

**ACCOUNTING FOR THE OTHER 95%: CONSERVATION AND ASSESSMENT OF
DATA LIMITED MARINE INVERTEBRATES IN THE CENTRAL PHILIPPINES**

by

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Abstract

Intense human pressures require that conservation be nimble and action-oriented even in the face of significant data limitations. In the ocean, invertebrates comprise over 95% of animal biodiversity and are a major component of fisheries catch. Yet, exceedingly little effort is dedicated to supporting conservation of these taxa. The goal of this thesis is to measure how coral reef invertebrates and invertebrate communities respond to conservation action based on limited data and then to suggest how such action can be tailored to maximize invertebrate abundance and reproductive output. I focused on no-fishing zones (marine reserves) and setting limitations on catch of juvenile animals in the Central Philippines—a region of immense ocean biodiversity, but also of enormous human fishing pressures. In my first data chapter (Chapter 2) I focused on the best timing for sampling invertebrates and I found that surveys at night significantly increased detection, having large impacts on both the number of animals and the number of taxa observed for mobile species. In Chapters 3 and 4, I examined if marine reserves increase invertebrate abundance and alter their communities. I found that reserves have 1.5 to 2.3 times more invertebrates for taxa important to local fisheries. The best outcomes were found in older reserves with complex habitats. Surprisingly, I found no correlation between abundance of fish and of invertebrates. Invertebrate communities often differed between fished and reserve areas, with the latter showing greater abundances for traits like bearing a shell and filter feeding. In Chapter 5, I used invertebrate catch data from intertidal fisheries and developed indicators for reproductive output and fishing mortality. For some species, a substantial proportion of catch was either juvenile animals or animals below a body size that would otherwise optimize yield. Introducing a minimum size limit would substantially increase spawning output and yield. Given

the significant challenges facing these taxa and the fisheries they support, I urge a combination of marine reserves and size-limits to conserve invertebrates. Such an approach should also support food security in the often marginalized fishers who rely upon them.

Lay Summary

Invertebrates—animals lacking a backbone—constitute 95% of ocean animal taxa but are largely overlooked in conservation despite being critical for food security and regulating ecosystem processes. This thesis explores conservation actions for invertebrates in the Central Philippines and how to increase their effectiveness. I focused on how invertebrates respond to 1) closing areas of the ocean to fishing and 2) applying fishing limits on juveniles. I found that on average, areas closed to fishing had 1.5 to 2.3 times more invertebrates important in fisheries.

Surprisingly, invertebrates respond differently to fish when they are protected. The largest effects were in areas protected for long periods of time and with complex habitats. Reserves also had more animals with particular traits, such as filtration capacity. Combining closed areas with catch limits for juvenile animals will likely increase the abundance of marine invertebrates and support human food security.

Preface

This thesis represents my own work, some of which has been published elsewhere. Two chapters in this thesis have been published in peer-reviewed journals (Chapters 3 and 4). Two chapters are being prepared for submission (Chapters 2 and 5) at peer-reviewed journals. I am (or will be) the lead author on all four papers. I was primarily responsible for conceptualization, experimental design, collecting information (with help from research assistants), data management, data analysis, and writing in each of the manuscripts. Dr. Vincent had a central role in facilitating research in the Philippines and conceptualizing the thesis and ideas for each chapter. Dr. Vincent played a critical role in securing funding for my research. My co-authors have made significant contributions and improved the manuscripts substantially. I list my co-authors and outline their contributions to each specific chapter below.

A version of Chapter 2 is in preparation for submission as “Gillespie KM, and Vincent ACJ. Night sampling is best for detection of coral reef invertebrates”. Dr. Vincent gave feedback on experimental design and provided edits throughout the analysis and writing of the manuscript.

A version of Chapter 3 has been published in *Aquatic Conservation: Marine and Freshwater Ecosystems* as “Gillespie, K.M., Vincent, A.C.J., 2019. Tropical invertebrate response to marine reserves varies with protection duration, habitat type, and exploitation history. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 29, 511–520”. Dr. Vincent gave feedback on the design of scientific surveys, fisher interviews and provided edits throughout the analysis and writing.

A version of Chapter 4 has been published in *Biodiversity and Conservation* as “Gillespie, K.M., Vincent, A.C.J., 2019. Marine reserves drive both taxonomic and functional change in coral reef invertebrate communities. *Biodivers. Conserv.* 28, 921–938”. Dr. Vincent gave feedback on the design of scientific surveys and provided edits throughout the analysis and writing.

A version of Chapter 5 is in preparation for submission as “Gillespie KM, Pauly D, Kleiber D, and Vincent ACJ. Using life history and size data for assessment and management of data-limited invertebrate fisheries”. Dr. Kleiber collected fisheries catch data and provided edits to the manuscript. Dr. Pauly guided the theoretical approach, supported modeling analyses, and provided edits to the manuscript. Dr. Vincent gave feedback on the design of scientific surveys and provided edits throughout the analysis and writing.

All fieldwork in this dissertation was approved by UBC’s Behavioural Research Ethics Board (certificate H13-00900; see appendix A3). Animal care approval was not required as UBC’s animal care committee does not oversee invertebrate research. All scuba dive based research was approved by UBC’s Canadian Association for Underwater Science panel.

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List of Symbols

a – exponent describing of the rate of change of weight with length in the length-weight formula

b – weight at unit length in the length-weight formula

F – fishing mortality (1/time)

F/M – ratio of fishing mortality (F) to natural mortality (M)

K – rate (1/time) at which the asymptotic length is approached

L_c – mean length at first capture

L_{inf} (or L_{∞}) – asymptotic length in a population

L_m – mean length at which 50% of the population has reached maturity

L_{m95} – mean length at which 95% of the population has reached maturity

L_{max} – maximum length reported from a population

L_{opt} – length at which biomass of an unfished cohort reaches its maximum

M – instantaneous rate (1/time) of natural mortality (1/time)

M/K – ratio of natural mortality to von Bertalanffy's K

ω – model weight

SPR – spawning potential ratio

$SPR_{current}$ – spawning potential ratio at selectivity observed in the fishery

$SPR_{L_{opt}}$ – spawning potential ratio at L_{opt} selectivity

Z – total mortality (1/time)

φ' – Phi prime: growth performance index ($\varphi' = \log K + 2 \log L_{\infty}$)

List of Abbreviations

AIC – Akaike information criterion

BTA – biological trait analysis

BHI – Beverton Holt life history invariant

CBD – Convention on Biological Diversity

CCEF – Coastal Conservation and Education Foundation

CI – confidence interval

CITES – Convention on International Trade in Endangered Species of Wild Fauna and Flora

CMS – Convention on Migratory Species

GLM – generalized linear model

GLMM – generalized linear mixed effects model

IUCN – International Union for Conservation of Nature

MANOVA – multivariate analysis of variance

MEA – multilateral environmental agreement

MDS – multidimensional scaling ordination

MPA – marine protected area

PERMANOVA – permutational multivariate analysis of variance

QAICc – quasi-Akaike information criterion corrected for small samples

SIMPER – similarity percentage analysis

VIF – variance inflation factor

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Dedication

To my parents, Mike and Andria Gillespie. Thank you for a loving home, garlic braids, and always being up for a game of cribbage. I am incredibly lucky to have you.

Chapter 1: Introduction

1.1 Rational

Intense pressures require that conservation programming use flexible, data-limited tools to support survival, growth, and reproduction in species impacted by humans. The current overwhelming focus on population dynamics in commercially dominant species is no longer adequate for improving recovery potential of populations and communities at broad geographic and taxonomic scales (Hall and Mainprize, 2004). This has driven a demand for more holistic management approaches that address biotic and abiotic needs in diverse taxa. This requires attention be paid to species and processes typically overlooked in conservation programming (Cardoso et al., 2012, 2011b; Collen et al., 2012; Travis et al., 2013). An added level complexity may seem at odds with the capabilities of ‘flexible and data-limited’—how do we account for taxa whose basic life history traits are unknown? Fortunately, a number of approaches have emerged that are practical in these scenarios. Management that requires relatively few data inputs but protects habitats and reduce mortality in key life-history stages—while not a panacea—can begin to address broader conservation issues faced by species, their habitats, and ultimately, ecosystems functioning.

Coastal, developing regions are often biodiverse, heavily threatened and have few management resources (Muallil et al., 2014). In these regions, fisheries support the protein diets of 1.4 billion people (Béné, 2006) and management tools that support ecosystems and the people who depend on them are required. Over the past several decades, depletion of populations, reductions in the size of individuals, destruction of habitats and loss of biodiversity have reduced the functioning

of marine ecosystems and threaten the multitude of benefits that people derive from oceans (Klain and Chan, 2012; Moberg and Folke, 1999; Nañola et al., 2011; Pauly et al., 1998; Worm et al., 2006). Many of these benefits, in addition to large amounts of protein for human consumption come from often overlooked marine invertebrate taxa and there is a pressing need to take invertebrate taxa into account (Anderson et al., 2011; Collen et al., 2012; Kleiber et al., 2014).

My thesis deploys a variety of analytical approaches to understand how data-limited and ecosystem-based tools support the survival, growth, and reproduction of taxa critical to fisheries and ocean functioning—marine invertebrates. While significant effort has been invested in designing sampling methods suitable for measuring biodiversity in coral reef finfish, detection of invertebrate biodiversity, to my knowledge, has not been taken into account in the design of these surveys. In Chapter 2, I present a case study comparing invertebrate biodiversity estimates from varying sample sizes and compare day-time and night-time sampling on coral reefs. To understand patterns of invertebrate response to MPAs I use a focused set of analyses (Chapters 3 and 4) to probe the drivers of response in abundance, diversity and functional traits. To do this I use a (Le Port et al., 2017) case studies from 10 protected areas in the Central Philippines—a heavily impacted coastal, developing region. I use various statistical modeling techniques to investigate how protected areas can better support recovery of invertebrate taxa and how these closures impact ecosystem functioning. Much of the ocean lies outside of protected areas. In the last section of this thesis (Chapter 5), I examine how data-limited, animal growth-based analyses can be employed to ensure fished invertebrate taxa have the opportunity to reproduce before capture in small scale fisheries. The analyses and questions addressed in this thesis are driven by

a desire to support conservation of invertebrate taxa in data-limited and resource-limited scenarios, contributing to healthy, well managed marine ecosystems.

1.2 Background and Context

Marine animal diversity is dominated by invertebrate species. Constituting 95% of all animal species in the ocean, invertebrate diversity of form and function has allowed them to thrive in environments from the deepest oceanic trenches to the shallows of every ocean on earth (Collen et al., 2012). Accordingly, they fill many roles in food webs and provide services invaluable to humans (Cardoso et al., 2011a). Corals act as buffers to storms, protecting coastlines from erosion (Moberg and Folke, 1999). Seasonal fluxes in zooplankton can drive fish numbers and dramatically influence fisheries (Ware and Thomson, 2005). Benthic species such as crabs and sea cucumbers act as “nutrient pumps”, dredging bottom habitat and returning nutrients back into food webs (Posey et al., 1995). And in the Antarctic, krill are notable for their astounding biomass and ability to sequester vast amounts of carbon in their wastes (Walsh et al., 2001).

Despite the critical roles invertebrates play in ocean ecosystems, they receive comparatively little attention in marine research (Cardoso et al., 2012; Collen et al., 2012). In part due to the astounding number of invertebrate taxa as well as their often cryptic nature, we know little about survival strategies or functional roles of most species (Cardoso et al., 2011b). Many species remain undescribed, and for most others, basic life-history and distributional data do not exist (Cardoso et al., 2011b; Collen et al., 2012). In food webs, invertebrate roles are sometimes heavily underestimated. Ecosystem modeling indicates that shifts in abundance of invertebrates in marine systems can have cascading effects of similar magnitude to that of shifts in forage

finfish (Eddy et al., 2017). This lack of basic life-history and baseline status information makes it difficult to observe and therefore manage changes within invertebrate populations.

Similar to finfish, many invertebrate populations are declining and there are examples of significant depletions (Anderson et al., 2011; Salomon et al., 2007). In the Caribbean, the overexploitation of queen conch, combined with a vulnerability to Allee effects, has resulted in large scale, basin-wide reductions (Stoner et al., 2012). In California, white abalone has suffered catastrophic declines of approximately ~99.99% (Davis et al., 1996; Hobday et al., 2000).

Similar patterns are seen globally. For instance, the popularity of sea cucumbers in the Asian seafood market has prompted worldwide serial depletions (Berkes et al., 2006). As with many marine conservation issues, invertebrate safeguarding is challenged by spatially massive and diverse habitats, unprecedented human pressures and a severe lack of resources to confront many of these problems (Allison et al., 1998). Further complicating these fisheries pressures has been the loss of key habitat such as coral reefs, mangrove forests and seagrass meadows (Munday, 2004), habitats that house large numbers of invertebrate taxa (Collen et al., 2012).

While there is an overall trend of decline for many invertebrates, human driven changes to marine ecosystems have led to benefits for some invertebrate species. On the north-east coast of North America, the collapse of cod stocks has led to increases in lobster densities – the result of the removal of a major lobster predator (McMahan et al., 2013). On coral reefs, fishing pressures on grazing fish species have changed herbivory dynamics (Mumby et al., 2006). For example, in the Indian and Pacific oceans, urchins and other invertebrate grazers have proliferated as fisheries have removed urchin predators or competing, grazing fish (McClanahan, 2014; Shears

and Babcock, 2003, 2002). Across the globe, there have been large increases in jellyfish blooms, the reasons for which are unclear (Brotz et al., 2012). Alteration of habitats and the use of active fishing gears have often resulted in “simplification” of complex habitats, shifting the balance toward species that thrive in less complex habitats (Alvarez-Filip et al., 2009; Harborne et al., 2012). The long-term ecological consequences of these human-driven changes are unclear and the complexities of ecosystem interactions are rarely as cut and dried as in these examples. Direct effects are often complicated by previously hidden interactions elsewhere in food webs and secondary and tertiary effects have proven difficult to predict and manage for (Travis et al., 2013).

Despite the numerous challenges facing marine invertebrate taxa, few conservation programs targeting marine invertebrates exist (Sloan, 2004). In fact, marine conservation remains largely focused on a small set of vertebrate species (Cardoso et al., 2011b). However, in some places where invertebrates have particularly high economic value, conservation-minded fisheries management has been introduced. For example, in the Bahamas, there is a focus on developing size limits and harvest refuges for economically important and CITES Appendix II listed queen conch (Stoner et al., 2012). In Chile, marine protected areas increased abundances of large adults and egg case density of loco snails *Concholepas concholepas* (Castilla and Duran, 1985; Manríquez and Castilla, 2001; Moreno et al., 1986). On the west coast of British Columbia, depletion of abalone has prompted larval seeding experiments. Unfortunately, this conservation program has not led to detectable increases in abalone densities (Campbell, 2000).

Throughout this thesis I refer to “survival, growth, and reproduction” in invertebrates—three elements important for persistence of populations (Kindsvater et al., 2016). I am referring to the rate of survival within and between life stages (e.g. survival from larval to juvenile stages; survival of sufficient numbers of adults to produce future cohorts). I am referring to the growth of animals to body sizes or maturity stages needed for key life history events (e.g. migrations, reproduction). And finally, I am referring to the production of offspring. Each invertebrate taxon in this thesis has its own unique morphology, growth rate, reproduction type, etc. (collectively, “life history strategy”). And while no single conservation practice will fully address each taxon’s needs, I aim to evaluate if two conservation practices (spatial fishing closures and catch size limits) contribute to improved survival (via abundance in reserves), growth (via proportion of adults in the catch) and reproduction (via reproductive output and yield) in invertebrate taxa and then suggest how these practices could be improved. Other life history elements are

1.3 Marine Protected Areas

A proposed alternative to species-specific conservation approaches is to set aside reserves where extractive pressures are removed (Bohnsack, 1998; Edgar et al., 2007). In these areas, species, habitats and food web relationships are given a chance to recover or achieve partial recovery (Micheli et al., 2005). The creation of these no-take areas often involves value-based decision making (Agardy et al., 2003; Lundquist and Granek, 2005). This has frequently resulted in reserve establishment with the explicit objective of protecting fish species of high economic value (Bohnsack, 1998; Halpern and Warner, 2003). In this regard, many reserves have been highly successful. A “fish-centric” approach has shifted how we evaluate marine reserves from a

holistic, biodiversity approach, to a model where fish abundance, diversity, biomass and body size are the metric of reserve success (Halpern, 2003).

Marine protected areas (MPAs) are a heavily advocated tool to conserve biodiversity and supplement fisheries (Agardy, 1994; Holland, 2002). There are many forms of MPAs: along with no-take areas (marine reserves) the term also describes areas that receive partial protection or temporally or spatially varying protection. The Convention on Biological Diversity (CBD), Aichi Target 11 called for 10% global MPA coverage by 2020, while the 2003 IUCN World Parks Congress called for 20-30% coverage by 2012. Despite these ambitious goals, MPA establishment has progressed slowly and as of 2020, global MPA coverage stood at 7.8% of the ocean (MPA Atlas, 2020). Gains in MPA coverage have been driven by establishment of a small number of very large MPAs (Boonzaier and Pauly, 2016). As of 2013, these large areas (>100,000 km²) form approximately 80% of total MPA coverage (Leenhardt et al., 2013). Theoretically, MPAs not only create a refuge for marine life to thrive but create positive effects in surrounding areas, making them simultaneous tools for marine conservation and resource management (Russ et al., 2004).

There is strong evidence that reserves are working to conserve fish and, in some cases, promote their spillover into adjacent fisheries (Russ et al., 2004; Russ and Alcala, 1996). Prominent meta-analyses examining fish response to reserves found 3.7 times more fish within reserves than out (Mosquera et al., 2000) and an overall increase in the density, biomass, size and diversity of fish species (Lester et al., 2009). The most pronounced positive responses have been observed in exploited species (Côté et al., 2001). These patterns are consistent across marine reserves in

tropical and temperate ecosystems and in reserves of varying sizes. Additionally, the spillover of both adult fish and larvae has been observed in several reserves (Abesamis and Russ, 2005; Goñi et al., 2008; Le Port et al., 2017; McClanahan and Mangi, 2000; Russ et al., 2004; Russ and Alcala, 1996). The magnitude and consistency of this spillover and its contribution to fisheries remains under question and some argue that benefits to fisheries from spillover are likely only present when outside fisheries have been severely mismanaged (e.g. Buxton et al., 2014). Recent studies, however, have found measurable spillover into surrounding areas among some taxa (e.g. exploited taxa, mobile taxa) and in certain conditions (larger and older protected areas) (Di Lorenzo et al., 2020; Kough et al., 2019; Lenihan et al., 2021).

Despite the successes observed in fish taxa, changes in abundance of marine invertebrates in response to reserves is not clear. This is, in part, due to the lack of focus on reserve response patterns in invertebrate taxa in conservation literature. MPA meta-analyses tend only to briefly touch on invertebrates and often indicate overall negative or non-significant trends in invertebrate taxa inside of reserves (Halpern, 2003; Lester et al., 2009). For example, a recent global MPA analysis measuring “conservation benefits” of MPAs does not mention the word “invertebrate” in any of the text or supplementary information (Edgar et al., 2014). Some individual studies have shown marine reserves to increase exploited invertebrate abundance and size (Ashworth et al., 2004; Edgar and Barrett, 1999). For example, lobster fisheries in New Zealand and South Africa quickly benefitted from spatial fisheries closures (Freeman et al., 2012; Shears et al., 2006). And densities of snails important to food security rapidly increased in Egyptian reserves when they were well enforced (Ashworth et al., 2004; Benzoni et al., 2006). Invertebrate responses may be slower to appear and more difficult to interpret (Pinnegar et al.,

2000). For example, decreases in abundance inside of reserves relative to outside may be due to restored trophic and competitive interactions as fish begin to recover within reserves (Micheli et al., 2005; Shears and Babcock, 2003).

Marine invertebrates play diverse roles in ecosystems and there is potential for shifts in the functioning of these ecosystems as their numbers are impacted by spatial management. These roles vary from filtration of water, to removal of parasites from fish to acting as a source of food for higher trophic levels. The term “ecosystem functioning” varies in definition but can include measures of energy or material flow through food webs (Diaz and Cabido, 2001) and the processes (e.g. filtration, nutrient cycling) that occur in ecosystems (Bengtsson, 1998; Naeem, 2004). These changes in the presence of traits possessed by species are often not quantified. There is evidence that life history traits like larger body size and adult longevity begin to increase in reserves, however these changes can take much longer to appear than increases in biomass and abundance (McClanahan and Graham, 2015). Nevertheless, the sheer diversity of roles of invertebrates in marine systems begs closer examination of functional change in invertebrate communities are that receiving protection from fishing pressures (Bremner et al., 2006a, 2006b).

The scarcity of analysis on macro-invertebrate response to reserves is especially alarming in light of invertebrate importance in fisheries. Commercial exploitation of invertebrate species has increased six-fold since 1950 and invertebrates now constitute one-fifth of the global commercial fisheries catch (Anderson et al., 2011). More countries than ever are reporting catches of invertebrate species. By 2004, 34% of commercial invertebrate fisheries were classified as over-

exploited, collapsed or closed (Anderson et al., 2011). However, unlike many commercially exploited finfish, tools for evaluating the status as well as management options for many invertebrate stocks have largely remained unexplored. This is surprising in view of their increasing social and economic importance (Anderson et al., 2011).

In developing regions, invertebrate fisheries are both important and enormously complex. These fisheries, which are often unreported and unregulated (Berkes, 2001; Palomares and Pauly, 2014), contain a diversity of methods, gears and target taxa (Mills et al., 2011; Selgrath et al., 2017). Conch and lobster are important fisheries species in the Caribbean, sea cucumbers in Asia and much of the Pacific and loco (Chilean abalone) in Patagonia are just a few examples. Globally, in coastal regions, marine invertebrates constitute a significant portion of fisher catch (Kleiber et al., 2014). In the Central Philippines, between a quarter and a third of all protein consumed in coastal villages comes from invertebrate catch and makes a significant contribution to local food security (Kleiber et al., 2015).

1.4 Managing Fisheries Outside of Reserves

Large areas of ocean fall outside of marine reserves and there is a need for data-poor invertebrate fisheries management tools. In regions with few management resources, setting total allowable catches or exploitation rates is often not feasible due to limited knowledge of stock status and exploitation, along with limited enforcement capabilities. A number of data-poor fisheries management tools have been suggested but few have been tested with invertebrate taxa (Carruthers et al., 2014). Despite these challenges, when stock status is unknown, imperfect but still highly useful management options are available (Baum and Worm, 2009; Johannes, 1998).

These can include spatial closures (MPAs), bans on harvest of female individuals, or animal size-based harvest rules.

Animal growth is an important factor in marine resource management as it can provide estimates on when animals reach sexual maturity and size at harvest for maximum yield. These estimates are important because a population requires a sufficient abundance or density of spawners to produce enough offspring to replenish itself. For much of the developing world, there are few resources to estimate stock biomass or enforce a total allowable catch. So, where controls of fisheries inputs (i.e. number of vessels and effort) are not practical, suggesting minimum sizes offers a potential management option given fisher buy-in. The effect of size limits on fisheries yield can be particularly powerful where limits are designed so that the biomass of a cohort is maximized (L_{opt}) (Froese et al., 2008). In instances where L_{opt} is used, the age structure of the population resembles that of an unfished stock, adding resilience within the population to withstand disturbance (Froese et al., 2016).

1.5 The Danajon Bank, Philippines as a Case Study

The Central Philippines is representative of challenges that have so far slowed attempts to stem marine biodiversity loss: a high and growing demand on the ocean for food and livelihoods, lack of management capacity, and little political will for environmental conservation (Berkes, 2001; Gill et al., 2017; Muallil et al., 2014; Selgrath et al., 2017; Weeks et al., 2010). The Danajon Bank, where the research in this thesis is focused, is a rare double barrier reef administered by the four surrounding provinces of Cebu, Bohol, Leyte and Southern Leyte. Marine management lies largely with municipal and village government (White et al., 2006). This region is also a

centre for biodiversity (Carpenter and Springer, 2005) but since 1960, extractive effort has increased 240%, heavily impacting these biodiversity rich communities and habitats on which they rely (Selgrath et al., 2017).

Fishing on the Danajon Bank is central to many livelihoods and includes a diverse set of gears that target a wide breadth of marine biodiversity. These fisheries are effectively open-access, and present a high level of fishing effort driven by a significant human population density and a lack of alternative livelihoods (Christie et al., 2006; Selgrath et al., 2017). These pressures are enormous: on a section of Danajon Bank that makes up approximately one third of the total Bank, over 90 different gears have been identified and the annual person days of fishing effort exceeds 1.3 million (Selgrath et al., 2017). Subtidal fishing is primarily conducted by small, outrigger boats (many with small engines), from which fishers skin dive and deploy gears like hook and line, poison, dynamite, nets and traps. The use of gears has evolved over time on the Danajon Bank, shifting from hooks and line and nets in the 1960s to predominantly nets and active methods like skin diving by 2010 (Selgrath et al., 2017). In intertidal zones, walking in intertidal habitat and gathering invertebrates, fish, and seaweeds is a major source of fishing effort, accounting for 13% of weekly catch that is sold, and 27% of catch that is retained for household consumption (Kleiber et al., 2014). While both subtidal and intertidal fisheries catch invertebrates, for intertidal gleaning fisheries, invertebrates are the primary target, accounting for >90% of gleaned catch by weight (Kleiber et al., 2014). This catch contains a high species diversity of invertebrates and common taxa in the catch include: snails and slugs (e.g. *Trochus*, *Dolabella*), urchins (e.g. *Tripneustes*), crabs (e.g. *Portunus*), bivalves (e.g. *Codakia*, *Crassostrea*), and sea cucumbers (e.g. *Holothuria*, *Stichopus*) (Kleiber et al., 2014).

