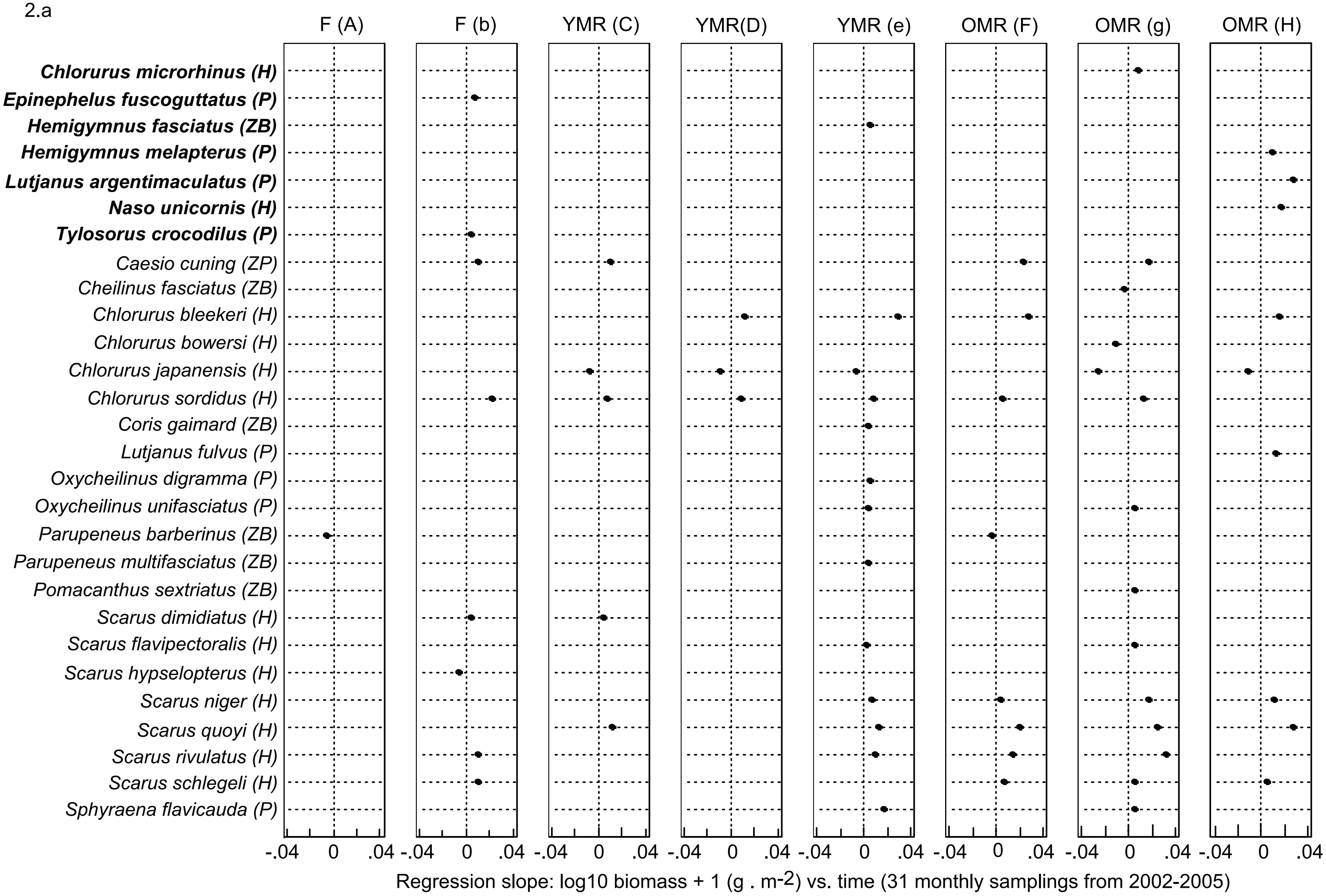
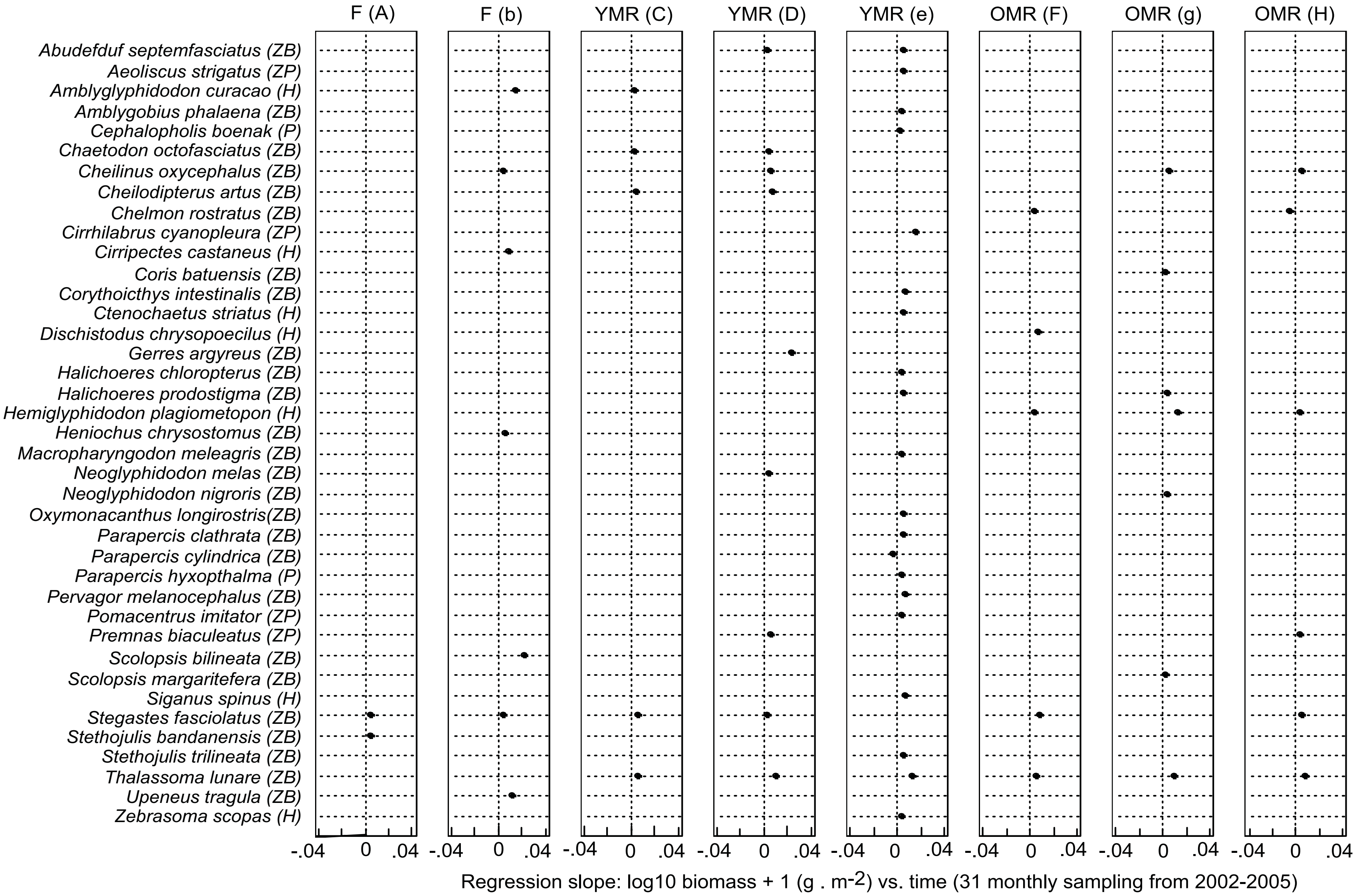


Figure 6.1 Two-way ANOVA testing the influence of protection-duration (F = fished, YMR = younger marine reserves (1-3 years old), OMR = older marine reserves (3-10 years old)) and site location (In = inshore and Off = offshore) on (a) the number of species found in 50 percent of the 31 monthly sampling within sites, (b) the percentage of species showing significant increase within sites over time, and (c) the percentage of species showing significant decline within sites over time. Also presented are the *F* and *P*-values (NS = non-significant). Error bars are standard errors.

2.a


F (A)
F (b)
YMR (C)
YMR(D)
YMR (e)
OMR (F)
OMR (g)
OMR (H)
Chlorurus microrhinus (H)
Epinephelus fuscoguttatus (P)
Hemigymnus fasciatus (ZB)
Hemigymnus melapterus (P)
Lutjanus argentimaculatus (P)
Naso unicornis (H)
Tylosorus crocodilus (P)
Caesio cuning (ZP)
Cheilinus fasciatus (ZB)
Chlorurus bleekeri (H)
Chlorurus bowersi (H)
Chlorurus japanensis (H)
Chlorurus sordidus (H)
Coris gaimard (ZB)
Lutjanus fulvus (P)
Oxycheilinus digramma (P)
Oxycheilinus unifasciatus (P)
Parupeneus barberinus (ZB)
Parupeneus multifasciatus (ZB)
Pomacanthus sextriatus (ZB)
Scarus dimidiatus (H)
Scarus flavipectoralis (H)
Scarus hypselopterus (H)
Scarus niger (H)
Scarus quoyi (H)
Scarus rivulatus (H)
Scarus schlegeli (H)
Sphyraena flavicauda (P)
-.04 0 .04 -.04 0 .04 -.04 0 .04 -.04 0 .04 -.04 0 .04 -.04 0 .04 -.04 0 .04 -.04 0 .04
Regression slope: log10 biomass + 1 (g . m-2) vs. time (31 monthly samplings from 2002-2005)

2.b


F (A)
F (b)
YMR (C)
YMR (D)
YMR (e)
OMR (F)
OMR (g)
OMR (H)
Abudefduf septemfasciatus (ZB)
Aeoliscus strigatus (ZP)
Amblyglyphidodon curacao (H)
Amblygobius phalaena (ZB)
Cephalopholis boenak (P)
Chaetodon octofasciatus (ZB)
Cheilinus oxycephalus (ZB)
Cheilodipterus artus (ZB)
Chelmon rostratus (ZB)
Cirrhilabrus cyanopleura (ZP)
Cirripectes castaneus (H)
Coris batuensis (ZB)
Corythoicthys intestinalis (ZB)
Ctenochaetus striatus (H)
Dischistodus chrysopoecilus (H)
Gerres argyreus (ZB)
Halichoeres chloropterus (ZB)
Halichoeres prodostigma (ZB)
Hemiglyphidodon plagiometopon (H)
Heniochus chrysostomus (ZB)
Macropharyngodon meleagris (ZB)
Neoglyphidodon melas (ZB)
Neoglyphidodon nigroris (ZB)
Oxymonacanthus longirostris(ZB)
Parapercis clathrata (ZB)
Parapercis cylindrica (ZB)
Parapercis hyxopthalma (P)
Pervagor melanocephalus (ZB)
Pomacentrus imitator (ZP)
Premnas biaculeatus (ZP)
Scolopsis bilineata (ZB)
Scolopsis margaritefera (ZB)
Siganus spinus (H)
Stegastes fasciolatus (ZB)
Stethojulis bandanensis (ZB)
Stethojulis trilineata (ZB)
Thalassoma lunare (ZB)
Upeneus tragula (ZB)
Zebrasoma scopas (H)
-.04
0
.04
Regression slope: log10 biomass + 1 (g . m-2) vs. time (31 monthly sampling from 2002-2005)

2.c

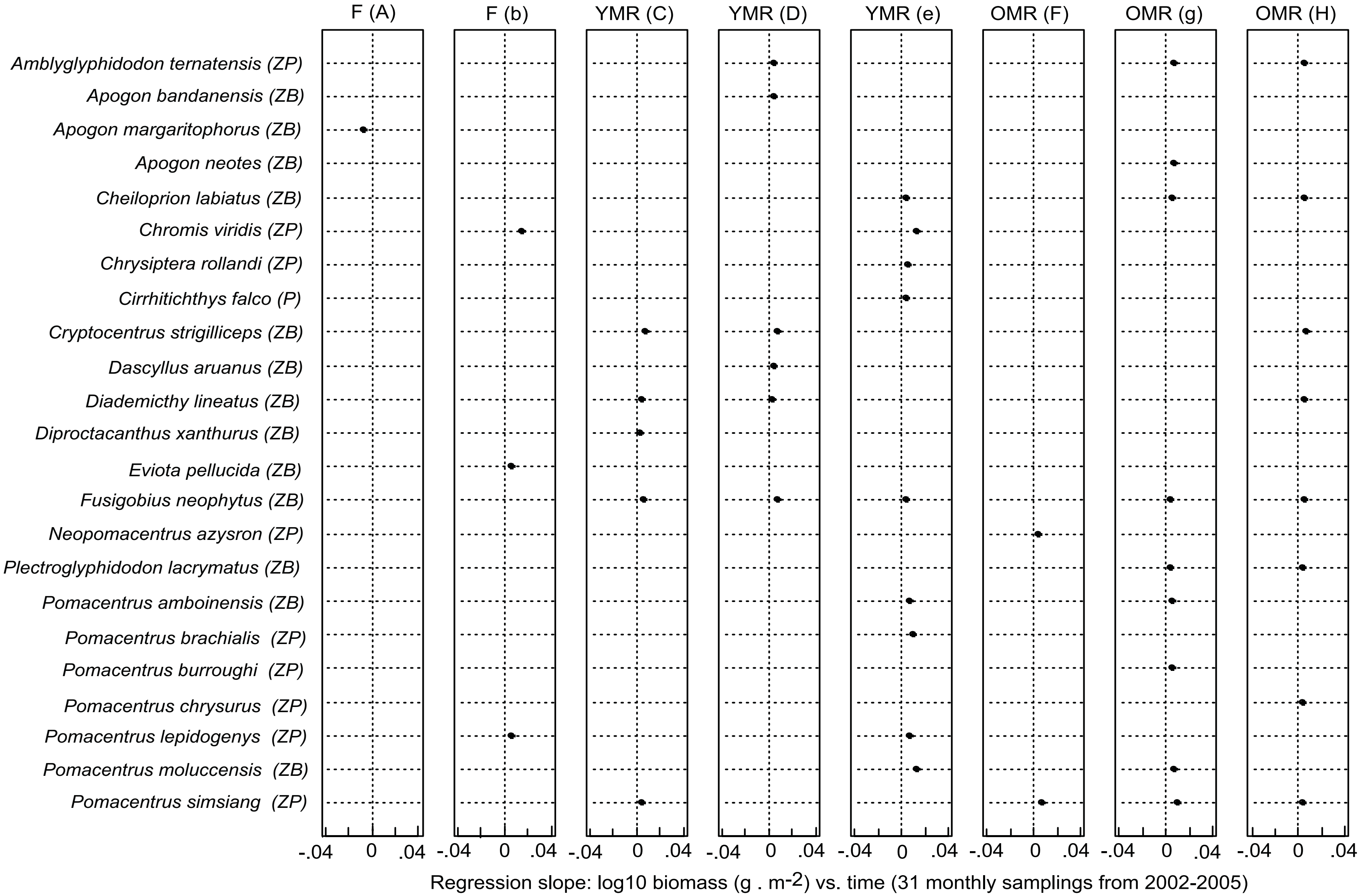

F (A)
F (b)
YMR (C)
YMR (D)
YMR (e)
OMR (F)
OMR (g)
OMR (H)
Amblyglyphidodon ternatensis (ZP)
Apogon bandanensis (ZB)
Apogon margaritophorus (ZB)
Apogon neotes (ZB)
Cheiloprion labiatus (ZB)
Chromis viridis (ZP)
Chrysiptera rollandi (ZP)
Cirrhitichthys falco (P)
Cryptocentrus strigilliceps (ZB)
Dascyllus aruanus (ZB)
Diademicthy lineatus (ZB)
Diproctacanthus xanthurus (ZB)
Eviota pellucida (ZB)
Fusigobius neophytus (ZB)
Neopomacentrus azysron (ZP)
Plectroglyphidodon lacrymatus (ZB)
Pomacentrus amboinensis (ZB)
Pomacentrus brachialis (ZP)
Pomacentrus burroughi (ZP)
Pomacentrus chrysurus (ZP)
Pomacentrus lepidogenys (ZP)
Pomacentrus moluccensis (ZB)
Pomacentrus simsiang (ZP)
-.04
0
.04
Regression slope: log10 biomass (g . m-2) vs. time (31 monthly samplings from 2002-2005)

Figure 6.2 Slope of the regression for the relationship between mean monthly biomass estimates of each species and time (3 years monthly sampling) for (a) extra-large bodied species or >60 cm maximum total length TL (bold) and large-bodied species or 30.1-60 cm TL (normal font), (b) medium-bodied species or 10.1-30 cm maximum TL, and (c) small-bodied species or 1-10 cm maximum TL. Also shown are the trophic categories of each species: H = herbivores, P = piscivores, ZB = zoobenthivores, and ZP = zooplanktivores.

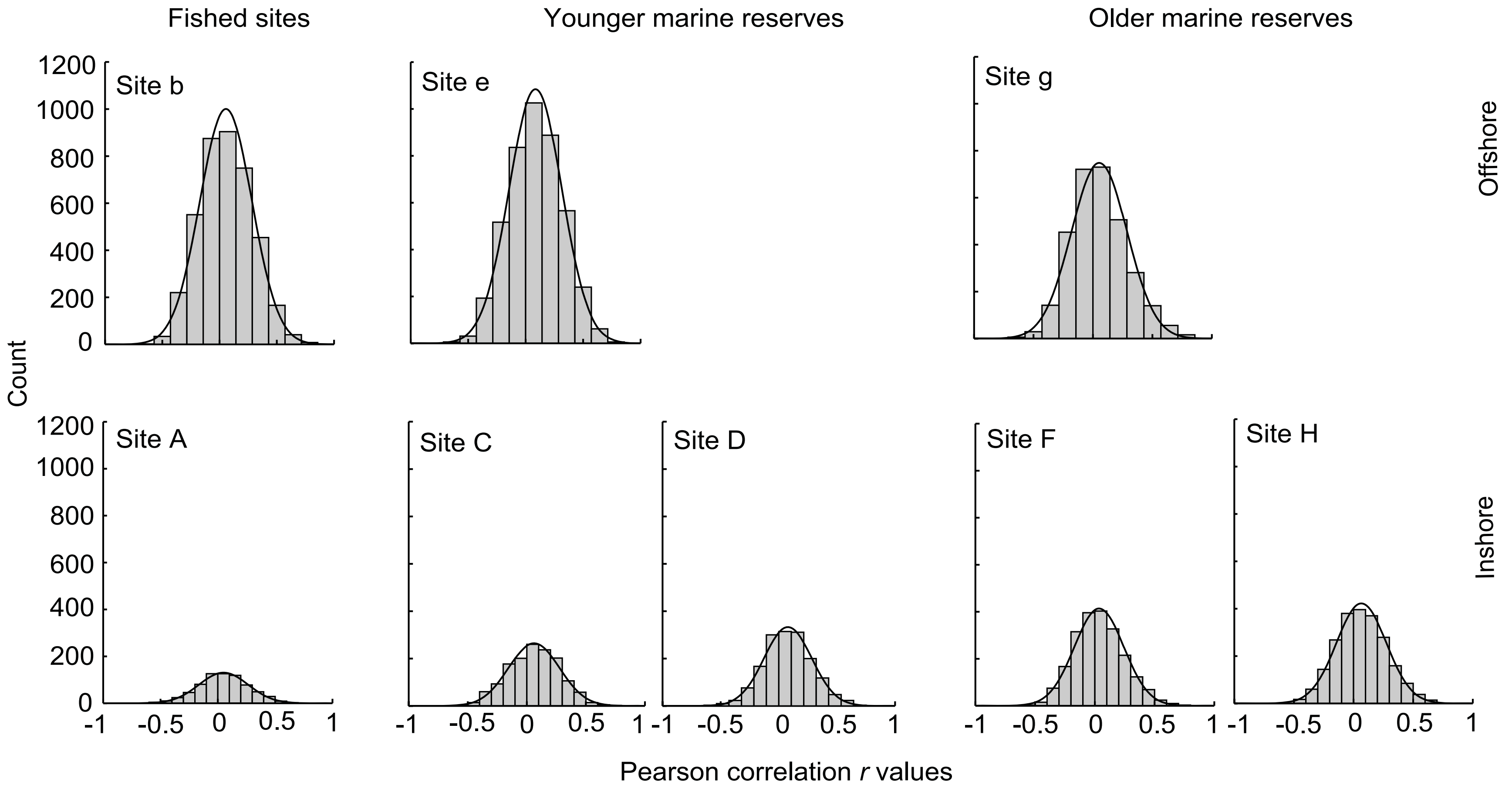


Figure 6.3 Histogram showing the frequency distribution of all the Pearson correlation *r* values between species that were found within 50% of the 31 monthly sampling within each study site.

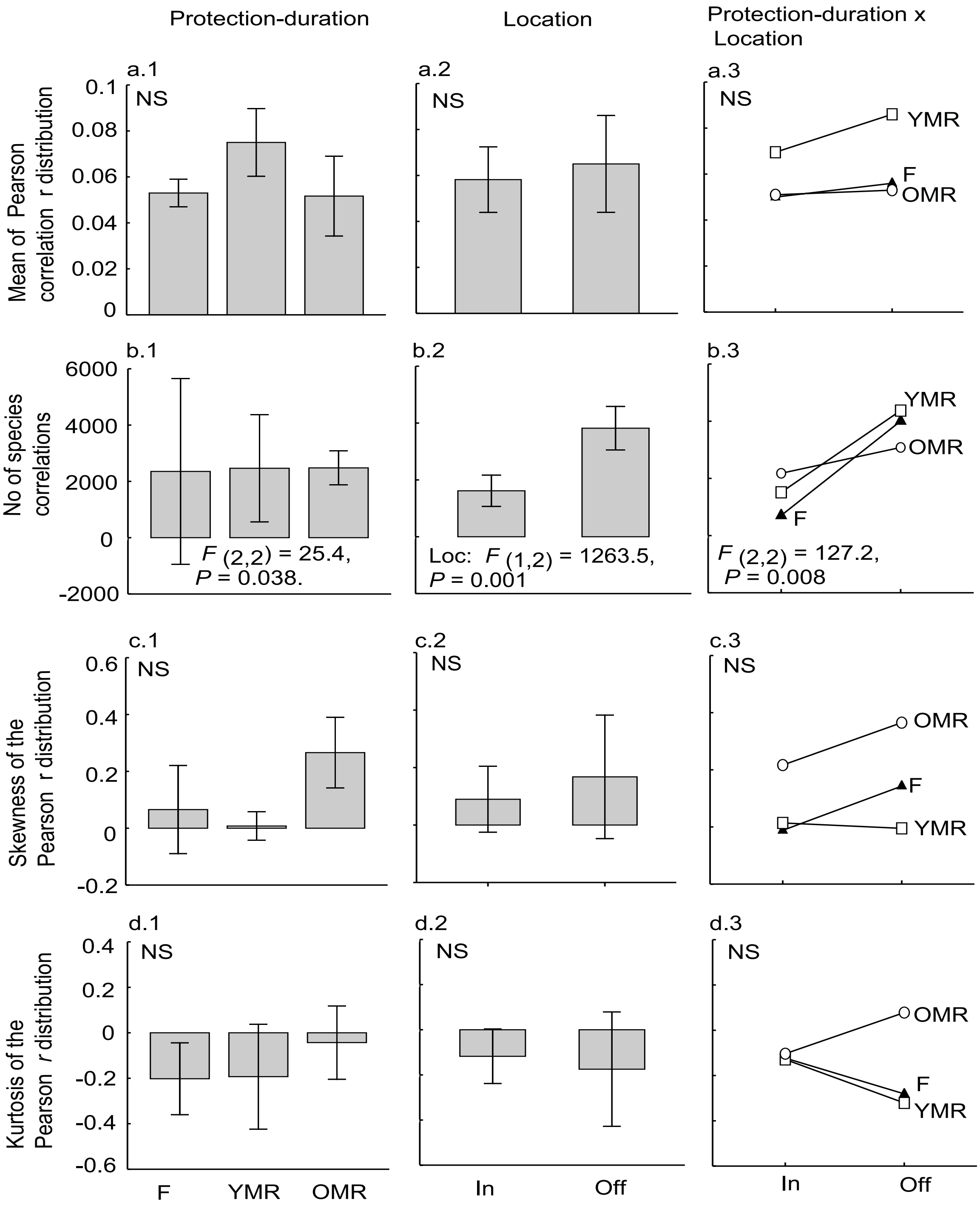


Figure 6.4 Two-way ANOVA testing the influence of protection-duration and site location on (F = fished, YMR = younger marine reserves (1-3 years old), OMR = older marine reserves (3-10 years old)) and site location (In = inshore and Off = offshore) on (a) the mean of the Pearson *r* values distributions, (b) number of unique species correlations, (c) skewness of the Pearson *r* values distributions, and (d) kurtosis of the Pearson *r* distributions within each study site. Also presented are the *F* and *P*-values (NS = non-significant).

References

Allen, J. C. 1975. Mathematical models of species interactions in time and space. The American Naturalist **109**:319-342.

Benedetti-Cecchi, L., I. Bertocci, F. Micheli, E. Maggi, E. Fosella, and S. Vaselli. 2003. Implications of spatial heterogeneity for management of marine protected areas (MPAs): examples from assemblages of rocky coasts in the northwest Mediterranean. Marine Environmental Research **55**:429-458.

Berlow, E. L. 1999. Strong effects of weak interactions in ecological communities. Nature **398**:330-334.

Bertness, M. D., and G. H. Leonard. 1997. The role of positive interactions in communities: lessons from intertidal habitats. Ecology **78**:1976-1989.

Borer, E. T., E. W. Seabloom, J. B. Shurin, K. E. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2005. What determines the strength of a trophic cascade? Ecology **86**:528-537.

Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. Trends in Ecology & Evolution **18**:119-125.

Chase, J. M., P. A. Abrams, J. P. Grover, S. Diehl, P. Chesson, R. D. Holt, S. A. Richards, R. M. Nisbet, and T. J. Case. 2002. The interaction between predation and competition: a review and synthesis. Ecology Letters **5**:302-315.

Connell, J. H. 1972. Community interactions on marine rocky intertidal shores. Annual Reviews in Ecology and Systematics **3**:169-192.

Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. The American Naturalist **122**:661.

Côté, I. M., I. Mosquera, and J. D. Reynolds. 2001. Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis. Journal of Fish Biology **59**:178-189.

Fath, B. D., and B. C. Patten. 1998. Network synergism: emergence of positive relations in ecological systems. Ecological Modelling **107**:127-143.

Freckleton, R. P., and A. R. Watkinson. 2001. Non-manipulative determination of plant community dynamics. Trends in Ecology & Evolution **16**:301-307.

Graham, N. A. J., R. D. Evans, and G. R. Russ. 2003. The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. Environmental Conservation **30**:200-208.

Hacker, S. D., and S. D. Gaines. 1997. Some implications of direct positive interactions for community species diversity. Ecology **78**:1990-2003.

Hastings, A., and L. W. Botsford. 2003. Comparing designs of marine reserves for fisheries and for biodiversity. Ecological Applications **13**:S65-S70.

Hoegh-Guldberg, O. 2006. Complexities of coral reef recovery. Science **311**:42-43.

Johnson, M. T. J., and A. A. Agrawal. 2003. The ecological play of predator–prey dynamics in an evolutionary theatre. Trends in Ecology & Evolution **18**:549-551.

Katz, C. H. 1985. A nonequilibrium marine predator-prey interaction. Ecology **66**:1426-1438.

Maestre, F. T., S. Bautista, and J. Cortina. 2003. Positive, negative, and net effects in grass-shrub interactions in Mediterranean semiarid grasslands. Ecology **84**:3186-3197.

McClanahan, T. R., N. A. J. Graham, J. M. Calnan, and M. A. MacNeil. 2007. Towards pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. Ecological Applications **17**:1055-1067.

Menge, B. A. 2000. Testing the relative importance of positive and negative effects on community structure. Trends in Ecology & Evolution **15**:46-47.

Micheli, F., P. Amarasekare, J. Bascompte, and L. R. Gerber. 2004a. Including species interactions in the design and evaluation of marine reserves: some insights from a predator-prey model. Bulletin of Marine Science **74**:653-669.

Micheli, F., L. Benedetti-Cecchi, S. Gambaccini, I. Bertocci, C. Borsini, G. C. Osio, and F. Romano. 2005. Cascading human impacts, marine protected areas, and the structure of Mediterranean assemblages. Ecological Monographs **75**:81-102.

Micheli, F., B. S. Halpern, L. W. Botsford, and R. R. Warner. 2004b. Trajectories and correlates of community change in no-take marine reserves. Ecological Applications **14**:1709-1723.

Mosquera, I., I. M. Côté, S. Jennings, and J. D. Reynolds. 2000. Conservation benefits of marine reserves for fish populations. Animal Conservation **4**:231-232.

Pennings, S. C., E. R. Selig, L. T. Houser, and M. D. Bertness. 2003. Geographic variations in positive and negative interactions among salt marshes plants. Ecology **84**:1527-1538.

Pikitch, E. K., C. Santora, E. A. Babcock, A. Bakun, R. Bonfil, D. O. Conover, P. Dayton, P. Doukakis, D. Fluharty, and B. Heneman. 2004. Ecosystem-based fishery management. Science **305**:346-347.

Russ, G. R., and A. C. Alcala. 1996. Marine reserves: rates and patterns of recovery and decline of large predatory fish. Ecological Applications **6**:947-961.

Russ, G. R., and A. C. Alcala. 1999. Management histories of Sumilon and Apo marine reserves, Philippines, and their influence on national marine resource policy. Coral Reefs **18**:307-319.

Russ, G. R., and A. C. Alcala. 2004. Marine reserves: long-term protection is required for full recovery of predatory fish populations. Oecologia **138**:622-627.

Schoener, T. W. 1983. Field experiments on interspecific competition. The American Naturalist **122**:240.

Shears, N. T., and R. C. Babcock. 2002. Marine reserves demonstrate top-down control of community structure on temperate reefs. Oecologia **132**:131-142.

Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2002. A cross-ecosystem comparison of the strength of trophic cascades. Ecology Letters **5**:785-791.

Tscharnke, T., and B. A. Hawkins. 2002. Multitrophic level interaction: an introduction. Pages 1-7 *in* T. Tscharnke and B. A. Hawkins, editors. Multitrophic level interactions. Cambridge University Press, Cambridge.

Underwood, A. J., M. G. Chapman, and S. D. Connell. 2000. Observations in ecology: you can't make progress on processes without understanding the patterns. Journal of Experimental Marine Biology and Ecology **250**:97-115.

Walters, C. J., D. Pauly, and V. Christensen. 1999. Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. Ecosystems **2**:539-554.

Wootton, J. T., and M. Emmerson. 2005. Measurement of interaction strength in nature. Annual Review of Ecology Evolution and Systematics **36**:419-444.

Worm, B., and R. A. Myers. 2003. Meta-analysis to cod-shrimp interactions reveal top-down control in oceanic food web. Ecology **84**:162-173.

Zhang, W. 2007. Computer inference of network of ecological interactions from sampling data. Environmental Monitoring and Assessment **124**:253-261.

7. Conclusions

First, our results indicated that although marine reserves could facilitate the recovery of previously disturbed reef fish communities, the details of this recovery were species-specific and site-specific (Chapters 3, 4 5, and 6). In addition, our data-intensive and species-comprehensive analyses illustrated that marine reserves facilitated reef fish community recovery mainly in terms of biomass, and less so in terms of abundance and species diversity (Chapters 3, 4, and 5).

Second, our results revealed that medium and large-bodied herbivores, zoobenthivores, and zooplanktivores drove most of the biomass recovery, while piscivores showed little recovery with protection-duration at the spatio-temporal scale that we observed (Chapter 3, 5, and 6). In terms of abundance and species richness, we found that the offshore sites consistently showed higher values than the inshore sites regardless of protection-duration (Chapters 3 and 4); this pattern is an indication of the importance of spatially heterogeneous factors and processes affecting reef fish communities (Williams 1991, Garcia Charton and Perez-Ruzafa 1999, Benedetti-Cecchi et al. 2003).

Third, our results demonstrated patterns of community succession within marine reserves wherein large-bodied ubiquitous species increased in biomass dominance, replacing ubiquitous, but medium or small-bodied species (Chapter 5). The trajectories of community succession across our study sites appeared to be parallel (Chapter 5), as is characteristic of spatially heterogeneous systems (Walker and del Moral 2003).

Finally, our results revealed net or overall positive interactions between species regardless of protection-duration (Chapter 6), a pattern which is consistent with previously disturbed ecosystems (Bertness and Leonard 1997) or highly diverse ecosystems (Fath and Patten 1998).

We now discuss the relationships among our main findings, their relevance to existing ecological and marine reserve knowledge, their main opportunities and limitations, and their implications for marine ecology and conservation.

Although small no-take marine reserves are reputed to facilitate recovery of reef fish communities (Halpern 2003, Alcala et al. 2005, McClanahan et al. 2007), we discovered that the actual magnitudes and rates of this recovery were low, at least within the spatio-temporal scale that we explored (Chapter 3). Our findings were, in fact, consistent with the so-called "rapid" community recovery extracted from meta-analyses of marine reserves effects (Halpern and Warner 2002). We must, therefore, caution that increases which appeared substantial when expressed relative (i.e. as a percentage) to the starting point, were actually very slow in absolute terms, especially for large piscivores or top predators (Russ and Alcala 1996, 2004, McClanahan et al. 2007). In comparison, the magnitudes and rates of recovery of herbivores, zoobenthivores, and zooplanktivores were higher than piscivores (Chapter 3). The relatively rapid recovery of herbivores (mainly family Scaridae) has also been demonstrated in other empirical marine reserve studies (Hoegh-Guldberg 2006, Mumby et al. 2006, McClanahan et al. 2007). The slower recovery of piscivores suggests that they are particularly vulnerable to high fishing exploitation and perhaps local extirpation (Dulvy et al. 2003, Cheung et al. 2005), and indicates that larger marine reserves may be required in order to protect viable populations of highly vulnerable and large predatory species (Polunin and Roberts 1993, Jennings 2001).

In contrast to fish biomass recovery, our analyses showed that marine reserves did not have a strong or significant influence on species richness (Chapter 3) or diversity indices (e.g. Simpson's 1-lambda, Pielou's evenness J, Shannon-Wiener diversity index ln(H), and Hill's N_1 diversity indices (Chapter 4) at the spatio-temporal scale of our study, although some trends of improvement could be discerned as marine reserves became older. Instead, the offshore sites consistently showed higher species richness than the inshore sites, a pattern found in other reef systems (Williams 1982, Adjeroud et al. 1998). However, detailed analyses of reef fish diversity using other indices hinted at lower values in the offshore sites than the inshore sites, thus indicating higher species dominance in the former (Chapter 4).

The cause of the inshore-offshore gradient across Danajon Bank reef systems was not explored in this thesis, but is a good target for future studies. In other systems, multiple biogeographic processes (e.g. habitat, distance from mainland, disturbance, island size or geomorphology, reef fish behaviour such as dispersal ability, and reef fish interactions) have been highlighted as factors influencing reef diversity distributions on a regional scale (Connell 1978, Williams and Hatcher 1983, Mora et al. 2003, Bouchon-Navaro et al. 2005, Nunez-Lara et al. 2005). In our case, habitats were grossly similar (e.g.

percentage cover of various benthic and coral life forms) across study sites so they did not explain the inshore-offshore diversity gradients at the spatio-temporal scale of our research. There was, however, a larger reef area in the offshore sites than the inshore sites, perhaps because sedimentation from the mainland limited reef development in the inshore sites (Pichon 1977); such sedimentation might have had a strong influence on inshore-offshore differences in most of the community recovery patterns that we observed throughout this thesis (Chapters 3, 4, 5, and 6), but needs further exploration in terms of how it actually affects reef fish communities. A good multi-factorial study could help tease apart the relative contribution of different factors on the spatial distribution of reef fish diversity across Danajon Bank.

Although protection-duration did not significantly influence spatio-temporal variation in reef fish diversity across study sites, older marine reserves had larger individuals than fished sites and younger marine reserves as indicated by the higher Biomass than Abundance comparison (ABC) curves (Chapter 3 and 4). The recovery of fish biomass in marine reserves (or the decline in fish biomass with fishing) appears to be more detectable than change in diversity indices (Russ and Alcala 1989, Jennings et al. 1996, Russ and Alcala 1998). Diversity (measured by common species richness and diversity measures as in Chapters 3 and 4) in highly diverse systems such as Danajon Bank may appear robust to exploitation (Naeem and Li 1997, McCann 2000), but the ecological and conservation implications of reduced quality or characteristics of diversity (e.g. mean body size of species) in fishing grounds needs further investigation.

As the biomass of a suite of species or life-history groups recovered with protection-duration (Chapter 3), patterns of community succession started to emerge within and across the study sites (Chapter 5). The most consistent trend of succession with protection-duration in our study sites was increasing biomass dominance of ubiquitous and large-bodied herbivore species (e.g *Chlorurus bleekeri*) and decreasing biomass dominance of ubiquitous, but medium-bodied zoobenthivore species (e.g. *Thalassoma lunare*). However, most species that showed biomass dominance with protection-duration were actually site-specific (Chapter 5).

The multivariate illustration (or grouping on MDS space) of community trajectories with protection-duration suggested convergent trends for communities at roughly similar distances from the mainland (Chapter 5). This result also suggested that if the inshore-offshore community gradient was somewhat maintained as communities recovered, then trajectories in communities might appear to be parallel (i.e. move in a similar direction, but never converge), as has been suggested for strongly spatially heterogeneous communities (Walker and del Moral 2003). The results of this analysis also demonstrated the value of multivariate approaches in the study of reef fish community succession patterns within marine reserves, contributing richer information than marine reserve succession studies which operate at the level of family (Micheli et al. 2004, McClanahan et al. 2007). However, longer term study will be needed to confirm some of the reef fish community succession patterns that our results identified.

Empirical and modelling studies suggest that marine reserves can restore negative community interactions (e.g. predation or competition) that are otherwise lost through fishing (Shears and Babcock 2003, Micheli et al. 2005, Guidetti 2006). Our correlation analyses of reef fish species biomass within sites over protection-duration indicated that the majority of the pairwise or interspecies Pearson correlation *r* values were positive (Chapter 6). This result could be interpreted to mean that the net community interactions within each marine reserve were mainly positive, regardless of protection-duration, which would be consistent with the hypothesis proposed for previously disturbed sites (Bertness and Leonard 1997, Menge 2000). Alternatively, the net positive correlation may be a general characteristic of highly diverse ecological systems (Fath and Patten 1998).

Net community interaction is becoming an important area of ecological research (Bertness and Leonard 1997, Fath and Patten 1998), expanding well beyond specific interactions (e.g. tightly linked competition, predator-prey, mutualistic, or parasitic interactions) (Maestre et al. 2003, Zhang 2007). Previous marine reserve studies showed that tightly linked predator-prey species may demonstrate strong negative interactions within marine reserves (Shears and Babcock 2002, Graham et al. 2003). However, our findings suggested that negative interactions were only one form of community interaction occurring in highly diverse systems such as reefs and might not be the most dominant or strongest interaction type (Chapter 6).

Our exploration of species correlation patterns is an important step in understanding species interactions in systems with limited prior knowledge (Underwood et al. 2000).

Although community interactions may be best demonstrated using controlled manipulations such as species removal experiments in intertidal interactions (Connell 1972, Connolly and Roughgarden 1999), such approaches are challenging in highly diverse coral reef environments. Controlling for all of the many species involved in reef fish communities is virtually impossible, even if one is able to address the open and mobile dynamics of these environments. Overall, inter-specific correlations within marine reserves of Danajon Bank over protection-duration were positive, partly because most of the species that recovered on the spatio-temporal scale that we tracked were herbivores, zoobenthivores, and zooplanktivores (Chapters 3, 5, and 6). The piscivores did not show significant recovery, so predation effects on prey species remained weaker (Chapters 3, 5, and 6). The positive net community interactions observed across the study sites also suggested weak competitive interactions among non-predatory species recovering marine reserves (Chapters 3, 5, and 6). Carefully designed multi-species interaction observation studies or experiments (Wootton and Emmerson 2005), which could be challenging logistically, will be needed to confirm the new hypothesis that net community interactions are positive in relatively younger marine reserves or are a characteristic of highly diverse systems (Chapter 6).

Strengths and challenges

Here we have presented comprehensive analyses of community changes within marine reserves, involving 423 species and based on intensive monthly sampling within eight study sites over three-year period. Recent empirical, review, and meta-analyses studies have cited the current limitations of using snapshot data (as in most extant coral reef research) to understand community recovery within marine reserves (Guidetti 2002, Russ 2002, Halpern 2003, Williamson et al. 2004, Sale et al. 2005). Our research has overcome some of the data limitations typical for marine reserve research to produce what may be the most detailed time-series analyses of reef fish community changes within marine reserves. Specifically, we have provided the following: (1) robust estimates of magnitudes and rates of community recovery within marine reserves in the total assemblage and by trophic groups and body size; (2) detailed analyses of species richness and diversity; (3) multivariate analyses of reef fish community succession within reserves, and (4) an evaluation of the overall or net species interactions or populations co-variations within marine reserves.

The main and inevitable limitations of our research relate to spatio-temporal replication. Ideally, there should be sufficient replication for all protection-duration and site location categories, to allow more robust testing by ANOVA. We should not, however, minimise the logistic challenges of greater spatial or temporal replication. In our case, the marine reserve sites that we presented here were the only well-enforced ones available in the northwest section of Danajon Bank at the time of data collection. While it certainly would have been possible to track more fished sites, the consequence would have been less sampling in each site. Additionally, a time-series longer than three years might help clarify or confirm some of the community recovery trends suggested in this thesis. Again, however, there are very real logistic and financial constraints on such intensive sampling. Finally, factors other than protection-duration and site location need to be explored. These might include factors such as (a) the relative importance of recruitment vs.

immigration in the observed biomass recovery and (b) the contribution of dispersal, predation, and microhabitat choice to diversity distribution in Danajon Bank. Addressing some of the processes and mechanisms that govern community recovery is an important next step for ecological marine reserve research.

Applications and implications of research to marine conservation

Results from this thesis suggested that there are ways to improve the selection and design of marine reserves according to the declared conservation objectives. Stakeholders, policy makers and collaborators must, therefore, clearly define their goals (Agardy et al. 2003, Halpern 2003). If the goal is to increase biomass, regardless of species, then any marine area seemingly can recover in biomass as long as it gets full protection and as long as there are source fish to initiate the recovery or perhaps migrate into the marine reserve (Jennings 2001, Samoilys et al. 2007). That said, the increase in biomass may be statistically significant but economically insignificant, begging the question of why communities in the Philippines and elsewhere support such marine reserves. Where the biomass in a reserve remains low, research clearly needs to focus on the other benefits that might accrue to communities. Among the myriad options might be fisher perceptions of more reliable catches over time or an improvement in social capital as communities organise to manage the reserve. If, on the other hand, the goal is primarily conservation – such as protecting and enhancing species richness and diversity – then we need to evaluate the these parameters across a defined geographic scale. More specifically, if the goal is to recover particular species (e.g. large-bodied piscivores), then we need to consider carefully their life history requirements (e.g. area required to maintain viable piscivore populations).

In all cases, carefully designed monitoring schemes will be needed to detect progress of marine reserves towards defined goals and thus to reduce the chance of the marine reserve being abandoned. For example, a goal of increased diversity may need intensive sampling for species richness (Willott 2001, Colwell et al. 2004), whereas a goal to recover particular species (e.g. large predators) will require a duration of monitoring appropriate for their life history (Russ and Alcala 2004, McClanahan et al. 2007).

Marine reserves can help degraded marine communities recover, but as with other conservation tools, they work better with some degree of ecological understanding. In the absence of prior knowledge, resources, and an organized scheme for designing and establishing a network of marine reserves, ad-hoc reserve selection and establishment might be the only option to reduce marine degradation and allow recovery of marine ecosystems (Allison et al. 1998, Gaston and Rodrigues 2003, Alcala and Russ 2006). Such reserves may still offer benefits (Hansen et al. in prep.), but the application of knowledge about marine systems and marine reserve effects – where available – might help achieve specific conservation goals of marine reserves (Roberts 1998, Hastings and Botsford 2003, Sale et al. 2005). However, it is worth contemplating that some coral reef systems may not be able to recovery quickly from heavy abuse, no matter how carefully we design and implement marine reserves. The best strategy, clearly, is to consider multiple management strategies such as managing fisheries exploitation outside marine reserves sustainably in addition to fully protecting portions of fishing grounds.

References

Adjeroud, M., Y. Letourneur, M. Porcher, and B. Salvat. 1998. Factors influencing spatial distribution of fish communities on a fringing reef at Mauritius, S.W. Indian Ocean. Environmental Biology of Fishes **53**:169-182.

Agardy, T., P. Bridgewater, M. P. Crosby, J. Day, P. K. Dayton, R. Kenchington, D. Laffoley, P. McConney, P. A. Murray, J. E. Parks, and L. Peau. 2003. Dangerous targets? Unresolved issues and ideological clashes around marine protected areas. Aquatic Conservation: Marine and Freshwater Ecosystems **13**:353-367.

Alcala, A. C., and G. R. Russ. 2006. No-take marine reserves and reef fisheries management in the Philippines: a new people power revolution. AMBIO: A Journal of the Human Environment **35**:245-254.

Alcala, A. C., G. R. Russ, A. P. Maypa, and H. P. Calumpong. 2005. A long-term, spatially replicated experimental test of the effect of marine reserves on local fish yields. Canadian Journal of Fisheries and Aquatic Sciences **62**:98-108.