The Philippines has nearly 2000 marine reserves and as of 2006, sixty marine reserves in the Danajon Bank area (Christie et al., 2006). In the Danajon Bank, Project Seahorse, and its Philippines partner organization Project Seahorse Foundation for Marine Conservation (PSF) have been instrumental in catalyzing the creation of 35 marine reserves. Marine reserves in the Danajon Bank vary in size as well as placement, with some found far offshore, while others abut the shore, covering areas typically used for intertidal collection of fish and invertebrates (“gleaning” fisheries). PSF hosted my field research, introduced me to local officials and guided me through the formal process of gaining research permission at the municipal and community levels. PSF staff members have also been critical for helping ground this work in the practicalities of conducting on the ground conservation programming.

1.6 Thesis Outline

This thesis addresses the conservation and management of marine invertebrates in an environment rich in diversity yet challenged by a lack of institutional resources, data, and political will (Andrew et al., 2007). I employ a diverse set of analytical approaches to evaluate current effectiveness in the conservation of these species and then suggest ways forward that are relevant to data and resource-poor scenarios. I wanted to know if current use and design of marine reserves is impacting the recovery or partial recovery of invertebrates and the types of reserves that are having the greatest impact. Does an animal’s life history and exploitation status influence their recovery potential? Do we see functional changes in ecosystems when invertebrates are protected? And how practical is it to establish data-limited fisheries size limits for the animals that live outside the boundaries of reserves?

In this thesis I combine fisheries independent and dependent field data, published literature and empirical relationships to understand impacts of marine reserves and size-based management in invertebrate conservation. In Chapter 2, I present a short pilot study on the impacts of survey timing (i.e. day or night) on detection rates for invertebrate abundance and diversity. I then focus on a set of community managed marine reserves in the Central Philippines to understand the factors affecting invertebrate response in both abundance (Chapter 3) and biodiversity and functional change (Chapter 4). In the last data chapter of this thesis (Chapter five), I address a growing recognition that marine reserves alone are not sufficient for achieving conservation and fisheries management goals. I assess the utility of data-limited, growth-based tools to set fisheries size limits in commonly captured invertebrate taxa. I conclude, in Chapter 6, with a synthesis of this body of work and offer direction on how it may be used to support healthy and more abundant marine invertebrate populations.

Chapter 2: Night sampling is best for detection of coral reef invertebrates

2.1 Summary

Marine invertebrates play important roles in ecosystems and support fisheries, yet are often overlooked in long-term monitoring. Establishing survey methods that effectively track changes in their abundance and diversity will be important for monitoring status and trend which are essential inputs for conservation and resource management decision making. On coral reefs, a popular survey method is day-time belt transects, but many invertebrates are nocturnal. In this short pilot study I compare day-time and night-time reef sampling methods to evaluate which method obtains highest detection of invertebrate individuals and taxa. My results indicate that night belt-transects provide significantly higher detection of exploited (504 times higher density) and mobile (22.5 times higher density) individuals and significantly higher richness estimates for all taxa (2.5 times greater family richness), and among various sub-groups including exploited taxa (16 times greater family richness), and mobile taxa (4.2 times greater family richness). As expected, there was no difference in sessile taxa for either metric. Night surveys required roughly double the sampling effort to reach 80-90% of asymptotic diversity but resulted in 2.5 times higher taxon richness value estimates compared to day surveys. These results have application for both researchers and resource managers who wish to increase taxon detection in their surveys and understand abundance patterns in coral reef invertebrate taxa.

2.2 Introduction

Reversing biodiversity loss requires knowledge of status and trend in populations and their environments. Conservationist and resource managers rely on monitoring data to set catch limits,

restrict trade in particular taxa, or set aside critical habitat for protection (Pereira and Cooper, 2006). These decisions rely on data that is representative of populations or an area's biodiversity (Kéry and Schmidt, 2008; Miloslavich et al., 2018). For example, good data for abundance and richness can lead to identification of biodiversity hotspots, estimates for species range or determination of sustainable exploitation limits (Collen et al., 2008; Williams et al., 2002). It is therefore important that sampling methods use approaches that are effective at detecting study taxa (Kellner and Swihart, 2014).

Marine invertebrates have earned greater recognition as a critical component of ocean biodiversity and capture fisheries (Anderson et al., 2011; Collen et al., 2012). The vast majority of marine animal diversity is made up from invertebrate taxa and they are involved in processes central to functioning in marine ecosystems (Cardoso et al., 2012; Moberg and Folke, 1999; Newell, 1988; Ware and Thomson, 2005). Over the past several decades, year-over-year growth in invertebrate fisheries has outpaced that of finfish and some invertebrate species rank among the most economically valuable in international seafood trade (Anderson et al., 2011; FAO, 2014). In developing regions, the magnitude of small-scale invertebrate fisheries has only recently been recognized (Kleiber et al., 2014; Palomares and Pauly, 2014).

Despite global and local importance, evaluations of the status of exploited invertebrate populations are often absent or severely deficient (Cardoso et al., 2012, 2011a; Collen et al., 2012; Jimenez et al., 2015). This presents challenges for those interested in designing marine invertebrate management programs, understanding their ranges or identifying invertebrate taxa that require conservation attention. It is therefore important that invertebrate survey methods

have reasonable levels of detection so that accurate status and trend data is available for understanding and responding to threats.

Coral reef surveys are typically completed during day-light hours but there are many invertebrate taxa that emerge only at night (McFarland, 1986; KMG, pers. obs.). Despite this nocturnal behaviour, an examination of the literature revealed only one record of invertebrate surveys occurring at night (Francis et al., 2019). The Reef Check program, for example, which operates with a standardized set of methods across several countries, uses the same day-time belt transects as are used for fish taxa (Hodgson et al., 1998). In this analysis I use data from a small pilot study and compare the ability of day and night belt transects to detect coral reef invertebrate density and richness. I focus on the Central Philippines—a region where between a quarter and a third of the protein diet is obtained from macro-invertebrates examined in this study—snails, bivalves, urchins and crabs—(Kleiber et al., 2014) and where pressures on invertebrate taxa come in many forms.

2.3 Methods

2.3.1 Study Taxa

I counted all non-coral, non-sponge macro-invertebrates greater than two centimetres in size (from here, referred to as “invertebrates”). Animals were identified to the finest taxonomic scale possible, however, the breadth of diversity in invertebrates often prevented species-level identification (and in some cases genus-level identification). For consistency in this analysis, I use family-level identification. Taxa were sorted into groups based on their exploitation status (exploited/non-exploited) and mobility (mobile/sessile). To determine the exploitation status of

each taxon, I consulted my local research assistants (who are fishers) as well as other local fishers.

2.3.2 Study Site

I sampled inside of Pinamgo marine reserve on Danajon Bank, Central Philippines. Danajon Bank is an approximately 1200-square-kilometre double-barrier reef in the north of Bohol Province. The region has particularly high levels of biodiversity and intensive human threats to the marine ecosystem (Anticamara et al., 2010; Selgrath et al., 2017). At the time of sampling, the reserve was 37.8 hectares and had been in place for 13 years. The reserve consisted mostly of corals as well as some seagrass, coral rubble and sand.

2.3.3 Sampling Methods

Sampling occurred in June, 2012. Sampling was divided into day-time and night-time scuba sampling. We conducted three 50 x 3 m haphazardly placed belt transects during the day and six 50 x 3 m haphazardly placed belt transects at night for a total of nine separate transects. All sampling was conducted within the reserve. So as not to impact observed densities of mobile species during sampling, we laid transects at least three hours before each visual survey. Night-time sampling began at least one hour after sunset and was conducted using mask-mounted and hand-held full spectrum dive lights. One trained biologist and one local research assistant with knowledge of local species and training in invertebrate identification completed the surveys. For each transect, we swam along the transect line, each surveying 1.5 m from centre line of the belt transect. We made two passes of each transect: a 15-minute survey for mobile species, followed

by a second, 30-minute pass for sessile species. Sampling was done at depths between 1 and 5 metres and was concentrated on coral habitat.

2.3.4 Data Analysis

For day-time and night-time surveys, I calculated the mean density of individuals for each group (all taxa, exploited taxa, unexploited taxa, mobile taxa, sessile taxa) and their respective 95% confidence intervals. If confidence intervals for day and night surveys did not overlap, I considered there to be a significant difference in the abundance detected by the two methods. Conversely, if confidence intervals did overlap, there was not a significant difference. A MANOVA and univariate tests were not conducted because of low sample sizes (i.e. 20+ taxon groups and only 9 total transects).

To account for uneven sampling and non-linear patterns in species accumulation curves, I conducted a rarefaction extrapolation analysis which extends the rarefaction curves to their asymptote to estimate absolute diversity (Chao et al., 2014). For each data set, a total of 5000 rarefaction sampling draws were made and bootstrapping was used to estimate confidence intervals around my estimates. Rarefaction analysis was completed using the iNext package in the R statistical environment (Chao et al., 2014; Hsieh et al., 2016; R Core Team, 2017).

To understand the sampling effort required to detect 80% or 90% of families estimated from each sampling method (day vs night), I then generated taxon accumulation curves by number of animals sampled and reef area (m²). Accumulation curves were calculated within the iNext package (Chao et al., 2014; Hsieh et al., 2016).

2.4 Results

Among all transects, we counted 6845 individual invertebrates with individual transect counts ranging from 216 to 1611. We detected a total of 33 families and individual transect family totals ranged from six to 22. Day-time sampling yielded 754 animals in 10 families along three transects (450 m²) for a total density of 1.68 animals/m². Night samples yielded 5337 animals along six transects (900 m²) for a total density of 5.93 animals/m² (Table 2.1 Invertebrate families detected during day-time and night-time transects and their mobility status. “x” indicates detection.. Summing across day and night surveys, bivalve and gastropod molluscs constituted most of the sample abundance, followed by malacostracan arthropods, annelids, and variety of families from the phyla echinodermata and platyhelminthes.

There was no statistical difference in abundance between day and night surveys when considering all invertebrate taxa as a single group (Figure 2.1). Examining taxa by their exploitation and mobility status on the other hand, revealed significant differences. A single animal from an exploited family (a cardiid cockle) was found during day-time sampling across all transects (0.002 animals/m²), whereas at night, 908 animals from 15 exploited families were found (1.0 animal/m²), a 504 fold difference in density. Mobile taxa were found at densities 22.5 times higher during night surveys (1489 from 22 families; 1.7 animals/m²) than day surveys (33 animals from 4 families; 0.1 animals/m²). There was no significant difference in densities of unexploited and sessile taxa between day and night surveys.

Night sampling detected significantly more invertebrate families across all categories except for sessile and unexploited taxa (Figure 2.1). An asymptotic taxon richness value of 14.5 (10.5 - 29.9, 95% CI) was estimated for day surveys compared with 36.1 (34.5 - 52.3, 95% CI) at night—a 2.5 fold difference. Day surveys almost never detected families collected in local fisheries (1 family) while night surveys had an estimated asymptotic richness value of 16 (15.1 – 26.1, 95% CI).

Mobile taxa asymptotic richness was estimated at 5.9 families (4.2 – 18.5, 95% CI) during the day and 24.7 (22.4 – 40.9, 95% CI) at night, a 4.2 fold difference. No difference was found in unexploited or sessile asymptotic family richness.

Taxon accumulation curves indicate that day sampling requires surveying 1274 animals (Figure 2.2) or 375 m² of reef area (Figure 2.3) to achieve 80% detection of the day-time asymptotic family diversity. To achieve 90% detection, 2051 animals and 600 m² of reef area is required. Night sampling, on the other hand, required approximately 2 and 2.5 times greater sampling effort for 80% and 90% thresholds, respectively but resulted in 2.5 times greater detection of invertebrate families than day surveys.

2.5 Discussion

Despite the preliminary nature of this study, the magnitude of difference between abundance and diversity values between day and night is notable. These results indicate that diurnal timing of surveys can have a significant impact on invertebrate abundance and richness estimates; particularly for exploited and mobile taxa. This has implications for management, biodiversity

research and conservation planning—disciplines that rely on abundance and richness sampling that has reasonable odds of detection (MacKenzie, 2006). In this MPA, for example, a practitioner using day-surveys would likely be unable to detect or monitor for trends in families that are an important component in local fisheries – fisheries that occur during the day in the shallow water areas (<1m) and largely at night in subtidal areas (see Chapters 1 & 5 for further description of these fisheries and taxa obtained in these fisheries). In my night surveys I detected many individuals and taxa that belong to these groups yet are “invisible” during day sampling. Sessile taxa (e.g. bivalves, burrowing annelids, etc.) did not suffer from this problem and were found at densities and richness levels no different between day and night sampling. This result should be expected as sessile individuals are unable to go into hiding during daylight hours and would have the same probability of detection regardless of sampling time.

Implementing day-time survey methodology for invertebrate taxa is likely problematic, however the night-time alternative comes with significant challenges. Sampling at night, underwater, often in remote coral reef locations adds additional layers of logistical planning and complexity to field studies. Divers must use additional safety measures, hire experienced boat drivers who have a depth of knowledge in hazardous reef formations, and be aware of night-time weather patterns (on Danajon Bank, large storms frequently passed through with little warning shortly after sunset—the ideal time for after-dark surveys). My estimate for night-sampling coverage needed to reach 90% detection of invertebrate taxa in this MPA is substantial, particularly given the extra logistical requirements. Practitioners, must evaluate the trade-offs between these logistical challenges and obtaining good monitoring data for mobile and/or exploited invertebrates.

As threats to coral reef systems grow there is a need to detect and respond to populations in decline (Collen et al., 2008). Coral reefs are some of the most taxon-rich ecosystems on the planet and much of that richness is in invertebrates (Gibson et al., 2011). Understanding the status and trend for taxa that are typically under-researched and rarely the focus of conservation programming is a critical next step in detecting and addressing threats. This work encourages practitioners to re-examine their coral reef invertebrate sampling methodology so that they can maximize the effectiveness of their conservation work.

Table 2.1 Invertebrate families detected during day-time and night-time transects and their mobility status.

“x” indicates detection.

Family	Day	Night	Mobility	Family	Day	Night	Mobility
Amphiuridae		x	Mobile	Penaeidae		x	Mobile
Cardiidae	x	x	Sessile	Phyllidiidae		x	Mobile
Cerithiidae	x		Mobile	Plakobrachidae		x	Mobile
Cypraeidae		x	Mobile	Portunidae		x	Mobile
Diadematidae		x	Mobile	Pseudocerotidae		x	Mobile
Diogenidae		x	Mobile	Sabellidae	x	x	Sessile
Hippolytidae		x	Mobile	Sepiidae		x	Mobile
Holothuriidae		x	Mobile	Spondylidae		x	Sessile
Malleidae		x	Sessile	Stenopodidae		x	Mobile
Mytilidae	x	x	Sessile	Stichopodidae		x	Mobile
Ophiocomidae	x	x	Mobile	Synaptidae	x	x	Mobile
Ostereidae		x	Sessile	Turbinidae		x	Mobile
Paguroidea		x	Mobile	Vermetidae	x	x	Sessile
Pectinidae	x	x	Sessile	Xanthidae		x	Mobile

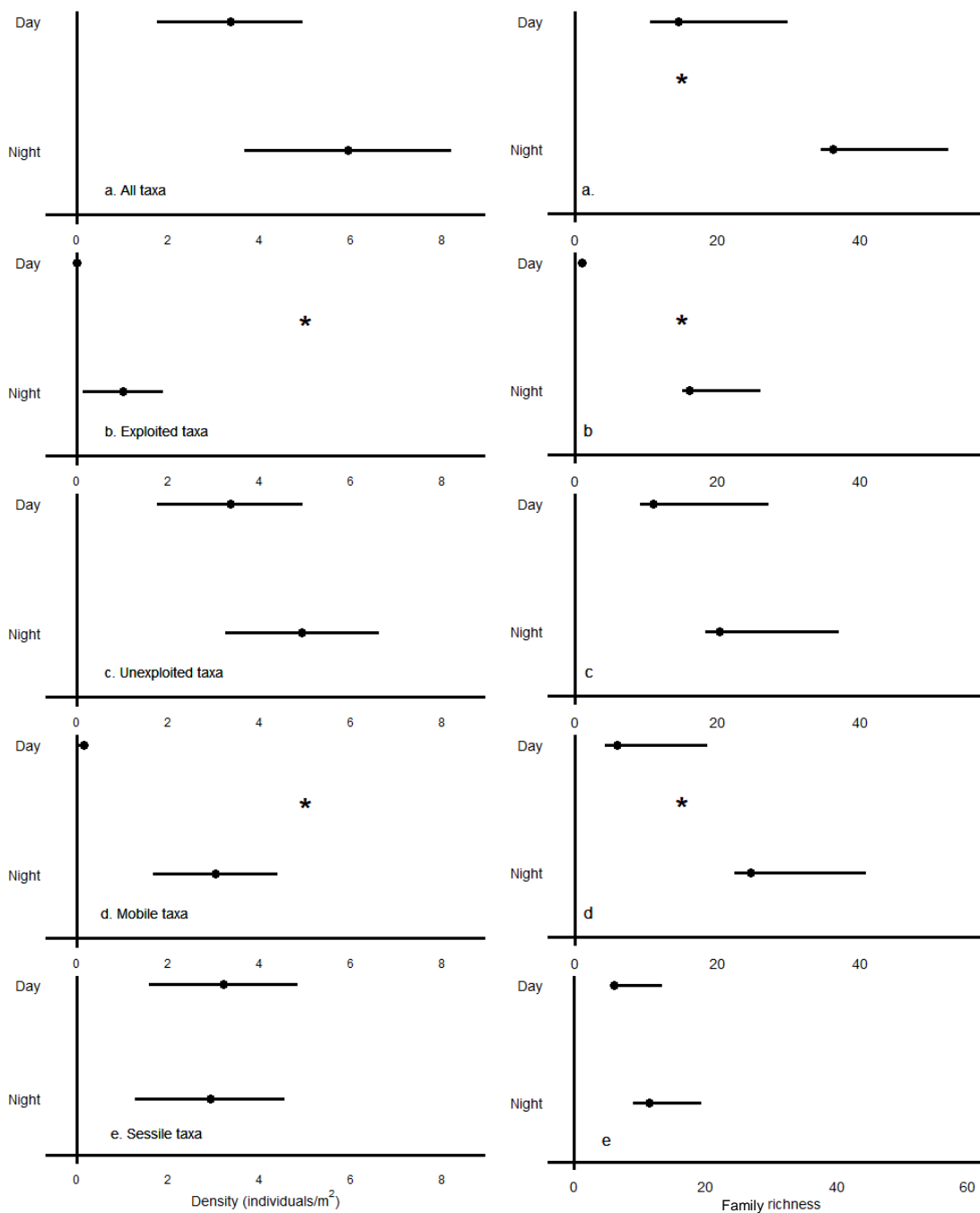


Figure 2.1 Mean density and family richness for five groupings of invertebrates (a. all taxa, b. exploited taxa, c. unexploited taxa, d. mobile taxa, and e. sessile taxa) by sampling method (day belt transects and night belt

transects). Error bars are 95% confidence intervals. Non-overlapping bars represent a significant difference between sampling methods and are noted with a “*”. Family richness estimates and associated confidence intervals were obtained from rarefaction extrapolation analysis where day and night-time data-sets were extrapolated to their asymptotes.

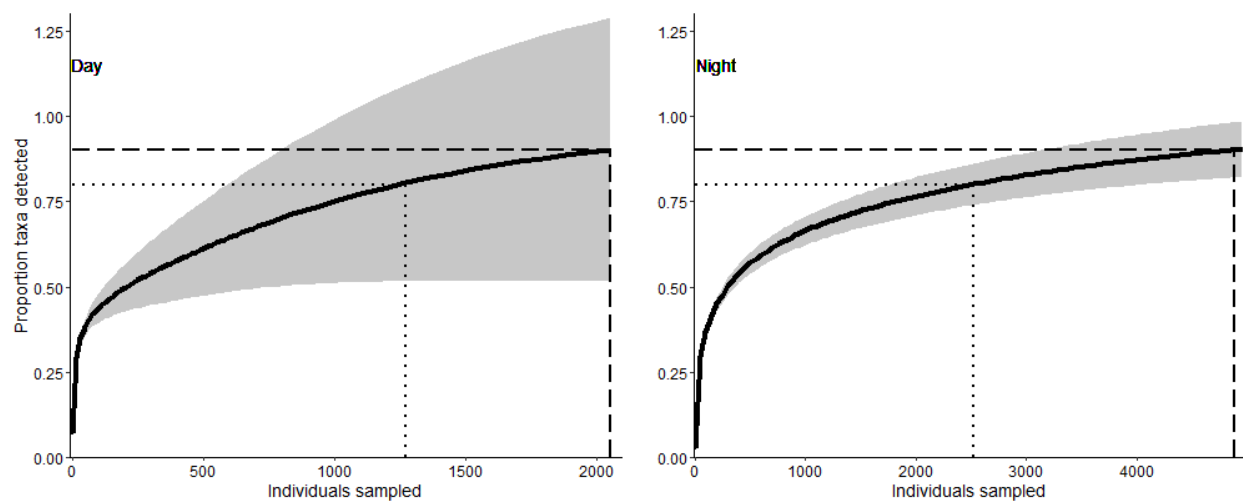


Figure 2.2 Taxon accumulation curves estimated from rarefaction, relative to number of individuals sampled.

Dotted lines indicate 80% taxa detection and dashed lines indicate 90% taxa detection. Error ribbons are 95% confidence intervals. Note difference in x-axis scale.

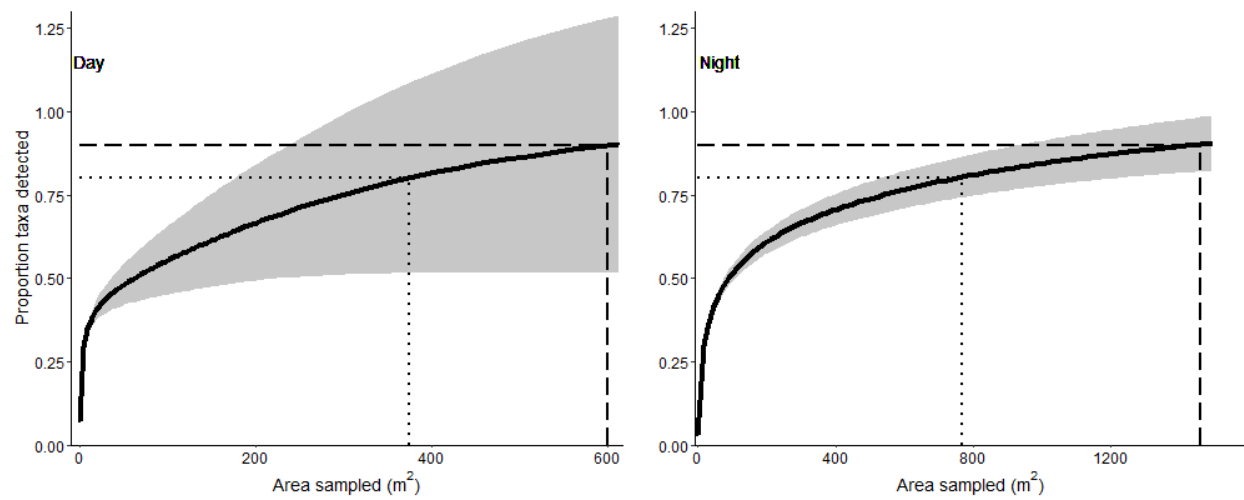


Figure 2.3 Taxon accumulation curves estimated from rarefaction, relative to area sampled. Dotted lines indicate 80% taxa detection and dashed lines indicate 90% taxa detection. Error ribbons are 95% confidence intervals. Note difference in x-axis scale.

Chapter 3: Tropical invertebrate response to marine reserves varies with protection duration, habitat type, and exploitation history

3.1 Summary

Macro-invertebrates play a critical role in marine processes, are important in global fisheries, and make up the vast majority of ocean biodiversity, yet are largely overlooked in fisheries stock assessment and conservation. Marine reserves are a heavily advocated method for promoting recovery of marine biodiversity but the design of reserves and the methods for evaluating their performance often neglect invertebrate taxa, instead assessing changes in fish abundance or biomass. The purpose of this study is to (1) measure the impacts of no-take marine reserves on marine macro-invertebrates, (2) identify the correlates of changes to macro-invertebrate abundance, and (3) determine if the typical taxa used to measure reserve success (finfish) can predict changes in invertebrate abundance. Non-coral, non-sponge, macro-invertebrates were sampled inside and immediately outside of 10 community-managed marine reserves in the Central Philippines and compared to abundances found at distant fished sites. Using generalized linear mixed effects models with multi-model inference, positive reserve effects were found in exploited invertebrate taxa both inside and outside of reserves (1.5 to 2.3 times greater abundances) but no effect was found in unfished taxa. Habitat composition and complexity were consistently associated with invertebrate abundance. Most surprisingly, invertebrate abundance was not consistently predicted by that of fish. These results indicate fish, in isolation, may not be an ideal indicator for biodiversity response to reserves and habitat considerations are important when creating reserves that support invertebrates. These results are particularly relevant to

practitioners in developing regions, where community-managed reserves are common and invertebrates are important in fisheries.

3.2 Introduction

Marine invertebrates make up over 95% of marine animal species diversity, so it is surprising that they—as a major component of fisheries catch—are largely overlooked in marine management and conservation (Collen et al., 2012). Their underrepresentation extends to IUCN conservation assessments (fewer than 3000 assessments, 38% of which are data deficient or no longer valid. For further analysis, see (Cardoso et al., 2012; IUCN, 2017) as well as evaluation and management within fisheries (Anderson et al., 2011; Perry et al., 1999). Commercial invertebrate fisheries experienced significant growth over the past six decades and the true scale of small-scale invertebrate fisheries in developing regions only recently began to emerge (Anderson et al., 2011; Kleiber et al., 2014; Palomares and Pauly, 2014). The most widespread extractive methods (dredging, benthic trawling) commonly result in impacts to habitat and have prompted a strong trend toward over-exploitation in many invertebrate taxa (Anderson et al., 2011)—issues particularly acute in tropical, developing regions. In these regions, a combination of heavy reliance on invertebrates, lack of invertebrate conservation assessment and near absence of management of invertebrate fisheries suggests enormous opportunity for making improvements in their conservation and management (Cardoso et al., 2012; Collen et al., 2012).