Allison, G. W., J. Lubchenco, and M. H. Carr. 1998. Marine reserves are necessary but not sufficient for marine conservation. Ecological Applications **8**:79-92.

Benedetti-Cecchi, L., I. Bertocci, F. Micheli, E. Maggi, E. Fosella, and S. Vaselli. 2003. Implications of spatial heterogeneity for management of marine protected areas (MPAs): examples from assemblages of rocky coasts in the northwest Mediterranean. Marine Environmental Research **55**:429-458.

Bertness, M. D., and G. H. Leonard. 1997. The role of positive interactions in communities: lessons from intertidal habitats. Ecology **78**:1976-1989.

Bouchon-Navaro, Y., C. Bouchon, M. Louis, and P. Legendre. 2005. Biogeographic patterns of coastal fish assemblages in the West Indies. Journal of Experimental Marine Biology and Ecology **315**:31-47.

Cheung, W. W. L., T. J. Pitcher, and D. Pauly. 2005. A fuzzy logic expert system to estimate intrinsic extinction vulnerabilities of marine fishes to fishing. Biological Conservation **124**:97-111.

Colwell, R. K., C. X. Mao, and J. Chang. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology **85**:2717-2727.

Connell, J. H. 1972. Community interactions on marine rocky intertidal shores. Annual Reviews in Ecology and Systematics **3**:169-192.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science **199**:1302-1310.

Connolly, S. R., and J. Roughgarden. 1999. Theory of marine communities: competition, predation, and recruitment-dependent interaction strength. Ecological Monographs **69**:277-296.

Dulvy, N. K., Y. Sadovy, and C. S. Reynolds. 2003. Extinction vulnerability in marine populations. Fish and Fisheries **4**:25-64.

Fath, B. D., and B. C. Patten. 1998. Network synergism: emergence of positive relations in ecological systems. Ecological Modelling **107**:127-143.

Garcia Charton, J. A., and A. Perez-Ruzafa. 1999. Ecological heterogeneity and the evaluation of the effects of marine reserves. Fisheries Research **42**:1-20.

Gaston, K. J., and A. S. L. Rodrigues. 2003. Reserve selection in regions with poor biological data. Conservation Biology **17**:188-195.

Graham, N. A. J., R. D. Evans, and G. R. Russ. 2003. The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. Environmental Conservation **30**:200-208.

Guidetti, P. 2002. The importance of experimental design in detecting the effects of protection measures on fish in Mediterranean MPAs. Aquatic Conservation: Marine and Freshwater Ecosystems **12**:619-634.

Guidetti, P. 2006. Marine reserves re-establish lost predatory interactions and cause community changes in rocky reefs. Ecological Applications **16**:963-976.

Halpern, B. S. 2003. The impact of marine reserves: do reserves work and does reserve size matter? Ecological Applications **13**:S117-S137.

Halpern, B. S., and R. R. Warner. 2002. Marine reserves have rapid and lasting effects. Ecology Letters **5**:361-366.

Hansen, G. J., N. Ban, M. L. Jones, L. Kaufman, H. Panes, M. Yasue, and A. C. J. Vincent. in prep. Hindsight in marine protected area designation and planning: a comparison of community-driven and systematic approaches in Danajon Bank, Philippines.

Hastings, A., and L. W. Botsford. 2003. Comparing designs of marine reserves for fisheries and for biodiversity. Ecological Applications **13**:S65-S70.

Hoegh-Guldberg, O. 2006. Complexities of coral reef recovery. Science **311**:42-43.

Jennings, S. 2001. Patterns and prediction of population recovery in marine reserves. Reviews in Fish Biology and Fisheries **10**:209-231.

Jennings, S., S. S. Marshall, and N. V. C. Polunin. 1996. Seychelles' marine protected areas: comparative structure and status of reef communities. Biological Conservation **75**:201-209.

Maestre, F. T., S. Bautista, and J. Cortina. 2003. Positive, negative, and net effects in grass-shrub interactions in Mediterranean semiarid grasslands. Ecology **84**:3186-3197.

McCann, K. S. 2000. The diversity-stability debate. Nature **405**:228-233.

McClanahan, T. R., N. A. J. Graham, J. M. Calnan, and M. A. MacNeil. 2007. Towards pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. Ecological Applications **17**:1055-1067.

Menge, B. A. 2000. Testing the relative importance of positive and negative effects on community structure. Trends in Ecology & Evolution **15**:46-47.

Micheli, F., L. Benedetti-Cecchi, S. Gambaccini, I. Bertocci, C. Borsini, G. C. Osio, and F. Romano. 2005. Cascading human impacts, marine protected areas, and the structure of Mediterranean assemblages. Ecological Monographs **75**:81-102.

Micheli, F., B. S. Halpern, L. W. Botsford, and R. R. Warner. 2004. Trajectories and correlates of community change in no-take marine reserves. Ecological Applications **14**:1709-1723.

Mora, C., P. M. Chittaro, P. F. Sale, J. P. Kritzer, and S. A. Ludsin. 2003. Patterns and processes in reef fish diversity. Nature **421**:933-936.

Mumby, P. J., C. P. Dahlgren, A. R. Harborne, C. V. Kappel, F. Micheli, D. R. Brumbaugh, K. E. Holmes, J. M. Mendes, K. Broad, and J. N. Sanchirico. 2006.

Fishing, Trophic Cascades, and the Process of Grazing on Coral Reefs. Science **311**:98-101.

Naeem, S., and S. Li. 1997. Biodiversity enhances ecosystem reliability. Nature **390**:507-509.

Nunez-Lara, E., J. E. Arias-Gonzales, and P. Legendre. 2005. Spatial patterns of Yucatan reef fish communities: testing models using multi-scale survey design. Journal of Experimental Marine Biology and Ecology **324**:157-169.

Pichon, M. 1977. Physiography, morphology, and ecology of the double barrier reef of North Bohol (Philippines). Pages 261-267 *in* Proceedings of the Third International Coral Reef Symposium, Miami, Florida.

Polunin, N., and C. Roberts. 1993. Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. Marine Ecology Progress Series **100**:167-176.

Roberts, C. M. 1998. Sources, sinks, and the design of marine reserve networks. Fisheries **23**:16-19.

Russ, G. R. 2002. Yet another review of marine reserves as reef fishery management tools. *in* P. F. Sale, editor. Coral Reef Fishes Dynamics and Diversity in a Complex Ecosystem. Academic Press, San Diego, California.

Russ, G. R., and A. C. Alcala. 1989. Effects of intense fishing pressure on an assemblage of coral reef fishes. Marine Ecology Progress Series **56**:13-27.

Russ, G. R., and A. C. Alcala. 1996. Marine reserves: rates and patterns of recovery and decline of large predatory fish. Ecological Applications **6**:947-961.

Russ, G. R., and A. C. Alcala. 1998. Natural fishing experiments in marine reserves 1983-1993: roles of life history and fishing intensity in family responses. Coral Reefs **17**:399-416.

Russ, G. R., and A. C. Alcala. 2004. Marine reserves: long-term protection is required for full recovery of predatory fish populations. Oecologia **138**:622-627.

Sale, P. F., R. K. Cowen, B. S. Danilowics, G. P. Jones, J. P. Kritzer, K. C. Lindeman, S. Planes, N. V. C. Polunin, G. R. Russ, Y. J. Sadovy, and R. S. Steneck. 2005. Critical science gaps impede use of no-take fishery reserves. Trends in Ecology and Evolution **20**:74-80.

Samoilys, M. A., K. M. Martin-Smith, B. G. Giles, B. Cabrera, J. A. Anticamara, E. O. Brunio, and A. C. J. Vincent. 2007. Effectiveness of five small Philippines' coral reef reserves for fish populations depends on site-specific factors, particularly enforcement history. Biological Conservation **136**:584-601.

Shears, N. T., and R. C. Babcock. 2002. Marine reserves demonstrate top-down control of community structure on temperate reefs. Oecologia **132**:131-142.

Shears, N. T., and R. C. Babcock. 2003. Continuing trophic cascade effects after 25 years of no-take marine reserve protection. Marine Ecology Progress Series **246**:1-16.

Underwood, A. J., M. G. Chapman, and S. D. Connell. 2000. Observations in ecology: you can't make progress on processes without understanding the patterns. Journal of Experimental Marine Biology and Ecology **250**:97-115.

Walker, L. R., and R. del Moral. 2003. Primary succession and ecosystem rehabilitation. Cambridge University Press, Cambridge.

Williams, D. M. 1982. Patterns in the distribution of fish communities across the central Great Barrier Reef. Coral Reefs **1**:35-43.

Williams, D. M. 1991. Patterns and processes in the distribution of coral reef fishes. Pages 437-474 *in* P. F. Sale, editor. The ecology of fishes on coral reefs. Academic Press, Inc., London.

Williams, D. M., and A. L. Hatcher. 1983. Structure of fish communities on outer slopes of inshore, mid-shelf and outer shelf reefs of the Great Barrier Reef. Marine Ecology Progress Series **10**:239-250.

Williamson, D. H., G. R. Russ, and A. M. Ayling. 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.

Willott, S. J. 2001. Species accumulation curves and the measure of sampling effort. Journal of Applied Ecology **38**:484-486.

Wootton, J. T., and M. Emmerson. 2005. Measurement of interaction strength in nature. Annual Review of Ecology Evolution and Systematics **36**:419-444.

Zhang, W. 2007. Computer inference of network of ecological interactions from sampling data. Environmental Monitoring and Assessment **124**:253-261.

8. Appendices

Appendix A. List of the 423 fish species found in the eight study sites during the three-year sampling period – 2002-2005. Also presented are life-history characteristics available for the species: (a) maximum total length; (b) size categories: small (1-10 cm), medium (10.1-30 cm), large (30.1-60 cm), and extra large (60.1+ cm); (c) parameters for length to weight conversion: Weight = a x Length ^{b}; and (d) trophic categories: detrivore, herbivore, piscivore, zoobenthivore, and zooplanktivore. The maximum length estimates were derived from FishBase. The length to weight conversion parameters a and b were either taken from FishBase (code FB) or estimated for the same genera of the similar body size and shape (code: SG). The numbers presented beside the length to weight conversion codes were the number of records available for each species or the number of similar genera records used in the estimation of parameters a and b. If records were greater than 1, then average values were presented. The trophic categories were either taken from FishBase (code FB) or based on other available information for the genera (code OT) from FishBase, fish identification books, or online websites (e.g. zipcodezoo.com and saltcorner.com) accessed in 2005. For species with varied diets, we assigned them to a trophic group based on their highest trophic food (e.g species that feed on algae, detritus, and zoobenthos were considered zoobenthivores).

Family; Scientific name	**Common name**	**Maximum length (cm)**	**Total length category**	**a**	**b**	**Trophic category**
Acanthuridae						
1 *Acanthurus auranticavus*	Surgeonfish_Orange socket	35	Large	0.0201[SG2]	3.072	Herbivore[OT]
2 *Acanthurus pyroferus*	Surgeonfish_Mimic	25	Medium	0.0018[FB1]	3	Herbivore[FB]
3 *Acanthurus thompsoni*	Surgeonfish_Thompson’s	27	Medium	0.0153[FB1]	3	Zoobenthivore[FB]
4 *Acanthurus xanthopterus*	Surgeonfish_Yellow fin	70	Extra large	0.0473[FB1]	2.787	Herbivore[FB]
5 *Ctenochaetus binotatus*	Surgeonfish_Two spot bristle tooth	22	Medium	0.081[FB1]	2.59	Herbivore[FB]
6 *Ctenochaetus striatus*	Surgeonfish_Lined bristle tooth	26	Medium	0.0137[FB1]	3.083	Herbivore[FB]
7 *Naso lituratus*	Surgeonfish_Orange spine unicorn fish	46	Large	0.0497[FB1]	2.839	Herbivore[FB]
8 *Naso unicornis*	Surgeonfish_Blue spine unicorn fish	70	Extra large	0.0328[FB1]	2.789	Herbivore[FB]
9 *Zebrasoma scopas*	Surgeonfish_Brush tail tang	20	Medium	0.0352[FB2]	2.912	Herbivore[FB]
10 *Zebrasoma veliferum*	Surgeonfish_Sail fin tang	40	Large	0.0339[FB1]	2.855	Herbivore[FB]

Appendix A continued

Family; Scientific name	Common name	Maximum length (cm)	Length category	a	b	Trophic category
Apogonidae						
11 *Apogon angustatus*	Cardinalfish_Striped	9	Small	0.0233^{FB1}	2.937	Zoobenthivore^{FB}
12 *Apogon aureus*	Cardinalfish_Ring tailed	14.5	Medium	0.017^{FB2}	2.95	Zoobenthivore^{FB}
13 *Apogon bandanensis*	Cardinalfish_Three saddled	10	Small	0.0228^{FB1}	2.966	Zoobenthivore^{OT}
14 *Apogon chrysopomus*	Cardinalfish_Spotted gill	10	Small	0.021^{SG22}	3.01	Zoobenthivore^{OT}
15 *Apogon compressus*	Cardinalfish_Split banded	12	Medium	0.0108^{FB1}	3	Zoobenthivore^{FB}
16 *Apogon cyanosoma*	Cardinalfish_Yellow striped	8	Small	0.011^{FB2}	3.24	Zoobenthivore^{FB}
17 *Apogon doederleini*	Cardinalfish_Doederlein's	14	Medium	0.0124^{FB1}	3.284	Zoobenthivore^{FB}
19 *Apogon exostigma*	Cardinalfish_Narrow striped	12	Medium	0.0205^{FB1}	2.985	Zoobenthivore^{FB}
19 *Apogon hartzfeldii*	Cardinalfish_Silver lined	10	Small	0.024^{SG2}	2.896	Zoobenthivore^{OT}
20 *Apogon kallopterus*	Cardinalfish_Spiny head	15	Small	0.0074^{FB1}	3.335	Piscivore^{FB}
21 *Apogon leptacanthus*	Cardinalfish_Long spined	6	Small	0.0127^{FB1}	3.161	Zoobenthivore^{FB}
22 *Apogon margaritophorus*	Cardinalfish_Red striped	6.5	Small	0.024^{SG2}	2.896	Zoobenthivore^{FB}
23 *Apogon melas*	Cardinalfish_Black	11	Medium	0.021^{SG22}	3.01	Zoobenthivore^{OT}
24 *Apogon multilineatus*	Cardinalfish_Many lined	11	Medium	0.021^{SG22}	3.01	Zoobenthivore^{OT}
25 *Apogon neotes*	Cardinalfish_Larval	2.7	Small	0.014^{FB1}	3.129	Zoobenthivore^{FB}
26 *Apogon notatus*	Cardinalfish_Spot nape	10	Small	0.021^{SG22}	3.01	Zoobenthivore^{FB}
27 *Apogon novemfasciatus*	Cardinalfish_Nine banded	9	Small	0.021^{SG22}	3.01	Zoobenthivore^{FB}
28 *Apogon selas*	Cardinalfish_Meteor	4	Small	0.021^{SG22}	3.01	Zoobenthivore^{FB}
29 *Apogon trimaculatus*	Cardinalfish_Three spot	14	Medium	0.0956^{FB1}	2.344	Zoobenthivore^{FB}
30 *Archamia fucata*	Cardinalfish_Narrow lined	9	Small	0.0199^{FB1}	2.921	Zoobenthivore^{FB}
31 *Archamia zosterophora*	Cardinalfish_Girdled	8	Small	0.0313^{FB1}	2.697	Piscivore^{FB}
32 *Cheilodipterus artus*	Cardinalfish_Wolf	18.7	Medium	0.0143^{SG1}	3	Zoobenthivore^{FB}
33 *Cheilodipterus macrodon*	Cardinalfish_Tiger	25	Medium	0.0041^{FB1}	3.577	Piscivore^{FB}

Appendix A continued

Family; Scientific name	Common name	Maximum length (cm)	Length category	a	b	Trophic category
34 *Cheilodipterus quinquilineatus*	Cardinalfish_Five lined	13	Medium	0.01^{FB1}	3.11	Piscivore^{FB}
35 *Fowleria variegata*	Cardinalfish_Variegated	8	Small	0.0185^{FB1}	3.191	Zoobenthivore^{FB}
36 *Rhabdamia gracilis*	Cardinalfish_Slender	6	Small	0.021^{SG22}	3.01	Zooplanktivore^{FB}
Atherinidae						
37 *Hypoatherina barnesi*	Hardyhead_Barne’s	7.9	Small	0.0105^{SG1}	2.9415	Zooplanktivore^{OT}
Balistidae						
38 *Balistapus undulatus*	Triggerfish_Orange lined	30	Medium	0.0516^{SG1}	2.875	Zoobenthivore^{FB}
39 *Balistoides viridescens*	Triggerfish_Titan	75	Extra large	0.0354^{SG1}	2.9	Zoobenthivore^{FB}
40 *Rhinecanthus verrucosus*	Triggerfish_Black patch	23	Medium	0.0522^{SG1}	2.641	Zoobenthivore^{OT}
Belonidae						
41 *Tylosorus crocodilus*	Longtom_Crocodile	150	Extra-large	0.0013^{FB2}	3.08	Piscivore^{FB}
Bleniidae						
42 *Aspidontus taeniatus*	Blenny_Mimic	12	Medium	0.0045^{SG4}	3.137	Zoobenthivore^{OT}
43 *Atrosalarias fuscus*	Blenny_Brown coral	10	Small	0.0102^{SG2}	3	Zoobenthivore^{FB}
44 *Cirrepectes castaneus*	Blenny_Chest nut	12.5	Medium	0.0064^{SG3}	2.981	Herbivore^{FB}
45 *Crossosalarias macrospilus*	Blenny_Triple spot	10	Small	0.0085^{SG2}	3.205	Herbivore^{FB}
46 *Ecsenius bimaculatus*	Blenny_Double spot	4.5	Small	0.0425^{SG1}	2.975	Herbivore^{FB}
47 *Ecsenius lividanalis*	Blenny_Blue and gold	5	Small	0.0425^{SG1}	2.975	Herbivore^{FB}
48 *Ecsenius midas*	Blenny_Midas	13	Medium	0.002^{SG1}	3.549	Herbivore^{FB}

Appendix A continued

Family; Scientific name	Common name	Maximum length (cm)	Length category	a	b	Trophic category
49 *Ecsenius yaeyamaensis*	Blenny_Coral	6	Small	0.0425[SG1]	2.975	Herbivore[FB]
50 *Enchelyurus ater*	Blenny_Black	5.5	Small	0.0425[FB1]	2.975	Herbivore[OT]
51 *Meiacanthus atrodorsalis*	Blenny_Yellow tail fang	11	Medium	0.0074[FB1]	3	Zooplanktivore[OT]
52 *Meiacanthus grammistes*	Blenny_Striped fang	11	Medium	0.002[FB1]	3.549	Zooplanktivore[OT]
53 *Meiacanthus lineatus*	Blenny_Lined fang	9.5	Small	0.002[SG1]	3.549	Zooplanktivore[OT]
54 *Plagiotremus rhinorhynchos*	Blenny_Blue striped fang	12	Medium	0.002[FB1]	3.594	Piscivore[FB]
55 *Salarias fasciatus*	Blenny_Jewelled	14	Medium	0.0099[FB1]	3	Zooplanktivore[FB]
56 *Salarias segmentatus*	Blenny_Twin spot	11	Medium	0.002[SG1]	3.549	Detrivore[FB]
Bothidae						
57 *Bothus pantherinus*	Flounder_Panther	39	Large	0.0038[FB1]	3.475	Zoobenthivore[FB]
Caesionidae						
58 *Caesio caerulaurea*	Fusilier_Scissor tail	35	Large	0.0221[FB1]	2.946	Zooplanktivore[FB]
59 *Caesio cuning*	Fusilier_Red bellied	60	Large	0.0137[FB2]	3	Zooplanktivore[FB]
60 *Caesio teres*	Fusilier_Blue and gold	40	Large	0.0137[SG1]	3	Zooplanktivore[FB]
61 *Caesio xanthonota*	Fusilier_Yellow back	40	Large	0.0137[SG1]	3	Zooplanktivore[FB]
62 *Pterocaesio pisang*	Fusilier_Yellow striped	60	Large	0.0074[FB1]	3.15	Zooplanktivore[FB]
63 *Pterocaesio tile*	Fusilier_Neon	30	Medium	0.0112[FB1]	3	Zoobenthivore[FB]
Callionymidae						
64 *Dactylopus dactylopus*	Dragonet_Fingered	30	Medium	0.0141[SG1]	2.7152	Zoobenthivore[OT]
65 *Synchiropus ocellatus*	Dragonet_Ocellated	8	Small	0.0307[SG1]	2.5334	Zoobenthivore[FB]
66 *Synchiropus splendidus*	Dragonet_Mandarin fish	6	Small	0.0307[SG1]	2.5334	Zoobenthivore[OT]

Appendix A continued

Family; Scientific name	Common name	Maximum length (cm)	Length category	a	b	Trophic category
Carangidae						
67 *Carangoides fulvoguttatus*	Trevally_Gold spotted	120	Extra large	0.0461[FB1]	2.705	Piscivore[FB]
68 *Caranx sexfasciatus*	Trevally_Big eye	120	Extra large	0.0248[FB1]	2.573	Piscivore[FB]
69 *Gnathonodon speciosus*	Trevally_Golden	110	Extra large	0.071[FB1]	2.68	Zoobenthivore[FB]
70 *Selaroides leptolepis*	Trevally_Smooth tailed	22	Medium	0.07074[FB2]	2.997	Piscivore[FB]
Centriscidae						
71 *Aeoliscus strigatus*	Razorfish	15	Medium	0.0061[SG1]	2.999	Zooplanktivore[FB]
Chaetodontidae						
72 *Chaetodon auriga*	Butterflyfish_Thread fin	23	Medium	0.0312[FB1]	2.953	Zoobenthivore[FB]
73 *Chaetodon baronessa*	Butterflyfish_Triangular	16	Medium	0.0355[SG13]	3.018	Zoobenthivore[FB]
74 *Chaetodon lineolatus*	Butterflyfish_Lined	30	Medium	0.0355[SG13]	3.018	Zoobenthivore[FB]
75 *Chaetodon lunula*	Butterflyfish_Racoon	20	Medium	0.0355[SG13]	3.018	Zoobenthivore[FB]
76 *Chaetodon melannotus*	Butterflyfish_Black back	15	Medium	0.038[FB1]	2.921	Zoobenthivore[FB]
77 *Chaetodon ocellicaudus*	Butterflyfish_Spot tail	15	Medium	0.0355[SG13]	3.018	Zoobenthivore[FB]
78 *Chaetodon octofasciatus*	Butterflyfish_Eight banded	12	Medium	0.0355[SG13]	3.018	Zoobenthivore[FB]
79 *Chaetodon oxycephalus*	Butterflyfish_Spot nape	25	Medium	0.0355[SG13]	3.018	Zoobenthivore[FB]
80 *Chaetodon rafflesii*	Butterflyfish_Latticed	18	Medium	0.0355[SG13]	3.018	Zoobenthivore[FB]
81 *Chaetodon speculum*	Butterflyfish_Oval spot	18	Medium	0.0355[SG13]	3.018	Zoobenthivore[FB]
82 *Chaetodon trifascialis*	Butterflyfish_Chevroned	15	Medium	0.0468[FB1]	2.758	Zoobenthivore[FB]
83 *Chaetodon trifasciatus*	Butterflyfish_Red fin	15	Medium	0.0294[FB3]	3.154	Zoobenthivore[FB]
84 *Chaetodon ulietensis*	Butterflyfish_Pacific double saddle	15	Medium	0.0355[SG13]	3.018	Zoobenthivore[FB]