In responding to biodiversity loss, major policy suggests the creation of no-take marine reserves, particularly in regions where data and capacity for complex management remains unavailable (CBD, 2012; Gaines et al., 2010; Johannes, 1998). Analyses demonstrate that reserves frequently

offer significant, positive effects on fish abundance and biomass, and sometimes, positive effects on fisheries in surrounding areas (Gell and Roberts, 2003; Lester et al., 2009; Palumbi, 2003; Roberts et al., 2001). Reserves offer a data-less (or near data-less) management strategy (Johannes, 1998), making them popular case studies of biological response to local marine management (Russ et al., 2004; Samoilys et al., 2007).

Analyses of marine reserves tend to concentrate on fish taxa and a handful of economically important invertebrates (Lester et al., 2009). Meta-analyses show large increases in the density, biomass, size and diversity of fish species (Lester et al., 2009; Mosquera et al., 2000), with the most pronounced recoveries in taxa important in fisheries (Côté et al., 2001). As with fish, there are some examples of economically important invertebrates (e.g. lobster) showing positive responses to reserves (Edgar and Barrett, 1999), but in many studies, invertebrates exhibit a combination of positive, negative and stable abundance trajectories after protection (Ashworth et al., 2004; Edgar and Barrett, 2012; Lester et al., 2009).

Considering that invertebrates make up the majority of marine animal diversity, the mechanisms of their reserve response represent a gap in our understanding of reserve biodiversity impacts and may be useful in designing reserves that account for non-fish taxa (Sale et al., 2005). The factors influencing invertebrate response may include reserve placement, habitat, whether they are exploited in fisheries and species interactions. As other species within food webs increase in abundance, trophic and competitive interactions may be restored, resulting in a combination of positive and negative trends in invertebrate abundance (Babcock et al., 2010; Micheli et al., 2005; Shears and Babcock, 2003). Habitat specialists, on the other hand may be more impacted

by changes in habitat types and quality (Cariglia et al., 2013; Dumas et al., 2013). Regardless of the drivers of differential responses among taxa inside of reserves, several examples of invertebrate responses in reserves show they do not match patterns observed in fish (Ashworth et al., 2004; Edgar and Barrett, 2012). With this in mind, a shift in approach away from one that emphasizes recovery to a more holistic one, where restored species interactions result in a combination of positive and negative abundance trajectories may be needed.

The capacity of invertebrates to respond to marine reserves is of particular interest in developing regions where invertebrates comprise a major share of local fisheries and community managed marine reserves have become widely used as a strategy for conservation and fisheries management (White et al., 2002; Yasue et al., 2010). In the Coral Triangle, establishment of approximately 2000 no-take marine reserves helps protect habitat, improve fisheries and offers alternative forms of income through tourism (White et al., 2014). In the rural areas in this region, a significant portion of the protein diet comes from invertebrate catch (Kleiber et al., 2014), especially during times when weather becomes unfavourable for boat-intensive finfish fisheries (D. Kleiber, pers. comm., September 2014). Given this importance, the ability of marine reserves to influence invertebrate species has important local implications for both food security and for design of reserves that consider invertebrate taxa. In this study, a set of 10 marine reserves and three distant fished sites in the Central Philippines are used to examine the effects of reserve age, placement, habitat and fish abundance on marine invertebrate response to reserves. Using this information, I comment on how reserves could be better evaluated for their biodiversity effects and how reserves may be designed with invertebrates in mind. Very few studies have considered the response of all taxa of macro-invertebrates in marine reserves, regardless of their economic

value (Dumas et al., 2017; Jimenez et al., 2015; Jimenez et al., 2010) and this is the first study to do this in the coral triangle.

3.3 Methods

3.3.1 Study Taxa

Non-coral, non-sponge, macro-invertebrates (from here, referred to as “invertebrates”) greater than two centimetres in size were counted (Table 3.1; see appendix A1 for taxon list with density by treatment). Unlike previous marine reserve work, which focused on species important in local fisheries, taxa were counted regardless of local value. Individuals were identified to the finest taxonomic scale possible, however, the breadth of diversity in invertebrates often prevented species-level identification (and even in some cases genus-level identification). For consistency in this analysis, family-level identification is used. Previous work has shown that family-level taxonomic resolution is sufficient to describe and detect patterns and changes in invertebrate assemblages (Jimenez et al., 2010). Several invertebrates in this analysis are heavily exploited in local fisheries (abalone, bivalves, crabs, etc.) while others (small sea slugs, brittlestars, flatworms, etc.) remain unexploited (see Table 3.1 for exploitation status). Invertebrate fisheries consist of intertidal collection (gleaning), skin diving (with and without crowbars for breaking apart corals), nets and traps for crabs and lobsters. To determine the exploitation status of each taxon, local research assistants (who are fishers) as well as other local fishers were consulted.

3.3.2 Study Sites

Reserve sites in 10 communities and three distant fished sites were sampled on Danajon Bank, an approximately 1200-square-kilometre double-barrier reef north of Bohol, Central Philippines

(Figure 3.1; see appendix A2 for site maps). The region has particularly high levels of biodiversity and intensive human threats to the marine ecosystem (Anticamara et al., 2010). Reserve sites were chosen to achieve a roughly evenly distributed temporal coverage of reserve ages ranging from 0 (distant fished sites) to 18 years since reserve establishment. Small island communities, with technical assistance from local government and non-governmental organizations, manage these permanently closed, no-take reserves, locally referred to as “sanktuaryo”. At the time of research, they ranged in size from 10.5 to 52.6 hectares and largely protected coral reef habitat. The three distant fished sites were chosen as ecologically similar comparisons to reserve sites—all, at minimum, two kilometres from the closest reserve site. These reserve sites and distant fished sites are surveyed as part of a long-running fish and habitat monitoring program (Samoilys et al., 2007). Areas sampled immediately outside of reserves were between 10 and 200 metres from the reserve boundaries.

To account for spatial processes related to reserve placement such as population density and coastal run-off, the linear distance from each site to the closest major land mass with a major population centre was recorded.

3.3.3 Sampling Design

Sampling occurred from June through August 2013. At each reserve, six 50 x 3 m haphazardly placed belt transects were surveyed inside and six outside the reserve for a total of 12 transects per reserve. At each of the three distant fished sites, six 50 x 3 m haphazardly placed belt transects were surveyed. Transects were placed in similar habitats and were limited to predominantly reef crest and slope areas that included occasional, small patches of soft bottom

and seagrass. Each transect was placed at a depth between 1.5 and 5 m. So as not to impact observed densities of mobile species during sampling, transects were laid at least 3 hours before each visual census. A preliminary study (Chapter 2) showed that night-time surveys yielded significantly higher densities and greater taxonomic richness of invertebrates when compared to daytime surveys. As a result, sampling began at least one hour after sunset when invertebrate density and diversity increased. One trained biologist and one local research assistant with knowledge of local species and training in invertebrate identification carried out the surveys using scuba. Each diver used two high powered, full spectrum flashlights: one mask mounted and the second, handheld. For each transect, surveyors swam along the transect line, each surveying 1.5 m from centre line of the belt transect. Two passes were made of each transect: the first, a 15-minute survey for mobile species, followed by a second, 30-minute pass for sessile species. Using the flashlights, close inspections were made of crevices and underhangs in the reef.

Habitat was characterized with two measures: structural complexity and coarse estimates of percentage cover of habitat types. Structural complexity was measured with a 10 m rugosity chain set at a random point (set with a random number table) on each transect. To account for finer-scale complexity not captured by the chain yet important invertebrate habitat (i.e. habitat for cryptic species), the depth of small crevices omitted by the rugosity chain was measured and doubled to simulate the distance the chain would cover had it been able to fit in the crevice and factored into the rugosity calculation. During each transect visual estimates of the percentage cover of seven habitat variables were estimated: algae, seagrass, sand and rubble, massive corals, branching corals, encrusting corals, dead corals and soft corals. After each transect, divers

discussed their estimates and agreed on a final percentage cover representative of the transect for each category. Live coral categories were summed to produce an estimate of percentage live coral cover.

To complement the invertebrate data set, fish count data were obtained from the same sites to be used as a predictor variable in this analysis. Fish visual census data were obtained from an existing long-term monitoring program, collected in the 3 months preceding data collection for this study (available for 11 of the 13 sites) (see Samoilys et al., 2007 for survey methods). Fish surveys were carried out during the day when fish are generally more active on the reef. These abundance data were used in generalized linear mixed effects modelling. Fish species were sorted into three trophic groups based on mean trophic level obtained from FishBase (Froese and Pauly, 2017) and are listed in Table 3.2: bottom trophic species, mid-trophic species, and top-trophic species.

To understand the fisheries exploitation status of each invertebrate taxon, eight to 14 semi-structured interviews were conducted with fishers in their native Cebuano language in each village associated with each of the reserve sites. A total of 110 interviews were conducted in which local fishers were asked about the types of fishing methods and gears they most commonly used and the invertebrate species they caught. In some cases, fishers were presented with a species photo-identification guide and asked if they caught particular taxa. Using this information, invertebrate taxa were sorted into exploitation history groupings (Table 3.1).

A set of reserve management criteria were measured to account for how these practices influence invertebrate response. Using a reserve scoring system developed in the Philippines by the Coastal Conservation and Education Foundation (CCEF) (Christie et al., 2006; White et al., 2006), 40 reserve management criteria were evaluated (appendix A3). In each community, two to four management interviews were conducted, asking both reserve management board members as well as local fishers about management criteria. An index that expressed the percentage of management categories that were fulfilled was created so that reserves were not penalized for criteria that did not apply to their management schemes. Reserve characteristics and management scores are found in Table 3.3.

3.3.4 Data Analysis

A set of tests was used to check for outliers, test covariates for collinearity, check for independence of predictor variables, and choose a suitable set of predictor variables based upon variance inflation factor values (Zuur et al., 2010). To test covariates for collinearity, Pearson correlation coefficients were used. In all but one case, correlations between covariates was 0.5 or lower, the exception being between reserve age and the management index (0.68). Using the same set of potential covariates, the variance inflation factor (VIF) values were then calculated. The management index received the highest score (6.5) and was dropped from the set of potential covariates (Zuur et al., 2010). VIF values were recalculated and all covariates received scores of less than 2. Based on both the correlation coefficients and VIF values, the management index was removed from the models. The same procedure was repeated for the habitat percentage cover data set and the “sand and rubble” covariate was removed. Again, all remaining covariates received VIF values of less than 2.

Invertebrate abundance was modelled for three response groups: all invertebrate taxa, unexploited invertebrate taxa, and exploited invertebrate taxa. The influence of variation due to site level effects and overdispersion proved statistically significant, so a site-level random effect and an transect-level random effect were used in the model to account for this (Bolker et al., 2009; Zuur et al., 2009). Models were run using the lme4 package, version 1.1-13 (Bates et al., 2015), in the R statistical environment, version 3.0.3 (R Core Team, 2017). Multi-model inference was completed using the MuMIn package, version 1.15.6 (Bartoń, 2015).

A global model was built using a set of standardized explanatory variables: reserve age, protections status (inside reserve, immediately outside reserve, distant fished site), habitat (percentage cover of live coral, rugosity), distance from land mass with major population centres, and fish abundance separated into low, medium, and high trophic taxa. Reserve age and protection status are included as an interaction term. Instead of choosing a single best model, a model averaging approach is used to select a set of top models and measure the average of effect sizes across models (Grueber et al., 2011). To do this, an information criterion approach was used to select a set of top models that individually may not be indistinguishable in their ability to model the data. As overdispersed count data were being used, the models were ranked using QAICc (quasi-Akaike information criterion corrected for small samples) and the top $\Delta 4\text{QAICc}$ models were kept. This yielded 19, 12 and 20 potential models for all invertebrate taxa, unexploited invertebrate taxa, and exploited invertebrate taxa, respectively (see appendices A4-A6 for top candidate models). From these model sets average effect sizes were calculated for each of the predictor variables and a corresponding 95% confidence interval. In all cases, none of

the top models had a model weight greater than 0.9 ω , indicating that averaging across models was appropriate in this analysis (Grueber et al., 2011).

To understand the relationship between invertebrate abundance and percentage cover of different habitats, a similar modelling methodology was used as described above. This yielded 10, 10 and 21 potential models for all invertebrate taxa, unexploited invertebrate taxa, and exploited invertebrate taxa, respectively (see appendices A7-A9 for top candidate models). Again, from these model sets, average effect sizes and a 95% confidence interval for each of the predictor variables was calculated. In all cases, none of the top models had a model weight greater than 0.9 ω , again indicating the appropriateness of this multi-model approach (Grueber et al., 2011).

3.4 Results

A total of 66 209 individual invertebrates from 74 families were counted inside and outside the 10 marine reserves and three distant fished sites for a mean density of 3.2 individuals/m². Individuals per transect ranged from 53 to more than 1600 and a mean of 23 families were detected per transect. Molluscs made up 56% of individuals counted, followed by arthropods (24%), echinoderms (12%), and annelids (8%). Forty-four percent of the families observed are collected in local fisheries, and individuals from these taxa accounted for 18% of the total abundance.

3.4.1 Abundance trends for invertebrates, as a single group

Examining invertebrates as a single group, protection status x age, distance from mainland, and fish density (at any trophic level) have no significant relationship with invertebrate abundance

while the habitat variables rugosity and live coral cover are positively related to abundance (Figure 3.2). The most parsimonious model ($\omega = 0.149$) in the set of 17 models used for model averaging (appendix A4) contained the rugosity, live coral cover, and low-trophic fish abundance variables. Two variables were present in all 17 models: rugosity and live coral cover.

Analysis of the relationship between total invertebrate abundance and percentage cover of habitat types shows significant positive relationships between invertebrates and each of algae, branching coral, massive coral, and seagrass. Dead coral, encrusting coral, and soft coral had no significant relationship with invertebrate abundance (Figure 3.3). The most parsimonious model ($\omega = 0.226$) of the set of 10 used for model averaging (appendix A7) contained algae, branching coral, massive coral, and seagrass. Branching coral, massive coral, and seagrass were found in all 10 top models.

3.4.2 Unexploited taxa

As with total invertebrate abundance, unexploited taxa appear unaffected by protection status and distance from mainland (Figure 3.2). Rugosity and live coral cover were positively associated with higher unfished invertebrate abundance. Unlike the “all taxa” grouping, abundance of fish showed some predictive power of unexploited invertebrate abundance. The low-trophic fish abundance group was positively associated with this groups’ abundance, however, top and mid trophic fish abundance had no relationship. The most parsimonious model ($\omega = 0.237$) out of the set of 9 top models contained rugosity, live coral, and low trophic fish abundance cover as contributing variables (appendix A5). Rugosity and live coral cover were found in all top models, while low trophic fish abundance was found in 6 of the top 9 models.

Following the same pattern observed in the “all invertebrate families” grouping, there were positive relationships between unfished invertebrate abundance and the percentage cover of algae, branching coral, massive coral, and seagrass (Figure 3.3). The most parsimonious model ($\omega = 0.203$) of the set of 10 models used for model averaging contained algae, branching coral, dead coral, massive coral, and seagrass as predictive variables (appendix A8). Percentage cover of branching coral, massive coral and seagrass were found in all 10 models.

3.4.3 Exploited taxa

The protection status x reserve age interaction term was associated with higher abundances of exploited invertebrates both within reserves and in areas immediately outside them, as compared to distant fished sites. The magnitude of this positive effect on invertebrate abundance was 54 and 130 percent higher density, respectively, with significant overlap in confidence intervals between inside and outside areas. Like the all invertebrates and unfished invertebrates groupings, rugosity was a significant positive predictor of abundance. Live coral cover, distance from mainland and the fish variables on the other hand, were not significant predictors of fished invertebrate abundance. The most parsimonious model ($\omega = 0.096$) of the 22 models used for model averaging contained two variables: protection status x reserve age and rugosity (appendix A6). Only rugosity was present in all 22 models.

The branching coral and seagrass percentage cover variables were significant predictors of fished invertebrate abundance (Figure 3.3). Unlike the other invertebrate groupings, algae and massive coral were not statistically important for predicting fished invertebrate abundance. A total of 21

top models were used for model averaging (appendix A9). The most parsimonious model ($\omega = 0.106$) contained branching coral, dead coral, and seagrass as explanatory variables. Branching coral and seagrass were found in all 21 top models.

3.5 Discussion

Marine invertebrate abundance in this study is associated with habitat characteristics, sometimes by presence of reserves and rarely by numbers of fish—the last being the typical metric of reserve effectiveness (e.g. Halpern, 2003; Lester et al., 2009). Furthermore, it was found that reserve protection appears to positively impact invertebrates that are exploited in adjacent fisheries and this effect is present both inside and immediately outside of reserves, suggesting potential spillover effects from reserves into adjacent areas. Habitat effects vary slightly by group but structural complexity consistently relates to higher invertebrate abundance. Reef fish abundance, does not consistently predict invertebrate patterns of abundance in this study. In tropical developing regions, reef invertebrates are important to local fisheries (Dalzell et al., 1996; Kleiber et al., 2015) and this work underscores the importance of designing reserves that address the requirements of both fish and invertebrates. Given the significance of invertebrates as contributors to biodiversity, ecosystem function and to fisheries, these results demonstrate a need for increased invertebrate attention in marine reserve planning, monitoring and species conservation.

The enormous diversity of life history strategies, morphologies and historical fishing pressures among groups of invertebrates make it no surprise that pooled, as a single group, invertebrates

fail to show a statistically significant response to reserves. Instead, a combination of protection, habitat characteristics and exploitation history affects whether a taxon responds to reserves. The result that exploited invertebrates show a reserve response aligns with several previous invertebrate studies (Benzoni et al., 2006; Cariglia et al., 2013; Dumas et al., 2013). This positive reserve response in exploited taxa is not the rule, as in other cases a combination of negative or neutral effects have been found across exploited taxa (Ashworth et al., 2004; Edgar and Barrett, 2012). The reserve effect that was observed in areas immediately outside protected sites may be due to spillover of mobile taxa and is unlikely due to larval processes which typically work on larger spatial scales than those considered in this study (Shanks, 2009). The impacts of fishing pressures immediately outside many reserves (i.e. fishing the line) appear to have lesser impact on adjacent areas than spillover. The lack of reserve response in many invertebrates in this study may be a result of restored trophic or competitive interactions, a lack of exploitation history, Allee effects, small reserve size, or simply that some taxa have not had sufficient time to respond to removal of fishing pressures (Babcock et al., 2010).

Reserve placement relative to human impacts is often an important predictor of biological recovery with reserves far from human population centres exhibiting the strongest recovery response (Edgar et al., 2014). While these results indicate a positive trend with reserve distance from major human settlement, the trend was not statistically significant. This positive (yet non-significant) trend may be the result of decreasing fishing pressures with increased distance from land. It may also be a result of environmental factors such as elevated sediment levels closer to land and estuaries. High sediment levels have been observed along Danajon Bank and may be due to runoff from Bohol, the closest major island to the double barrier reef.

My finding that complex habitat and live coral cover is often associated with higher invertebrate abundance is not surprising in light of the close association between epibenthic organisms and physical structures on which they live (Canion and Heck Jr, 2009; Heck et al., 2003; Orth et al., 1984; Stoner, 1980). Corals and the small crevices between them serve as locations for important life history events (reproduction, feeding) and as protection from predators (Dumas et al., 2013; Graham and Nash, 2013; Heck et al., 2003). The importance of habitat in predicting invertebrate numbers suggests that complex, live benthic substrate is likely a key factor in determining whether there will be a reserve effect (McClanahan, 1994). This result is further borne out in the finding that percentage cover of branching coral is positively associated with invertebrate abundance across all groupings in this analysis. During surveys, invertebrate “hot-spot” areas both inside and outside reserves were observed which appeared to be associated with structurally complex habitat and high live coral cover. Changes in coral cover and composition within reserves are often difficult to detect, particularly over short time scales (Lester et al., 2009). Assuming that coral composition and cover changes within reserves over time and destructive fishing is reduced immediately outside reserves, temporal changes in invertebrate abundance may be a result of both release from exploitation and regrowth of corals. This may also explain the lack of response in unexploited species within and around reserves. While exploited species are released from fishing pressure, unexploited species may have to first wait for improvements in coral habitat (McClanahan, 1994). Restoration of trophic interactions is commonly observed in marine systems receiving protection (Pinnegar et al., 2000) and the lack of response of some taxa in this study may be the result of increased predatory pressures from recovering taxa.

The relationships found between habitat percentage cover and invertebrate abundance is consistent with previous work on the use of physical habitats and animal abundance across diverse taxa (Hughes and Ward, 1993; McClanahan, 1994; Nonacs and Dill, 1990; Orth et al., 1984; Stoner, 1980). In aquatic systems, macroalgae are a platform for diverse herbivore communities and complex ecological interactions (Lubchenco and Gaines, 1981). Here, the finding that unexploited taxa are positively associated with algal cover is borne out by large numbers of small herbivorous snails that feed on epiphytes found on the surface of macroalgae. Similarly, the relationship between unexploited invertebrates and massive corals may be driven by burrowing taxa (e.g. serpulids, sabellids, muricids) that are not captured in fisheries. The finding that seagrass percentage cover is consistently associated with higher invertebrate numbers is of interest given that species living on seagrass shoots fall outside of the minimum size threshold for counting in the visual census surveys. This would seem to suggest that the presence of seagrass is positively associated with higher invertebrate numbers in adjacent habitats. The mechanism is unclear but may be related to high levels of epiphytic primary and associated secondary production or cover from predation during juvenile life stages (Hall and Bell, 1988; Orth and Van Montfrans, 1984; Terrados and Borum, 2004).

Fish are the common metric for reserve performance yet the results indicate that the number of fish is seldom associated with invertebrate abundance at sample sites. This is contrary to an expectation that changes in fish abundance coincide with shifts in abundance in other taxa. For example, an overall increase in the number of fish would seem to indicate recovery (or partial recovery) of a system. Conversely an increase in predatory fish would result in increased predation pressures on prey species and result in a decline in those species (Pinnegar et al.,

2000). In the case of the latter, a negative relationship would be expected between mid and top-trophic fish species and invertebrates. These relationships likely exist at much finer, species:species scale than can be captured by the coarse-scale groupings of taxa used in this analysis. The finding that unfished invertebrate abundance is positively associated with low-trophic fish abundance may be a further indication of recovery across low trophic species not important in fisheries. Despite the near absence of relationships between fish groupings and invertebrates, in the reserve literature it is not uncommon to see the terms “fish abundance” and “fish species richness” used interchangeably with the term “biodiversity” (e.g. Edgar et al., 2014). This analysis leads us to believe that further studies would benefit from avoiding the assumption that fish are representative of changes to broader ecosystem biodiversity.

The importance of considering both fish and invertebrates in reserve assessment and design will likely be of significant importance in tropical developing regions where both marine finfish and invertebrates are heavily exploited. During low tides and in shallow reef areas, gleaning and skin diving (often using metal rods to break coral apart to find invertebrates) are popular methods for obtaining invertebrate catch (Kleiber et al., 2015). These activities are largely carried out by women, children and the elderly and contribute to household food security (Kleiber et al., 2014). This work shows that a reserve response exists for exploited species both inside and immediately outside of reserves which indicates a potential positive fisheries outcome as a result of the reserves. This is serendipitous as reserves in the region are typically designed as a tool to supplement finfish stocks (White et al., 2002), despite the importance of invertebrates in local diets. Between a quarter and third of the protein diet at the sample sites in this study is obtained from invertebrate catch (Kleiber et al., 2014). Explicitly incorporating invertebrates into reserve

planning and including areas both farther away from the mainland and with complex habitat (or with potential for recovery of complex habitat) may further increase effects on invertebrate abundance and fisheries.

Marine reserves are often created with a set of goals in mind, the most popular being biodiversity protection and fisheries sustainability (Holland, 2002). As both the scale of invertebrate biodiversity and invertebrate fisheries becomes more apparent, marine managers must begin to consider the need for monitoring and conservation planning beyond finfish. This analysis suggests that there are positive impacts on exploited invertebrate groups inside and immediately outside reserves but also that other factors are important for positive responses. Many invertebrates are closely associated with the physical structure of bottom habitat and protection of complex habitat on the reef crest is important. It is therefore critical that reserve planners prioritize protection of areas with habitat attributes associated with invertebrate recovery (or areas with good potential for recovery of these attributes): live coral cover, seagrass, and structurally complexity. This analysis also has implications for how marine reserves are assessed since change in fish abundance is a typical indicator of biodiversity response to marine reserves. Given the roles played by invertebrates in ecosystems and their importance in fisheries, closer examination of invertebrates in marine reserve assessment and their inclusion in reserve planning should become a priority.