Appendix A continued

Family; Scientific name	Common name	Maximum length (cm)	Length category	a	b	Trophic category
85 *Chaetodon vagabundus*	Butterflyfish_Vagabond	23	Medium	0.0355[SG13]	3.018	Zoobenthivore[FB]
86 *Chelmon rostratus*	Butterflyfish_Beaked	20	Medium	0.0689[FB2]	3.208	Zoobenthivore[FB]
87 *Heniochus acuminatus*	Butterflyfish_Long fin banner fish	25	Medium	0.0271[FB1]	3.061	Zoobenthivore[FB]
88 *Heniochus chrysostomus*	Butterflyfish_Pennant banner fish	18	Medium	0.0132[FB1]	3.369	Zoobenthivore[FB]
89 *Heniochus singularis*	Butterflyfish_Singular banner fish	30	Medium	0.0301[FB1]	3	Zoobenthivore[FB]
90 *Heniochus varius*	Butterflyfish_Hump head banner fish	19	Medium	0.025[FB1]	3	Zoobenthivore[FB]
91 *Parachaetodon ocellatus*	Butterflyfish_Ocellated coral fish	18	Medium	0.0355[SG13]	3.018	Zoobenthivore[FB]
Cirrhitidae						
92 *Cirrhitichthys falco*	Hawkfish_Dwarf	7	Small	0.0172[FB1]	2.977	Piscivore[FB]
93 *Cirrhitichthys oxecephalus*	Hawkfish_Pixy	8.5	Small	0.0331[FB1]	3	Piscivore[OT]
94 *Paracirrhites forsteri*	Hawkfish_Black side	22	Medium	0.0214[SG1]	3	Piscivore[FB]
Dasyatidae						
95 *Dasyatis kuhlii*	Stingray_Kuhl's	70	Extra large	0.034[FB1]	2.989	Zoobenthivore[FB]
96 *Taeniura lymma*	Stingray_Blue spotted	30	Medium	0.0087[SG1]	3	Zoobenthivore[FB]
Diodontidae						
97 *Diodon liturosus*	Porcupinefish_Black blotch	65	Extra large	0.1065[SG1]	2.535	Piscivore[FB]

Appendix A continued

Family; Scientific name	Common name	Maximum length (cm)	Length category	a	b	Trophic category
Ephippidae						
98 *Platax orbicularis*	Batfish_Orbicular	50	Large	0.0425[FB1]	2.975	Zoobenthivore[FB]
99 *Platax pinnatus*	Batfish_Long finned	30	Medium	0.0676[SG1]	2.289	Herbivore[OT]
100 *Platax teira*	Batfish_Teira	70	Extra large	0.0425[FB1]	2.975	Herbivore[FB]
Fistularidae						
101 *Fistularia commersonii*	Flutemouth_Smooth	160	Extra large	0.0006[FB1]	3	Piscivore[FB]
102 *Fistularia tabacaria*	Flutemouth_Blue spotted	200	Extra large	0.0053[FB1]	2.59	Piscivore[FB]
Gerreidae						
103 *Gerres argyreus*	Mojarra_Common	20	Medium	0.0193[SG2]	3.099	Zoobenthivore[FB]
Gobiesocidae						
104 *Diademicthys lineatus*	Clingfish_Urchin	5	Small	0.0124[SG1]	3.047	Zoobenthivore[FB]
Gobiidae						
105 *Amblyeleotris randalli*	Goby_Randall’s shrimp	12	Medium	0.0107[SG1]	3	Zoobenthivore[OT]
106 *Amblyeleotris steinitzi*	Goby_Steinitz’ shrimp	8	Small	0.0107[FB1]	3	Zoobenthivore[FB]
107 *Amblygobius decussatus*	Goby_Orange striped	8	Small	0.0133[SG1]	3	Zoobenthivore[FB]
108 *Amblygobius hectori*	Goby_Hector’s	5.5	Small	0.0212[SG1]	2.9168	Zoobenthivore[FB]
109 *Amblygobius nocturnus*	Goby_Pyjama	10	Small	0.0212[FB1]	2.9168	Zoobenthivore[OT]
110 *Amblygobius phalaena*	Goby_Banded	15	Medium	0.0245[FB1]	3	Zoobenthivore[FB]
111 *Amblygobius sphynx*	Goby_Sphinx	18	Medium	0.0069[SG1]	3	Zoobenthivore[OT]
112 *Asterropteryx semipunctata*	Goby_Starry	4	Small	0.0158[FB1]	3	Zoobenthivore[FB]

Appendix A continued

Family; **Scientific name**	**Common name**	**Maximum length (cm)**	**Length category**	**a**	**b**	**Trophic category**
113 *Cryptocentrus cinctus*	Goby_Yellow shrimp	7.5	Small	0.0096^{SG1}	3.0187	Zoobenthivore^{OT}
114 *Cryptocentrus leucostictus*	Goby_Saddled shrimp	7	Small	0.0096^{SG1}	3.0187	Zoobenthivore^{OT}
115 *Cryptocentrus strigilliceps*	Goby_Target shrimp	10	Small	0.0096^{SG1}	3.0187	Zoobenthivore^{OT}
116 *Ctenogobiops pomastictus*	Goby_Spot shrimp	6	Small	0.0096^{SG1}	3.0187	Zoobenthivore^{OT}
117 *Eviota pellucida*	Goby_Red pygmy	2.1	Small	0.0096^{SG1}	3.0187	Zoobenthivore^{OT}
118 *Exyrias belissimus*	Goby_Beautiful	13	Medium	0.0096^{SG1}	3.0187	Detrivore^{FB}
119 *Fusigobius neophytus*	Goby_Novice	7.5	Small	0.0096^{SG1}	3.0187	Zoobenthivore^{FB}
120 *Gobiodon quinquestrigatus*	Goby_Five bar coral	3.5	Small	0.0352^{FB1}	2.7196	Zoobenthivore^{OT}
121 *Paragobiodon echinocephalus*	Goby_Red head	4	Small	0.0096^{SG1}	3.0187	Zoobenthivore^{OT}
122 *Signigobius biocellatus*	Goby_Twin spot	8.5	Small	0.0096^{SG1}	3.0187	Zoobenthivore^{FB}
123 *Trimma striata*	Goby_Stripe head	3	Small	0.0096^{SG1}	3.0187	Zoobenthivore^{FB}
124 *Valenciennea sexguttata*	Goby_Six spot	14	Medium	0.0174^{FB1}	3	Zoobenthivore^{OT}
125 *Valenciennea strigata*	Goby_Blue band	15	Medium	0.0096^{SG1}	3.0187	Zoobenthivore^{OT}
Haemulidae						
126 *Diagramma labiosum*	Sweetlips_Painted	90	Extra large	0.0077^{SG1}	3.131	Zoobenthivore^{OT}
127 *Plectorhinchus chaetonoides*	Sweetlips_Many spotted	72	Extra large	0.0148^{FB1}	3.083	Zoobenthivore^{FB}
128 *Plectorhinchus lessonii*	Sweetlips_Striped	40	Large	0.0209^{SG1}	2.9474	Zoobenthivore
129 *Plectorhinchus lineatus*	Sweetlips_Diagonal banded	72	Extra large	0.044^{SG1}	2.786	Zoobenthivore^{FB}
130 *Plectorhinchus orientalis*	Sweetlips_Oriental	86	Extra large	0.044^{SG1}	2.786	Zoobenthivore^{FB}

Appendix A continued

Family; Scientific name	Common name	Maximum length (cm)	Length category	a	b	Trophic category
Holocentridae						
131 *Myripristis berndti*	Squirrelfish_Big scale	30	Medium	0.0168[FB1]	2.0612	Zoobenthivore[FB]
132 *Myripristis murdjan*	Squirrelfish_Blotch eye	27	Medium	0.0191[FB2]	3.017	Piscivore[FB]
133 *Myripristis violacea*	Squirrelfish_Latticed	35	Large	0.0411[FB1]	2.903	Zoobenthivore[FB]
134 *Sargocentron rubrum*	Squirrelfish_Red coat	32	Large	0.1185[FB2]	2.8365	Piscivore[FB]
Kyphosidae						
135 *Kyphosus cinerascens*	Drummer_Top sail	50	Large	0.0218[SG1]	3.0053	Herbivore[FB]
Labridae						
136 *Anampses geographicus*	Wrasse_Graphic tusk fish	24	Medium	0.0147[SG1]	3	Zoobenthivore[FB]
137 *Bodianus axillaris*	Wrasse_Axil spot hog fish	20	Medium	0.0145[SG2]	3.0265	Zoobenthivore[FB]
138 *Bodianus diana*	Wrasse_Diana's hog fish	25	Medium	0.0145[SG2]	3.0265	Zoobenthivore[FB]
139 *Bodianus mesothorax*	Wrasse_Split level hog fish	25	Medium	0.0145[SG2]	3.0265	Zoobenthivore[FB]
140 *Cheilinus chlorurus*	Wrasse_Floral maori	45	Large	0.0293[FB1]	2.849	Zoobenthivore[FB]
141 *Cheilinus fasciatus*	Wrasse_Red breasted	40	Large	0.0149[FB1]	3	Zoobenthivore[FB]
142 *Cheilinus oxycephalus*	Wrasse_Snooty maori	17	Medium	0.021[SG1]	2.972	Zoobenthivore[OT]
143 *Cheilinus trilobatus*	Wrasse_Triple tail maori	45	Large	0.021[FB1]	2.972	Zoobenthivore[FB]
144 *Cheilinus undulatus*	Wrasse_Hump head maori	225	Extra large	0.0123[FB1]	3.115	Zoobenthivore[OT]
145 *Cheilio inermis*	Wrasse_Cigar	50	Large	0.0036[FB1]	3.066	Piscivore[FB]
146 *Choerodon anchorago*	Wrasse_Anchor tusk fish	38	Large	0.0145[SG3]	3.125	Piscivore[FB]
147 *Choerodon cyanodus*	Wrasse_Blue tusk fish	70	Extra large	0.208[SG1]	3	Zoobenthivore[FB]
148 *Cirrhilabrus cyanopleura*	Wrasse_Blue side	15	Medium	0.0097[SG2]	3.167	Zooplanktivore[FB]
149 *Cirrhilabrus exquisitus*	Wrasse_Exquisite	12	Medium	0.0138[SG1]	3.018	Zooplanktivore[FB]

Appendix A continued

Family; Scientific name	Common name	Maximum length (cm)	Length category	a	b	Trophic category
150 *Coris aurilineata*	Wrasse_Gold lined	11.5	Medium	0.0142[SG1]	3	Zoobenthivore[OT]
151 *Coris aygula*	Wrasse_Clown coris	120	Extra large	0.0145[FB2]	3	Zoobenthivore[FB]
152 *Coris batuensis*	Wrasse_Batu coris	17	Medium	0.0048[SG1]	3.378	Zoobenthivore[FB]
153 *Coris dorsomacula*	Wrasse_Pale barred coris	20	Medium	0.0124[SG1]	2.2946	Zoobenthivore[OT]
154 *Coris gaimard*	Wrasse_Yellow tail coris	40	Large	0.0109[FB1]	3	Zoobenthivore[FB]
155 *Coris julis*	Wrasse_Mediterranean rainbow	30	Medium	0.0081[FB1]	3	Zoobenthivore[FB]
156 *Diproctacanthus xanthurus*	Wrasse_Yellow tail tube lip	10	Small	0.0109[SG1]	3	Zoobenthivore[FB]
157 *Epibulus insidiator*	Wrasse_Sling jaw	54	Large	0.0165[FB1]	3	Piscivore[FB]
158 *Gomphosus varius*	Wrasse_Bird	30	Medium	0.0099[FB1]	3	Piscivore[FB]
159 *Halichoeres argus*	Wrasse_Argus	12	Medium	0.0128[SG3]	3.006	Zoobenthivore[OT]
160 *Halichoeres biocellatus*	Wrasse_Biocellate	12	Medium	0.0148[FB1]	3	Zoobenthivore[OT]
161 *Halichoeres chloropterus*	Wrasse_Pastel green	19	Medium	0.016[FB1]	2.87	Zobenthivore[FB]
162 *Halichoeres hortulanus*	Wrasse_Checkerboard	27	Medium	0.0133[FB2]	3.03	Zoobenthivore[FB]
163 *Halichoeres margaritaceus*	Wrasse_Pink belly	12.5	Medium	0.0106[FB1]	3	Zoobenthivore[FB]
164 *Halichoeres marginatus*	Wrasse_Dusky	17	Medium	0.0091[FB2]	3.207	Zoobenthivore[FB]
165 *Halichoeres melanurus*	Wrasse_Tail spot	12	Medium	0.0109[FB1]	3	Zoobenthivore[FB]
166 *Halichoeres melaspomus*	Wrasse_Ocellated	24	Medium	0.0119[FB1]	3.064	Zoobenthivore[FB]
167 *Halichoeres nebulosus*	Wrasse_Nebulous	12	Medium	0.0128[SG1]	3.006	Zoobenthivore[FB]
168 *Halichoeres ornatissimus*	Wrasse_Ornate	18	Medium	0.0133[FB2]	3	Zoobenthivore[FB]
169 *Halichoeres prodostigma*	Wrasse_Breast spot	18.5	Medium	0.0053[SG2]	3.398	Zoobenthivore[FB]
170 *Halichoeres prosopeion*	Wrasse_Two tone	13	Medium	0.0145[SG2]	2.935	Zoobenthivore[OT]

Appendix A continued

Family; Scientific name	Common name	Maximum length (cm)	Length category	a	b	Trophic category
171 *Halichoeres purpurescens*	Wrasse_Silty	13	Medium	0.016[SG1]	2.82	Zoobenthivore[FB]
172 *Halichoeres scapularis*	Wrasse_Zigzag	20	Medium	0.0052[FB1]	3.382	Zoobenthivore[FB]
173 *Halichoeres trimaculatus*	Wrasse_Three spot	27	Medium	0.0227[FB1]	2.804	Zoobenthivore[FB]
174 *Hemigymnus fasciatus*	Wrasse_Barred thick lip	80	Extra large	0.0227[FB1]	2.804	Zoobenthivore[FB]
175 *Hemigymnus melapterus*	Wrasse_Black eye thick lip	90	Extra large	0.0182[FB1]	3	Piscivore[FB]
176 *Hologymnosus annulatus*	Wrasse_Ring	40	Large	0.0214[SG1]	3	Piscivore[FB]
177 *Hologymnosus doliatus*	Wrasse_Pastel ring	50	Large	0.0352[SG1]	3	Piscivore[FB]
178 *Labrichthys unilineatus*	Wrasse_Tube lip	17.5	Medium	0.015[FB1]	3	Zoobenthivore[FB]
179 *Labroides bicolor*	Wrasse_Bicolor	15	Medium	0.0058[SG1]	3.1716	Zoobenthivore[FB]
180 *Labroides dimidiatus*	Wrasse_Cleaner	11.5	Medium	0.0076[FB1]	3.105	Piscivore[FB]
181 *Macropharyngodon meleagris*	Wrasse_Black spotted	15	Medium	0.0182[FB1]	3	Zoobenthivore[FB]
182 *Novaculichthys taeniourus*	Wrasse_Rock mover	30	Medium	0.013[SG1]	2.91	Zoobenthivore[FB]
183 *Oxychelinus bimaculatus*	Wrasse_Two spot maori	15	Medium	0.0565[FB1]	2.499	Zoobenthivore[OT]
184 *Oxycheilinus digramma*	Wrasse_Cheek lined maori	40	Large	0.0145[FB1]	3	Piscivore[FB]
185 *Oxycheilinus unifasciatus*	Wrasse_Ring tail maori	46	Large	0.0169[FB1]	3	Piscivore[FB]
186 *Pseudocheilinus hexataenia*	Wrasse_Six stripe	10	Small	0.0167[FB1]	3	Zoobenthivore[FB]
187 *Pseudocheilinus octotaenia*	Wrasse_Eight stripe	14	Medium	0.0049[SG1]	3.51	Zoobenthivore[FB]
188 *Pteragogus cryptus*	Wrasse_Cryptic	9.5	Small	0.0028[SG1]	3.693	Zoobenthivore[FB]
189 *Stethojulis bandanensis*	Wrasse_Blue lined	15	Medium	0.015[FB2]	3.167	Zoobenthivore[FB]

Appendix A continued

Family; Scientific name	**Common name**	**Maximum length (cm)**	**Length category**	**a**	**b**	**Trophic category**
190 *Stethojulis strigiventer*	Wrasse_Stripe belly	15	Medium	0.0168[FB1]	2.934	Zoobenthivore[FB]
191 *Stethojulis trilineata*	Wrasse_Three ribbon	15	Medium	0.0072[FB1]	3.257	Zoobenthivore[FB]
192 *Thalassoma amblycephalum*	Wrasse_Blunt head	16	Medium	0.0095[FB1]	3	Zooplanktivore[FB]
193 *Thalassoma hardwicke*	Wrasse_Six bar	20	Medium	0.0105[FB2]	3.048	Zooplanktivore[FB]
194 *Thalassoma hebraicum*	Wrasse_Hebrew	23	Medium	0.0271[FB1]	3	Zoobenthivore[FB]
195 *Thalassoma jansenii*	Wrasse_Jansen's	20	Medium	0.0112[FB2]	3	Piscivore[FB]
196 *Thalassoma lunare*	Wrasse_Moon	25	Medium	0.0183[FB2]	2.862	Zoobenthivore[FB]
197 *Thalassoma lutescens*	Wrasse_Sunset	30	Medium	0.0123[FB1]	3.077	Zoobenthivore[FB]
198 *Wemorella albofasciata*	Wrasse_White banded sharp nose	6	Small	0.0138[SG1]	3.018	Zoobenthivore[OT]
Lethrinidae						
199 *Lethrinus genivittatus*	Emperor_Lancer	25	Medium	0.0204[FB1]	2.946	Piscivore[FB]
200 *Lethrinus harak*	Emperor_Thumb print	50	Large	0.0178[FB1]	3.026	Zoobenthivore[FB]
201 *Lethrinus lentjan*	Emperor_Pink eared	52	Large	0.0189[FB1]	2.938	Piscivore[FB]
202 *Lethrinus obsoletus*	Emperor_Orange striped	60	Large	0.0197[FB1]	2.979	Zoobenthivore[FB]
203 *Lethrinus ornatus*	Emperor_Yellow striped	45	Large	0.0236[SG2]	2.98	Zoobenthivore[FB]
204 *Lethrinus variegatus*	Emperor_Variegated	20	Medium	0.182[FB1]	2.284	Zoobenthivore[FB]
205 *Monotaxis grandoculis*	Emperor_Big eye bream	43	Large	0.036[FB1]	2.851	Zoobenthivore[FB]
Lutjanidae						
206 *Lutjanus argentimaculatus*	Snapper_Mangrove jack	150	Extra large	0.0062[FB2]	3.193	Piscivore[FB]
207 *Lujanus carponotatus*	Snapper_Spanish flag	40	Large	0.0162[SG2]	3.045	Piscivore[FB]

Appendix A continued

Family; Scientific name	Common name	Maximum length (cm)	Length category	a	b	Trophic category
208 *Lutjanus decussatus*	Snapper_Checkered	35	Large	0.0192^{SG3}	2.959	Piscivore^{FB}
209 *Lutjanus fulviflamma*	Snapper_Black spot	35	Large	0.0239^{FB1}	2.906	Piscivore^{FB}
210 *Lutjanus fulvus*	Snapper_Yellow margined	40	Large	0.0243^{FB1}	2.928	Piscivore^{FB}
211 *Lutjanus monostigma*	Snapper_One spot	50	Large	0.0184^{FB1}	2.97	Piscivore^{FB}
212 *Lutjanus rivulatus*	Snapper_Maori	80	Extra large	0.0178^{FB1}	3	Piscivore^{FB}
213 *Lutjanus russellii*	Snapper_Moses	50	Large	0.0071^{FB1}	3.234	Piscivore^{FB}
214 *Lutjanus vitta*	Snapper_Brown stripe	40	Large	0.0169^{FB1}	2.978	Piscivore^{FB}
Malacanthidae						
215 *Hoplolatilus starcki*	Tilefish_Blue	15	Medium	0.0049^{SG1}	3	Piscivore^{FB}
Monacanthidae						
216 *Acreicthys radiatus*	Filefish_Radial	7	Small	0.011^{SG1}	3.242	Zoobenthivore^{OT}
217 *Acreicthys tomentosus*	Filefish_Bristle tailed	10	Small	0.216^{SG2}	3.0165	Zoobenthivore^{OT}
218 *Aluterus scriptus*	Filefish_Scrawled	110	Extra large	0.0022^{FB1}	3	Zoobenthivore^{FB}
219 *Amanses scopas*	Filefish_Brush sided	20	Medium	0.0216^{SG2}	3.0165	Zoobenthivore^{OT}
220 *Monacanthus chinensis*	Filefish_Fan bellied	38	Large	0.0704^{FB2}	2.447	Zoobenthivore^{FB}
221 *Oxymonacanthus longirostris*	Filefish_Beaked	12	Medium	0.0132^{FB1}	3	Zoobenthivore^{FB}
222 *Paramonacanthus japonicus*	Filefish_Japanese leather jacket	10	Small	0.0557^{FB1}	2.474	Zoobenthivore^{FB}
223 *Pervagor alternans*	Filefish_Yellow eyed	16	Medium	0.0250^{SG1}	2.946	Zoobenthivore^{OT}
224 *Pervagor aspricaudus*	Filefish_Orange tailed	13	Medium	0.025^{SG1}	2.946	Zoobenthivore^{OT}
225 *Pervagor melanocephalus*	Filefish_Black headed	16	Medium	0.0047^{FB6}	3.25	Zoobenthivore^{FB}
226 *Pseudomonacanthus macrurus*	Filefish_Small spotted	18	Medium	0.0407^{SG7}	2.744	Zoobenthivore^{OT}