Table 3.1 Invertebrate families († superfamily) censused in this study and their respective exploitation status

Phylum	Family	Exploited?	Phylum	Family	Exploited?
Annelida	Sabellidae	N	Mollusca	Cassidae	Y
	Serpulidae	N		Chromodorididae	N
Arthropoda	Calappidae	Y		Conidae	N
	Diogenidae	N		Cypraeidae	Y
	Dromiidae	Y		Discodorididae	N
	Ethusidae	N		Fasciariidae	Y
	Hippolytidae	N		Gryphaeidae	Y
	Inachidae	N		Haliotidae	Y
	Majidae	N		Hexabranidae	N
	Majoidea	N		Limidae	N
	Paguroidea†	N		Loliginidae	Y
	Parthenopidae	N		Malleidae	Y
	Penaeidae	N		Muricidae	Y
	Portunidae	Y		Mytilidae	N
	Scyllaridae	Y		Naticidae	Y
	Stenopodidae†	N		Octopodidae	Y
	Xanthidae	Y		Ostreidae	Y
Echinodermata	Acanthasteridae	N		Pectinidae	Y
	Amphiuridae	N		Phyllidiidae	N
	Asteropseidae	N		Pinnidae	Y
	Comasteridae	N		Plakobranidae	N
	Cucumariidae	N		Pleurobranchidae	N
	Diadematidae	N		Polyceridae	N
	Echinometridae	N		Pteriidae	Y
	Eurypatagidae	N		Ranellidae	Y
	Gorgonocephalidae	N		Sepiidae	Y
	Holothuriidae	Y		Sepiolidae	N
	Mithrodiidae	N		Spondylidae	Y
	Ophiocomidae	N		Strombidae	Y
	Oreasteridae	N		Tonnidae	Y
	Stichopodidae	Y		Trochidae	Y
	Synaptidae	N		Turbinidae	Y
	Temnopleuridae	N		Velutinidae	N
Mollusca	Aplysiidae	Y		Vermetidae	N
	Arcidae	N		Volutidae	Y
	Cardiidae	Y	Platyhelminthes	Pseudocerotidae	N

Table 3.2 Fish family trophic groupings used in this study. Numbers in brackets indicate mean family trophic level obtained from FishBase

Low trophic fish families	Mid trophic fish families	Top trophic fish families
Acanthuridae (2.3)	Balistidae (3.4)	Lutjanidae (4)
Pomacanthidae (2.8)	Caesionidae (3.4)	Synodontidae (4.3)
Pomacentridae (2.8)	Chaetodontidae (3.2)	
Scaridae (2)	Cirrhitidae (3.7)	
Siganidae (2.3)	Haemulidae (3.6)	
	Holocentridae (3.6)	
	Labridae (3.5)	
	Lethrinidae (3.7)	
	Mullidae (3.5)	
	Nemipteridae (3.6)	
	Serranidae (3.9)	

Table 3.3 Characteristics of reserves used in this study. Letters beside reserve names correspond with reserve

IDs in figure 3.1

Reserve	Age (yrs)	Size (ha)	Management score
Matabao (A)	2	52.6	69.8
Tugas (B)	5	10.4	58.8
Busalian (C)	6	17.4	49.0
Bantiguian (D)	9	10.6	64.5
Jandayan Norte (E)	11	24.9	47.5
Pinamgo (F)	13	37.8	54.4
Bilang-Bilangan West (G)	14	10.5	62.7
Batasan (H)	14	21.0	62.5
Cataban (I)	17	19.9	72.5
Handumon (J)	18	50.0	73.8

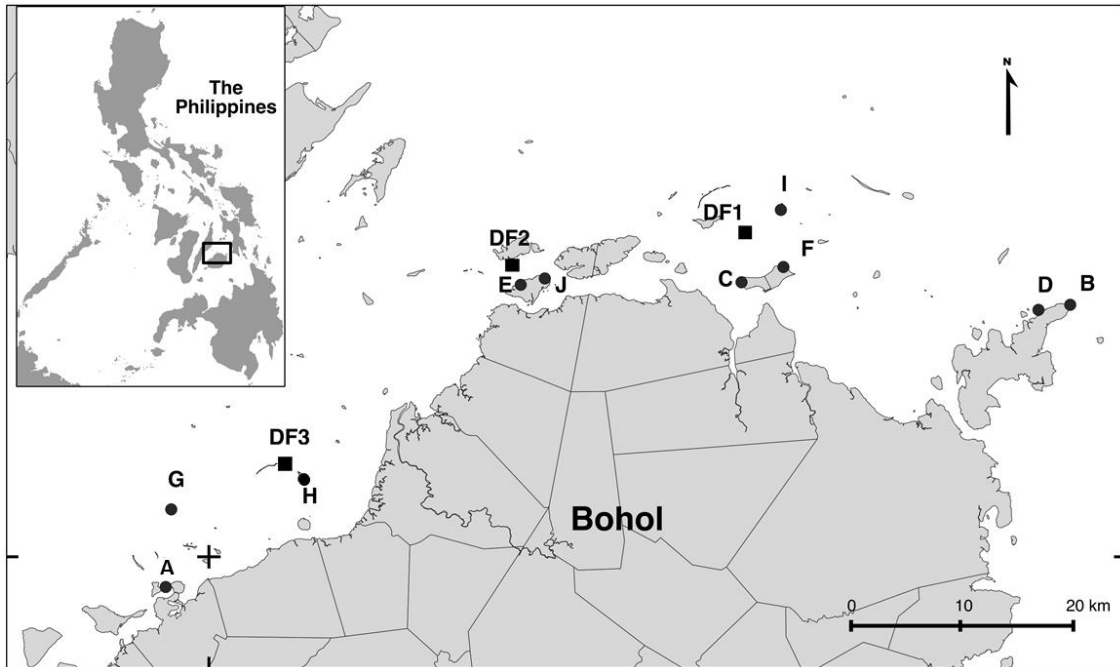


Figure 3.1 The Danajon Bank region of the Central Philippines. The Danajon Bank is a rare double-barrier reef formation to the north of Bohol, Philippines. Letter codes indicate sample sites. Letters are sorted by how recently a marine reserve was established (e.g. A = youngest reserve sampled). “DF” codes are distant fished sites.

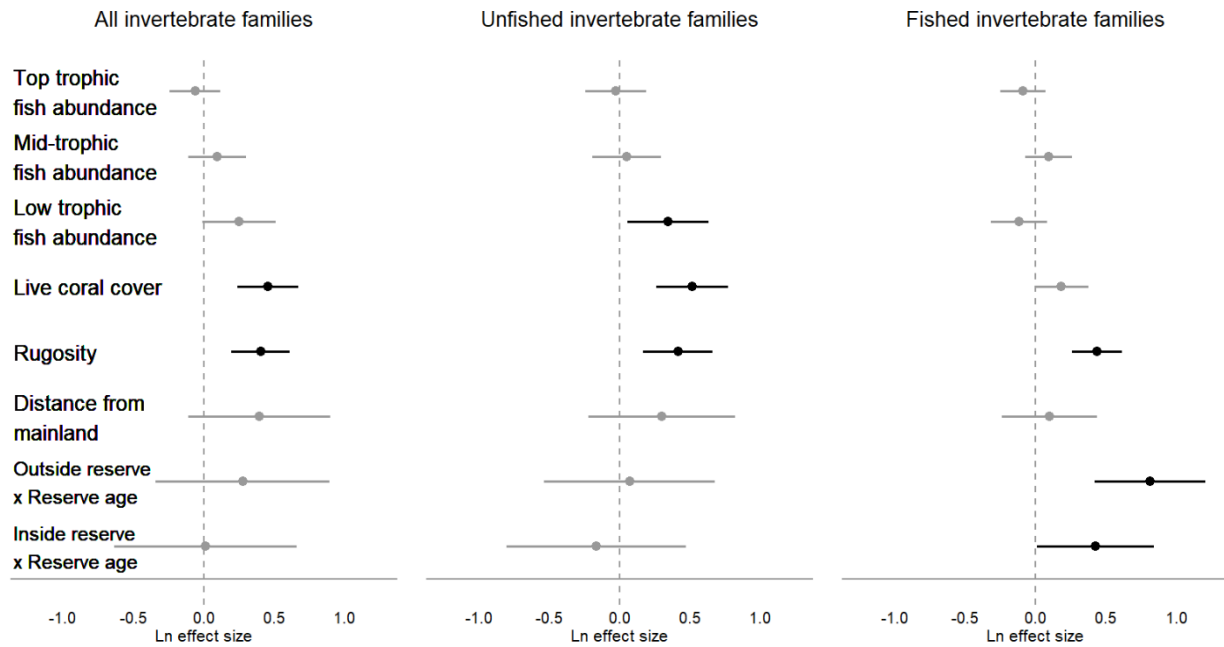


Figure 3.2 Model-averaged effect sizes with 95% confidence intervals for mixed effects models. Confidence intervals that do not intersect with zero (black bars) indicate the presence of an effect on invertebrate abundance. The reference category for protection status variables is “distant fished sites”. Distant fished sites are areas far from the marine reserves and are not subject to spillover effects or “fishing the line” effects.

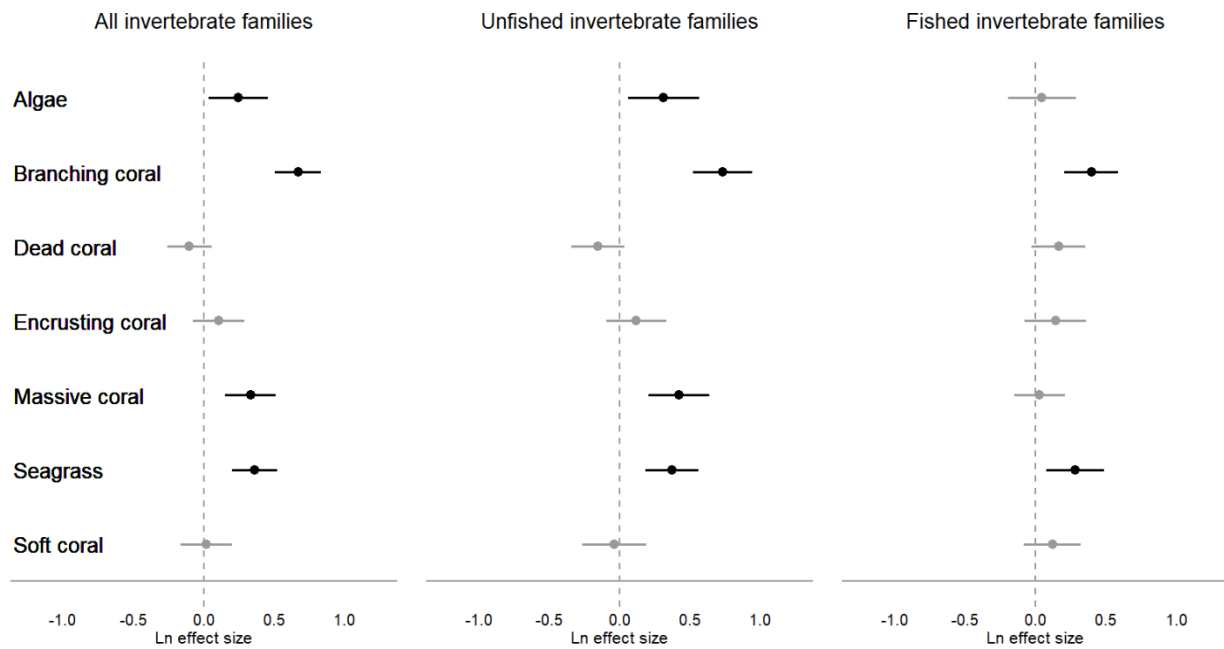


Figure 3.3 Model-averaged effect sizes with 95% confidence intervals for mixed effects models for habitat percent cover. Confidence intervals that do not intersect with zero (black bars) indicate the presence of an effect on invertebrate abundance.

Chapter 4: Marine reserves drive both taxonomic and functional change in coral reef invertebrate communities

4.1 Summary

A leading argument for no-take marine protected area (marine reserve) establishment is their contribution to the conservation of biodiversity, but the impacts of reserves on ecosystem functioning have seldom been quantified. This is unusual given the value of services provided by ocean ecosystems to human well-being. While no single index can describe ecosystem function, a set of life-history attributes possessed by taxa can be used to infer differences in ecosystem function across space and time. In this study, I use Biological Trait Analysis (BTA) to determine whether the attributes of invertebrate taxa differ between inside of six no-take marine reserves and outside, in fished areas in the Central Philippines. Using permutational multivariate analyses, I found that the composition of traits and taxa were significantly different between reserve and non-reserve areas. Habitat use, morphology and mobility traits were the biggest contributors to dissimilarity, indicating that reserves can have community-wide effects that change the functional composition of invertebrate assemblages. Notably, traits associated with coral habitat use, bearing a shell, lacking mobility and filter feeding are the most important traits associated with differences in community structure between reserve and non-reserve areas. At the taxa composition level, small shrimps, three families of bivalve, two families of burrowing snails and brittle stars are the most important contributors to differences in taxonomic community composition. The addition of organismal attributes to traditional taxa composition approaches

provides richer insight into how ecosystems respond to protection and has the potential to inform practitioners on conserving for ecosystem traits.

4.2 Introduction

Many marine systems have undergone significant changes in biodiversity and functioning as a result of habitat disturbance and fishing, jeopardizing their ability to provide services important to humans (Cardinale et al., 2012). On some Caribbean reefs, loss of herbivores contributed to a shift from coral to algae and cyanobacteria dominated substrates (de Bakker et al., 2017; Knowlton and Jackson, 2008; McCook et al., 2001), resulting in coral mortality, loss of stony habitats and reduction in species important in local fisheries (Jackson et al., 2014). Depletion of oysters in Chesapeake Bay resulted in substantial loss of water filtration capacity linked to reductions in water quality (Newell, 1988). These ecosystem changes are further complicated by previously hidden interactions elsewhere in food webs resulting in cascading effects in other taxa (Eddy et al., 2017; Shears and Babcock, 2003, 2002; Travis et al., 2013). The current prevalence of active gears like trawls can often result in reductions in biomass, diversity, body size and alterations in the trait composition (e.g. reduction in filter feeders and larger animals in impacted areas) present in marine communities (Tillin et al., 2006). The consequences of the loss of services provided by species (e.g. herbivory, filtration, habitat creation) underscores the importance of considering how ecosystems respond to pressures and managing for the conservation of ecosystem function (Shears and Babcock, 2003).

The functioning of ecosystems can be described in many ways and no single index is capable of quantifying the many processes, interactions, and services present (Darling et al., 2012; Giller et

al., 2004). The term “ecosystem functioning” varies in definition but can include measures of energy or material flow through food webs (Díaz and Cabido, 2001) and the processes (e.g. filtration, nutrient cycling) that occur in ecosystems (Bengtsson, 1998; Naeem, 2004). Many of these flows of energy, material or processes can be inferred by examining the characteristics of organisms living in the system (Bremner et al., 2003a, 2003b). Biological Trait Analysis (BTA) attempts to do this by describing ecosystem functioning based on traits possessed by members of biological assemblages (Bremner et al., 2006a). By scoring taxa on a multiple traits relating to their life history, behaviour, and morphology, the relative presence of ecosystem processes can be compared over time and space—a critical step in accounting for hidden processes that may impact ecosystems and human well-being (Cardinale et al., 2012; Gagic et al., 2015; Travis et al., 2013). In terrestrial ecology, for example, trait based analysis has been successfully used to link functional traits across taxa in plant systems to resource availability and disturbance (Lavorel and Garnier, 2002). Until recently, BTA has typically been used to describe functional differences in plant and freshwater invertebrate communities living in varying abiotic conditions (Castella and Speight, 1996). Despite strong interest in incorporating functional traits in MPA design and management (Frid et al., 2008), to my knowledge, BTA has been applied few times in the context of MPAs (Coleman et al., 2015; Haizea Jimenez et al., 2015).

Invertebrates play diverse roles in ecosystem functioning but are often overlooked in marine reserve and conservation science (Donaldson et al., 2016; Ricard et al., 2012). This is surprising, given the global scale of invertebrate fisheries and the expansion of these fisheries in recent decades both in biomass and number of taxa fished (Anderson et al., 2011). These species provide numerous services including water filtration, bioturbation, benthic-pelagic coupling, and

creation of hard habitat (Anderson et al., 2011; Eddy et al., 2017). However, many of these traits are associated with increased vulnerability to fisheries: low mobility, surface dwelling, long lifespans, suspension feeding and large body size (Bremner et al., 2003b; Cesar and Frid, 2009; Dulvy et al., 2003). Determining whether community structure is different between reserve and non-reserve areas has been examined frequently and many studies have found taxonomic and community differences between reserve and non-reserve areas (Babcock et al., 1999; Dumas et al., 2013; Jimenez et al., 2015; Lasiak and Field, 1995; Powell et al., 2014). These studies can be useful for identifying the species that drive differences in communities but often do not quantify what traits or functions differ between the systems.

Marine reserves are a popular tool for rebuilding ecosystems impacted by fisheries but current metrics of reserve success often emphasize change in abundance of economically important fish species rather than ecosystem processes and services (e.g. Côté et al., 2001; Lester et al., 2009). And while the current metrics provide strong evidence that reserves can contribute to increases in abundance, biomass and diversity, the changes in the presence of traits possessed by those species are often not quantified. There is evidence that life history traits like larger body size and adult longevity begin to increase in reserves, however these changes can take much longer to appear than increases in biomass and abundance (McClanahan and Graham, 2015). Animal size and longevity are indicators of higher extinction risk in marine species (Dulvy et al., 2003) but increases in the presence of these traits may not be indicative of broader functional changes (Bremner et al., 2006a).

The capacity of invertebrates in marine reserves to contribute to coastal ecosystem functioning is of particular interest in developing regions where invertebrates comprise a major share of local fisheries and marine reserves are widely used as a strategy for conservation and fisheries management (White et al., 2002; Yasue et al., 2010). In the coral triangle, approximately 2000, usually very small no-take marine reserves have been established with the purpose of protecting habitat, improving fisheries and offering alternative forms of income through tourism (White et al., 2014). In the rural areas in this region, a significant portion of the protein diet comes from invertebrate catch (Kleiber et al., 2015), especially during times when weather becomes unfavourable for boat-intensive finfish fisheries (Kleiber et al., 2014). Given this importance, the ability of marine reserves to impact invertebrates and the functions they contribute to has important local implications.

In this study, I use a set of six marine reserves in the Central Philippines to examine the effects of reserves on the trait and taxon structure of invertebrate communities. Using this information, I comment on how reserves could be better evaluated for their biodiversity effects.

4.3 Methods

4.3.1 Study taxa

I counted all non-coral, non-sponge macro-invertebrates (from here, referred to simply as “invertebrates”) greater than two centimetres in length. Individuals were identified to the finest taxonomic scale possible, however, the breadth of diversity in invertebrates often prevented species-level identification (and even in some cases genus-level identification). For consistency in this analysis I use family-level identification. Despite challenges presented by Linnaean

classification (Bertrand et al., 2006), a body of previous work has shown that family-level taxonomic resolution is often sufficient to describe and detect patterns and changes in invertebrate assemblages (Jimenez et al., 2010; Olsgard and Somerfield, 2000; Vanderklift et al., 1998). Many invertebrates in this analysis are heavily exploited in local fisheries (abalone, bivalves, crabs, etc.) while others (sea slugs, brittle stars, flatworms, etc.) remain unexploited. To determine the exploitation status of each taxon, local research assistants (who are fishers) as well as other local fishers were consulted. A complete list of sample taxa is found in appendix A1.

4.3.2 Study sites

I studied six no-take reserve sites on Danajon Bank, an approximately 1200-square-kilometre double-barrier reef north of Bohol, Central Philippines (Figure 4.1). Reserves were grouped into three regions off the coast of Bohol: two on the northern coast; two on the north-western coast; and two on the western coast. In each of the three regions, I also sampled a “distant fished site”—sites, at minimum, two kilometres from the closest reserve sites and were evaluated as containing similar habitat at the time of reserve establishment. The region has particularly high levels of biodiversity and intensive human threats to the marine ecosystem (Anticamara et al., 2010; Carpenter and Springer, 2005; White et al., 2006). I chose reserves established for at least 10 years as protection effects have often been found to take several years before their effects are measurable (McClanahan, 2014). My six sites ranged in age from 10 to 18 years since establishment and were all located adjacent to island communities. These communities, with technical assistance from local government and non-governmental organizations, manage these reserves, locally referred to as “sanktuaryo”. At the time of research, they ranged in size from 10.5 to 50 hectares and largely consisted of coral reef, soft bottom, and seagrass habitat.

4.3.3 Sampling design

Sampling occurred from June through August 2013. At each reserve, we conducted six 50 x 3 m haphazardly placed belt transects inside and six outside the reserve for a total of 12 transects per reserve. At each of the three distant fished sites, six 50 x 3 m haphazardly placed belt transects were surveyed. Areas sampled immediately outside of reserves were between 10 and 200 metres from the reserve boundaries. Transects were at a depth of between 1 and 4 metres and in all cases were placed in similar habitats (predominantly reef crest and slope areas that included small patches of soft bottom and seagrass). So as not to impact observed densities of mobile species during sampling, we laid transects at least three hours before each visual census. A preliminary study (Chapter 2) showed that nighttime surveys yielded significantly higher densities and greater taxonomic richness of invertebrates when compared to daytime surveys. As a result, we chose to begin our sampling at least one hour after sunset when invertebrate density and diversity increased. Each diver used two high powered, full spectrum flashlights: one mask mounted and the second, handheld. The senior author and one Filipino research assistant with knowledge of local species and training in invertebrate identification did the surveys. For each transect, we swam along the transect line, each surveying 1.5 m from the centre line of the belt transect. We made two passes of each transect: a 15-minute survey for mobile species and a 30-minute pass for sessile species. When we encountered an area containing a very high density (hundreds) of a single taxon, we counted individuals within a limited section of that area and then extrapolated to the larger area. We used this approach infrequently and in situations where, for example, a high density of small snails or serpulid worms was encountered.

Habitat was characterized using coarse estimates of percentage cover of habitat types. During each transect, visual estimates of the percentage cover of seven habitat variables were estimated: algae, seagrass, sand and rubble, massive corals, branching corals, encrusting corals, dead corals and soft corals. After each transect, divers discussed their estimates and agreed on a final percentage cover representative of the transect for each category.

4.3.4 Biological Trait Description and Scoring

For each taxonomic family in my data set I assigned a set of scores based on life history, feeding habits, and morphology (Bremner et al., 2006; Jimenez et al., 2015). I chose 11 traits to characterize my set of taxa and then further divided these traits into 43 trait categories (Table 4.1), largely mimicking Jimenez et al. (2015) so as to allow comparisons. I used fuzzy-coding approach to score categories within each trait as this scoring method allows for use of diverse kinds of biological information derived from a variety of sources (Chevene et al., 1994). For each trait, a taxon could receive a maximum score of 3, distributed across its categories. A score of 0 indicated no affinity to a trait category and 3 signified total affinity. For example, an organism that is largely predatory but is occasionally known to scavenge was given a score of “2” in the predator category and “1” in the scavenger category. In this case, the deposit-feeder, grazer, and suspension-feeder categories all receive a score of “0”. I based scoring on a variety of sources, including published and grey literature and field observations. Where information was unavailable for a particular category, I assigned a score of 0. Scores were then multiplied by the abundance of that taxon for each transect, creating a matrix best described as being composed of “trait abundances”.

4.3.5 Data Analysis

To detect differences in the trait and family and habitat cover composition among reserve, non-reserve, and distant fished areas, I used a combination of ordination (MDS) with 95% confidence ellipses, permutational multivariate analysis of variance (PERMANOVA) and analysis of similarity percentages (SIMPER). To estimate the relationship between the biological community and the habitat characteristics, I used a relational analysis. The majority of analysis was done in Primer (v.6.1.16) with the PERMANOVA extension (v 1.0.6) (Clarke and Gorley, 2006). MDS bootstrapping and 95% confidence ellipse estimation was conducted in Primer version 7 (7.0.13) (Clarke and Gorley, 2015).

A set of tests was used to check for outliers, test covariates for collinearity, test for homogeneity of variance, check for independence of predictor variables, and choose a suitable set of predictor variables based upon variance inflation factor values (Zuur et al., 2010).

Before analysis, trait occurrence and family abundance matrices were square-root transformed to avoid over-emphasizing abundant or rare trait categories or families (Clarke and Green, 1988). The biological data sets (trait and taxon) were each transformed into Bray-Curtis similarity matrices with resemblance between transects being measured. Multi-dimensional scaling with 95% confidence ellipses were used to visualize differences between reserve, non-reserve, and distant fished areas. To generate the ellipses, community structure and habitat resemblance matrices were bootstrapped 100 times at each treatment level. Ordination points were plotted in 2-d space with smoothed 95% region estimates (“confidence ellipses”) for each treatment level.

For my primary, whole dataset analysis, I conducted two hierarchical PERMANOVA analyses, each with 9999 permutations: one on the trait resemblance matrix and the second on the taxon resemblance matrix. I used a single fixed effect with three levels: inside the reserve, outside the reserve, and distance fished site. To account for spatial autocorrelation, I applied a site-level random effect nested within a regional random effect. The regional effect was applied because sites spatially cluster into three regions (Figure 4.2). To evaluate statistical significance I used the treatment x site nested within region interaction term. Because of the unbalanced design (6 reserve sites and 3 distant fished sites), pairwise comparisons between treatment levels in the global models were not possible. To examine these pairwise relationships, I conducted a post-hoc PERMANOVA for each reserve individually, comparing among inside the reserve, outside the reserve, and the distant fished site corresponding to that region.

I explored the trait and taxon based characteristics of difference in community composition using SIMPER. This analysis does not test the statistical significance of differences in community structure, but partitions Bray-Curtis dissimilarity for groups being compared and helps explain which traits or taxa are most relevant in differentiating communities. I used a one-way test using protection status as the level of comparison.

To estimate relationships between biological community structure and habitat percent cover, I used the RELATE routine to estimate the amount of variation in the community structure matrix that is explained by the habitat cover matrix.

The map of the study region was produced in QGIS (QGIS Development Team, 2014).

4.4 Results

4.4.1 Taxon composition

We observed 51 363 individual invertebrates from 74 families inside and outside six marine reserves for a mean density of 3.8 individuals m^{-2} (s.e. 0.23). Individuals per transect ranged from 133 to more than 1600 and we detected a mean of 23.4 families per transect (s.e. 0.40). Molluscs made up 58% of individuals counted (mean 215.1 individuals per transect, s.e. 20.27), followed by arthropods (23%, mean 128.5 individuals per transect, s.e. 17.58), echinoderms (12%, mean 66.7 individuals per transect, s.e. 8.34), and annelids (7%, mean 41.3 individuals per transect, s.e. 4.14). Forty-four percent of the families observed contain species that are collected in local fisheries, and individuals from these taxa accounted for 17% of the total abundance (mean 98.1 individuals per transect, s.e. 9.70).