Appendix A continued

Family; Scientific name	Common name	Maximum length (cm)	Length category	a	b	Trophic category
Mullidae						
227 *Parupeneus barberinoides*	Goatfish_Bicolor	30	Medium	0.0151[SG1]	3.078	Zoobenthivore[FB]
228 *Parupeneus barberinus*	Goatfish_Dash dot	60	Large	0.0063[FB1]	3.195	Zoobenthivore[FB]
229 *Parupeneus ciliatus*	Goafish_Gold saddled	38	Large	0.0122[FB1]	3.188	Zoobenthivore[FB]
230 *Parupeneus indicus*	Goatfish_Indian	45	Large	0.0152[FB1]	3.087	Zoobenthivore[FB]
231 *Parupeneus multifasciatus*	Goatfish_Many barred	35	Large	0.0915[FB1]	2.415	Zoobenthivore[FB]
232 *Parupeneus trifasciatus*	Goatfish_Double barred	35	Large	0.0047[FB1]	3.3786	Zoobenthivore[OT]
233 *Upeneus tragula*	Goatfish_Freckled	30	Medium	0.0093[FB1]	3.0235	Zoobenthivore[FB]
Muraenidae						
234 *Echidna nebulosa*	Moray eel_Starry	100	Extra large	0.0012[FB1]	3	Piscivore[FB]
235 *Gymnothorax javanicus*	Moray eel_Giant	300	Extra large	0.0035[FB1]	3	Zoobenthivore[FB]
236 *Gymnothorax ruepelli*	Moray eel_Banded	80	Extra large	0.0014[FB1]	3	Piscivore[FB]
Nemipteridae						
237 *Pentapodus bifasciatus*	Bream_White shoulder	18	Medium	0.0164[SG2]	3	Zoobenthivore[FB]
238 *Pentapodus caninus*	Bream_Banded thread fin	35	Large	0.106[FB2]	3	Zoobenthivore[FB]
239 *Pentapodus nagasakiensis*	Bream_Japanese butter fish	20	Medium	0.0146[SG2]	3	Zoobenthivore[FB]
240 *Pentapodus paradiseus*	Bream_Paradise butter fish	30	Medium	0.0164[SG2]	3	Zoobenthivore[FB]
241 *Scolopsis bilineata*	Bream_Bridled monocle	23	Medium	0.0149[FB1]	3.141	Zoobenthivore[FB]
242 *Scolopsis ciliata*	Bream_White streak monocle	19	Medium	0.0641[FB1]	2.48	Zoobenthivore[FB]

Appendix A continued

Family; Scientific name	Common name	Maximum length (cm)	Length category	a	b	Trophic category
243 *Scolopsis lineata*	Bream_Lined monocle	23	Medium	0.027[SG4]	2.944	Zoobenthivore[FB]
244 *Scolopsis margaritifera*	Bream_Pearly monocle	28	Medium	0.027[SG4]	2.944	Zoobenthivore[FB]
245 *Scolopsis monogramma*	Bream_Monocle	31	Large	0.027[SG4]	2.944	Zoobenthivore[FB]
246 *Scolopsis trilineata*	Bream_Three lined monocle	20	Medium	0.027[SG4]	2.944	Zoobenthivore[OT]
Ostraciidae						
247 *Ostracion cubicus*	Boxfish_Yellow	45	Large	0.101[FB1]	2.588	Zoobenthivore[FB]
248 *Ostracion meleagris*	Boxfish_Spotted	25	Medium	0.0101[SG1]	2.588	Zoobenthivore[FB]
249 *Ostracion solorensis*	Boxfish_Striped	11	Medium	0.0101[SG1]	2.588	Zoobenthivore[OT]
Pinguipedidae						
250 *Parapercis clathrata*	Sandperch_Latticed	24	Medium	0.0081[FB1]	3	Zoobenthivore[OT]
251 *Parapercis cylindrica*	Sandperch_Sharp nose	23	Medium	0.0143[FB1]	2.95	Zoobenthivore[FB]
252 *Parapercis hexopthalma*	Sandperch_Speckled	29	Medium	0.0085[FB1]	3.159	Piscivore[FB]
253 *Parapercis nebulosa*	Sandperch_Barred	25	Medium	0.0081[FB1]	3	Zoobenthivore[OT]
254 *Parapercis snyderi*	Sandperch_U marked	10	Small	0.0143[SG1]	2.95	Zoobenthivore[OT]
255 *Parapercis xanthozona*	Sandperch_Yellow barred	23	Medium	0.0081[SG1]	3	Zoobenthivore[OT]
Platycephalidae						
256 *Cymbacephalus beauforti*	Flathead_Giant	50	Large	0.0041[SG1]	3.205	Zoobenthivore[OT]
Plotosidae						
257 *Plotosus lineatus*	Catfish_Striped	32	Large	0.008[FB2]	2.95	Piscivores[FB]

Appendix A continued

Family; Scientific name	Common name	Maximum length (cm)	Length category	a	b	Trophic category
Pomacanthidae						
258 *Centropyge vrolikii*	Angelfish_Pearl scaled	12	Medium	0.0795[SG2]	2.63	Zoobenthivore[FB]
259 *Chaetodontoplus mesoleucus*	Angelfish_Vermiculated	18	Medium	0.0305[SG1]	3	Zoobenthivore[FB]
260 *Pomacanthus sextriatus*	Angelfish_Six banded	46	Large	0.0052[FB2]	3	Zoobenthivore[FB]
261 *Pomacanthus xanthometopon*	Angelfish_Yellow masked	38	Large	0.0281[SG2]	3	Zoobenthivore[FB]
262 *Pygoplites diacanthus*	Angelfish_Regal	25	Medium	0.0276[FB2]	3	Herbivore[FB]
Pomacentridae						
263 *Abudefduf abdominalis*	Damselfish_Maomao	30	Medium	0.0178[FB1]	3	Zoobenthivore[FB]
264 *Abudefduf bengalensis*	Damselfish_Bengal sergeant	17	Medium	0.0099[SG1]	3.267	Zoobenthivore[FB]
265 *Abudefduf lorenzi*	Damselfish_Black tail sergeant	18	Medium	0.0239[SG2]	2.9	Zooplanktivore[FB]
266 *Abudefduf septemfasciatus*	Damselfish_Banded sergeant	23	Medium	0.0246[SG1]	3	Zoobenthivore[FB]
267 *Abudefduf sexfasciatus*	Damselfish_Scissortail sergeant	16	Medium	0.0612[FB1]	2.747	Zoobenthivore[FB]
268 *Abudefduf vaigiensis*	Damselfish_Indo Pacific sergeant	20	Medium	0.0199[FB2]	3.0335	Piscivore[FB]
269 *Amblygliphidodon aureus*	Damselfish_Golden	13	Medium	0.0174[SG1]	3.0514	Zooplanktivore[FB]
270 *Amblyglyphidodon curacao*	Damselfish_Stag horn	11	Medium	0.0413[FB1]	2.886	Zoobenthivore[FB]
271 *Amblyglyphidodon leucogaster*	Damselfish_White belly	13	Medium	0.0048[FB1]	3	Zooplanktivore[FB]

Appendix A continued

Family; Scientific name	Common name	Maximum length (cm)	Length category	a	b	Trophic category
272 *Amblyglyphidodon ternatensis*	Damselfish_Ternate	10	Small	0.023[SG2]	2.943	Zooplanktivore
273 *Amblypomacentrus breviceps*	Damselfish_Black banded	8.5	Small	0.0243[SG1]	2.9586	Zooplanktivore[OT]
274 *Amphiprion clarkii*	Damselfish_Clark's anemone fish	15	Medium	0.034[SG3]	2.893	Zoobenthivore[FB]
275 *Amphiprion frenatus*	Damselfish_Tomato anemone fish	14	Medium	0.0166[SG1]	3	Zoobenthivore[FB]
276 *Amphiprion ocellaris*	Damselfish_False clown anemone fish	11	Medium	0.0239[SG1]	2.9828	Zoobenthivore[FB]
277 *Amphiprion percula*	Damselfish_Clown anemone fish	11	Medium	0.034[SG3]	2.893	Zoobenthivore[OT]
278 *Amphiprion peridaraion*	Damselfish_Pink anemone fish	10	Small	0.0239[SG1]	2.9828	Zooplanktivore[FB]
279 *Cheiloprion labiatus*	Damselfish_Big lip	6	Small	0.0211[SG2]	3	Zoobenthivore[FB]
280 *Chromis amboinensis*	Damselfish_Ambon chromis	9	Small	0.123[FB1]	3	Zooplanktivore[FB]
281 *Chromis analis*	Damselfish_Yellow chromis	17	Medium	0.0204[SG1]	2.9574	Zooplanktivore[FB]
282 *Chromis atripectoralis*	Damselfish_Black axil chromis	12	Medium	0.0204[FB1]	3.217	Zoobenthivore[FB]
283 *Chromis lepidolepis*	Damselfish_Scaly chromis	8	Small	0.195[FB1]	1.939	Zooplanktivore[FB]
284 *Chromis margaritifer*	Damselfish_Bicolor chromis	9	Small	0.0099[SG1]	3.267	Zooplanktivore[FB]
285 *Chromis retrofasciata*	Damselfish_Black bar chromis	4	Small	0.009[FB1]	2.773	Zooplanktivore[FB]
286 *Chromis ternatensis*	Damselfish_Ternate chromis	10	Small	0.043[FB1]	2.889	Zooplanktivore[FB]
287 *Chromis viridis*	Damselfish_Blue green chromis	8	Small	0.0642[FB1]	2.518	Zooplanktivore[FB]

Appendix A continued

Family; Scientific name	Common name	Maximum length (cm)	Length category	a	b	Trophic category
288 *Chromis xanthura*	Damselfish_Pale tail chromis	15	Medium	0.009[FB1]	2.773	Zooplanktivore[FB]
289 *Chrysiptera brownriggii*	Damselfish_Surge	7.5	Small	0.0318[SG1]	3	Zoobenthivore[FB]
290 *Chrysiptera cyanea*	Damselfish_Blue devil	8.5	Small	0.0294[SG1]	2.9505	Zoobenthivore[FB]
291 *Chrysiptera flavipinnis*	Damselfish_Yellow fin	8	Small	0.0377[SG1]	2.702	Zooplanktivore[FB]
292 *Chrysiptera glauca*	Damselfish_Grey	10	Small	0.0217[FB2]	3	Zoobenthivore[FB]
293 *Chrysiptera rex*	Damselfish_King	7	Small	0.0294[SG1]	2.9505	Zoobenthivore[FB]
294 *Chrysiptera rollandi*	Damselfish_Rolland's	7.5	Small	0.0294[SG1]	2.9505	Zooplanktivore[FB]
295 *Chrysiptera springeri*	Damselfish_Springer's	5.5	Small	0.0294[SG1]	2.9505	Zooplanktivore[FB]
296 *Chrysiptera talboti*	Damselfish_Talbot's	6	Small	0.0294[SG1]	2.9505	Zooplanktivore[FB]
297 *Chrysiptera tricinta*	Damselfish_Two spot	6	Small	0.0213[SG1]	3	Zooplanktivore[FB]
298 *Dascyllus aruanus*	Damselfish_Hambug	10	Small	0.0716[FB3]	2.635	Zoobenthivore[FB]
299 *Dacyllus melanurus*	Damsefish_Black tailed dascyllus	8	Small	0.0294[SG1]	2.9505	Zoobenthivore[FB]
300 *Dascyllus reticulatus*	Damselfish_Reticulated dascyllus	9	Small	0.0612[FB1]	2.747	Zooplanktivore[FB]
301 *Dascyllus trimaculatus*	Damselfish_Three spot dascyllus	11	Medium	0.108[FB1]	2.75	Zooplanktivore[FB]
302 *Dischistodus chrysopoecilus*	Damselfish_White patch	15	Medium	0.0178[SG1]	3	Herbivore[FB]
303 *Dischistodus melanotus*	Damselfish_Black vent	16	Medium	0.0179[SG1]	3.126	Herbivore[FB]
304 *Dischistodus perspicillatus*	Damselfish_White	18	Medium	0.0178[SG1]	3	Herbivore[FB]
305 *Dischistodus prosopotaenia*	Damselfish_Honey head	17	Medium	0.0179[SG1]	3.126	Herbivore[FB]

Appendix A continued

Family; Scientific name	Common name	Maximum length (cm)	Length category	a	b	Trophic category
306 *Hemiglyphidodon plagiometopon*	Damselfish_Lagoon	18	Medium	0.0174[SG3]	3.089	Herbivore[FB]
307 *Lepidozygus tapeinosoma*	Damselfish_Fusilier	10	Small	0.0294[SG1]	2.9505	Zooplanktivore[FB]
308 *Neoglyphidodon melas*	Damselfish_Black	18	Medium	0.0254[SG1]	3.054	Zoobenthivore[FB]
309 *Neoglyphidodon nigroris*	Damselfish_Behn’s	13	Medium	0.0254[SG1]	3.054	Zoobenthivore[FB]
310 *Neopomacentrus azysron*	Damselfish_Yellow tail	7.5	Small	0.0297[FB1]	2.868	Zooplanktivore[FB]
311 *Neopomacentrus filamentosus*	Damselfish_Brown	11	Medium	0.0294[SG1]	2.9505	Zooplanktivore[FB]
312 *Neopomacentrus violascens*	Damselfish_Violet	7.5	Small	0.0489[SG1]	2.565	Zooplanktivore[FB]
313 *Plectroglyphidodon dickii*	Damselfish_Dick’s	11	Medium	0.0294[SG1]	2.9505	Zoobenthivore[FB]
314 *Plectroglyphidodon lacrymatus*	Damselfish_Jewel	10	Small	0.0612[SG1]	2.635	Zoobenthivore[FB]
315 *Pomacentrus amboinensis*	Damselfish_Ambon	9	Small	0.123[FB1]	2.302	Zoobenthivore[FB]
316 *Pomacentrus bankanensis*	Damselfish_Speckled	10	Small	0.0586[FB1]	2.683	Zoobenthivore[FB]
317 *Pomacentrus brachialis*	Damselfish_Charcoal	8	Small	0.0135[FB1]	3.312	Zooplanktivore[FB]
318 *Pomacentrus burroughi*	Damselfish_Burrough’s	8.5	Small	0.0411[SG5]	2.9166	Zooplanktivore[FB]
319 *Pomacentrus chrysurus*	Damselfish_White tail	9	Small	0.0215[FB1]	3.225	Zooplanktivore[FB]
320 *Pomacentrus coelestis*	Damselfish_Neon	9	Small	0.037[FB1]	2.63	Zooplanktivore[FB]
321 *Pomacentrus imitator*	Damselfish_Imitator	11	Medium	0.0102[FB1]	3.469	Zooplanktivore[OT]
322 *Pomacentrus lepidogenys*	Damselfish_Scaly	9	Small	0.0281[FB1]	3.084	Zooplanktivore[FB]
323 *Pomacentrus moluccensis*	Damselfish_Lemon	9	Small	0.0703[FB1]	2.646	Zoobenthivore[FB]
324 *Pomacentrus nigromarginatus*	Damselfish_Black margined	8	Small	0.0294[SG1]	2.9505	Zooplanktivore[FB]
325 *Pomacentrus pavo*	Damselfish_Blue	8.5	Small	0.0365[FB1]	2.775	Zooplanktivore[FB]

Appendix A continued

Family; Scientific name	Common name	Maximum length (cm)	Length category	a	b	Trophic category
326 *Pomacentrus philippinus*	Damselfish_Philippine	10	Small	0.0508[FB1]	2.707	Zooplanktivore[FB]
327 *Pomacentrus simsiang*	Damselfish_Simsiang	7	Small	0.0586[FB1]	2.683	Zooplanktivore[FB]
328 *Pomacentrus stigma*	Damselfish_Black spot	13	Medium	0.0264[SG1]	2.9684	Zooplanktivore[FB]
329 *Pomacentrus tripunctatus*	Damselfish_Three spot	7.5	Small	0.0484[SG1]	2.7607	Zoobenthivore[FB]
330 *Pomacentrus vaiuli*	Damselfish_Princess	10	Small	0.0619[FB1]	2.628	Zooplanktivore[FB]
331 *Pomacentrus wardi*	Damselfish_Ward's	11	Medium	0.0407[SG3]	2.91	Herbivore[FB]
332 *Premnas biaculeatus*	Damselfish_Spine cheek anemone fish	17	Medium	0.0234[SG3]	2.995	Zooplanktivore[FB]
333 *Stegastes fasciolatus*	Damselfish_Pacific gregory	15	Medium	0.0179[SG1]	3.126	Zoobenthivore[FB]
334 *Stegastes lividus*	Damselfish_Blunt snout gregory	13	Medium	0.0642[FB1]	2.518	Zoobenthivore[FB]
335 *Stegastes nigricans*	Damselfish_Dusky	15	Medium	0.022[FB1]	3.086	Piscivore[FB]
Pseudochromidae						
336 *Congrogadus subducens*	Dottyback_Carpet eel blenny	45	Large	0.0157[SG1]	3.0016	Piscivore[FB]
337 *Labracinus cyclopthalmus*	Dottyback_Fire tail	22	Medium	0.0182[SG2]	2.965	Zoobenthivore[FB]
338 *Ogilbyina queenslandiae*	Dottyback_Queensland	15	Medium	0.0182[SG2]	2.965	Piscivore[OT]
339 *Pseudochromis fuscus*	Dottyback_Brown	9	Small	0.0207[SG2]	3	Zoobenthivore[OT]
340 *Pseudochromis paranox*	Dottyback_Mid night	7	Small	0.0207[SG2]	3	Zoobenthivore[OT]
Scaridae						
341 *Bolbometopon muricatum*	Parrotfish_Bump head	130	Extra large	0.0352[SG1]	2.88	Zoobenthivore[FB]
342 *Calotomus carolinus*	Parrotfish_Star eye	30	Medium	0.0179[FB2]	2.95	Herbivore[FB]
343 *Calotomus spinidens*	Parrotfish_Ragged tooth	30	Medium	0.0115[FB2]	3.2115	Herbivore[FB]

Appendix A continued

Family; Scientific name	Common name	Maximum length (cm)	Length category	a	b	Trophic category
344 *Cetoscarus bicolor*	Parrotfish_Bicolor	90	Extra large	0.0157[FB1]	3	Herbivore[FB]
345 *Chlorurus bleekeri*	Parrotfish_Bleeker's	49	Large	0.0925[SG1]	2.85	Herbivore[FB]
346 *Chlorurus bowersi*	Parrotfish_Bower's	40	Large	0.0295[FB1]	2.85	Herbivore[FB]
347 *Chlorurus japanensis*	Parrotfish_Red tail	31	Large	0.0204[SG1]	3	Herbivore[FB]
348 *Chlorurus microrhinus*	Parrotfish_Steep head	70	Extra large	0.0133[FB1]	3.132	Herbivore[OT]
349 *Chlorurus sordidus*	Parrotfish_Bullet head	40	Large	0.0204[FB2]	3.111	Herbivore[FB]
350 *Chlorurus longiceps*	Parrotfish_Pacific long nose	60	Large	0.0159[SG1]	3	Zoobenthivore[FB]
351 *Leptoscarus vaigiensis*	Parrotfish_Slender	35	Large	0.0173[FB1]	2.965	Herbivore[FB]
352 *Scarus altipinnis*	Parrotfish_Mini fin	60	Large	0.0233[FB1]	2.98	Herbivore[FB]
353 *Scarus chameleon*	Parrotfish_Chameleon	31	Large	0.0228[SG2]	3.03	Herbivore[FB]
354 *Scarus dimidiatus*	Parrotfish_Yellow barred	40	Large	0.0185[SG2]	3.029	Herbivore[FB]
355 *Scarus flavipectoralis*	Parrotfish_Yellow fin	40	Large	0.0185[SG2]	3.029	Herbivore[FB]
356 *Scarus frenatus*	Parrotfish_Bridled	47	Large	0.0279[FB1]	3.06	Herbivore[FB]
357 *Scarus ghobban*	Parrotfish_Blue barred	90	Extra large	0.0233[FB1]	2.919	Herbivore[FB]
358 *Scarus globiceps*	Parrotfish_Globe head	27	Medium	0.0155[FB1]	3	Herbivore[FB]
359 *Scarus hypselopterus*	Parrotfish_Yellow tail	31	Large	0.0175[SG2]	3.07	Herbivore[OT]
360 *Scarus niger*	Parrotfish_Swarthy	40	Large	0.0257[FB1]	3.09	Herbivore[FB]
361 *Scarus oviceps*	Parrotfish_Egg head	35	Large	0.018[FB1]	3	Herbivore[FB]
362 *Scarus psittacus*	Parrotfish_Pale nose	30	Medium	0.0258[FB1]	2.903	Herbivore[FB]
363 *Scarus quoyi*	Parrotfish_Quoy's	40	Large	0.0185[SG2]	3.029	Herbivore[FB]
364 *Scarus rivulatus*	Parrotfish_Surf	40	Large	0.0173[FB1]	3.14	Herbivore[FB]
365 *Scarus rubroviolaceous*	Parrotfish_Ember	70	Extra large	0.0136[FB1]	3.109	Herbivore[FB]
366 *Scarus schlegeli*	Parrotfish_Schlegel's	40	Large	0.0309[FB1]	2.87	Herbivore[FB]

Appendix A continued

Family; Scientific name	Common name	Maximum length (cm)	Length category	a	b	Trophic category
Scombridae						
367 *Rastrelliger kanagurta*	Mackerel_Long jawed	35	Large	0.0022[FB18]	3.287	Piscivore[FB]
Scorpaenidae						
368 *Dendrochirus zebra*	Scorpionfish_Zebra lion fish	25	Medium	0.0129[SG1]	3.201	Zoobenthivore[FB]
369 *Pterois antenanata*	Scorpionfish_Ragged finned lion fish	20	Medium	0.0265[SG1]	3	Piscivore[FB]
370 *Pterois volitans*	Scorpionfish_Red lion fish	38	Large	0.0171[SG1]	3	Piscivore[FB]
371 *Scorpaenopsis diabolus*	Scorpionfish_False	30	Medium	0.0044[FB2]	3	Zoobenthivore[FB]
Serranidae						
372 *Anyperodon leucogrammicus*	Grouper_White lined	30	Medium	0.0032[FB1]	3.328	Zoobenthivore[FB]
373 *Cephalopholis argus*	Grouper_Peacock	60	Large	0.014[FB1]	3.092	Piscivore[FB]
374 *Cephalopholis boenak*	Grouper_Brown barred	30	Medium	0.0132[FB1]	3.0826	Piscivore[FB]
375 *Cephalopholis cyanostigma*	Grouper_Blue spotted	40	Large	0.0172[SG2]	2.993	Piscivore[FB]
376 *Cephalopholis fulva*	Grouper_Coney	41	Large	0.0729[FB4]	2.574	Zoobenthivore[FB]
377 *Cephalopholis microprion*	Grouper_Dot head	25	Medium	0.0135[FB1]	3.044	Piscivore[FB]
378 *Cromileptes altivelis*	Grouper_Barramundi rock cod	66	Extra large	0.0052[SG1]	3.3	Piscivore[FB]
379 *Epiniphelus coerulupunctatus*	Grouper_White spotted	76	Extra large	0.0214[FB1]	2.907	Zoobenthivore[FB]
380 *Epinephelus coioides*	Grouper_Estuary	120	Extra large	0.0124[FB1]	3.054	Piscivore[FB]