4.4.2 Habitat composition

Amongst the habitat categories used to characterize the transects, coral categories accounted for the largest amount of habitat cover at 53% (s.e. 1.97). Within the coral category, massive corals made up a mean of 18% of the total bottom substrate (s.e. 1.07), followed by thin branching coral (17%, s.e. 1.57), encrusting coral (7%, s.e. 0.68), soft coral (6%, s.e. 0.81), and thick branching coral (5%, s.e. 0.82). Mean cover of sand and rubble was 26% of bottom substrate (s.e. 1.28), while dead coral was 15% (s.e. 0.62). Mean algal coverage was 3% (s.e. 0.98), and seagrass coverage was 2% (s.e. 0.83).

4.4.3 Trait composition

Trait categories most dominant in the community were living on corals (8% of occurrences), sessile lifestyle (6%), surface dwelling (6%), suspension feeding (5%), broadcast spawning (5%), have a shell (5%) and are of a small body size (5%). The least common traits include deposit feeding, non-substrate dwelling, burrowing, swimming and mud dwelling, accounting for less than half of 1% of total occurrences.

4.4.4 Community and habitat ordination

For all sites combined, ordination plots with 95% confidence ellipses for community structure and habitat composition showed separation between most groupings (Figure 4.2). The trait based ordination shows inside reserve trait communities forming a distinct cluster, separated from the outside and distant fished site confidence ellipses, which have substantial overlap. Taxon based ordination shows distinct separation between all groups and no overlap amongst ellipses. Habitat ordination shows minor overlap between inside and outside of reserve ellipses while distant fished site habitat composition grouped separately from the in and out reserve areas.

Site-by-site ordination of community structure and habitat composition showed distinct clustering of protection types (Figure 4.3). Ordination based on traits tend to have more overlap between groupings than in taxonomic groupings based ordination, where there is no overlap of confidence ellipses at any site. Ordination of habitat cover data showed distinct groupings based on protection level but separation of confidence ellipses is less consistent than in taxon community analysis.

4.4.5 PERMANOVA community composition test

My test for differences in community composition based on PERMANOVA of the full data set (Table 4.2) indicates a significant difference between protection groups based on taxonomic groupings (pseudo-F = 2.433, $p = 0.0001$). Trait based PERMANOVA, however, showed no significant difference between groups (pseudo-F = 1.613, $p = 0.1258$). Similarly, PERMANOVA for differences in habitat composition showed no significant difference between groups (pseudo-F = 1.533, $p = 0.0795$).

At the site level, the main PERMANOVA tests indicate a significant difference between protection types for three of six sites when using BTA and five of six sites using taxon-based analysis (Table 4.2). Habitat composition PERMANOVA showed a significant difference between protection groups at four of six sites. Post-hoc pairwise PERMANOVA between treatment levels at each site indicates protection effect varies by reserve. Trait-based analysis comparisons showed statistically significant differences in seven of 18 comparisons of community structure, while taxon-based analysis shows differences between 12 of 18 comparisons. In all cases, where there was a difference in community structure based on traits, there was also a difference in community structure based on taxonomic groupings for both the main test and the post-hoc pairwise test. Habitat composition pairwise comparisons indicate differences in 10 of 18 tests.

4.4.6 Habitat composition as an explanatory effect

Differences in community composition may be the result of differences in available habitat types in each protection type. Pairwise comparisons allow us to examine for situations where there are

community composition differences but no habitat differences between protection types. In cases where there is a statistically significant difference in community composition in protected versus unprotected area (an in-out or in-reference site comparison) but no difference in habitat composition, I consider there to be a greater chance of the effect being driven by protection. I found this to be the case in three of six reserves (Batasan, Bilang-Bilangan, and Pinamgo). In these cases, there was a difference in community structure (based on either traits or taxonomic groupings) but no difference in habitat composition between the protected and unprotected area comparison. My test for the amount of variation in community composition explained by habitat composition, showed the range of variation as between 18.9% and 51.3% (Table 4.2). In all cases the variation in community composition explained by habitat was statistically significant.

4.4.7 Taxon differences by protection status

Family level data indicates that small reef shrimp (hippolytidae, unexploited), coral burrowing bivalves (arcidae, unexploited), coral burrowing snails (vermetidae, unexploited), small grazing gastropods (cerithiidae, unexploited), habitat forming bivalves (malleidae and mytilidae, exploited), brittle stars (ophiocomidae, unexploited), and feather duster worms (sabellidae, unexploited) are the top contributors to differences in community structure both between reserve and immediately outside reserve areas and between reserve and distant fished areas (see Table 4.3a and Table 4.4a for direction of the effects).

4.4.8 Traits differences by protection status

Invertebrate morphology and adult habitat use contributed most to dissimilarity in trait occurrence between reserve and non-reserve areas (both immediately outside and distant fished

sites), with these categories accounting for 29% and 27% of the total dissimilarity, respectively (Table 4.3b and Table 4.4b; note that 29% and 27% include traits that fall outside of the 50% cumulative contribution cut-off in the table). Trait categories associated with movement accounted for 18% of dissimilarity, followed by feeding (11%), reproduction (8%), and lifespan (7%). Similarity percentage analysis does not conduct statistical tests but rather helps explain which traits or taxa contribute to differences in community structure. The top contributor to differences in both trait-based and taxon-based community structure was the use of corals as habitat. In this case, taxa with an affinity for coral during the adult life stage were very slightly more abundant inside of reserves than outside. Of the traits associated with morphology, having a shell, and having a small or medium body sizes, and medium meat to body mass ratio trait categories contributed to differences in community structure. Trait categories associated with movement were the next most important, contributing to 18% of total dissimilarity. Sessile trait categories had higher occurrences inside of reserves relative to outside. The largest contributors to dissimilarity in the next most important trait category, feeding (11 % of total dissimilarity), is suspension feeding, with greater occurrence inside reserves. The scavenger trait was also an important contributor to dissimilarity, with a higher occurrence of the scavenger trait found outside of reserves. Internal fertilization is the most important trait category related to dissimilarity within the set of traits associated with reproduction and is the second most important trait in contributing to dissimilarity overall. Other reproduction and lifespan trait categories, however, contribute little to dissimilarity between reserve and non-reserve areas.

4.5 Discussion

Marine reserves have community wide effects on both taxonomic composition and the occurrence of traits in this coral reef system, particularly traits related to body morphology and habitat preference, and movement type. I show that shifts in trait composition within reserves are associated with coral habitat use, sessile taxa that are associated with filter feeding and have shells. Traits associated with vulnerability to fishing (large body size, large edible meat to body size ratio) and grazing on the other hand were of little importance in explaining community patterns. Both taxon based and trait based analysis provide informative results on the effect of reserves on biological communities and their use in tandem appears to provide a much more nuanced understanding of reserve impacts on ecosystems than the typical approach of using taxon-based analysis in isolation. This type of information has potential uses in conserving for ecosystem functional traits (e.g. conservation of bivalves for filtration function) and prioritizing management activities.

My taxonomic analysis, without data on the autoecology of each taxon, shows a more simplistic and arguably less informative picture of differences in the communities in reserve versus non-reserve areas. That the top contributing taxa to these differences in community structure are small shrimps, a few families of bivalve, snail, brittle star and a worm is likely of small biological significance without knowledge of how these taxa interact with their environment and other taxa. Instead, knowing that differences in communities among protection types are characterized by coral associations, suspension feeding and low or no mobility provides a broader understanding of the system that extends beyond a list of taxon names.

My result that trait differences between protection types was associated with patterns of coral habitat use, low or no mobility and taxa that are associated with filter feeding and have shells is similar to results found in New Caledonia (Dumas et al., 2013) and South Africa (Lasiak and Field, 1995). In New Caledonia, the occurrence of surface dwelling traits and coral associated traits were also major components of dissimilarity between reserve and non-reserve areas (Dumas et al., 2013; Jimenez et al., 2015). Similarly, in South Africa, higher levels of filter feeder abundance was found in unexploited areas. My result that sessile traits and taxa are a major contributor to dissimilarity corresponds with previous work showing the impacts of fisheries on benthic, sessile communities (Collie et al., 2000; Kaiser, 2005). Taxa unable to evade capture in fisheries (i.e. taxa with low or zero mobility) have the greatest recovery potential from cessation of fishing (Sainsbury et al., 1997). Many of these sessile taxa are suspension feeders (another top ranked dissimilarity trait) that contribute to removal and cycling of organics from the water column. These filter feeders (i.e. bivalves) tend to have shells, are desirable in fisheries and are likely contributing to the importance of the highly ranked “shell” body morphology category in my dissimilarity analysis. The importance of shelled filter feeders and the suspension feeding trait in explaining differences in community composition requires further investigation but suggests that reserves could be related to increased filtering capacity and the creation of three-dimensional habitat as a result of animal shells.

The link between community structure and both protection type and habitat composition is interesting in that I find evidence for both reserve effects and habitat effects on community structure. In all reserves studied here, I found a statistically significant relationship between habitat composition and community structure. What’s notable is that in some cases, habitat

composition did not differ between protection types yet community composition did. This could suggest that differences are being driven by removal of exploitation pressures rather than inherent differences in the habitat composition of inside reserves versus outside and distant fished sites. I suspect that differences in community composition are the result of a combination of protection from exploitation and habitat differences. At the time of reserve establishment, comparison sites were chosen on the basis of their similarity in habitat to reserve areas and I feel it probable that habitat building species may have also responded to removal of exploitation pressures and habitat composition shifted over time.

These results challenge the idea that reserves can promote recovery of traits particularly vulnerable to fishing pressure (Sala et al., 2002). Some traits, particularly those associated with extinction vulnerability and grazing processes, have been identified as being important for ocean and coastal systems (Dulvy et al., 2003; Mumby et al., 2006). These however, did not appear to be important contributors to dissimilarity between reserve and non-reserve areas. Taxa at higher risk to vulnerability typically are longer lived and have larger body size (and more edible meat). This lack of observed effect may be due to an absence of a reserve impact of these effects occurring over time scales not present in this study or simply because they were not well captured in my trait categories. It is likely that organisms with large body sizes and long life spans require substantial time periods before increases in their abundance are detectable—potentially longer than the 10 to 18 year protection time spans used in this study. A significant lag in the recovery of larger, longer lived species has also been observed in reserves in the western Indian Ocean (McClanahan and Graham, 2015). However, my use of the term “large body size” is used relative to other taxa in this study and it’s likely that my “large bodied”

animals are smaller than those imagined by Dulvy et al. (2003) and Mumby et al. (2006). The near absence of grazing taxa or grazing traits as important components differences in community structure is also unexpected. Grazing, also a trait often vulnerable to fishing pressures, is a process that has received considerable attention in marine protected area and reserve science and changes in grazing dynamics have been observed over much shorter time scales (McClanahan and Shafir, 1990; Mumby et al., 2006). Grazing by both fish and invertebrates is important for the removal of algal overgrowth of corals, which appeared to be an issue at some of my sites. The lack of response in invertebrate grazers could be a result of functional redundancy in the system through taxa not measured in this study (i.e balanced by increases in grazing fish) (Ogden and Lobel, 1978).

The predominant approach to reserve evaluation, to date, has been through measures of change in abundance, biomass and diversity of fish taxa (e.g. Côté et al., 2001; Halpern and Warner, 2002; Lester et al., 2009), which while indicative of change, overlooks functional and trait aspects of ecosystem change. For many stakeholders involved in reserve establishment, the former set of criteria are often a primary interest (Halpern and Warner, 2003) and in many cases these measures will likely satisfy their informational needs. Trait analysis of often overlooked taxa expands our understanding of reserve effects and allows for discussion of reserve impacts on management for ecosystem resilience and functional traits that provide important services associated with fisheries, storm surge mitigation, algal control and others valuable to human wellbeing (Berkes et al., 2000).

Resilient ecosystems are able to buffer the effects of external pressures while maintaining their same basic functional properties (Hughes et al., 2005; Levin and Lubchenco, 2008; Pikitch et al., 2004). In many cases it may be difficult to manage for the maintenance of functional traits because (1) it may be unclear what traits are out of balance in a system and (2) it may be unclear which taxa are contributing to particular functions. Evaluating biological communities using both taxonomy and biological traits may help overcome these challenges by tracking change in traits and identifying the taxa linked with these traits and ecosystem functions. This may allow managers and practitioners to direct management or restoration towards taxa that support resilient biological systems or traits that may be absent in the system. This type of management is important for incorporating critical services in protected area planning and to buffer the effects of human encroachment.

In this analysis I show that invertebrate community structure differs both taxonomically and functionally inside of reserves as compared to outside. I identified taxa that characterize these differences and then extend upon typical biodiversity analyses by incorporating biological traits to understand the functional effects of reserve implementation. This combination of analyses provides a richer information relevant to biodiversity and management on taxa rarely examined in marine reserve science. Furthermore, these analyses show how reserves can increase water filtration and complex habitat traits in a coral reef system.

Table 4.1 Trait variables used to describe functional characteristics of invertebrates on coral reefs in the Central Philippines

Type	Trait	Category	Type	Trait	Category
Feeding	Feeding habit	Predator	Morphology	Adult size (mm)	Small < 50
		Deposit-feeder			Medium 50-150
		Grazer			Large >150
		Suspension-feeder		Body form	Worm-like
		Scavenger			Shell
Habitat	Adult life habitat	Sand	Movement	Edible meat to total body mass ratio	Cuticle
		Mud			Irregular
		Seagrass			Small
		Algae			Medium
		Corals			Large
	Living habit	Endofauna		Adult mobility	None
		Epifauna			Low
		Epizoic			Medium
		Endozoic			High
	Substrate localisation	Surface		Movement method	Sessile
		1cm depth			Burrow
		>1cm depth			Crawl
		Other			Slip
Lifespan	Adult longevity (years)	Small <1	Reproduction	Reproductive method	Swim
		Medium 1-5			External fertilization, planktonic
		Large >5			Benthic stage
					Internal Fertilization

Table 4.2 PERMANOVA p-values and RELATE analysis explained variation for all sites combined (first data row) and each individual site. “Main” refers to the main PERMANOVA test and “Pair-wise” refers to post-hoc pair-wise tests between treatment levels (levels of protection). The “BTA” results are for trait scored community data, “Taxon” for taxon based community data, and “Habitat” for habitat percent cover data. The “Relate” column indicates the amount of variation of in community composition data that is explained by habitat composition data. I-O is the comparison between inside the reserve and outside the reserve; I-DF the comparison between inside and the distant fished site; O-DF the comparison between outside the reserve and the distant fished site. Bold numbers emphasize statistically significant results.

Site	<u>BTA</u>			<u>Taxon</u>			<u>Habitat</u>	
	Main	Pair-wise	Relate	Main	Pair-wise	Relate	Main	Pair-wise
All sites	0.1258	NA	20.5% (p = 0.013)	0.0001	NA	24.9% (p = 0.0421)	0.0795	NA
Batasan	0.0524	I-O: 0.0455 I-DF: 0.0997 O-DF: 0.2187	18.9% (p = 0.0342)	0.0007	I-O: 0.023 I-DF: 0.0192 O-DF: 0.089	19.2% (p = 0.047)	0.0654	I-O: 0.7789 I-DF: 0.014 O-DF: 0.0958
Bilang-Bilangan	0.0144	I-O: 0.1916 I-DF: 0.0988 O-DF: 0.0064	35.1% (p = 0.011)	0.0012	I-O: 0.1426 I-DF: 0.0022 O-DF: 0.0035	28.5% (p = 0.025)	0.1387	I-O: 0.8918 I-DF: 0.098 O-DF: 0.0442
Cataban	0.0032	I-O: 0.0156 I-DF: 0.0027 O-DF: 0.1776	33.9% (p = 0.004)	0.0001	I-O: 0.0019 I-DF: 0.0031 O-DF: 0.0261	41.2% (p = 0.0001)	0.0001	I-O: 0.0032 I-DF: 0.0026 O-DF: 0.0035
Handumon	0.4647	I-O: 0.4688 I-DF: 0.3096 O-DF: 0.3927	37.2% (p = 0.003)	0.0025	I-O: 0.061 I-DF: 0.0073 O-DF: 0.0488	34.4% (p = 0.001)	0.0037	I-O: 0.0639 I-DF: 0.0022 O-DF: 0.0217
Jandayan Norte	0.6065	I-O: 0.6967 I-DF: 0.4449 O-DF: 0.3775	51.3% (p = 0.0001)	0.2265	I-O: 0.8295 I-DF: 0.1505 O-DF: 0.0757	33.8% (p = 0.0007)	0.0292	I-O: 0.6595 I-DF: 0.004 O-DF: 0.0116
Pinamgo	0.0015	I-O: 0.0306 I-DF: 0.0023 O-DF: 0.0158	30.1% (p = 0.013)	0.0001	I-O: 0.0023 I-DF: 0.0018 O-DF: 0.0017	19.0% (p = 0.0421)	0.018	I-O: 0.1799 I-DF: 0.3575 O-DF: 0.0046

Table 4.3 Variables contributing to 50 percent dissimilarity between reserve and immediately outside reserve areas. Section (a) is taxa that contribute to dissimilarity and section (b) is traits that contribute to dissimilarity. Bold lettering is used to indicate the larger abundance value.

a) Taxon	Class	Reserve average abundance	Outside reserve average abundance	Dissimilarity contribution	Cumulative % of dissimilarity
Hippolytidae	Arthropoda	86	110	9.67	9.67
Arcidae	Mollusca	155	98	8.14	17.81
Vermetidae	Mollusca	76	78	7.79	25.60
Cerithiidae	Mollusca	42	39	5.92	31.52
Malleidae	Mollusca	29	59	5.55	37.06
Mytilidae	Mollusca	30	18	5.28	42.34
Ophiocomidae	Echinodermata	15	34	5.24	47.58
Sabellidae	Annelida	50	35	4.02	51.60
b) Trait	Type				
Adult habitat: Corals	Habitat	1450	1396	4.33	4.33
Internal fertilization	Reproduction	759	827	3.82	8.15
Movement method: sessile	Movement	1243	1096	3.77	11.92
Adult mobility: None	Movement	1127	944	3.65	15.57
Surface dweller	Habitat	994	1146	3.64	19.20
Medium meat:body mass ratio	Morphology	791	850	3.63	22.84
Suspension feeder	Feeding	1055	855	3.57	26.40
Shell	Morphology	966	838	3.49	29.90
Epizoic	Habitat	609	706	3.43	33.32
Small body size	Morphology	881	884	3.42	36.75
Planktonic fertilization	Reproduction	983	858	3.39	40.14
Endozoic	Habitat	700	536	3.31	43.45
Cuticle	Morphology	362	405	3.14	46.58
Medium body size	Morphology	666	531	3.09	49.67
Scavenger	Feeding	302	427	3.03	52.70

Table 4.4 Variables contributing to 50 percent dissimilarity between reserve and distant fished areas. Section (a) are taxa that contribute to dissimilarity and section (b) are traits that contribute to dissimilarity. Bold numbering is used to indicate the larger abundance value.

a) Taxon	Class	Reserve average abundance	Distant fished site average abundance	Dissimilarity contribution	Cumulative % of dissimilarity
Hippolytidae	Arthropoda	86	57	8.59	8.59
Vermetidae	Mollusca	76	27	7.63	16.22
Arcidae	Mollusca	155	113	7.07	23.29
Ophiocomidae	Echinodermata	15	48	6.89	30.18
Cerithiidae	Mollusca	42	50	5.94	36.12
Mytilidae	Mollusca	30	7	4.85	40.97
Sabellidae	Annelida	50	35	4.58	45.55
Malleidae	Mollusca	29	34	4.51	50.06
b) Trait	Type				
Adult habitat: Corals	Habitat	1450	1171	4.33	4.33
Internal fertilization	Reproduction	759	610	3.84	8.17
Small body size	Morphology	881	598	3.69	11.86
Movement method: sessile	Movement	1243	831	3.68	15.53
Adult mobility: None	Movement	1127	741	3.52	19.06
Surface dweller	Habitat	994	1023	3.51	22.57
Suspension feeder	Feeding	1055	664	3.50	26.06
Epizoic	Habitat	966	629	3.35	29.41
Endozoic	Habitat	700	391	3.30	32.70
Medium meat:body mass ratio	Morphology	791	591	3.29	36.00
Planktonic fertilization	Reproduction	983	827	3.07	39.06
Shell	Morphology	966	775	2.97	42.03
Medium body size	Morphology	666	616	2.95	44.98
Short lifespan (<1 year)	Lifespan	211	233	2.93	47.91
Worm-like	Morphology	318	240	2.91	50.82

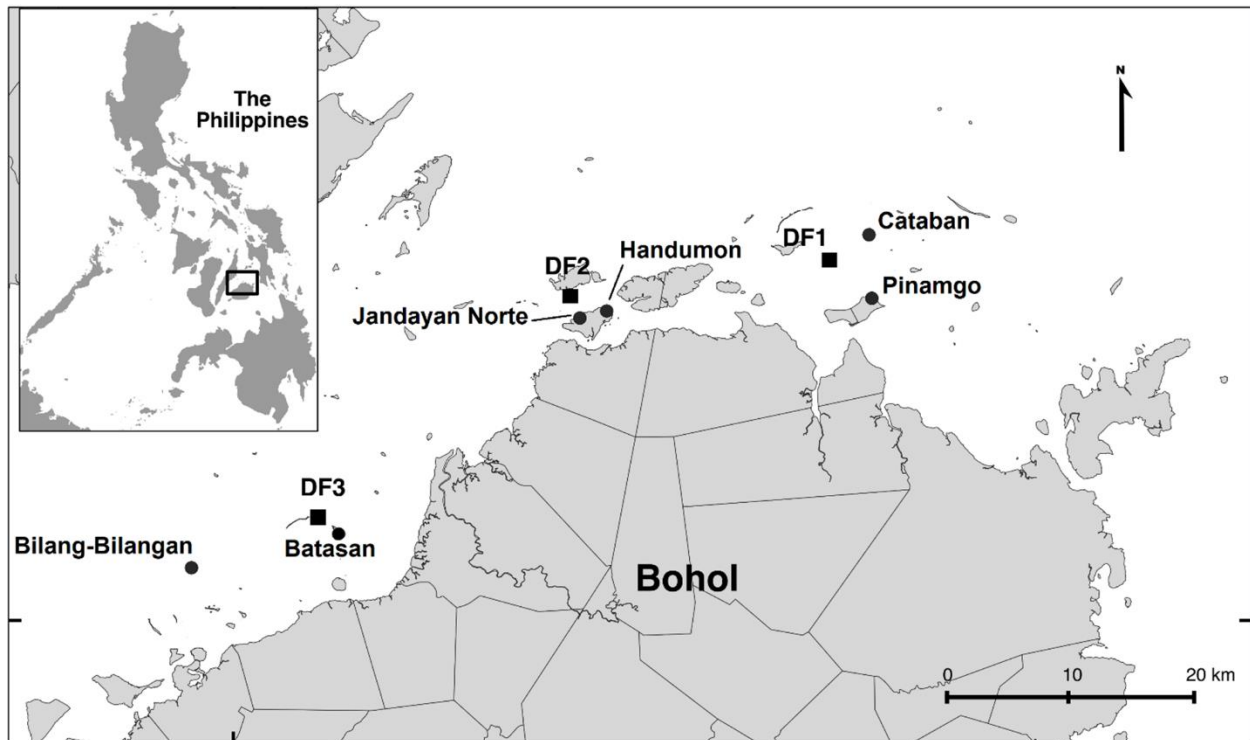


Figure 4.1 The Danajon Bank region of the Central Philippines. The Danajon Bank is a rare double-barrier reef formation to the north of Bohol, Philippines. Dots (•) indicate MPA sites and squares (■) indicate distant fished (or DF) sites.

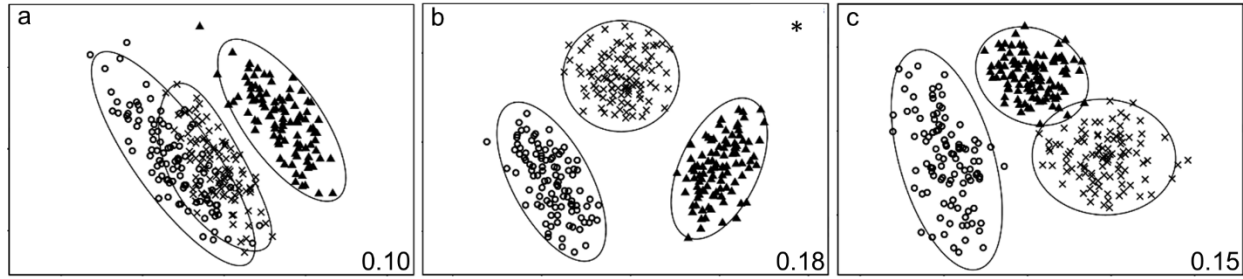


Figure 4.2 Community and habitat composition as represented by MDS plots with 95% confidence ellipses. Marine reserves are represented by filled triangles (▲), non-reserves by x symbols (x), and distant fished sites by empty circles (○). Numbers indicate stress and asterisks (*) indicate a statistically significant result was found in the corresponding PERMANOVA. Plot (a) is ordination based on biological trait composition; (b) based on taxonomic composition; (c) based on habitat percent cover composition. Community composition plots (a and b) were computed on Bray-Curtis similarity matrices from trait and taxonomic occurrence data that were square-root transformed. The habitat composition plot is computed on a matrix of Euclidean distance data that were normalised.