Appendix A continued

Family; Scientific name	Common name	Maximum length (cm)	Length category	a	b	Trophic category
381 *Epinephelus corallicola*	Grouper_Coral rock cod	49	Large	0.0136[FB1]	3	Piscivore[OT]
382 *Epinephelus fuscoguttatus*	Grouper_Flowery	120	Extra large	0.0124[FB2]	3.054	Piscivore[FB]
383 *Epinephelus hexagonatus*	Grouper_Hexagon	27.5	Medium	0.014[FB1]	3	Piscivore[FB]
384 *Epinephelus malabaricus*	Grouper_Malabar	234	Exra large	0.0128[FB1]	3.034	Zoobenthivore[FB]
385 *Epinephelus ongus*	Grouper_Speckled fin	40	Large	0.0216[FB1]	2.887	Piscivore[FB]
386 *Epinephelus qouyanus*	Grouper_Long finned	40	Large	0.0216[SG1]	2.887	Piscivore[FB]
387 *Grammistes sexlineatus*	Grouper_Six lined soap fish	30	Medium	0.0205[FB1]	3	Piscivore[FB]
388 *Plectropomus areolatus*	Grouper_Square tail	73	Extra large	0.0119[SG1]	3.057	Piscivore[FB]
389 *Plectropomus leopardus*	Grouper_Coral trout	120	Extra large	0.0114[FB1]	3.2	Piscivore[FB]
390 *Plectropomus maculatus*	Grouper_Barred cheek coral trout	100	Extra large	0.0156[FB1]	3	Piscivore[FB]
391 *Pseudanthias huchtii*	Grouper_Thread fin anthias	12	Medium	0.0113[SG2]	3	Zooplanktivore[FB]
392 *Pseudanthias tuka*	Grouper_Purple anthias	12	Medium	0.0113[SG2]	3	Zooplanktivore[FB]
Siganidae						
393 *Siganus argenteus*	Rabbitfish_Fork tail	40	Large	0.025[FB1]	2.883	Herbivore[FB]
394 *Siganus canaliculatus*	Rabbitfish_White spotted	30	Medium	0.012[FB1]	3.011	Herbivore[FB]
395 *Siganus doliatus*	Rabbitfish_Barred	24	Medium	0.0143[FB1]	3.164	Herbivore[FB]
396 *Siganus guttatus*	Rabbitfish_Gold spotted	42	Large	0.0254[SG1]	2.948	Herbivore[FB]
397 *Siganus lineatus*	Rabbitfish_Gold lined	43	Large	0.0254[FB1]	2.948	Herbivore[FB]
398 *Siganus luridus*	Rabbitfish_Indian	30	Medium	0.0196[FB3]	2.947	Zoobenthivore[FB]
399 *Siganus puellus*	Rabbitfish_Blue lined	38	Large	0.0109[FB1]	3	Zoobenthivore[FB]
400 *Siganus punctatissimus*	Rabbitfish_Fine spotted	30	Medium	0.012[SG1]	3.011	Herbivore[FB]
401 *Siganus spinus*	Rabbitfish_Spiny	28	Medium	0.055[FB1]	2.88	Herbivore[FB]
402 *Siganus virgatus*	Rabbitfish_Virgate	30	Medium	0.0248[SG2]	2.885	Zooplanktivore[FB]
403 *Siganus vulpinus*	Rabbitfish_Fox face	24	Medium	0.0162[FB1]	3	Herbivore

Appendix A continued

Family; Scientific name	Common name	Maximum length (cm)	Length category	a	b	Trophic category
Soleidae						
404 *Pardachirus pavoninus*	Sole_Peacock	25	Medium	0.066[SG1]	3.001	Zoobenthivore[FB]
Sphyraenidae						
405 *Sphyraena barracuda*	Barracuda_Great	200	Extra large	0.0192[FB9]	2.84	Piscivore[FB]
406 *Sphyraena flavicauda*	Barracuda_Yellow tail	60	Large	0.0082[FB1]	2.861	Piscivore[FB]
407 *Sphyraena genie*	Barracuda_Chevron	170	Extra large	0.0056[FB1]	3	Piscivore[FB]
Syngnathidae						
408 *Corythoichthys intestinalis*	Pipefish_Banded	16	Medium	0.001[SG1]	3	Zoobenthivore[FB]
409 *Doryrhamphus dactyliophorus*	Pipefish_Ringed	19	Medium	0.0043[SG1]	2.66	Zoobenthivore[FB]
Synodontidae						
410 *Saurida gracilis*	Lizardfish_Slender	32	Large	0.0047[FB1]	3.216	Piscivore[FB]
411 *Synodus dermatogenys*	Lizardfish_Clear fin	24	Medium	0.0066[FB1]	3.201	Piscivore[OT]
412 *Synodus variegatus*	Lizardfish_Reef	40	Large	0.0026[FB1]	3.431	Piscivore[FB]
Tetraodontidae						
413 *Arothron hispidus*	Pufferfish_Stars and stripes	50	Large	0.057[FB1]	2.801	Zoobenthivore[FB]
414 *Arothron manilensis*	Pufferfish_Striped	31	Large	0.0469[FB1]	2.704	Zoobenthivore[FB]
415 *Arothron mappa*	Pufferfish_Map	65	Extra large	0.0047[SG1]	3	Zoobenthivore[FB]
416 *Arothron nigropunctatus*	Pufferfish_Black spotted	33	Large	0.0266[FB1]	3	Zoobenthivore[FB]
417 *Arothron stellatus*	Pufferfish_Star	120	Extra large	0.0947[FB1]	2.664	Zoobenthivore[OT]
418 *Canthigaster bennetti*	Pufferfish_Bennet’s	10	Small	0.0947[SG1]	2.664	Herbivore[FB]

Appendix A continued

Family; Scientific name	Common name	Maximum length (cm)	Length category	a	b	Trophic category
419 *Canthigaster coronata*	Pufferfish_Three barred	14	Medium	0.0947[SG1]	2.664	Zoobenthivore[FB]
420 *Canthigaster papua*	Pufferfish_False eye	9	Small	0.0947[SG1]	2.664	Zoobenthivore[OT]
421 *Canthigaster solandri*	Pufferfish_Solander	11.5	Medium	0.0947[SG1]	2.664	Zoobenthivore[FB]
422 *Canthigaster valentini*	Pufferfish_Black saddled	11	Medium	0.0729[FB1]	2.5	Zoobenthivore[FB]
Zanclidae						
423 *Zanclus cornutus*	Moorish idol	23	Medium	0.0172[FB1]	3.171	Zoobenthivore[FB]

Appendix B. Diagnostics of the regression on abundance, biomass, species richness, and other diversity indices vs. time (three-year monthly sampling) at the whole assemblage level, and by defined body size and trophic categories. Only species richness was calculated for the defined body size and trophic groups. Presented are the following: (1) intercept (a); (2) slope and *P*-value (b; significant values in bold), and (3) r^2; (4) PRESS or *Predicted Error Sum of Squares* (a measure of how good the model is at predicting new data – the smaller the PRESS value the better); (5) Durbin-Watson statistic of correlation between the residuals – the more the value differs from 2 the greater the likelihood that the residuals are correlated (i.e. values <1.5 and >2.5); (6) Kolmogorov-Smirnov test of normality statistic and *P*-value; and (7) *P*-value of the constant variance test of the regression.

Site; Variables	**a**	**b (*P*)**	r^2	$F_{(df)}$	**PRESS**	**Durbin-Watson (Note)**	**Normality: Kolmogorov-Smirnov; *P* (Note)**	**Constant Variance *P* (Note)**
Total Abundance								
A (F; In)	0.46	**0.01 (0.01)**	0.09	$2.22_{(1, 22)}$	2.0	1.59 **(Passed)**	0.14; 0.71 **(Passed)**	0.2 **(Passed)**
b (F; Off)	-0.01	**0.13 (<0.0001)**	0.51	$22.67_{(1, 22)}$	18.46	2.52 (Failed)	0.07; 0.99 **(Passed)**	0.09 **(Passed)**
C (YMR; In)	0.45	**0.01 (0.008)**	0.2	$7.39_{(1, 30)}$	1.99	0.95 **(Passed)**	0.09; 0.95 **(Passed)**	0.56 **(Passed)**
D (YMR; In)	0.35	**0.02 (<0.0001)**	0.43	$22.01_{(1, 30)}$	2.21	1.52 **(Passed)**	0.13; 0.61 **(Passed)**	0.75 **(Passed)**
e (YMR; Off)	0.38	**0.13 (<0.0001)**	0.7	$62.79_{(1, 27)}$	17.93	1.49 (Failed)	0.09; 0.94 **(Passed)**	0.39 **(Passed)**
F (OMR; In)	0.74	**0.03 (0.0006)**	0.31	$12.69_{(1, 29)}$	9.09	1.98 **(Passed)**	0.11; 0.76 **(Passed)**	0.34 **(Passed)**
g (OMR; Off)	1.14	**0.04 (<0.0001)**	0.44	$22.58_{(1,29)}$	8.93	1.59 **(Passed)**	0.08; 0.97 **(Passed)**	0.04 (Failed)
H (OMR; In)	0.66	**0.03 (0.005)**	0.22	$8.59_{(1, 30)}$	10.31	2.19 **(Passed)**	0.17; 0.25 **(Passed)**	0.23 **(Passed)**
Proportion: Passed/Failed						**(75%)/(25%)**	**(100%)/(0)**	**(88%)/(12%)**
Total Biomass								
A (F; In)	4.19	**0.12 (0.002)**	0.16	$4.06_{(1, 22)}$	98.04	1.77 **(Passed)**	0.18; 0.38 **(Passed)**	0.42 **(Passed)**
b (F; Off)	-3.91	**1.15 (<0.0001)**	0.64	$38.1_{(1, 22)}$	844.29	1.7 **(Passed)**	0.13; 0.78 **(Passed)**	0.051 **(Passed)**
C (YMR; In)	2.47	**0.62 (0.001)**	0.29	$12.29_{(1, 30)}$	3107.99	1.97 **(Passed)**	0.22; 0.06 **(Passed)**	0.001 (Failed)
D (YMR; In)	1.9	**0.85 (<0.0001)**	0.41	$20.44_{(1, 30)}$	3456.47	1.06 (Failed)	0.23; 0.06 **(Passed)**	0.09 **(Passed)**
e (YMR; Off)	2.69	**1.38 (0.02)**	0.13	$3.93_{(1, 27)}$	26928.23	1.91 **(Passed)**	0.38; 0.0004 (Failed)	0.28 **(Passed)**
F (OMR; In)	2.93	**1.39 (<0.0001)**	0.49	$27.41_{(1, 29)}$	5900.88	1.27 (Failed)	0.13; 0.6 **(Passed)**	<0.0001 (Failed)
g (OMR; Off)	51.02	0.83 (0.14)	0.06	$2.09_{(1, 29)}$	29103.5	1.77 **(Passed)**	0.08; 0.96 **(Passed)**	0.2 **(Passed)**
H (OMR; In)	5.68	2.53 **(0.003)**	0.24	$9.5_{(1, 30)}$	67312.85	1.53 **(Passed)**	0.21; 0.09 **(Passed)**	0.007 (Failed)
Proportion: Passed/Failed						**(75%)/(25%)**	**(88%)/(12%)**	**(63%)/(37%)**

Appendix B Continued

Site; Variables	**a**	**b (*P*)**	**r^2**	**$F_{(df)}$**	**PRESS**	**Durbin-Watson (Note)**	**Normality: Kolmogorov-Smirnov; *P* (Note)**	**Constant Variance *P* (Note)**
Total Species Richness								
A (F; In)	46.1	**0.63 (0.005)**	0.13	$3.18_{(1, 22)}$	2977.38	2.15 **(Passed)**	0.12; 0.85 **(Passed)**	0.95 **(Passed)**
b (F; Off)	55.8	**1.83 (<0.0001)**	0.52	$23.3_{(1, 22)}$	3364.3	1.51 **(Passed)**	0.14; 0.68 **(Passed)**	0.06 **(Passed)**
C (YMR; In)	52.01	**0.84 (0.002)**	0.25	$9.92_{(1, 30)}$	6584.25	1.02 (Failed)	0.14; 0.48 **(Passed)**	0.54 **(Passed)**
D (YMR; In)	38.34	**1.5 (<0.0001)**	0.48	$26.98_{(1, 30)}$	7592.65	1.32 (Failed)	0.12; 0.72 **(Passed)**	0.35 **(Passed)**
e (YMR; Off)	49.24	**3.18 (<0.0001)**	0.72	$67.44_{(1, 27)}$	8975.11	0.47 (Failed)	0.16; 0.42 **(Passed)**	0.79 **(Passed)**
F (OMR; In)	54.07	**1.25 (<0.0001)**	0.6	$43.6_{(1, 29)}$	3032.33	1.64 **(Passed)**	0.10; 0.85 **(Passed)**	0.46 **(Passed)**
g (OMR; Off)	70.1	**1.23 (<0.0001)**	0.71	$71.14_{(1, 29)}$	1902.63	1.21 (Failed)	0.08; 0.97 **(Passed)**	0.10 **(Passed)**
H (OMR; In)	50.05	**1.36 (<0.0001)**	0.61	$45.71_{(1, 30)}$	3677.95	2.79 (Failed)	0.10; 0.84 **(Passed)**	0.28 **(Passed)**
Proportion: Passed/Failed						**(37%)/(63%)**	**(100%)/(0)**	**(100%)/(0)**
Hill's N1								
A (F; In)	20.18	-0.06 (0.63)	0.003	$0.08_{(1, 22)}$	1427.81	2.11 **(Passed)**	0.17; 0.48 **(Passed)**	0.66 **(Passed)**
b (F; Off)	22.34	-0.14 (0.13)	0.03	$0.82_{(1, 22)}$	612.82	1.27 (Failed)	0.16; 0.55 **(Passed)**	0.11 **(Passed)**
C (YMR; In)	22.67	0.17 (0.20)	0.05	$1.55_{(1, 30)}$	1764.1	1.46 (Failed)	0.08; 0.98 **(Passed)**	0.34 **(Passed)**
D (YMR; In)	16.22	**0.4 (0.009)**	0.2	$7.31_{(1, 30)}$	2074.47	1.06 (Failed)	0.08; 0.95 **(Passed)**	0.41 **(Passed)**
e (YMR; Off)	21.53	-0.07 (0.55)	0.009	$0.24_{(1, 27)}$	1482.1	0.87 (Failed)	0.12; 0.7 **(Passed)**	0.21 **(Passed)**
F (OMR; In)	15.79	**0.18 (0.04)**	0.11	$3.68_{(1, 29)}$	766.25	1.54 **(Passed)**	0.07; 0.99 **(Passed)**	0.99 **(Passed)**
g (OMR; Off)	23.15	0.001 (0.99)	0.0	$0.00_{(1, 29)}$	1066.9	1.34 (Failed)	0.12; 0.7 **(Passed)**	0.53 **(Passed)**
H (OMR; In)	20.39	0.19 (0.25)	0.04	$1.28_{(1, 30)}$	2718.29	2.39 **(Passed)**	0.13; 0.56 **(Passed)**	0.96 **(Passed)**
Proportion: Passed/Failed						**(38%)/(62%)**	**(100%)/(0)**	**(100%)/(0)**
Pielou's J								
A (F; In)	0.76	-0.003 (0.11)	0.04	$0.94_{(1, 22)}$	0.22	2.13 **(Passed)**	0.14; 0.72 **(Passed)**	0.79 **(Passed)**
b (F; Off)	0.7	**-0.003 (0.04)**	0.06	$1.51_{(1, 22)}$	0.13	1.44 (Failed)	0.15; 0.61 **(Passed)**	0.25 **(Passed)**
C (YMR; In)	0.78	-0.001 (0.37)	0.02	$0.76_{(1, 30)}$	0.11	1.49 (Failed)	0.13; 0.56 **(Passed)**	0.82 **(Passed)**
D (YMR; In)	0.76	-0.001 (0.62)	0.01	$0.41_{(1, 30)}$	0.2	1.25 (Failed)	0.16; 0.36 **(Passed)**	0.09 **(Passed)**
e (YMR; Off)	0.73	**-0.005 (0.0002)**	0.31	$12.1_{(1, 27)}$	0.12	1.6 **(Passed)**	0.17; 0.3 **(Passed)**	0.27 **(Passed)**
F (OMR; In)	0.67	-0.0002 (0.88)	0.0007	$0.019_{(1, 29)}$	0.13	1.98 **(Passed)**	0.13; 0.58 **(Passed)**	0.35 **(Passed)**
g (OMR; Off)	0.72	-0.001 (0.17)	0.06	$1.8_{(1, 29)}$	0.16	1.4 (Failed)	0.18; 0.21 **(Passed)**	0.47 **(Passed)**
H (OMR; In)	0.73	-0.001 (0.64)	0.007	$0.2_{(1, 30)}$	0.46	2.31 **(Passed)**	0.18; 0.22 **(Passed)**	0.13 **(Passed)**
Proportion: Passed/Failed						**(50%)/(50%)**	**(100%)/(0)**	**(100%)/(0)**

Appendix B Continued

Site; Variables	a	b (*P*)	r^2	$F_{(df)}$	PRESS	Durbin-Watson (Note)	Normality: Kolmogorov-Smirnov; *P* (Note)	Constant Variance *P* (Note)
Shannon-Weiner ln(H')								
A (F; In)	2.96	-0.005 (0.5)	0.007	$0.15_{(1, 22)}$	4.83	2.0 **(Passed)**	0.18; 0.35 **(Passed)**	0.75 **(Passed)**
b (F; Off)	2.93	-0.001 (0.81)	0.001	$0.01_{(1, 22)}$	3.01	1.23 (Failed)	0.18; 0.38 **(Passed)**	0.03 (Failed)
C (YMR; In)	3.07	0.007 (0.18)	0.05	$1.69_{(1, 30)}$	2.8	1.31 (Failed)	0.08; 0.97 **(Passed)**	0.64 **(Passed)**
D (YMR; In)	2.77	**0.01 (0.03)**	0.13	$4.49_{(1, 30)}$	5.8	1.35 (Failed)	0.17; 0.3 **(Passed)**	0.74 **(Passed)**
e (YMR; Off)	2.97	-0.002 (0.72)	0.003	$0.08_{(1, 27)}$	4.23	1.05 (Failed)	0.01; 0.93 **(Passed)**	0.59 **(Passed)**
F (OMR; In)	2.71	**0.01 (0.05)**	0.11	$3.57_{(1, 29)}$	2.74	1.64 **(Passed)**	0.11; 0.82 **(Passed)**	0.54 **(Passed)**
g (OMR; Off)	3.08	0.001 (0.87)	0.0009	$0.02_{(1, 29)}$	3.54	1.43 (Failed)	0.17; 0.30 **(Passed)**	0.91 **(Passed)**
H (OMR; In)	2.88	0.01 (0.3)	0.03	$1.01_{(1, 30)}$	8.89	2.43 **(Passed)**	0.21; 0.09 **(Passed)**	0.25 **(Passed)**
Proportion: Passed/Failed						**(38%)/(62%)**	**(100%)/(0)**	**(88%)/(12%)**
Simpson's 1-lambda								
A (F; In)	0.91	-0.002 (0.2)	0.02	$0.59_{(1, 22)}$	0.15	1.89 **(Passed)**	0.21; 0.19 **(Passed)**	0.8 **(Passed)**
b (F; Off)	0.85	0.001 (0.36)	0.01	$0.29_{(1, 22)}$	0.1	1.35 (Failed)	0.20; 0.27 **(Passed)**	0.015 (Failed)
C (YMR; In)	0.91	0.0001 (0.88)	0.0007	$0.02_{(1, 30)}$	0.04	1.64 **(Passed)**	0.20; 0.11 **(Passed)**	0.65 **(Passed)**
D (YMR; In)	0.88	0.001 (0.35)	0.02	$0.83_{(1, 30)}$	0.12	1.59 **(Passed)**	0.23; 0.05 **(Passed)**	0.25 **(Passed)**
e (YMR; Off)	0.89	-0.001 (0.18)	0.04	$1.23_{(1, 27)}$	0.08	1.66 **(Passed)**	0.20; 0.1 **(Passed)**	0.87 **(Passed)**
F (OMR; In)	0.85	0.001 (0.12)	0.07	$2.11_{(1, 29)}$	0.11	2.17 **(Passed)**	0.20; 0.14 **(Passed)**	0.19 **(Passed)**
g (OMR; Off)	0.89	0.0002 (0.84)	0.001	$0.03_{(1, 29)}$	0.11	1.65 **(Passed)**	0.21; 0.09 **(Passed)**	0.93 **(Passed)**
H (OMR; In)	0.86	0.001 (0.47)	0.01	$0.48_{(1, 30)}$	0.4	2.3 **(Passed)**	0.28; 0.009 (Failed)	0.01 (Failed)
Proportion: Passed/Failed						**(88%)/(12%)**	**(88%)/(12%)**	**(75%)/(25%)**
Total Proportion: Passed/Failed						**(57%)/(43%)**	**(96%)/(4%)**	**(88%)/(22%)**