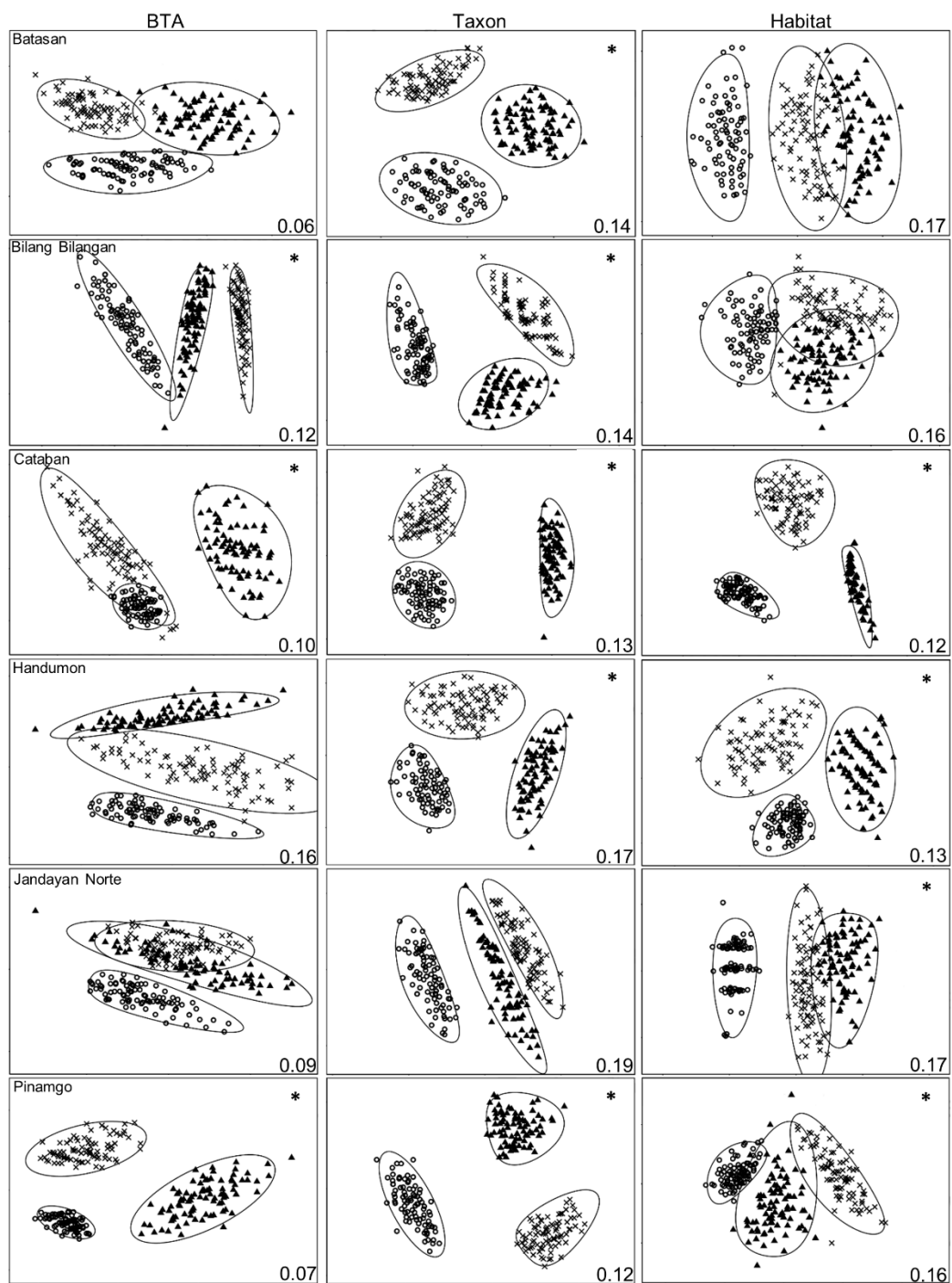


Figure 4.3 Community and habitat composition as represented by MDS plots with 95% confidence ellipses. Marine reserves are represented by filled triangles (\blacktriangle), non-reserves by x symbols (x), and distant fished sites by empty circles (\circ). Site names are in the top right corner of each row and numbers indicate stress. Asterisks (*) indicate a statistically significant result was found in the corresponding PERMANOVA. The first column

is ordination based on biological trait composition; the second column based on taxonomic composition; the last column based on habitat percent cover composition. Community composition plots (columns 1 and 2) were computed on Bray-Curtis similarity matrices from trait and taxonomic occurrence data that were square-root transformed. The habitat composition plot is computed on a matrix of Euclidean distance data that were normalized.

Chapter 5: Using life history and size data for assessment and management of data-limited invertebrate fisheries

5.1 Summary

Invertebrate fisheries offer a critical source of protein in developing regions but are data-limited and lack methods for assessment and management. Advances in size frequency methods offer new techniques for assessing data-limited taxa and providing management recommendations. Here, I apply a set of life history ratios, length-based spawning potential ratio (SPR) analyses, and population simulation modeling to a multi-species, data-limited invertebrate fishery in the Central Philippines. I calculated life history parameters for nine invertebrate taxa important in local fisheries and then estimated stock status based on length-based SPR and fishing mortality rate. I found that the majority of the extraction was of animals below their size at first maturity, most taxa were being fished at high fishing mortality rates, and many had low SPR. I tested different selectivity assumptions in mobile species and found that accounting for spatial dynamics of the fishery and the target taxa is important for estimation of fisheries mortality and SPR. I conducted a simulation analysis to test the effect of setting minimum size limits for each species at L_{opt} , the optimal length at capture to maximize yield, while still maintaining a high exploitation rate. I found that setting selectivity at L_{opt} would increase fisheries yield by an average of 573%. However, the spatial footprint in this fishery likely means that this additional yield in mobile species may not be accessible to the fishers who currently depend on these taxa for their catch.

5.2 Introduction

As the importance of data-limited fisheries is realized, appropriate tools for their management are increasingly needed (Pauly and Zeller, 2016; Sadovy, 2005; Worm and Branch, 2012). Most fisheries falling into this category are considered “small-scale fisheries”, which contribute about half of the global catch for direct human consumption and employ the overwhelming majority of the world’s fishers (Jacquet and Pauly, 2008; World Bank et al., 2012). Characterized by a high diversity of gears, spatially diffuse fleets, and weak management structures, input control measures are often not practical in these fisheries (Berkes, 2001; Sadovy, 2005). “Data-less management” approaches are often proposed in these situations, consisting of a set of rules designed to conserve spawning biomass (Johannes, 1998). These can include seasonal fisheries closures, increased mesh sizes, bans on retention of some species, or escape hatches in traps. One of the most heavily promoted data-less management approaches is the creation of marine protected areas (MPAs). MPAs can be effective tools for conserving biodiversity but limitations in both their current coverage (less than 8% of world ocean in 2020 is encompassed by MPAs, with less than 30% of that area as no-take) and the scale of spillover (spillover from MPAs can take a very long time and can be of small magnitude) of biomass into adjacent fisheries requires that they be augmented with additional conservation approaches (Boersma and Parrish, 1999; Di Franco et al., 2016). This is particularly true in locations where fishing effort is high and dependence on fisheries resources is intense (e.g. Selgrath et al. 2017). In these locations, practical tools that reflect management capacities and species life histories are needed to maintain the productivity of the resource base, and thus maintain its ability to meet nutritional needs (Bell et al., 2009).

Central to assessment and management of data-limited fisheries are estimates of how target taxa grow, survive, and reproduce (Adams, 1980; Kindsvater et al., 2016). This information can help determine timing, locations and optimal size at which fish should be caught (Froese et al., 2008; Pardo et al., 2016). Similarly, the size at which a fish reaches maturity and the number of eggs it produces can, for example, inform fisheries exploitation rates and size limits or lead to protection of spawning areas (Jensen, 1996; Pardo et al., 2016). For many economically important species in developed countries, these data are readily available and stored in fisheries databases, e.g. FishBase for fishes (www.fishbase.org) and SeaLifeBase for invertebrates (www.sealifebase.org). When these life history data are combined with catch time series, indices of abundance, and stock-recruit relationships, the processes for estimating stock status and sustainable exploitation rates are well established. But a near absence of catch and effort data and limitations in capacity for species assessment in many of the world's regions mean many of these techniques cannot be used (Berkes, 2001).

Fisheries targeting invertebrate taxa have undergone enormous growth and typically lack formal assessment and management (Anderson et al., 2011; Perry et al., 1999). Despite a long-held belief that invertebrates are more resilient to fishing pressures (Jamieson, 1993), 34% of assessed invertebrate fisheries are over-exploited, collapsed, or closed (Anderson et al., 2011). A six-fold increase in global invertebrate catch from 1950 to 2004 and large growth in the number of exploited taxa (Anderson et al., 2011) is not reflected in conservation assessments: fewer than 3000 marine invertebrates have been assessed for extinction risk—less than one sixth of one percent of the estimated 1-2 million marine invertebrate species (IUCN, 2017). Likewise, a dearth of basic life-history data means that the leading aggregator for aquatic invertebrate life

history data, SeaLifeBase, still contains relatively few measures for invertebrate growth and reproduction when compared to the information available for fishes on FishBase (Froese and Pauly, 2017; Palomares and Pauly, 2017). The near absence of assessment is concerning given the growth of invertebrate catch and the high-profile declines in data-limited populations such as abalones, sea cucumbers, and lobsters (Berkes et al., 2006; Hobday et al., 2000; Salomon et al., 2007).

Establishing size limits appropriate for an animal's growth and maturity is an established method for mitigating overfishing (Donaldson and Donaldson, 1992; Froese and Binohlan, 2000; Holt, 2014; Perry et al., 1999). Minimum size limits help maintain a spawning stock that supports future cohorts, supporting the long-term viability of the population. They can also help increase yield in a fishery by growing the available exploitable biomass (Allen, 1953; Beverton and Holt, 1957). However, where empirical data are available for key life-history attributes (e.g. size at maturity, natural mortality), determination of size limits can be arbitrarily set, or can be estimated through a set of ratios among life history variables like rate of growth and maximum size (Froese and Binohlan, 2000; Pauly, 1980). While these ratios are imperfect (Prince et al., 2015a), a large body of work demonstrates that they can provide adequate estimates of key life history events, like size at maturity (Froese and Binohlan, 2003, 2000; Jensen, 1996; Williams and Shertzer, 2003). L_{opt} , the length where cohort biomass is at its maximum in an unexploited population (Holt, 1958), is a product of these ratios and can inform size limits for supporting populations that are robust to exploitation (Froese et al., 2008).

Recently, many data-limited approaches have been developed to meet a demand for science-based assessment and management. These approaches fall into two main categories: catch-based and length-based models. Catch-based models (e.g. SRA, Catch-MSY, CMSY) use catch time-series data to estimate biomass and sustainable catch for a stock, and thus are vulnerable to errors due to catch misreporting (Martell and Froese, 2013). Length-based models (e.g. LBSPR, LBB, LIME) use length-frequency data to estimate exploitation and the spawning potential relative to that of an unfished stock (SPR), relying on catch size frequencies that are representative of the exploited population (Froese et al., 2019, 2018; Hordyk et al., 2016). Given large data gaps and poor record keeping for catch in small scale and developing world fisheries, advancement of tools (or methods) to estimate stock status on the basis of length frequencies is an area of research undergoing rapid growth (Froese et al., 2019, 2018, Hordyk et al., 2014a, 2014b, 2016, 2015; Rudd and Thorson, 2017).

It is particularly important that we develop management tools for data-limited invertebrate fisheries in developing countries. In such areas, intertidal gleaning fisheries make important contributions to diets and livelihoods (Kleiber et al., 2015, 2014). These fisheries are conducted primarily by woman fishers—a demographic whose catch is often overlooked, yet constitutes a major extractive effort (Fröcklin et al., 2014; Harper et al., 2020, 2013; Kleiber et al., 2014). In this study area invertebrate gleaning fisheries contribute to both household diets and local trade. On average 32% of gleaning fisheries catch goes directly to feed the family of the gleaner. Gleaning can be disproportionately important to community members that cannot access other forms of fishing, and can also be important to all families during bad weather when fishing in

boats is too dangerous. The impacts to target species in this fishery are rarely quantified and comprise a large “invisible fishery” (Kleiber et al., 2015, 2014).

In this study I attempt to assess and make management recommendations for near data-less invertebrate taxa. I apply a length and growth-based approach to nine invertebrate taxa important in intertidal gleaning fisheries. I calculate life-history attributes, estimate their stock status, and then estimate the impact on fisheries yield of setting minimum size limits. This work attempts to illustrate methods beyond marine reserves that could contribute to sustainability in small scale fisheries.

5.3 Methods

In this analysis I use a variety of tools to obtain information about the life history of each taxon. I then use two length-based reproductive output models (Length-Based Spawning Potential Ratio, LBSPR; and Length-based Integrated Mixed Effects, LIME) to estimate the status of the stocks, and an equilibrium simulation model within the LBSPR package to estimate the potential effect of introducing a minimum size limit in the fishery.

5.3.1 Study area

I focused on a biodiverse, and heavily fished region of the Philippines, dominated by fisheries that lack basic data on catch species composition, biomass extraction and fishing effort. Danajon Bank is an approximately 1200-square-kilometre double-barrier reef north of Bohol, Central Philippines (Figure 5.1). Invertebrate fisheries are conducted through skin diving, traps, nets, and notably through intertidal gleaning fisheries. This gleaning fishery is predominantly done by

women, children, and the elderly—often marginalized groups that lack access to boats.

Invertebrate catch is an important part of local food security. Between a quarter and a third of household protein is obtained from these gleaning fisheries (Kleiber et al., 2014). This combination of biodiversity, heavy fishing pressures, and data limitations make it a striking case study to test these methods.

5.3.2 Focal species

I chose nine macro-invertebrate taxa common in local gleaning fisheries: six bivalves, one gastropod, one crustacean, and one echinoid (Table 5.1). I selected taxa based on (i) availability of size-frequency data ($n > 80$ size observations) and (ii) for which I had a high degree of confidence in taxonomic identification.

5.3.3 Estimating life-history variables

I estimated life history parameters through a combination of literature data, life history records from closely related species (Costello et al., 2012), and use of Beverton-Holt life-history invariants (BHI). For each taxon, I searched SeaLifeBase, online museum records, government reports, and peer reviewed scientific literature for size, maturity and growth data. In data-limited scenarios, a few basic pieces of life history information can be used to estimate critical stages in animal growth (Table 5.1 and Table 5.2). I created a conceptual model for estimating life-history parameters and estimating status (Figure 5.2). The most critical life stages I sought to estimate were: (i) its natural mortality rate (M), (ii) how quickly and how large an animal grows (L_{∞} & K), and (iii) at what size it reaches reproductive maturity (L_m).

The von Bertalanffy growth function (VBGF; eq. 1) estimates length at time, L_t , incorporating the rate (K) at which the size of an animal approaches a theoretical maximum or asymptotic size (W_∞ or L_∞)

$$L_t = L_\infty(1 - e^{-K(t-t_0)}) \quad (1)$$

I assumed that asymptotic length is approximately five percent larger than the average observed maximum length (Pauly, 1984) and can be estimated by examining records from museum specimens, guide books, or SeaLifeBase (Palomares and Pauly, 2017). I calculated asymptotic size using maximum size observations from areas that were geographically as close as possible to the population of interest. This is because asymptotic size varies with seawater temperature, as warmer water has lower oxygen levels available for use in metabolism (Pauly, 2019; Pauly and Cheung, 2018). With increasing animal size, the ratio of gill surface area to body tissues decreases, resulting in lower maximum body size than areas with cooler water (Pauly, 2019; Pauly and Cheung, 2018).

The rate at which growth approaches asymptotic length, K can be estimated with or without size frequency data. In cases where length frequency observations were collected at regular intervals over several months, electronic length frequency analysis (ELEFAN) can be used to track the growth of cohorts over time and then fit a growth curve (Pauly, 1998). For taxa where these data are unavailable, K can be calculated using the growth performance index (eq. 2),

$$\varphi' = \log K + 2\log L_\infty \quad (2)$$

This index is a measure of the relationship between asymptotic size of an animal and the rate it approaches that size. The relationship is relatively conserved among closely related taxa (Pauly, 1998). Estimating K for a taxon with no growth data requires averaging φ' values of closely

related taxa and incorporating their asymptotic length, both of which I obtained from SeaLifeBase (Figure 5.2).

Mean size at first reproduction (L_m) can be obtained from direct measurements in the field (as was the case for *P. viridis*, *T. niloticus* and *P. pelagicus* where I used literature values), from the relative size at maturity in closely related taxa, or, in the complete absence of reproductive data, by assuming that maturity occurs at one-half the asymptotic length (Pauly, 1983). The one-half asymptotic length maturity assumption is a crude estimate and I am aware that some invertebrate taxa mature at sizes below this point—however in the absence of additional data, I deemed it to be an appropriate and conservative estimate.

Natural mortality (M) is particularly difficult to measure but is important for understanding population dynamics of stock response to fishing pressures (Pauly, 1980). Determining M is data and resource-intensive, requiring mark-recapture assessment, modelling of predation analysis or other data-intensive methods (Pauly, 1984). To bypass these data-heavy methods, considerable effort has been invested in finding correlates of M , particularly for fishes (Pauly 1980). For invertebrates, it may be necessary to resort to simple ratios, for example that M is approximately one and a half times the value of K (Pauly, 1983). However, recent evidence has shown that this ratio is does not always hold when comparing taxa that are not closely related (Prince et al., 2015a; Thorson et al., 2017); also, variation around the $M = 1.5 K$ assumption can differ significantly differ among taxa while closely related taxa tend to have similar M/K ratios (Prince et al., 2015a). Thus, using meta-analysis results from Prince et al. (2015) I set the M/K ratio for

bivalves, the crustacean, and the echinoid in this analysis at 1.2, while it was set to 0.59 for gastropods.

5.3.3.1 Estimating optimal size at capture

Optimal size at capture, L_{opt} , is the length where cohort biomass is maximum in an unexploited population (Holt, 1958). L_{opt} was calculated using three life history values obtained above (K , L_{∞} , and M) using the estimation process in Figure 5.2.

5.3.3.2 Length frequency sampling design

I obtained length frequency data indirectly, from intertidal invertebrate gleaning fisheries in 11 villages on Danajon Bank from September 2011 to January 2012 (Figure 5.1). Fishing catches were evaluated opportunistically, typically by asking interview respondents if they would be willing to let us measure the catch of their next fishing trip. In other cases, fishers returning with their catch were opportunistically approached at points along the seashore to sample both subsistence and commercial catch. For each fishing trip I noted the weight of each animal, their taxon and their local name. I measured catch from 160 gleaning trips. For each trip, I measured the wet weight for each animal in the catch. For the nine taxa examined in this analysis, I obtained sizes for 11 055 animals (Table 5.1).

I next needed to calculate the length of each specimen. For each taxon, I searched the literature and online database SeaLifeBase to deduce length from weight ($W = aL^b$). For taxa with no established length-weight relationship, I assumed that length was proportional to the cube root of weight. This proportional length-weight relationship is particularly useful in soft bodied

invertebrates and has been used previously on invertebrate taxa in the same region as this study (Pauly and Calumpong, 1984).

5.3.3.3 Estimating length-based spawning potential ratio

I used calculated lengths to deduce the spawning potential ratio (SPR). SPR is a measure of the reproductive output of a fished stock relative to the same stock in an unfished state (Goodyear, 1993). Length-based SPR methods use a per-recruit, length structured model that can account for size-dependent selectivity and estimate fecundity at size. These methods account for within-cohort size variability to select the largest individuals in a cohort into the fishery at a higher rate than smaller individuals (Hordyk et al., 2016). Recently developed length-based SPR analyses (e.g. LBSPR and LIME) differ from previous size or age structured SPR models where size dependent selectivity is not considered and are vulnerable to overestimates of fishing mortality and negative bias in SPR estimates (Froese et al., 2018; Hordyk et al., 2016; Rudd and Thorson, 2017). These methods also provide estimates of selectivity and the ratio of fishing mortality to natural mortality. The default assumption in these methods is a logistic selectivity curve and the same von Bertalanffy growth curve and catchability in both sexes. LIME allows for specification of a Gaussian selectivity curve. For my catch data, I used the life-history parameters found in Table 5.1.

For many taxa, a typical assumption is that once a stock is fully selected in fishery, it remains fully selected for the rest of its life span (logistic selectivity). For mobile species in this gleaning fishery, this is likely not the case. Many species of fish and invertebrates undergo depth migration with growth. *Trochus*, for example, is found to have greater frequencies of larger

individuals with increasing depth, suggesting depth migration with growth (Heslinga et al., 1984; Nash, 1993). Similar patterns have been found in the other mobile taxa in this analysis: *Portunus* (Batoy et al., 1988), and *Tripneustes* (Lewis, 1958). Bivalves, on the other hand, are confined to the same patch of substrate for the duration of their post-larval life cycle. In practical terms, this means that for species that undergo depth migrations, data obtained from this intertidal gleaning fishery likely omit large individuals—not because they are absent in the population, but because the spatial footprint of the fishery does not overlap with the depth habitat of large animals. To account for reductions in selectivity in larger individuals, I applied a second length frequency analysis tool with capabilities for assuming a Gaussian (“dome-shaped”) selectivity curve. The length-based integrated mixed effects model (LIME) has several of the same assumptions as LBSPR for single year length-frequency data sets but with an important difference: a Gaussian selectivity pattern can be specified in the model (Rudd and Thorson, 2017). In LIME, I analysed all taxa using a logistic selectivity curve and then for the three mobile taxa in my analysis I applied a Gaussian selectivity curve. To specify the standard deviation for each Gaussian curve, I used the standard deviation from the respective taxon’s length frequencies. I then conducted a sensitivity analysis by varying the standard deviation by $\pm 20\%$.

5.3.4 Simulation analysis

To understand the impacts of setting a minimum size limit on fisheries yield, I ran simulation models in the LBSPR package. For each taxon in this analysis, I simulated a population, and then used two different assumptions for size at selection into the fishery. I then assessed differences in population size structure and fisheries yield among size at first capture assumptions. I used the same set of life-history values as above (Table 5.1) and set steepness for all taxa at a relatively

conservative 0.7. In the first scenario, I used the size at first capture currently observed for each taxon, estimated in the LBSPR analysis above. In the second scenario I simulated implementation of a minimum size limit by setting recruitment as a knife edge selectivity pattern for each taxon's L_{opt} value (i.e., zero catch below the size limit and full selection into the fishery above the size limit). In all cases, the exploitation rate was set very high ($F/M = 4$) to mimic high exploitation rates observed in the fishery. For each scenario I generated population size frequencies and catch size frequencies. I also calculated the difference in available fishable yield for each taxon in each scenario. To do this I used the length frequency distributions generated above, converted lengths to mass, and compared total mass between scenarios for each species. My mass estimates do not describe edible mass but instead total animal mass, shell included.

Length frequency data were analysed in the LBSPR and LIME packages in R (Hordyk et al., 2016; Rudd and Thorson, 2017) to produce estimates of SPR, selectivity and fishing mortality.

5.4 Results

5.4.1 Catch size composition relative to reference points

Of the nine species examined in this analysis, five had a mean L_c (mean length at capture) that exceeded my calculated L_m (length at 50% maturity; Table 5.3), while the remaining four species had L_c of less than L_m (Table 5.3). In only one of nine species did the length at capture exceed L_{opt} (optimal length at capture; *Tegillarca granosa*).

5.4.1.1 Bivalve catch size composition

Among the bivalves, mean L_c for five of the six species was greater than their L_m . The one exception, *Perna viridis*, had a mean L_c that was 17 mm less than its L_m . Only one bivalve

species reached L_{opt} before L_c . Catch of *T. granosa* consisted of over 80% individuals at sizes larger than L_{opt} . Mean length at capture falls short of L_{opt} by between 5% (*Amusium pleuronectes*; 4 mm) and 106% (*P. viridis*; 64 mm). With the exception of *P. viridis* and *Crassostrea iredalei*, in bivalves, a small fraction of the catch consists of juvenile individuals (Figure 5.3). In four of six species, more than half of the catch (by count) is of individuals smaller than L_{opt} (Figure 5.3). 90% of the catch of *P. viridis* is smaller than L_m and nearly half the catch of *C. iredalei* is smaller than L_m .

5.4.1.2 Gastropod catch size composition

In the gastropod species (*Trochus niloticus*), mean L_c is less than both L_m and L_{opt} . *T. niloticus* falls short of L_{opt} by 262% (76 mm) and in my gleaning data set, it is captured exclusively at sizes less than its L_m .

5.4.1.3 Crustacean catch size composition

The crustacean, *Portunus pelagicus*'s mean L_c is 30% less (23 mm) than L_m and 86% less (66 mm) than L_{opt} . All but a small percentage of the catch (~1%) were of individuals smaller than L_m .

5.4.1.4 Echinoderm catch size composition

The single echinoderm in this analysis, the urchin *Tripneustes gratilla*, has a mean L_c which is 40% smaller (31 mm) than L_m and 58% less (65 mm) than L_{opt} . The entirety of the catch of *T. gratilla* was caught at sizes smaller than L_{opt} and L_m .

5.4.2 Length-based spawning potential ratio

SPR analyses in both LBSPP and LIME showed a pattern consistent with my observed catch pattern by life stage: The bivalve species in which L_c exceeded L_m and/or L_{opt} also had relatively

higher reproductive output in fished populations (Table 5.3). These taxa were all sessile and mean SPR among them was 0.34 (s.e. ± 0.09) in LBSPR and 0.33 (s.e. ± 0.08) in LIME. The single sessile taxon with a high proportion of catch below L_m , *P. viridis*, had the lowest SPR, at 0.01 (LBSPR) and 0.03 (LIME). The SPRs among the other sessile species ranged from 0.15 to 0.61; in these species, mean L_c exceeded L_m .