Appendix B Continued

Site; **Variables**	**a**	**b (*P*)**	**r^2**	**$F_{(df)}$**	**PRESS**	**Durbin-Watson (Note)**	**Normality: Kolmogorov-Smirnov; *P* (Note)**	**Constant Variance *P* (Note)**
Extra Large Abundance								
A (F; In)	0.01	-0.0002 (0.11)	0.04	$0.91_{(1, 22)}$	0.0007	1.48 (Failed)	0.11; 0.89 **(Passed)**	0.02 (Failed)
b (F; Off)	0.01	**0.0005 (0.03)**	0.07	$1.62_{(1, 22)}$	0.003	1.69 **(Passed)**	0.17; 0.43 **(Passed)**	0.41 **(Passed)**
C (YMR; In)	0.03	-0.0002 (0.30)	0.03	$0.98_{(1, 30)}$	0.005	1.30 (Failed)	0.16; 0.35 **(Passed)**	0.33 **(Passed)**
D (YMR; In)	0.03	-0.0002 (0.46)	0.01	$0.51_{(1, 30)}$	0.008	1.71 **(Passed)**	0.19; 0.17 **(Passed)**	0.06 **(Passed)**
e (YMR; Off)	0.01	**0.0006 (0.01)**	0.15	$4.78_{(1, 27)}$	0.004	1.82 **(Passed)**	0.14; 0.56 **(Passed)**	0.28 **(Passed)**
F (OMR; In)	0.03	-0.0002 (0.56)	0.01	$0.29_{(1, 29)}$	0.007	1.58 **(Passed)**	0.20; 0.13 **(Passed)**	0.77 **(Passed)**
g (OMR; Off)	0.05	-0.0003 (0.39)	0.02	$0.69_{(1, 29)}$	0.01	1.67 **(Passed)**	0.12; 0.72 **(Passed)**	0.35 **(Passed)**
H (OMR; In)	0.04	0.01 (0.69)	0.005	$0.15_{(1, 30)}$	0.02	1.38 (Failed)	0.10; 0.85 **(Passed)**	0.33 **(Passed)**
Proportion: Passed/Failed						**(62%)/(38%)**	**(100%)/(0)**	**(88%)/(12%)**
Extra Large Biomass								
A (F; In)	0.73	**-0.01 (0.01)**	0.09	$2.22_{(1,22)}$	2.8	2.14 **(Passed)**	0.26; 0.06 **(Passed)**	0.78 **(Passed)**
b (F; Off)	0.45	**0.03 (0.01)**	0.10	$2.57_{(1, 22)}$	9.51	1.80 **(Passed)**	0.19; 0.33 **(Passed)**	0.98 **(Passed)**
C (YMR; In)	0.72	**0.03 (0.05)**	0.11	$3.78_{(1, 30)}$	24.48	2.07 **(Passed)**	0.17; 0.27 **(Passed)**	0.09 **(Passed)**
D (YMR; In)	0.75	0.09 (0.11)	0.07	$2.45_{(1, 30)}$	386.72	1.27 (Failed)	0.24; 0.03 (Failed)	0.04 (Failed)
e (YMR; Off)	4.06	0.12 (0.81)	0.001	$0.03_{(1, 27)}$	23391.23	2.08 **(Passed)**	0.48; <0.0001 (Failed)	<0.0001 (Failed)
F (OMR; In)	2.85	0.04 (0.37)	0.02	$0.70_{(1, 29)}$	225.35	1.96 **(Passed)**	0.13; 0.64 **(Passed)**	0.41 **(Passed)**
g (OMR; Off)	8.23	0.09 (0.57)	0.01	$0.29_{(1, 29)}$	2629.15	2.27 **(Passed)**	0.23; 0.05 **(Passed)**	0.19 **(Passed)**
H (OMR; In)	-5.07	**1.37 (0.02)**	0.14	$5.09_{(1, 30)}$	37668.33	1.30 (Failed)	0.26; 0.02 (Failed)	<0.0001 (Failed)
Proportion: Passed/Failed						**(75%)/(25%)**	**(62%)/(38%)**	**(62%)/(38%)**
Extra Large Species Richness								
A (F; In)	4.67	**-0.06 (0.004)**	0.14	$3.45_{(1, 22)}$	32.41	3.10 (Failed)	0.08; 0.99 **(Passed)**	0.14 **(Passed)**
b (F; Off)	2.76	**0.09 (0.0004)**	0.22	$6.11_{(1, 22)}$	33.45	2.29 **(Passed)**	0.10; 0.95 **(Passed)**	0.47 **(Passed)**
C (YMR; In)	3.86	0.02 (0.28)	0.03	$1.12_{(1, 30)}$	69.67	2.00 **(Passed)**	0.11; 0.77 **(Passed)**	0.98 **(Passed)**
D (YMR; In)	3.83	**0.07 (0.006)**	0.21	$7.96_{(1, 30)}$	68.40	2.37 **(Passed)**	0.11; 0.78 **(Passed)**	0.95 **(Passed)**
e (YMR; Off)	3.02	**0.12 (0.009)**	0.16	$5.18_{(1, 27)}$	162.60	1.93 **(Passed)**	0.14; 0.52 **(Passed)**	0.36 **(Passed)**
F (OMR; In)	4.81	0.06 (0.07)	0.09	$2.94_{(1, 29)}$	110.45	2.53 (Failed)	0.16; 0.36 **(Passed)**	0.54 **(Passed)**
g (OMR; Off)	5.97	0.04 (0.18)	0.05	$1.67_{(1, 29)}$	125.60	2.02 **(Passed)**	0.12; 0.72 **(Passed)**	0.85 **(Passed)**
H (OMR; In)	5.49	**0.16 (0.002)**	0.25	$9.89_{(1, 30)}$	252.52	2.43 **(Passed)**	0.10; 0.83 **(Passed)**	0.41 **(Passed)**
Proportion: Passed/Failed						**(75%)/(25%)**	**(100%)/(0)**	**(100%)/(0)**

Appendix B Continued

Site; Variables	**a**	**b (*P*)**	**r^2**	**$F_{(df)}$**	**PRESS**	**Durbin-Watson (Note)**	**Normality: Kolmogorov-Smirnov; *P* (Note)**	**Constant Variance *P* (Note)**
Large Abundance								
A (F; In)	0.01	0.003 (0.07)	0.05	$1.21_{(1, 22)}$	0.23	1.29 (Failed)	0.28; 0.04 (Failed)	0.003 (Failed)
b (F; Off)	0.32	0.009 (0.15)	0.03	$0.74_{(1, 22)}$	2.80	2.34 **(Passed)**	0.17; 0.40 **(Passed)**	0.73 **(Passed)**
C (YMR; In)	0.09	**0.004 (0.02)**	0.15	$5.43_{(1, 30)}$	0.39	1.40 (Failed)	0.13; 0.56 **(Passed)**	0.58 **(Passed)**
D (YMR; In)	0.14	0.002 (0.30)	0.03	$1.01_{(1, 30)}$	0.48	1.29 (Failed)	0.16; 0.32 **(Passed)**	0.56 **(Passed)**
e (YMR; Off)	-0.03	**0.010 (0.0005)**	0.28	$10.6_{(1, 27)}$	1.38	1.98 **(Passed)**	0.19; 0.20 **(Passed)**	<0.0001 (Failed)
F (OMR; In)	0.24	0.007 (0.18)	0.05	$1.54_{(1, 29)}$	2.52	2.10 **(Passed)**	0.17; 0.28 **(Passed)**	0.43 **(Passed)**
g (OMR; Off)	0.31	0.006 (0.27)	0.03	$1.11_{(1, 29)}$	2.77	2.22 **(Passed)**	0.20; 0.12 **(Passed)**	0.66 **(Passed)**
H (OMR; In)	0.24	0.007 (0.24)	0.04	$1.31_{(1, 30)}$	4.22	1.85 **(Passed)**	0.27; 0.01 (Failed)	0.46 **(Passed)**
Proportion: Passed/Failed						**(62%)/(38%)**	**(75%)/(25%)**	**(75%)/(25%)**
Large Biomass								
A (F; In)	1.54	0.05 (0.07)	0.05	$1.19_{(1, 22)}$	57.81	2.01 **(Passed)**	0.13; 0.73 **(Passed)**	0.02 (Failed)
b (F; Off)	-1.48	**0.35 (<0.0001)**	0.52	$23.40_{(1, 22)}$	129.52	1.79 **(Passed)**	0.14; 0.68 **(Passed)**	0.04 (Failed)
C (YMR; In)	-0.45	**0.49 (0.006)**	0.21	$8.13_{(1, 30)}$	2964.81	1.93 **(Passed)**	0.23; 0.05 **(Passed)**	0.002 (Failed)
D (YMR; In)	2.04	**0.32 (0.001)**	0.29	$12.19_{(1, 30)}$	851.86	1.60 **(Passed)**	0.19; 0.16 **(Passed)**	0.18 **(Passed)**
e (YMR; Off)	-2.80	**0.55 (<0.0001)**	0.54	$31.64_{(1, 27)}$	565.04	2.22 **(Passed)**	0.24; 0.06 (**Passed**)	0.03 (Failed)
F (OMR; In)	-3.10	**1.11 (<0.0001)**	0.46	$24.75_{(1, 29)}$	4150.44	1.09 (Failed)	0.15; 0.43 **(Passed)**	<0.0001 (Failed)
g (OMR; Off)	37.30	0.48 (0.26)	0.04	$1.18_{(1, 29)}$	17133.55	1.46 (Failed)	0.11; 0.78 **(Passed)**	0.19 **(Passed)**
H (OMR; In)	7.28	**0.98 (0.0004)**	0.34	$15.11_{(1, 30)}$	5909.70	2.14 **(Passed)**	0.08; 0.95 **(Passed)**	0.01 (Failed)
Proportion: Passed/Failed						**(75%)/(25%)**	**(100%)/(0)**	**(25%)/(75%)**
Large Species Richness								
A (F; In)	11.82	0.08 (0.12)	0.04	$0.87_{(1, 22)}$	216.73	2.71 (Failed)	0.15; 0.60 **(Passed)**	0.44 **(Passed)**
b (F; Off)	10.84	**0.45 (<0.0001)**	0.43	$16.19_{(1, 22)}$	293.58	1.55 **(Passed)**	0.08; 0.99 **(Passed)**	0.49 **(Passed)**
C (YMR; In)	12.66	**0.19 (0.006)**	0.21	$8.04_{(1, 30)}$	429.68	1.64 **(Passed)**	0.12; 0.66 **(Passed)**	0.25 **(Passed)**
D (YMR; In)	9.80	**0.29 (0.002)**	0.26	$10.55_{(1, 30)}$	740.63	1.71 **(Passed)**	0.09; 0.92 **(Passed)**	0.85 **(Passed)**
e (YMR; Off)	7.16	**0.84 (<0.0001)**	0.75	$78.10_{(1, 27)}$	534.02	0.69 (Failed)	0.08; 0.97 **(Passed)**	0.31 **(Passed)**
F (OMR; In)	14.10	**0.32 (<0.0001)**	0.59	$40.61_{(1, 29)}$	205.87	2.02 **(Passed)**	0.08; 0.96 **(Passed)**	0.54 **(Passed)**
g (OMR; Off)	18.99	**0.34 (<0.0001)**	0.61	$44.08_{(1, 29)}$	232.00	1.21 (Failed)	0.08; 0.97 **(Passed)**	0.22 **(Passed)**
H (OMR; In)	14.21	**0.31 (0.0002)**	0.37	$17.18_{(1, 30)}$	523.28	2.58 (Failed)	0.09; 0.92 **(Passed)**	0.75 **(Passed)**
Proportion: Passed/Failed						**(50%)/(50%)**	**(100%)/(0)**	**(100%)/(0)**

Appendix B Continued

Site; Variables	**a**	**b (*P*)**	r^2	$F_{(df)}$	**PRESS**	**Durbin-Watson (Note)**	**Normality: Kolmogorov-Smirnov; *P* (Note)**	**Constant Variance *P* (Note)**
Medium Abundance								
A (F; In)	0.18	**0.005 (0.01)**	0.1	$2.38_{(1, 22)}$	0.27	1.89 **(Passed)**	0.15; 0.6 **(Passed)**	0.87 **(Passed)**
b (F; Off)	0.22	**0.02 (<0.0001)**	0.36	$1.09_{(1, 22)}$	0.96	2.08 **(Passed)**	0.09; 0.97 **(Passed)**	0.30 **(Passed)**
C (YMR; In)	0.24	0.0006 (0.73)	0.003	$0.11_{(1, 30)}$	0.30	1.68 **(Passed)**	0.13; 0.58 **(Passed)**	0.22 **(Passed)**
D (YMR; In)	0.11	**0.009 (<0.0001)**	0.45	$24.10_{(1, 30)}$	0.31	1.67 **(Passed)**	0.11; 0.79 **(Passed)**	0.68 **(Passed)**
e (YMR; Off)	0.34	**0.38 (<0.0001)**	0.38	$16.14_{(1, 27)}$	5.37	1.68 **(Passed)**	0.12; 0.73 **(Passed)**	0.02 (Failed)
F (OMR; In)	0.24	**0.009 (0.004)**	0.22	$8.33_{(1, 29)}$	0.89	1.88 **(Passed)**	0.13; 0.64 **(Passed)**	0.15 **(Passed)**
g (OMR; Off)	0.38	**0.009 (0.004)**	0.24	$8.89_{(1, 29)}$	0.83	1.88 **(Passed)**	0.13; 0.65 **(Passed)**	0.07 **(Passed)**
H (OMR; In)	0.16	**0.009 (0.0003)**	0.32	$15.54_{(1, 30)}$	0.49	2.00 **(Passed)**	0.12; 0.64 **(Passed)**	0.01 (Failed)
Proportion: Passed/Failed						**(100%)/(0)**	**(100%)/(0)**	**(75%)/(25%)**
Medium Biomass								
A (F; In)	1.75	**0.07 (0.003)**	0.23	$6.27_{(1, 22)}$	19.98	2.20 **(Passed)**	0.10; 0.93 **(Passed)**	0.81 **(Passed)**
b (F; Off)	-3.81	**0.57 (<0.0001)**	0.61	$33.91_{(1, 22)}$	234.80	1.65 **(Passed)**	0.13; 0.74 **(Passed)**	0.04 (Failed)
C (YMR; In)	2.05	**0.07 (0.002)**	0.25	$10.14_{(1, 30)}$	50.74	1.55 **(Passed)**	0.10; 0.87 **(Passed)**	0.45 **(Passed)**
D (YMR; In)	-0.92	**0.38 (0.0005)**	0.33	$14.31_{(1, 30)}$	10009.79	2.03 **(Passed)**	0.17; 0.27 **(Passed)**	<0.0001 (Failed)
e (YMR; Off)	0.34	**0.03 (<0.0001)**	0.38	$16.14_{(1, 27)}$	5.37	1.68 **(Passed)**	0.12; 0.73 **(Passed)**	0.02 (Failed)
F (OMR; In)	2.96	**0.14 (0.0005)**	0.32	$13.33_{(1, 29)}$	133.65	1.94 **(Passed)**	0.15; 0.42 **(Passed)**	0.85 **(Passed)**
g (OMR; Off)	4.20	**0.11 (0.02)**	0.14	$4.89_{(1, 29)}$	259.86	2.24 **(Passed)**	0.17; 0.29 **(Passed)**	0.35 **(Passed)**
H (OMR; In)	3.14	**0.12 (0.01)**	0.16	$5.74_{(1, 30)}$	250.58	1.93 **(Passed)**	0.15; 0.38 **(Passed)**	0.82 **(Passed)**
Proportion: Passed/Failed						**(100%)/(0)**	**(100%)/(0)**	**(62%)/(38%)**
Medium Species Richness								
A (F; In)	23.21	**0.23 (0.01)**	0.10	$2.35_{(1, 22)}$	565.34	1.89 **(Passed)**	0.12; 0.81 **(Passed)**	0.37 **(Passed)**
b (F; Off)	31.00	**0.61 (<0.0001)**	0.34	$10.86_{(1, 22)}$	814.25	1.91 **(Passed)**	0.09; 0.98 **(Passed)**	0.02 (Failed)
C (YMR; In)	27.7	0.22 (0.06)	0.10	$3.31_{(1, 30)}$	1376.62	1.19 **(Passed)**	0.09; 0.90 **(Passed)**	0.46 **(Passed)**
D (YMR; In)	17.94	**0.62 (<0.0001)**	0.44	$23.66_{(1, 30)}$	1509.03	1.50 **(Passed)**	0.11; 0.75 **(Passed)**	0.11 **(Passed)**
e (YMR; Off)	26.94	**1.59 (<0.0001)**	0.74	$76.63_{(1, 27)}$	1984.80	0.69 (Failed)	0.14; 0.55 **(Passed)**	0.54 **(Passed)**
F (OMR; In)	25.51	**059 (<0.0001)**	0.51	$29.51_{(1, 29)}$	1023.24	1.47 (Failed)	0.11; 0.80 **(Passed)**	0.36 **(Passed)**
g (OMR; Off)	36.73	**0.26 (0.007)**	0.21	$0.21_{(1, 29)}$	830.10	1.34 (Failed)	0.10; 0.90 **(Passed)**	0.29 **(Passed)**
H (OMR; In)	22.64	**0.44 (<0.0001)**	0.50	$29.62_{(1, 30)}$	613.99	2.48 **(Passed)**	0.08; 0.90 **(Passed)**	0.57 **(Passed)**
Proportion: Passed/Failed						**(62%)/(38%)**	**(100%)/(0)**	**(88%)/(12%)**

Appendix B Continued

Site; **Variables**	**a**	**b (*P*)**	r^2	$F_{(df)}$	**PRESS**	**Durbin-Watson (Note)**	**Normality: Kolmogorov-Smirnov; *P* (Note)**	**Constant Variance *P* (Note)**
Small Abundance								
A (F; In)	0.24	0.005 (0.17)	0.03	$0.65_{(1, 22)}$	1.00	2.01 **(Passed)**	0.09; 0.98 **(Passed)**	0.77 **(Passed)**
b (F; Off)	-0.57	**0.09 (<0.0001)**	0.58	$29.30_{(1, 22)}$	8.14	2.39 **(Passed)**	0.20; 0.26 **(Passed)**	0.04 (Failed)
C (YMR; In)	0.07	**0.007 (0.0006)**	0.32	$13.71_{(1, 30)}$	0.37	1.30 (Failed)	0.12; 0.65 **(Passed)**	0.55 **(Passed)**
D (YMR; In)	0.05	**0.01 (<0.0001)**	0.41	$20.78_{(1, 30)}$	0.62	1.75 **(Passed)**	0.15; 0.37 **(Passed)**	0.54 **(Passed)**
e (YMR; Off)	0.06	**0.08 (<0.0001)**	0.52	$29.27_{(1, 27)}$	13.81	1.73 **(Passed)**	0.18; 0.26 **(Passed)**	0.04 (Failed)
F (OMR; In)	0.21	**0.02 (0.0004)**	0.32	$13.50_{(1, 29)}$	2.76	1.78 **(Passed)**	0.18; 0.21 **(Passed)**	0.003 (Failed)
g (OMR; Off)	0.39	**0.03 (<0.0001)**	0.50	$28.39_{(1, 29)}$	3.35	1.84 **(Passed)**	0.14; 0.49 **(Passed)**	0.18 **(Passed)**
H (OMR; In)	0.21	**0.01 (0.03)**	0.14	$4.82_{(1, 30)}$	3.26	2.23 **(Passed)**	0.20; 0.14 **(Passed)**	0.44 **(Passed)**
Proportion: Passed/Failed						**(88%)/(12%)**	**(100%)/(0)**	**(62%)/(38%)**
Small Biomass								
A (F; In)	0.15	**0.01 (0.02)**	0.08	$1.99_{(1, 22)}$	4.11	1.55 **(Passed)**	0.16; 0.53 **(Passed)**	0.10 **(Passed)**
b (F; Off)	0.94	**0.19 (<0.0001)**	0.39	$13.52_{(1, 22)}$	68.47	2.04 **(Passed)**	0.11; 0.91 **(Passed)**	0.23 **(Passed)**
C (YMR; In)	0.14	**0.02 (0.0002)**	0.37	$17.37_{(1, 30)}$	2.78	1.04 (Failed)	0.09; 0.94 **(Passed)**	0.09 **(Passed)**
D (YMR; In)	0.02	**0.04 (<0.0001)**	0.43	$22.68_{(1, 30)}$	8.28	1.28 (Failed)	0.10; 0.86 **(Passed)**	0.15 **(Passed)**
e (YMR; Off)	0.44	**0.24 (<0.0001)**	0.37	$15.29_{(1, 27)}$	221.50	1.79 **(Passed)**	0.13; 0.64 **(Passed)**	0.16 **(Passed)**
F (OMR; In)	0.30	**0.09 (<0.0001)**	0.48	$26.46_{(1, 29)}$	26.07	1.73 **(Passed)**	0.12; 0.72 **(Passed)**	0.31 **(Passed)**
g (OMR; Off)	1.22	**0.13 (<0.0001)**	0.44	$22.13_{(1, 29)}$	75.19	1.26 (Failed)	0.09; 0.94 **(Passed)**	0.01 (Failed)
H (OMR; In)	0.32	**0.05 (0.0002)**	0.36	$16.96_{(1, 30)}$	16.80	1.61 **(Passed)**	0.19; 0.16 **(Passed)**	0.22 **(Passed)**
Proportion: Passed/Failed						**(62%)/(38%)**	**(100%)/(0)**	**(88%)/(12%)**
Small Species Richness								
A (F; In)	0.39	**0.37 (<0.0001)**	0.28	$8.54_{(1, 22)}$	389.83	1.74 **(Passed)**	0.14; 0.70 **(Passed)**	0.31 **(Passed)**
b (F; Off)	11.21	**0.67 (<0.0001)**	0.55	$25.71_{(1, 22)}$	416.80	1.15 (Failed)	0.12; 0.84 **(Passed)**	0.15 **(Passed)**
C (YMR; In)	7.71	**0.39 (0.0006)**	0.32	$13.92_{(1, 30)}$	1039.24	0.61 (Failed)	0.15; 0.40 **(Passed)**	0.72 **(Passed)**
D (YMR; In)	6.76	**0.50 (<0.0001)**	0.49	$28.68_{(1, 30)}$	804.65	0.78 (Failed)	0.08; 0.95 **(Passed)**	0.34 **(Passed)**
e (YMR; Off)	12.11	**0.63 (<0.0001)**	0.51	$27.24_{(1, 27)}$	858.15	0.85 (Failed)	0.10; 0.92 **(Passed)**	0.13 **(Passed)**
F (OMR; In)	9.60	**0.27 (<0.0001)**	0.42	$20.77_{(1, 29)}$	296.55	2.13 **(Passed)**	0.11; 0.81 **(Passed)**	0.86 **(Passed)**
g (OMR; Off)	8.48	**0.57 (<0.0001)**	0.72	$72.92_{(1, 29)}$	384.19	1.56 **(Passed)**	0.11; 0.82 **(Passed)**	0.59 **(Passed)**
H (OMR; In)	13.18	**0.60 (<0.0001)**	0.57	$39.26_{(1, 30)}$	853.75	2.39 **(Passed)**	0.09; 0.92 **(Passed)**	0.34 **(Passed)**
Proportion: Passed/Failed						**(50%)/(50%)**	**(100%)/(0)**	**(100%)/(0)**
Total Proportion: Passed/Failed						**(72%)/(28%)**	**(95%)/(5%)**	**(77%)/(33%)**