Among mobile species, estimated SPR values are exceedingly low when applying a logistic selectivity curve. *T. niloticus*, a gastropod with a low mean L_c relative to L_m and L_{opt} , has an estimated SPR of zero and 0.03 in LBSPR and LIME, respectively. Similarly, both the crustacean and the urchin in this analysis register SPRs very close to zero. While this pattern of low SPR values is consistent with high proportions of catch in small animals, these SPR estimates unrealistically low given that these taxa persist in the catch and have not become locally extirpated. For these three taxa, I specified a Gaussian (“dome shaped”) selectivity pattern in LIME (Table 5.4) as this option was unavailable in LBSPR. In the gastropod and crustacean, SPR increases to 0.19 and 0.18, respectively, while in the urchin, the SPR value remains similar to that found when assuming logistic selectivity (0.02). SPR values for each taxon vary depending on the standard deviation of the assumed Gaussian curve used in the analysis. In my sensitivity analysis, when the standard deviation of the Gaussian selectivity curve decreases by 20% for each species, estimated SPR increases in all cases. Conversely, an increase in the standard deviation in each curve resulted in decreases in estimated SPR (Table 5.4).

Estimates for fisheries mortality rate relative to natural mortality rate show a similar pattern to those found in SPR analysis: lower SPR values were associated with higher estimates for F/M

ratios (Table 5.3 & Table 5.4, Figure 5.4). When considering all species, the F/M ratio has a mean value of 6.78 (s.e. ± 2.0) and ranges from 0.64 to 19.03 in LBSPR, assuming logistic selectivity (Table 5.3). In LIME, the ratio, assuming logistic selectivity is 4.3 (s.e. ± 1.9) and ranges from 0.59 to 18.24 (Table 5.3). However, when Gaussian selectivity is assumed for mobile species in LIME, the mean F/M ratio among all species decreases to 2.84 (s.e. ± 1.1) and ranges from 0.59 to 11.35 (Table 5.3 and Table 5.4). F/M ratio estimates in LBSPR and LIME are roughly similar, however for three taxa (*C. tigerina*, *G. tumidum*, and *T. gratilla*), estimates produced by LIME are substantially lower than those produced by LBSPR.

5.4.3 Simulation analysis

Comparing populations under three scenarios: fishing at current selectivity and fishing at L_{opt} selectivity (i.e., a minimum size limit), and zero fishing, I found that setting minimum size limits would have a notable effect on the reproductive output for these taxa. I compare SPR for simulated populations fished with varying selectivity patterns. Increases in SPR when using L_{opt} selectivity relative to current selectivity range from 0.14 to 0.61, with an average increase of 0.40 (s.e. ± 0.05), (Table 5.5). SPR at simulated selectivity patterns observed in the catch have a mean of 0.15 (s.e. ± 0.06) and a range of values spanning 0.01 to 0.52, while $SPR_{L_{opt}}$ has a mean value of 0.55 (s.e. ± 0.02) and range from 0.48 to 0.66. For the bivalves, mean $SPR_{current}$ is 0.21 (s.e. ± 0.08) while $SPR_{L_{opt}}$ is 0.54 (s.e. ± 0.03). For the gastropod, SPR increases from 0.03 to 0.58 while the crustacean increases from 0.02 to 0.63, and the urchin from 0.02 to 0.51. In all cases, fishing with a minimum size limit set at L_{opt} results in substantial shifts in size frequencies and increases in SPR and fisheries yield relative to selectivity observed in the current catch (Figure 5.5). Population size frequency plots indicate that a larger proportion of the populations are

reaching larger sizes and, in many cases, size frequency distributions are similar to those found in an unfished population (Figure 5.6 and Figure 5.7). Catch size frequencies indicate dramatic differences between current selectivity and L_{opt} selectivity (Figure 5.6 and Figure 5.7).

Introduction of an L_{opt} -based minimum size limit results in large increases in the amount of biomass available, as deduced from yield under identical exploitation rates. Yield increases by an average of 573% with a minimum increase of 103% and a maximum increase of 1383% (Table 5.5). Among the bivalves, yield increased by a mean of 395%. The largest increases were in species that also have large increases to SPR, *C. iredalei* and *P. viridis* with yield increases of 617 and 982%, respectively. This is also true for the gastropod, crustacean and echinoid, all of which undergo substantial increases in SPR and have fisheries yield increases ranging from 609% (*T. gratilla*) to 1383% (*T. niloticus*). This simulation analysis indicates that moving to an L_{opt} -based minimum size limit, while still maintaining high fishing pressure, results in large improvements to both stock status (SPR) and fisheries yield.

5.5 Discussion

In this analysis, I estimated life history values for data-limited tropical invertebrates using von Bertalanffy growth and Beverton-Holt life-history invariants, assessed stock status and then estimated effects of setting a minimum size limit. I found that large portions of the catch are fished at sizes too small to support productive populations or maximize fisheries yield. Setting minimum size limits would likely benefit reproductive output and have substantial impacts to catch biomass.

My finding that a large proportion of the invertebrate catch is retained at sizes smaller than size at maturity and L_{opt} are unsurprising given the intensity of fishing effort. In this study area it was found that and estimated 97% of women and 55% of men participated in gleaning, and the gleaning fisheries accounted for 35% of the total reported weekly catch volume (Kleiber et al. 2014b). On average people reported gleaning over 5.5 hours per week, with an average catch of just over 6 kg per week (Kleiber et al., 2014).

My finding that heavily exploited target taxa (i.e. those with very high exploitation rates) have not been fully depleted and are still present in the catch has potential ecological and economic explanations. For two thirds of species in this analysis, fishing mortality is estimated to be greater, and in some cases, much greater than natural mortality; yet populations of these animals persist. Assuming these fishing mortality estimates are correct, this pattern could be explained by source-sink dynamics—spawners from elsewhere could be supporting populations found in these fishing grounds through larval transport or migration from adjacent areas. These source populations could be found at depths beyond the range of fishing gears, in sparsely fished areas or protected areas, which are common in the region. If local reproduction is not important for persistence of these animals in gleaning areas, an argument could be made for continued high mortality rates in smaller size classes. In this case, larval transport from source populations could sustain these sinks. However, given the dramatic expansion of fisheries footprints and the increases in the diversities in gear in the region (Selgrath et al., 2017), it becomes difficult to justify an assumption of a source population for continuation of intensive sink fisheries. Persistence of these species in the catch despite high exploitation may also be linked with the economics of this fishery. These gleaning fisheries have few overhead costs typically found in

subtidal fisheries (boats, fuel, nets, etc.)—all that is required is time and a plastic bucket. Where subtidal species may no longer be economically viable for targeting below a particular abundance, exceedingly low overhead costs in gleaning fisheries may mean the fishery has potential to persist even where catch per unit effort is low.

I found that characterizing selectivity patterns within the fishery was important for obtaining realistic model estimates for SPR. The combined effects of species ecology and spatial dynamics within the fishery may introduce bias in estimates of fishing mortality rate and SPR when assuming logistic selectivity. In many cases, even with the possibility of source-sink dynamics and favourable economic aspects, fishing mortality rates relative to natural mortality rates in mobile species appeared to be unrealistically high (up to 19 times higher than natural mortality) and SPR unrealistically low. The LBSPR model assumes that once animals reach a size where the selectivity curve levels off, their probability of capture remains near constant through the rest of their lifecycle, regardless of size (Hordyk et al., 2016). This means that the LBSPR model assumes catch size data are representative of the exploited population size structure. In LBSPR the model estimates for SPR and F/M are heavily influenced by whether large animals are present in the catch (Hordyk et al., 2016). Very low SPR values or very high F/M values may be a result of an absence, or near absence, of large animals in the catch. Many species of fish and invertebrates undergo depth migration with growth. *Trochus*, for example, is found to have greater frequencies of larger individuals with increasing depth, suggesting depth migration with growth (Heslinga et al., 1984; Nash, 1993). Similar patterns have been found in the other mobile taxa in this analysis: *Portunus* (Batoy et al., 1988), and *Tripneustes* (Lewis, 1958). Bivalves, on the other hand, are confined to the same patch of substrate for the duration of their post-larval

life cycle. In practical terms, this means that for species that undergo depth migrations, data obtained from this intertidal gleaning fishery likely omit large individuals—not because they are absent in the population, but because the spatial footprint of the fishery does not overlap with the depth habitat of large animals. This Gaussian selectivity pattern, where large animals are not selected into the fishery, violates the assumption of logistic selectivity in the LBSPR model and may be leading to extreme values for SPR and F/M for some mobile species (Hordyk et al., 2016). When I applied a Gaussian selectivity curve for mobile species in the LIME model, F/M and SPR estimates appeared within ranges that were more realistic. Similarly, Pons et al. (2019), found that length-based models better estimated stock status in small tunas when catch length-frequency data was obtained from fisheries that target a broad range of sizes, adhering to the assumption of logistic selectivity among size classes.

I am surprised by the scale of increases to yield and SPR from introduction of an L_{opt} minimum size limit. Allowing animals to reproduce before capture, particularly large, highly fecund spawners could result in substantial increases in reproductive output in these stocks, contributing to higher abundances of animals available in this fishery, assuming they are an allowable size to catch. Similar to this, L_{opt} -based size limits have been found to substantially increase stock biomass, contribute to an age structure similar to an unfished stock, eliminate growth overfishing and contribute to resilience within populations (Froese et al., 2008). For example, in the Mediterranean, a shift towards an L_{opt} size limit is estimated to result in a 9.3 fold increase in stock biomass for assessed stocks (Colloca et al., 2013).

Despite the increases in biomass and SPR, a blanket ban on mobile invertebrate taxa smaller than L_m or L_{opt} is likely unrealistic for those involved in this fishery. For many mobile species, juvenile stages are spent in intertidal and shallow water areas before moving to deeper waters with growth. My estimates for increases in exploitable biomass are based on increases in yield per recruit—accumulation of biomass from growth in individual animals. This means that YPR benefits are achieved through growth of those animals—and in this case movement to deeper water before capture. Should size limits be implemented, fishers whose spatial footprint is limited to walk-able areas—marginalized members of the community who lack boats and exploit invertebrates in their juvenile stages—become excluded from a fishery important for food security (Kleiber et al., 2014). An important next step is an analysis of trade-offs required to achieve similar biological results, but with management strategies that combine spatial zoning of effort and size limits. For example, there may be options to close small sections of gleaning areas in conjunction with setting size limits in sub-tidal zones fished by skin-divers. Evaluating the plausibility of trade-offs between closed areas and size limits will require significant consultation with village groups.

This analysis and a growing body of work indicates that management and conservation of invertebrate taxa, particularly those in data-limited fisheries, is required for increasing populations and improving fisheries—even if the assessment tools used are imperfect (Anderson et al., 2011; Benbow et al., 2014; Collen et al., 2012; Mobrand et al., 2005; Perry et al., 1999; Prince and Hordyk, 2019; Rhyne et al., 2009; Worm and Branch, 2012). Data-limited fisheries, particularly those where animal life history is lacking, require assumptions that introduce uncertainty in outputs. Within every step in this analysis, I was required to either extrapolate

from related species (e.g. growth parameters, M/K ratios), use approximate life-history estimates and their ratios (e.g., L_m to L_∞ ratios; assuming uniform growth and maturity between sexes) or make assumptions about population dynamics (e.g. equilibrium dynamics). Despite these sources of uncertainty, these estimates may be “good enough”—they are consistent with established principles for lessening fisheries impacts and achieving “pretty good yield”: allowing animals to reproduce at least once before capture (Froese et al., 2008; Hilborn, 2010; Johannes, 1998).

The high intensity and widespread nature of extractive pressures in these gleaning fisheries require that multiple tools be used to manage human impacts. In my study region, MPAs are a common conservation tool and recent evidence suggests they are effective at increasing the abundance of exploited invertebrate taxa (Gillespie and Vincent, 2019; Lester et al., 2009). While MPAs can support biodiversity and contribute to spillover of biomass into adjacent areas, their ability to singularly compensate for wide-spread, intensive fisheries is not realistic (Boersma and Parrish, 1999; Hilborn et al., 2004). Managing for size-selectivity may be another tool for tempering exploitation within artisanal fisheries (Johannes, 2002, 1998; Prince et al., 2015b), requires fewer resources than quota-based management (Berkes, 2001; Copes, 1986), and offers a promising supplement to existing conservation and fisheries management undertakings. I demonstrate a procedure for applying data-limited methods and identify their biological and social caveats in species and fisheries that are typically overlooked. While imperfect, these size-based methods offer a tool to achieve higher yields and larger, more productive populations of target invertebrate species.

Table 5.1 Life history values and sample sizes for nine commonly fished invertebrate taxa on the Danajon

Bank. All length values are in millimetres.

Type	Species	n	L_{∞} (mm)	ϕ'	K (year ⁻¹)	M (year ⁻¹)	M/K ratio
Bivalve	<i>Amusium</i>						1.2
	<i>pleuronectes</i>	80	114	2.04	0.85	1.02	
	<i>Codakia tigerina</i>	332	126	1.3	0.13	0.15	1.2
	<i>Crassostrea iredalei</i>	286	95	2.06	1.29	1.54	1.2
	<i>Gafrarium tumidum</i>	1651	51	0.97	0.35	0.42	1.2
	<i>Perna viridis</i>	369	173	2.09	0.41	0.49	1.2
	<i>Tegillarca granosa</i>	4260	95	1.49	0.35	0.42	1.2
Gastropod	<i>Trochus niloticus</i>	3101	126	1.53	0.21	0.13	0.59
Crustacean	<i>Portunus pelagicus</i>	702	183	2.55	0.89	1.07	1.2
Urchin	<i>Tripneustes gratilla</i>	272	157	2.32	0.85	1.02	1.2

Table 5.2 Common symbols and abbreviations in Chapter 5

Variable	Description
F	Fishing mortality (1/time)
F/M	Ratio of fishing mortality (F) to natural mortality (M)
K	Rate (1/time) at which the asymptotic length is approached
L_{∞}	Asymptotic length in a population
L_c	Mean length at first capture
L_m	Mean length at which 50% of the population has reached maturity
L_{m95}	Mean length at which 95% of the population has reached maturity
L_{max}	Maximum length reported from a population
L_{opt}	Length at which biomass of an unfished cohort reaches its maximum
M	Instantaneous rate (1/time) of natural mortality (1/time)
M/K	Ratio of natural mortality to von Bertalanffy's K
SPR	Spawning potential ratio
$SPR_{current}$	Spawning potential ratio at selectivity observed in the fishery
$SPR_{L_{opt}}$	Spawning potential ratio at L_{opt} selectivity
Z	Total mortality (1/time)
ϕ'	Phi prime: growth performance index ($\phi' = \log K + 2 \log L_{\infty}$)

Table 5.3 Length at maturity, mean length at capture, estimated optimal size at capture and SPR and F/M indicators of stock status in nine invertebrate taxa obtained from LBSPR and LIME.

Type	Species	L _m (mm)	Mean L _c (mm)	Estimated L _{opt} (mm)	<u>LBSPR</u>		<u>LIME</u>	
					SPR	F/M	SPR	F/M
Bivalve	<i>Amusium pleuronectes</i>	57	77	81	0.47	0.64	0.42	1.04
	<i>Codakia tigerina</i>	63	77	90	0.18	9.12	0.15	0.82
	<i>Crassostrea iredalei</i>	47	53	68	0.21	1.14	0.2	1.39
	<i>Gafrarium tumidum</i>	26	28	37	0.22	7.00	0.27	1.56
	<i>Perna viridis</i>	87	60	124	0.01	4.10	0.03	2.62
	<i>Tegillarca granosa</i>	47	78	68	0.61	2.62	0.61	0.59
Gastropod	<i>Trochus niloticus</i>	63	29	105	0.00	19.03	0.03	18.24
Crustacean	<i>Portunus pelagicus</i>	100	77	143	0.01	5.01	0.00	7.62
Urchin	<i>Tripneustes gratilla</i>	78	47	112	0.00	12.37	0.02	4.82

Table 5.4 SPR and F/M indicators of stock status in three mobile invertebrate taxa under varying selectivity assumptions in LIME.

Type	Species	<u>Logistic</u>		<u>Gaussian 1.2 SD</u>		<u>Gaussian 1.0 SD</u>		<u>Gaussian 0.8 SD</u>	
		SPR	F/M	SPR	F/M	SPR	F/M	SPR	F/M
Gastropod	<i>Trochus niloticus</i>	0.03	18.24	0.14	12.12	0.19	11.35	0.42	7.11
Crustacean	<i>Portunus pelagicus</i>	0.00	7.62	0.14	1.48	0.18	1.39	0.30	1.14
Urchin	<i>Tripneustes gratilla</i>	0.02	4.82	0.02	4.81	0.02	4.80	0.03	4.76

Table 5.5 SPR estimates for simulated populations of nine invertebrate taxa. I calculated SPR based on my life history parameter estimates, held $F/M = 4$ and then varied selectivity. I compare SPR based on my estimate for current selectivity to SPR based on knife-edge selectivity at L_{opt} .

Type	Species	SPR _{current}	SPR _{L_{opt}}	Increase in fisheries yield at L_{opt} (%)
Bivalve	<i>Amusium pleuronectes</i>	0.11	0.48	270
	<i>Codakia tigerina</i>	0.32	0.54	195
	<i>Crassostrea iredalei</i>	0.03	0.51	617
	<i>Gafrarium tumidum</i>	0.25	0.51	203
	<i>Perna viridis</i>	0.01	0.51	982
	<i>Tegillarca granosa</i>	0.52	0.66	103
Gastropod	<i>Trochus niloticus</i>	0.03	0.58	1383
Crustacean	<i>Portunus pelagicus</i>	0.02	0.63	793
Urchin	<i>Tripneustes gratilla</i>	0.02	0.51	609

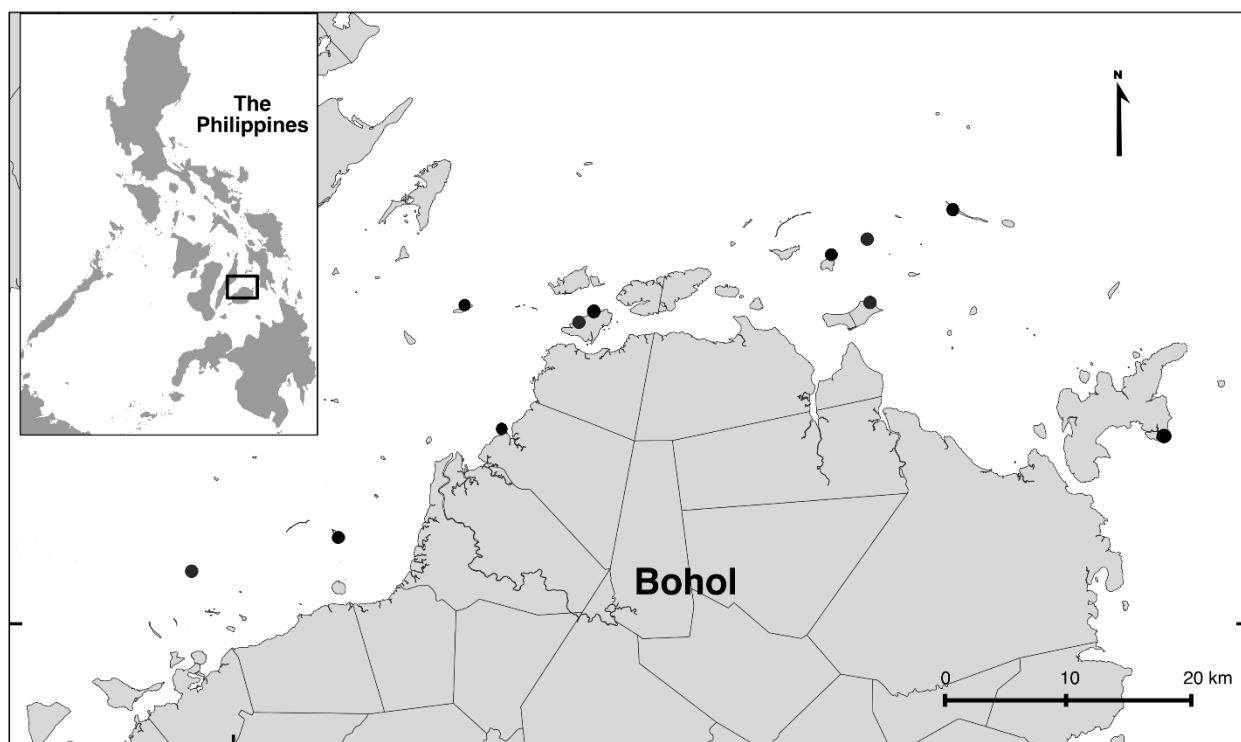


Figure 5.1 Gleaning catch sampling sites in the Danajon Bank region, Philippines. I sampled catch from 160 fishing trips at 11 intertidal sites on the north coast of Bohol.

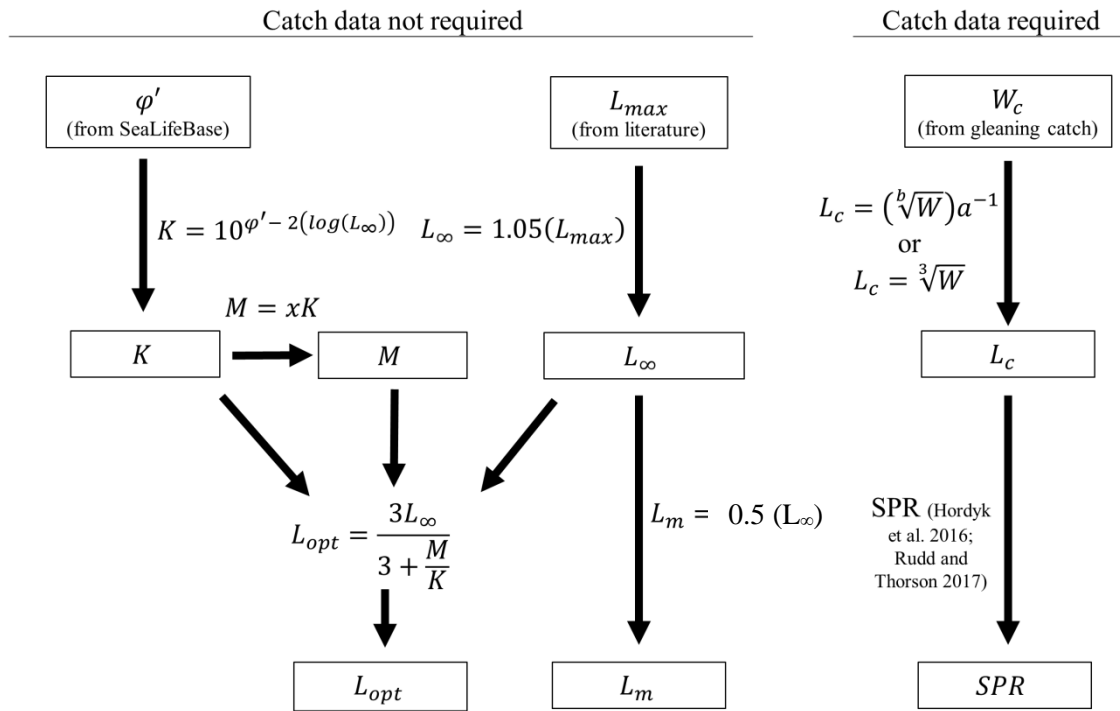


Figure 5.2 Schematic of my analytical approach. I obtained both literature and field data to estimate growth parameters and calculate L_{opt} and L_m . These values were compared to length at catch data, L_c , obtained from gleaning fisheries in the Central Philippines.

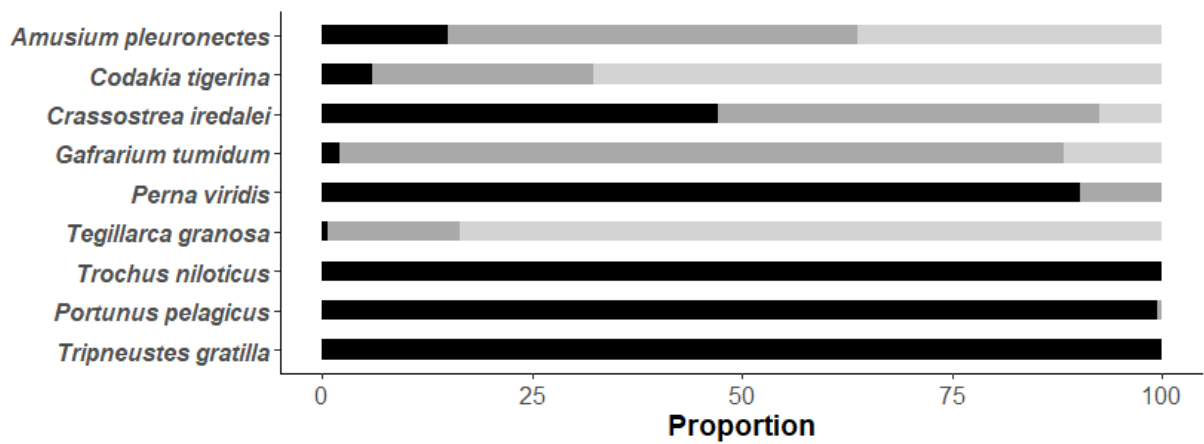


Figure 5.3 Proportion of gleaning catch that is smaller than L_m (black segments), larger than L_m but less than L_{opt} (dark grey segments), and larger than L_{opt} (light grey segments).