Appendix B Continued

Site; Variables	**a**	**b (*P*)**	**r^2**	**$F_{(df)}$**	**PRESS**	**Durbin-Watson (Note)**	**Normality: Kolmogorov-Smirnov; *P* (Note)**	**Constant Variance *P* (Note)**
Herbivore Abundance								
A (F; In)	0.10	**-0.002 (<0.0001)**	0.31	$9.77_{(1, 22)}$	0.01	2.08 **(Passed)**	0.14; 0.72 **(Passed)**	0.29 **(Passed)**
b (F; Off)	0.10	**0.002 (0.05)**	0.06	$1.44_{(1, 22)}$	0.06	1.51 **(Passed)**	0.12; 0.81 **(Passed)**	0.55 **(Passed)**
C (YMR; In)	0.07	0.0002 (0.81)	0.001	$0.04_{(1, 30)}$	0.07	1.26 (Failed)	0.13; 0.61 **(Passed)**	0.12 **(Passed)**
D (YMR; In)	0.05	0.001 (0.33)	0.02	$0.89_{(1, 30)}$	0.12	2.15 **(Passed)**	0.15; 0.38 **(Passed)**	0.42 **(Passed)**
e (YMR; Off)	0.05	**0.004 (0.0004)**	0.29	$10.88_{(1, 27)}$	0.09	1.04 (Failed)	0.13; 0.69 **(Passed)**	0.10 **(Passed)**
F (OMR; In)	0.01	**0.003 (0.0005)**	0.32	$13.20_{(1, 29)}$	0.05	1.19 (Failed)	0.16; 0.36 **(Passed)**	0.21 **(Passed)**
g (OMR; Off)	0.13	0.0009 (0.36)	0.02	$0.78_{(1, 29)}$	0.08	1.87 **(Passed)**	0.10; 0.89 **(Passed)**	0.02 (Failed)
H (OMR; In)	0.06	**0.002 (0.04)**	0.12	$4.13_{(1, 30)}$	0.17	2.03 **(Passed)**	0.11; 0.74 **(Passed)**	0.07 **(Passed)**
Proportion: Passed/Failed						**(50%)/(50%)**	**(100%)/(0)**	**(88%)/(12%)**
Herbivore Biomass								
A (F; In)	2.30	-0.01 (0.59)	0.004	0.10	32.74	2.19 **(Passed)**	0.11; 0.91 **(Passed)**	0.33 **(Passed)**
b (F; Off)	-2.26	**0.40 (<0.0001)**	0.41	16.64	274.91	1.96 **(Passed)**	0.15; 0.60 **(Passed)**	0.08 **(Passed)**
C (YMR; In)	3.67	0.08 (0.15)	0.06	$1.98_{(1, 30)}$	300.36	1.92 **(Passed)**	0.15; 0.44 **(Passed)**	0.13 **(Passed)**
D (YMR; In)	1.40	**0.25 (0.001)**	0.28	$11.66_{(1, 30)}$	523.06	1.67 **(Passed)**	0.11; 0.77 **(Passed)**	0.03 (Failed)
e (YMR; Off)	-1.87	**0.43 (<0.0001)**	0.62	$44.03_{(1, 27)}$	252.08	2.00 **(Passed)**	0.16; 0.37 **(Passed)**	0.12 **(Passed)**
F (OMR; In)	-0.66	**0.64 (<0.0001)**	0.40	$18.88_{(1, 29)}$	1831.55	0.95 (Failed)	0.15; 0.43 **(Passed)**	0.01 (Failed)
g (OMR; Off)	38.82	0.22 (0.62)	0.008	$0.22_{(1, 29)}$	20215.68	1.63 **(Passed)**	0.17; 0.30 **(Passed)**	0.18 **(Passed)**
H (OMR; In)	9.24	**0.86 (0.004)**	0.23	$8.74_{(1, 30)}$	7939.94	2.30 **(Passed)**	0.11; 0.82 **(Passed)**	0.17 **(Passed)**
Proportion: Passed/Failed						**(88%)/(12%)**	**(100%)/(0)**	**(75%)/(25%)**
Herbivore Species Richness								
A (F; In)	9.56	0.02 (0.68)	0.003	$0.08_{(1, 22)}$	195.47	2.74 (Failed)	0.17; 0.42 **(Passed)**	0.18 **(Passed)**
b (F; Off)	5.39	**0.41 (<0.0001)**	0.56	$27.43_{(1, 22)}$	146.00	2.78 (Failed)	0.12; 0.84 **(Passed)**	0.20 **(Passed)**
C (YMR; In)	9.07	**0.14 (0.001)**	0.28	$11.64_{(1, 30)}$	175.54	1.70 **(Passed)**	0.08; 0.97 **(Passed)**	0.01 (Failed)
D (YMR; In)	7.96	**0.20 (0.01)**	0.16	$5.68_{(1, 30)}$	650.93	1.67 **(Passed)**	0.13; 0.61 **(Passed)**	0.85 **(Passed)**
e (YMR; Off)	3.95	**0.68 (<0.0001)**	0.68	$56.99_{(1, 27)}$	483.79	0.71 (Failed)	0.09; 0.94 **(Passed)**	0.63 **(Passed)**
F (OMR; In)	7.73	**0.34 (<0.0001)**	0.58	$38.83_{(1, 29)}$	256.06	1.69 **(Passed)**	0.11; 0.81 **(Passed)**	0.29 **(Passed)**
g (OMR; Off)	12.05	**0.27 (<0.0001)**	0.51	$29.51_{(1, 29)}$	220.13	1.27 (Failed)	0.11; 0.77 **(Passed)**	0.53 **(Passed)**
H (OMR; In)	9.79	**0.26 (0.0008)**	0.31	$13.11_{(1, 30)}$	495.77	2.49 **(Passed)**	0.07; 0.99 **(Passed)**	0.10 **(Passed)**
Proportion: Passed/Failed						**(50%)/(50%)**	**(100%)/(0)**	**(88%)/(12%)**

Appendix B Continued

Site; Variables	**a**	**b (*P*)**	r^2	$F_{(df)}$	**PRESS**	**Durbin-Watson (Note)**	**Normality: Kolmogorov-Smirnov; *P* (Note)**	**Constant Variance *P* (Note)**
Piscivore Abundance								
A (F; In)	-0.01	**0.005 (0.005)**	0.13	$3.18_{(1, 22)}$	0.21	1.63 **(Passed)**	0.22; 0.18 **(Passed)**	0.008 (Failed)
b (F; Off)	0.53	-0.005 (0.29)	0.01	$0.38_{(1, 22)}$	1.93	1.99 **(Passed)**	0.11; 0.88 **(Passed)**	0.67 **(Passed)**
C (YMR; In)	0.12	0.002 (0.21)	0.04	$1.47_{(1, 30)}$	0.28	1.82 **(Passed)**	0.15; 0.45 **(Passed)**	0.94 **(Passed)**
D (YMR; In)	0.13	0.001 (0.47)	0.01	$0.49_{(1, 30)}$	0.28	1.98 **(Passed)**	0.21; 0.08 **(Passed)**	0.28 **(Passed)**
e (YMR; Off)	0.03	**0.01 (0.004)**	0.20	$6.52_{(1, 27)}$	1.31	1.94 **(Passed)**	0.20; 0.14 **(Passed)**	<0.0001 (Failed)
F (OMR; In)	0.23	0.001 (0.80)	0.001	$0.05_{(1, 29(}$	2.66	2.03 **(Passed)**	0.21; 0.11 **(Passed)**	0.58 **(Passed)**
g (OMR; Off)	0.24	0.0003 (0.94)	0.0002	$0.005_{(1, 29)}$	1.68	1.54 **(Passed)**	0.21; 0.11 **(Passed)**	0.54 (Passed)
H (OMR; In)	0.22	0.007 (0.28)	0.03	$1.11_{(1, 30)}$	4.76	1.98 **(Passed)**	0.30; 0.004 (Failed)	0.39 **(Passed)**
Proportion: Passed/Failed						**(100%)/(0)**	**(88%)/(12%)**	**(75%)/(25%)**
Piscivore Biomass								
A (F; In)	0.39	**0.02 (0.05)**	0.06	$1.41_{(1, 22)}$	15.31	1.73 **(Passed)**	0.20; 0.27 **(Passed)**	0.02 (Failed)
b (F; Off)	0.62	**0.05 (0.0009)**	0.19	$5.03_{(1, 22)}$	15.61	1.48 (Failed)	021; 0.20 **(Passed)**	0.58 **(Passed)**
C (YMR; In)	-2.65	**0.35 (0.04)**	0.12	$4.12_{(1, 30)}$	3001.37	2.10 **(Passed)**	0.32; 0.001 (Failed)	<0.0001 (Failed)
D (YMR; In)	1.43	0.06 (0.12)	0.07	$2.39_{(1, 30)}$	165.53	2.13 **(Passed)**	0.21; 0.10 **(Passed)**	0.07 **(Passed)**
e (YMR; Off)	3.97	0.26 (0.63)	0.005	$0.15_{(1, 27)}$	25694.56	2.08 **(Passed)**	0.45; <0.0001 (Failed)	<0.0001 (Failed)
F (OMR; In)	2.09	**0.05 (0.06)**	0.10	$3.18_{(1, 29)}$	85.24	1.77 **(Passed)**	0.20; 0.15 **(Passed)**	0.09 **(Passed)**
g (OMR; Off)	4.01	0.04 (0.33)	0.03	$0.88_{(1, 29)}$	239.73	1.71 **(Passed)**	0.16; 0.37 **(Passed)**	0.96 **(Passed)**
H (OMR; In)	-1.08	**0.87 (0.01)**	0.17	$6.12_{(1, 30)}$	12192.33	1.55 **(Passed)**	0.24; 0.03 (Failed)	<0.0001 (Failed)
Proportion: Passed/Failed						**(88%)/(12%)**	**(75%)/(25%)**	**(50%)/(50%)**
Piscivore Species Richness								
A (F; In)	5.58	**0.10 (0.005)**	0.13	$3.19_{(1, 22)}$	86.90	**1.81 (Passed)**	0.16; 0.52 **(Passed)**	0.62 **(Passed)**
b (F; Off)	9.39	**0.18 (0.002)**	0.16	$4.18_{(1, 22)}$	182.66	**1.69 (Passed)**	0.13; 0.77 **(Passed)**	0.01 (Failed)
C (YMR; In)	9.21	0.05 (0.35)	0.02	$0.81_{(1, 30)}$	351.97	1.31 (Failed)	0.12; 0.73 **(Passed)**	0.78 **(Passed)**
D (YMR; In)	7.00	**0.13 (0.009)**	0.19	$7.13_{(1, 30)}$	235.75	1.47 (Failed)	0.13; 0.62 **(Passed)**	0.40 **(Passed)**
e (YMR; Off)	7.75	**0.47 (<0.0001)**	0.59	$38.80_{(1, 27)}$	335.23	1.15 (Failed)	0.08; 0.97 **(Passed)**	0.10 **(Passed)**
F (OMR; In)	9.15	**0.16 (0.0003)**	0.34	$14.44_{(1, 29(}$	159.72	1.80 **(Passed)**	0.08; 0.97 **(Passed)**	0.50 **(Passed)**
g (OMR; Off)	11.95	**0.11 (0.05)**	0.11	$3.72_{(1, 29)}$	282.69	1.56 **(Passed)**	0.10; 0.89 **(Passed)**	0.84 **(Passed)**
H (OMR; In)	10.33	**0.15 (0.0002)**	0.36	$16.96_{(1, 30)}$	124.75	2.74 (Failed)	0.12; 0.65 **(Passed)**	0.29 **(Passed)**
Proportion: Passed/Failed						**(50%)/(50%)**	**(100%)/(0)**	**(88%)/(12%)**

Appendix B Continued

Site; Variables	**a**	**b (*P*)**	r^2	$F_{(df)}$	**PRESS**	**Durbin-Watson (Note)**	**Normality: Kolmogorov-Smirnov; *P* (Note)**	**Constant Variance *P* (Note)**
Zoobenthivore Abundance								
A (F; In)	0.15	**0.01 (0.002)**	0.16	$4.13_{(1, 22)}$	1.09	2.04 **(Passed)**	0.16; 0.53 **(Passed)**	0.27 **(Passed)**
b (F; Off)	-0.03	**0.07 (<0.0001)**	0.50	$21.01_{(1, 22)}$	5.70	2.44 **(Passed)**	0.10; 0.93 **(Passed)**	0.03 (Failed)
C (YMR; In)	0.20	**0.006 (0.01)**	0.17	$6.15_{(1, 30)}$	0.53	1.30 (Failed)	0.11; 0.78 **(Passed)**	0.81 **(Passed)**
D (YMR; In)	0.11	**0.01 (0.0001)**	0.39	$18.96_{(1, 30)}$	0.90	1.48 (Failed)	0.10; 0.86 **(Passed)**	0.23 **(Passed)**
e (YMR; Off)	0.40	**0.05 (<0.0001)**	0.57	$34.64_{(1, 27)}$	4.49	0.76 (Failed)	0.15; 0.50 **(Passed)**	0.28 **(Passed)**
F (OMR; In)	0.33	**0.009 (0.003)**	0.23	$8.41_{(1, 29)}$	0.23	2.12 **(Passed)**	0.12; 0.68 **(Passed)**	0.002 (Failed)
g (OMR; Off)	0.58	**0.02 (<0.0001)**	0.42	$21.04_{(1, 29)}$	2.12	1.48 (Failed)	0.15; 0.45 **(Passed)**	0.06 **(Passed)**
H (OMR; In)	0.97	-0.88 (0.17)	0.06	$1,94_{(1, 30)}$	1.97	1.60 **(Passed)**	0.15; 0.39 **(Passed)**	0.56 **(Passed)**
Proportion: Passed/Failed						**(50%)/(50%)**	**(100%)/(0)**	**(75%)/(25%)**
Zoobenthivore Biomass								
A (F; In)	1.46	**0.07 (0.0003)**	0.22	$6.16_{(1, 22)}$	22.44	2.17 **(Passed)**	0.13; 0.73 **(Passed)**	0.05 **(Passed)**
b (F; Off)	-0.68	**0.48 (<0.0001)**	0.59	$30.37_{(1, 22)}$	189.54	1.51 **(Passed)**	0.08; 0.98 **(Passed)**	0.003 (Failed)
C (YMR; In)	1.54	**0.08 (0.008)**	0.31	$13.11_{(1, 30)}$	54.61	1.64 **(Passed)**	0.10; 0.86 **(Passed)**	0.27 **(Passed)**
D (YMR; In)	-1.73	**0.46 (<0.0001)**	0.42	$21.38_{(1, 30)}$	982.36	0.94 (Failed)	0.17; 0.24 **(Passed)**	<0.0001 (Failed)
e (YMR; Off)	0.67	**0.46 (<0.0001)**	0.67	$53.11_{(1, 27)}$	231.39	1.05 (Failed)	0.16; 0.39 **(Passed)**	0.14 **(Passed)**
F (OMR; In)	2.78	**0.20 (0.0002)**	0.36	$16.15_{(1, 29)}$	214.36	1.96 **(Passed)**	0.11; 0.79 **(Passed)**	0.07 **(Passed)**
g (OMR; Off)	7.28	**0.28 (0.04)**	0.12	$3.82_{(1, 29)}$	1782.22	2.59 (Failed)	0.19; 0.19 **(Passed)**	0.16 **(Passed)**
H (OMR; In)	-2.85	**0.70 (0.01)**	0.16	$5.82_{(1, 30)}$	8671.72	1.18 (Failed)	0.32; 0.001 (Failed)	<0.0001 (Failed)
Proportion: Passed/Failed						**(50%)/(50%)**	**(88%)/(12%**	**(62%)/(38%)**
Zoobenthivore Species Richness								
A (F; In)	0.15	**0.01 (0.002)**	0.16	$4.13_{(1, 22)}$	1.09	2.04 **(Passed)**	0.16; 0.53 **(Passed)**	0.27 **(Passed)**
b (F; Off)	32.04	**0.77 (<0.0001)**	0.43	$16.47_{(1, 22)}$	851.10	1.59 **(Passed)**	0.08; 0.99 **(Passed)**	0.02 (Failed)
C (YMR; In)	26.24	**0.38 (0.007)**	0.20	$7.67_{(1, 30)}$	1762.58	1.14 (Failed)	0.10; 0.89 **(Passed)**	0.22 **(Passed)**
D (YMR; In)	18.90	**0.79 (<0.0001)**	0.53	$33.16_{(1, 30)}$	1707.81	1.08 (Failed)	0.09; 0.95 **(Passed)**	0.22 **(Passed)**
e (YMR; Off)	29.29	**1.57 (<0.0001)**	0.67	$53.54_{(1, 27)}$	2762.05	0.67 (Failed)	0.10; 0.87 **(Passed)**	0.57 **(Passed)**
F (OMR; In)	27.83	**0.55 (<0.0001)**	0.50	$28.06_{(1, 29)}$	914.23	1.97 **(Passed)**	0.07; 0.98 **(Passed)**	0.61 **(Passed)**
g (OMR; Off)	36.75	**0.57 (<0.0001)**	0.69	$62.59_{(1, 29)}$	467.93	1.50 **(Passed)**	0.08; 0.97 **(Passed)**	1.50 **(Passed)**
H (OMR; In)	21,11	**0.69 (<0.0001)**	0.60	$44.09_{(1, 30)}$	1000.41	2.27 **(Passed)**	0.10; 0.82 **(Passed)**	0.03 (Failed)
Proportion: Passed/Failed						**(62%)/(38%)**	**(100%)/(0)**	**(75%)/(25%)**

Appendix B Continued

Site; Variables	**a**	**b (*P*)**	**r^2**	**$F_{(df)}$**	**PRESS**	**Durbin-Watson (Note)**	**Normality: Kolmogorov-Smirnov; *P* (Note)**	**Constant Variance *P* (Note)**
Zooplanktivore Abundance								
A (F; In)	0.20	**-0.003 (0.13)**	0.03	$0.81_{(1, 22)}$	0.25	1.98 **(Passed)**	0.14; 0.68 **(Passed)**	0.30 **(Passed)**
b (F; Off)	-0.61	**0.06 (<0.0001)**	0.48	$20.01_{(1, 22)}$	5.14	1.72 **(Passed)**	0.18; 0.34 **(Passed)**	0.002 (Failed)
C (YMR; In)	0.04	**0.004 (0.004)**	0.23	$9.05_{(1, 30)}$	0.18	1.50 **(Passed)**	0.18; 0.21 **(Passed)**	0.09 **(Passed)**
D (YMR; In)	0.25	-0.15 (0.31)	0.03	$1.04_{(1, 29)}$	0.38	1.26 (Failed)	0.14; 0.52 **(Passed)**	0.45 **(Passed)**
e (YMR; Off)	-0.70	**0.06 (<0.0001)**	0.49	$25.63_{(1, 27)}$	11.14	1.64 **(Passed)**	0.20; 0.16 **(Passed)**	0.27 **(Passed)**
F (OMR; In)	0.15	**0.02 (0.0001)**	0.36	$16.41_{(1, 29)}$	2.77	1.54 **(Passed)**	0.19; 0.19 **(Passed)**	0.30 **(Passed)**
g (OMR; Off)	0.18	**0.02 (0.002)**	0.26	$10.29_{(1, 30)}$	4.96	2.00 **(Passed)**	0.02; 0.12 **(Passed)**	0.002 (Failed)
H (OMR; In)	0.19	0.003 (0.44)	0.01	$0.57_{(1, 30)}$	2.43	2.15 **(Passed)**	0.25; 0.03 (Failed)	0.31 **(Passed)**
Proportion: Passed/Failed						**(88%)/(12%)**	**(88%)/(12%)**	**(75%)/(25%)**
Zooplanktivore Biomass								
A (F; In)	-0.11	**0.03 (0.005)**	0.13	$3.20_{(1, 22)}$	7.62	1.83 **(Passed)**	0.17; 0.46 **(Passed)**	0.003 (Failed)
b (F; Off)	-1.59	**0.20 (<0.0001)**	0.49	$20.67_{(1, 22)}$	50.90	2.33 **(Passed)**	0.11; 0.89 **(Passed)**	0.008 (Failed)
C (YMR; In)	-0.12	**0.09 (0.01)**	0.18	$6.73_{(1, 30)}$	132.61	1.58 **(Passed)**	0.23; 0.06 **(Passed)**	<0.0001 (Failed)
D (YMR; In)	0.74	0.06 (0.07)	0.10	$3.30_{(1, 30)}$	121.67	1.83 **(Passed)**	0.27; 0.01 (Failed)	0.26 **(Passed)**
e (YMR; Off)	-0.08	**0.21 (<0.0001)**	0.42	$19.36_{(1, 27)}$	137.01	2.24 **(Passed)**	0.26; 0.02 (Failed)	0.05 (Failed)
F (OMR; In)	-1.31	**0.48 (0.0003)**	0.33	$14.33_{(1, 29)}$	1383.87	2.00 **(Passed)**	**0.13; 0.63 (Passed)**	0.002 (Failed)
g (OMR; Off)	0.89	**0.27 (0.001)**	0.28	$11.05_{(1, 29)}$	574.67	2.33 **(Passed)**	**0.15; 0.39 (Passed)**	0.04 (Failed)
H (OMR; In)	0.35	**0.09 (0.02)**	0.14	$5.02_{(1, 30)}$	150.94	2.19 **(Passed)**	0.23; 0.05 **(Passed)**	0.002 (Failed)
Proportion: Passed/Failed						**(100%)/(0)**	**(75%)/(25%)**	**(12%)/(88%)**

Appendix B Continued

Site; **Variables**	**a**	**b (*P*)**	**r^2**	**$F_{(df)}$**	**PRESS**	**Durbin-Watson (Note)**	**Normality: Kolmogorov-Smirnov; *P* (Note)**	**Constant Variance *P* (Note)**
Zooplanktivore Spp. Richness								
A (F; In)	4.21	**0.14 (0.004)**	0.14	$3.44_{(1, 22)}$	139.23	1.89 **(Passed)**	0.11; 0.92 **(Passed)**	0.87 **(Passed)**
b (F; Off)	9.39	**0.38 (<0.0001)**	0.38	$13.22_{(1, 22)}$	273.07	1.31 (Failed)	0.13; 0.74 **(Passed)**	0.53 **(Passed)**
C (YMR; In)	6.55	**0.25 (0.001)**	0.30	$12.5_{(1, 30)}$	465.97	0.81 (Failed)	0.12; 0.71 **(Passed)**	0.24 **(Passed)**
D (YMR; In)	3.50	**0.36 (<0.0001)**	0.58	$41.39_{(1, 30)}$	293.13	1.64 **(Passed)**	0.11; 0.74 **(Passed)**	0.92 **(Passed)**
e (YMR; Off)	8.20	**0.44 (<0.0001)**	0.54	$30.71_{(1, 27)}$	375.22	1.20 (Failed)	0.07; 0.99 **(Passed)**	0.53 **(Passed)**
F (OMR; In)	8.93	**0.16 (0.003)**	0.23	$8.60_{(1, 29)}$	251.68	1.31 (Failed)	0.11; 0.77 **(Passed)**	0.37 **(Passed)**
g (OMR; Off)	9.25	**0.26 (<0.0001)**	0.55	$35.24_{(1, 29)}$	177.00	1.67 (Passed)	0.13; 0.63 **(Passed)**	0.89 **(Passed)**
H (OMR; In)	8.09	**0.23 (<0.0001)**	0.51	$31.16_{(1, 30)}$	160.89	2.38 **(Passed)**	0.11; 0.75 **(Passed)**	0.12 **(Passed)**
Proportion: Passed/Failed						**(38%)/(62%)**	**(100%)/(0)**	**(100%)/(0)**
Total Proporion: Passed/Failed						**(64%)/(36%)**	**(92%)/(8%)**	**(71%)/(29%)**