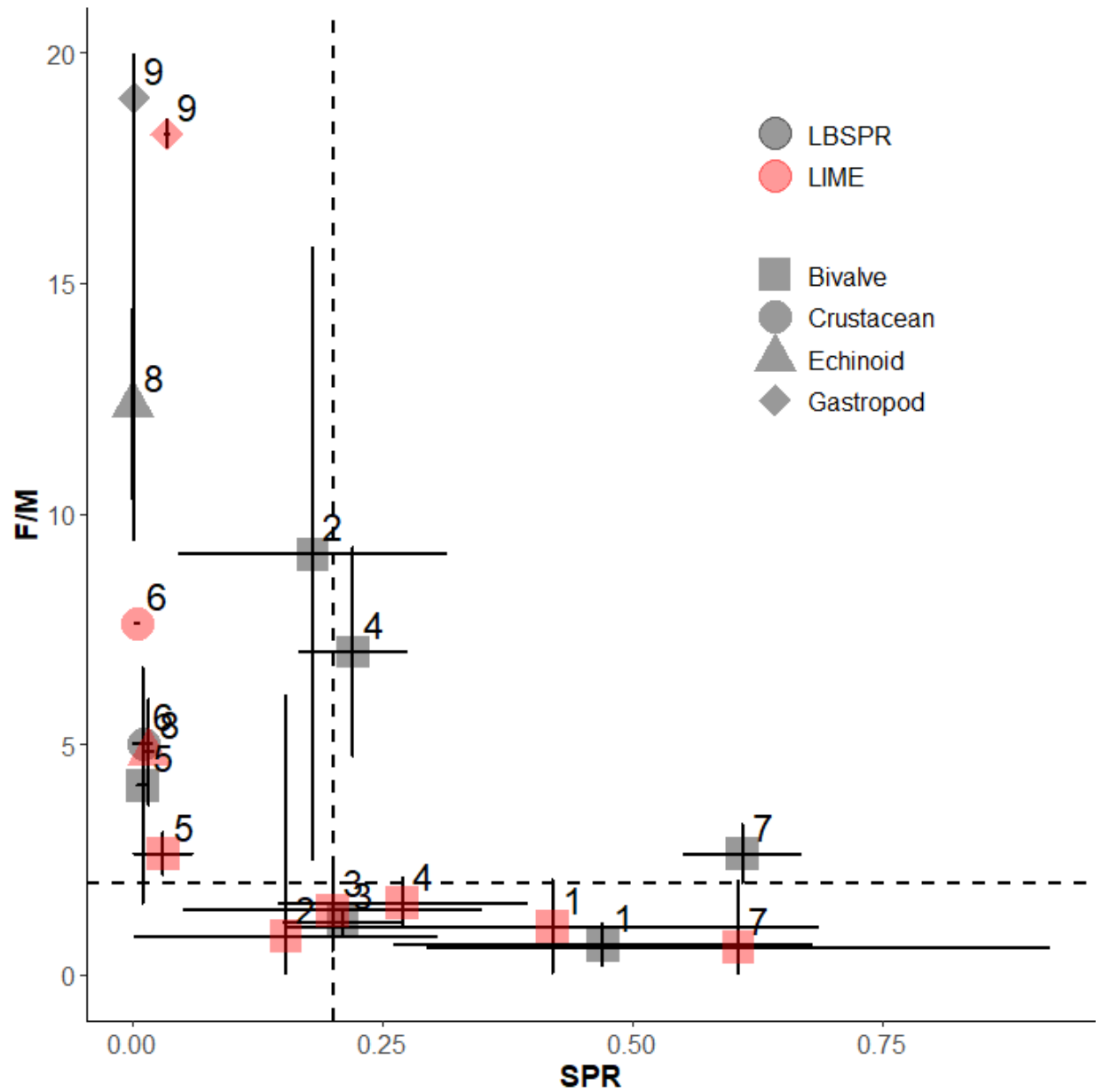


Figure 5.4 Stock status for nine species of intertidal macroinvertebrates as estimated by length-based SPR and length-based F/M methods where logistic selectivity is assumed. Solid horizontal and vertical lines are 95% confidence intervals for SPR and F/M. Dotted lines indicate typical SPR and F/M thresholds for assessing stock health. The vertical dotted line is where SPR = 20%. The horizontal line is where F/M = 2. Number labels correspond with the nine taxa in this analysis: 1 = *A. pleuronectes*, 2 = *C. tigerina*, 3 = *C. iredalei*, 4 = *G. tumidum*, 5 = *P. viridis*, 6 = *P. pelagicus*, 7 = *T. granosa*, 8 = *T. gratilla*, 9 = *T. niloticus*

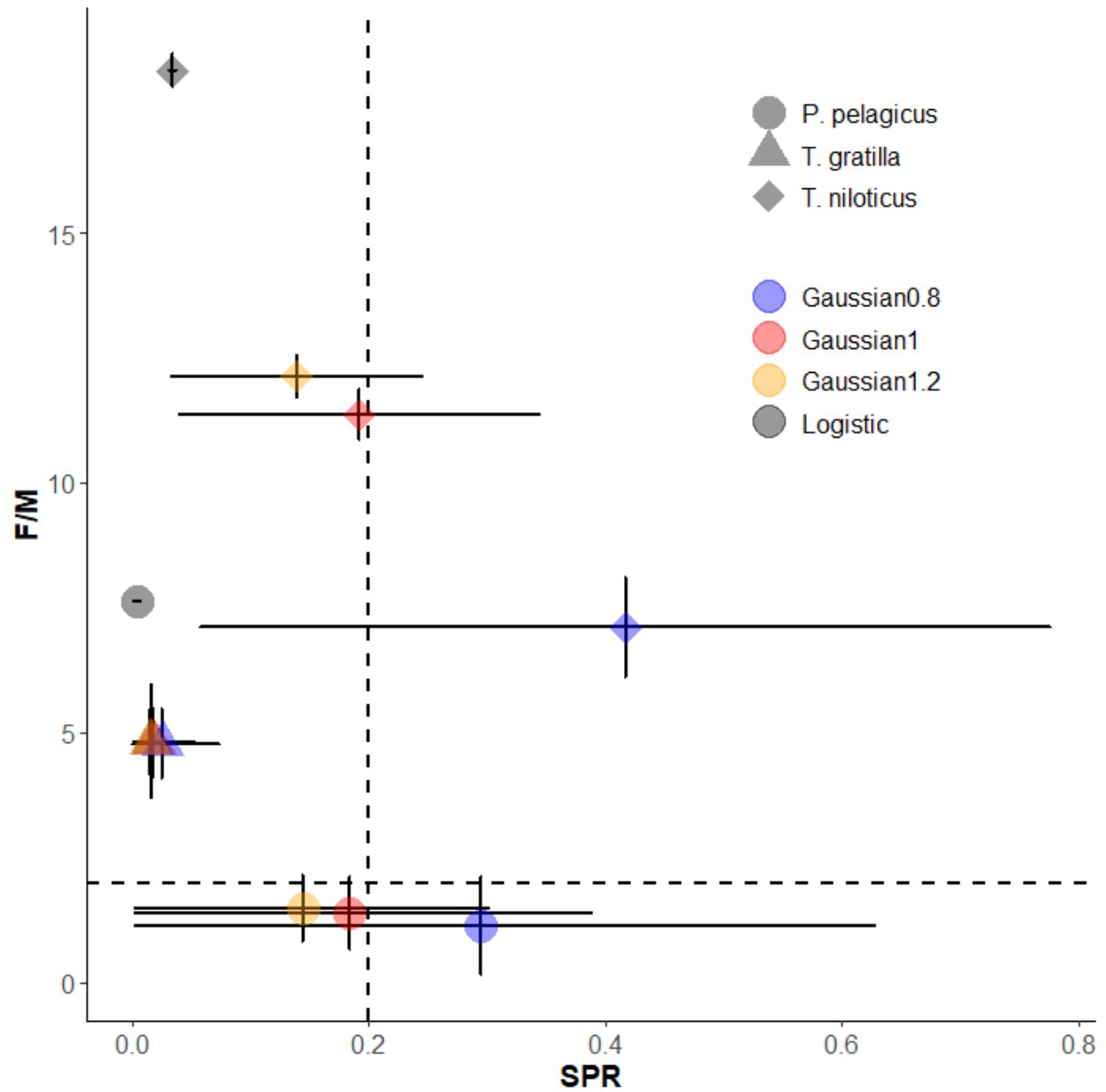


Figure 5.5 Stock status for three species of mobile intertidal macroinvertebrates as estimated by length-based SPR and length-based F/M methods where logistic and Gaussian selectivities are applied. Solid horizontal and vertical lines are 95% confidence intervals for SPR and F/M. Dotted lines indicate typical SPR and F/M thresholds for assessing stock health. The vertical dotted line is where SPR = 20%. The horizontal line is where F/M = 2.

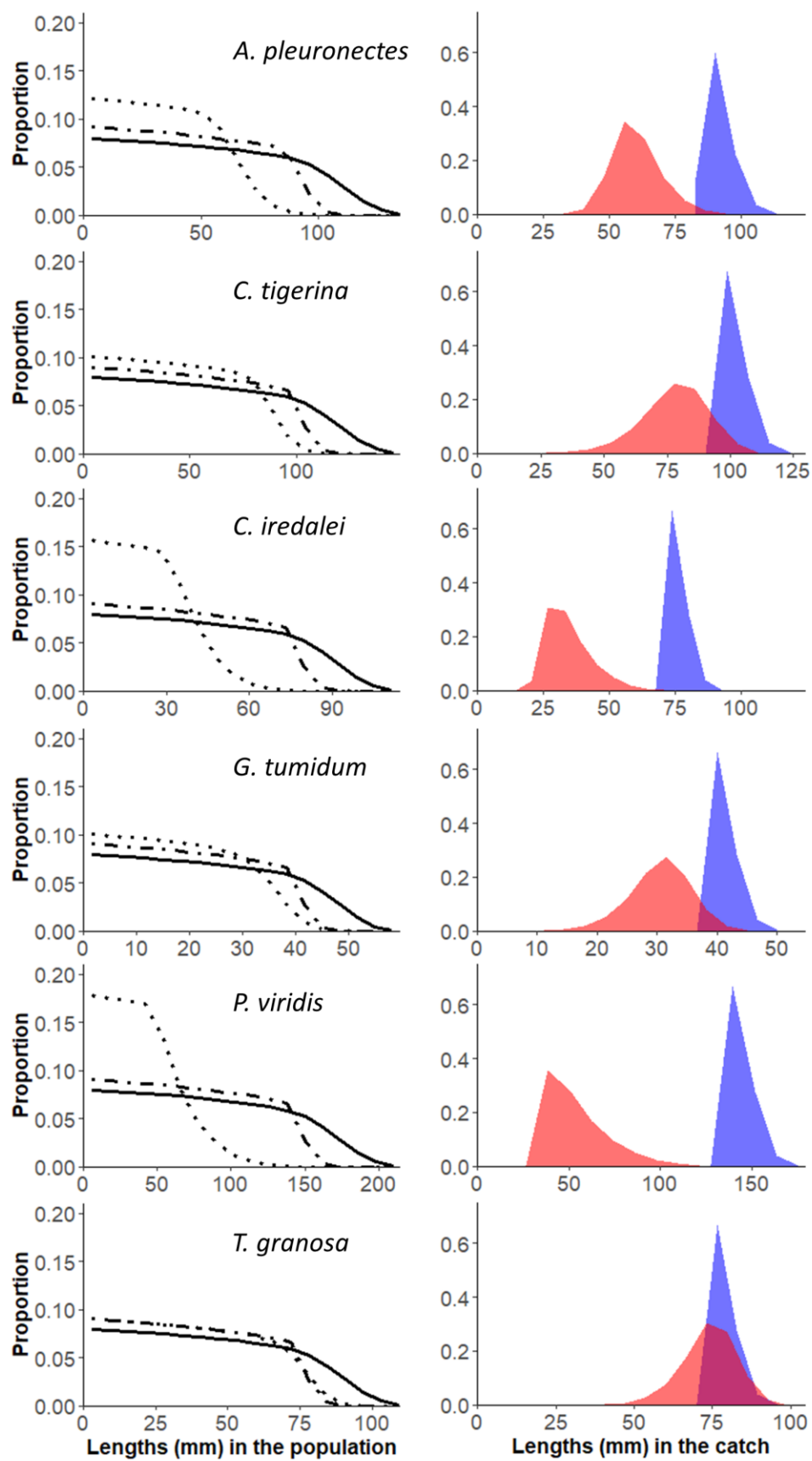


Figure 5.6 Population size structure and catch size structure for six simulated populations for sessile taxa.

Each simulated population was given life-history attributes for a taxon of interest in this study and then “fished” with two different selectivity patterns. In the population size distribution plots, on the left, the solid lines correspond with the body sizes of a population that is unfished; the dash-dot lines correspond with a population fished at L_{opt} ; and the dotted lines show a population at current estimated fishing. In the catch size distribution plots, on the right, the red area represents catch size frequency under current selectivity patterns and the blue bars represent catch size distribution in a knife-edge L_{opt} selectivity pattern. In all cases, I set a high exploitation rate of $F/M = 4$. Note the differing x-scale among taxa.

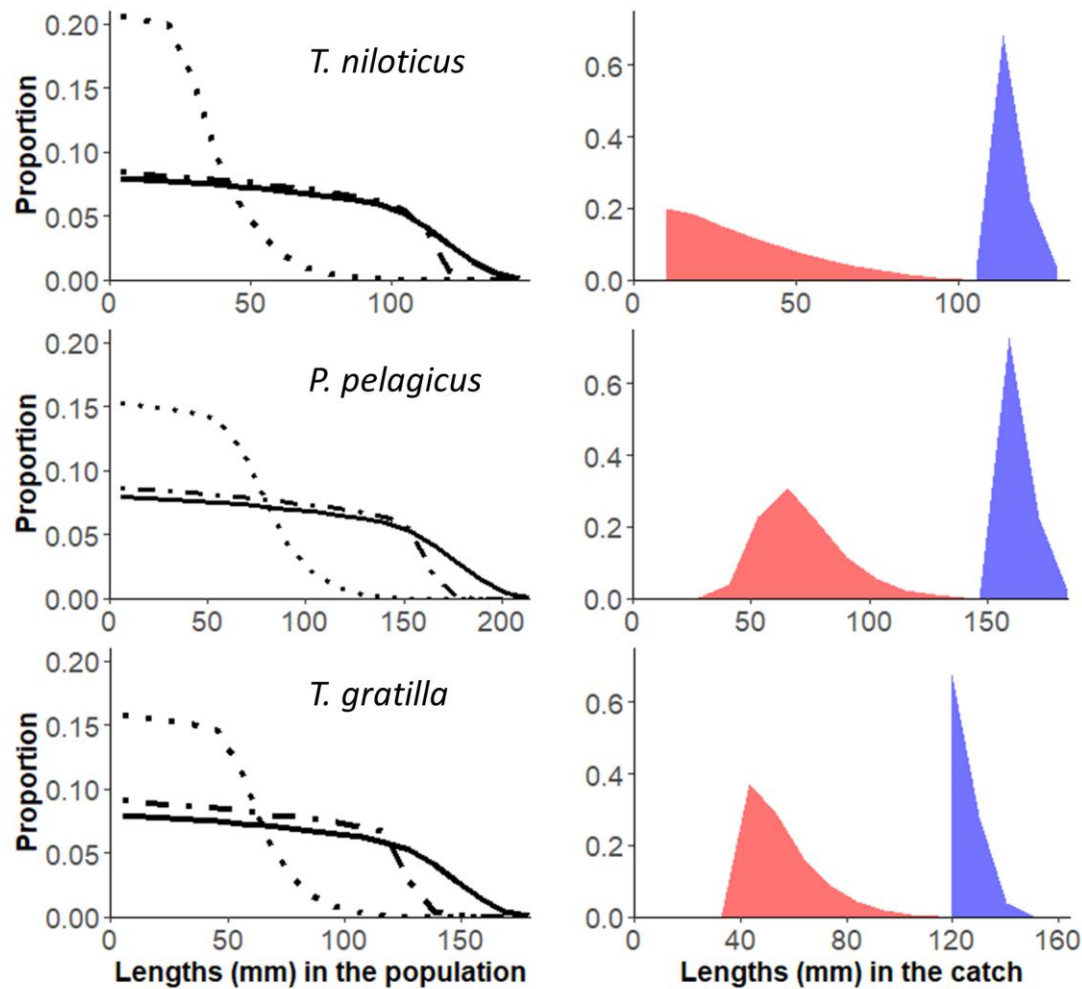


Figure 5.7 Population size frequency distributions and catch size frequency distributions for three simulated populations of mobile taxa. Each simulated population was given life-history attributes for a taxon of interest in this study and then “fished” with two different selectivity patterns. In the population size distribution plots, on the left, the solid lines correspond with the body sizes of a population that is unfished; the dash-dot lines correspond with a population fished at L_{opt} ; and the dotted lines show a population at current estimated fishing. In the catch size distribution plots, on the right, the red area represents catch size frequency under current selectivity patterns and the blue bars represent catch size distribution in a knife-edge L_{opt} selectivity pattern. In all cases, I set a high exploitation rate of $F/M = 4$. Note the differing x-scale among taxa.

Chapter 6: Conclusion

6.1 Introduction

This thesis addresses three significant research gaps by creating new knowledge that will contribute to conservation of marine invertebrate taxa: (i) survey approaches necessary for effective detection and monitoring of invertebrates, (ii) impacts of marine reserves on invertebrates and their communities, and (iii) the need for complementary conservation measures to secure reproductive output. In Chapter 2, I found that tailoring sampling to invertebrate ecology—shifting data collection to night-time—dramatically increases detection of mobile invertebrates. Such a shift, in turn, has a substantial bearing on estimates of invertebrate biodiversity. In Chapter 3, I found that marine reserves increase the abundance of invertebrate taxa important in fisheries and that presence of structurally complex habitat can amplify this effect. I also found that fish response to MPAs serves as a poor indicator for abundance trends in invertebrates. In Chapter 4, I found that marine reserves changed both the composition of invertebrate communities and the traits and functions present in those communities. This results in marine reserves that are functionally different than fished areas. Lastly, in Chapter 5, I found that for commonly exploited invertebrate taxa invertebrates with poor data, minimum size restrictions can improve the reproductive output and fisheries yield.

Marine conservation science has shifted in the years since I began this work—something I have attempted to reflect in this thesis. In the 2000s to mid-2010s, the state of art in marine conservation was MPA science. A number of influential meta-analyses had been published, which examined response trends among taxa and ecosystems (Côté et al., 2001; Grorud-Colvert et al., 2014; Halpern, 2003; Lester et al., 2009). This work paralleled an effort from governments

and civil society for increased establishment of MPAs. Chapters 2-4 of this thesis contribute to this body of work. In recent years, the field has shifted, embracing a broader swathe of conservation techniques that compliment MPA establishment—notably, development of methods for establishing effort controls in data-limited fisheries (Carruthers et al., 2014; Hordyk et al., 2015). This shift is reflected in Chapter 5 and is consistent with calls to “stack” complementary actions to achieve rebuilding of populations and habitats (Duarte et al., 2020).

For each chapter in this thesis, I present my research question and place my findings in the context of the broader academic and conservation field. I discuss the limitations of my work and then conclude by describing practical applications of my research, broader conservation implications, and directions for future research.

6.2 Research findings and broader context

6.2.1 How does time of sampling affect detection of coral reef invertebrate taxa?

In Chapter 2, I tested whether night time invertebrate surveys result in different biodiversity estimates than those completed during daylight hours. This chapter is notable because it provides guidance for other researchers on gathering baseline information and detecting trends in invertebrate abundance and diversity.

I found that sampling at night increases detection and results in large differences in the estimates of total biodiversity, as compared to daytime sampling. Ecological monitoring relies on the assumption that methods produce data representative of the system they are measuring (Kellner and Swihart, 2014). In my search of the marine invertebrate monitoring literature, sampling methods were similar to those for fish: day-time belt transects or day-time quadrats. However,

through trial and error in the field I found that this provides disappointing results: densities and species richness values were exceedingly low given the biodiversity of my study region. By shifting sampling to night-time, I found substantially more mobile taxa and higher taxon richness. This results in large differences between day and night in estimates of total taxon richness in rarefaction extrapolation analyses. The difference in results delivers a compelling message: sampling strategy must be tailored to the ecology of the focal taxa. Use of daytime sampling in this thesis, would likely have resulted no difference in detection for sessile taxa. However, some of the most interesting trends in Chapters 3 and 4 are related to mobile taxa—those with poor detection rates during the day. It is likely that many of the mobile focal taxa in this work would have had counts too low to have enough statistical power to understand response patterns had I not switched to night sampling. This is an important lesson for other MPA ecologists.

6.2.2 How and why do marine invertebrates respond to no-take marine reserves?

My work in Chapter 3 found that marine reserves do indeed increase the overall abundance of exploited invertebrate taxa while there is no significant effect in taxa unimportant in local fisheries. Positive effects take time, being stronger in older reserves, and are found both inside and immediately outside reserves. These effects are also associated with structurally complex habitat. Notably, however, there is almost no relationship between fish abundance trends, and invertebrate abundance trends—even when controlling by trophic group.

My finding that only some invertebrate taxa – a general group of fished species – responded positively to reserves is initially unexpected. However, considering the enormous diversity of

invertebrate life history strategies, exploitation histories, and trophic positions, this observation becomes far less surprising and aligns with variability in abundance trajectories of fish in MPAs (e.g. García-Rubies et al., 2013). Invertebrate taxa previously exploited in fisheries gain the most from removal of exploitation pressures, and this positive response is notable in my results—again similar to reserve response ratios for some fish taxa (Claudet et al., 2006). The group of unfished taxa, on the other hand show no response to reserves—perhaps they are subject to greater predation in reserves because of increases in larger-bodied, previously fished invertebrates and fish. This mix of abundance responses is consistent with other marine and terrestrial protected area studies which show winners, losers, or an absence of effect (Claudet et al., 2006; Fanshawe et al., 2003; Lester et al., 2009). For example, marine protected areas in California, created in part to support fisheries sustainability, resulted in decreases in abalone numbers as their predators increased in abundance (Fanshawe et al., 2003). This theme is not confined to the marine realm; conservation interventions in terrestrial and freshwater areas can have unexpected cascading effects. The creation of a terrestrial protected area in Utah, for example, was linked with declines in predatory taxa, an increase in grazing which led to alteration of erosion patterns and ultimately, declines in both terrestrial and aquatic species (Ripple and Beschta, 2006).

My analysis of habitat effects on invertebrate abundance illustrates the importance of complex coral structuring on reefs. I found that level of rugosity and abundance of branching corals consistently predict invertebrate abundance. These are areas where invertebrates live, feed, reproduce, and use for protection from predation (Castro, 1988; Idjadi and Edmunds, 2006; Luckhurst and Luckhurst, 1978; McClanahan, 1994; Sale, 1991; Vytöpil and Willis, 2001). This

finding indicates that reserve planning should include areas with complex habitat or areas that have potential for recovery of complex habitat. It also adds to the call for limits on use of destructive gears (e.g. Cinner, 2009; Mangi and Roberts, 2006; McManus et al., 1997). While use of active gears may provide good fishing yields in the short-term, this work supports the idea that harm to habitats can take a long time to recover, likely limiting an area's ability to support high abundances of invertebrates for many years.

The near absence of relationship between fish abundance and invertebrate abundance is an important finding. The vast majority of marine reserve studies compare abundance of fish in exploited and unexploited areas (see meta-analyses: Côté et al., 2001; Halpern, 2003; Lester et al., 2009). My results indicate that it is important that the scope of current monitoring be broadened in taxonomic scope to include and track changes in invertebrates—taxa that constitute the majority of marine life on coral reefs (Gibson et al., 2011).

6.2.3 How do protected invertebrate communities differ from those in adjacent fished areas?

Chapter 3 offers a notably different approach from typical reserve in-out studies, which tend to focus solely on abundances. Instead, I investigated community composition and functional abundance in reserve versus non-reserve areas. I found that invertebrate communities in reserves differed from those in surrounding, fished areas at the taxonomic, trait, and functional levels. Each species fills different trophic and functional roles in an ecosystem and fishing activities can change the relative presence and quantity of those roles. Fishing of bivalves, for example, can reduce water filtration capacity. The implication of my work is that elimination of fishing should,

theoretically, improve water quality. Through my comparison of community structure between reserve and non-reserve areas I found a set of top contributors to community differences. While interesting, this list of taxa (small shrimps, a few bivalves and snails) becomes much more informative when combined with measures of their trait abundances: I found community and trait differences between reserve and non-communities are driven by increases in species with filter feeding capacity, sessile taxa, and taxa with shells.

Surprising among my results is the lack of effect in traits typically associated with vulnerability: relatively larger body size and a higher ratio of edible meat to body size (Dulvy et al., 2008; Kindsvater et al., 2016). I can hypothesize that perhaps these traits are either not well captured in my trait categories or that time scales are insufficient in this study to capture the effect. For example, a significant lag (up to 45 years) in the recovery of larger, longer lived species was observed in reserves in the Western Indian Ocean (McClanahan and Graham, 2015). Furthermore, “larger” body size is highly relative. In this study, maximum body size for my focal taxa is approximately 20 centimetres—ten times larger than the smallest of my study taxa but still much smaller than other fish taxa on the same reefs, and may not fit into the category of “large body size”. Also notable is my finding that even when habitat composition does not differ between reserve and non-reserve area, community and trait composition still differs. This suggests that removal of fishing pressures, alone, can be an important driver of taxonomic and functional composition.

My results are notable in the context of a push for ecosystem and resilience-based management (Duarte et al., 2020; Obura, 2005; Worm, 2017). My finding that functional abundances differ in

reserves is important given that diverse functional traits help confer the resilience that ecosystems rely on for buffering fishing and climate change pressures (Hughes et al., 2005; Levin and Lubchenco, 2008; Pikitch et al., 2004). For example, loss of filtration capacity from bivalves can impair light transmission to photosynthetic organisms, imperiling their ability to synthesize food (La Peyre et al., 2014). In many cases it may be difficult to manage for the maintenance of functional traits because it may be unclear which taxa are contributing to particular functions. Evaluating biological communities using both taxonomy and biological traits (e.g. grazing, habitat forming), as I do in Chapter 4, may help overcome this challenge by identifying the taxa linked with these traits and ecosystem functions. This may eventually allow managers and practitioners to direct management or restoration towards taxa that support resilient biological systems or traits that may be absent or at low abundances in the system.

6.2.4 How can we generate minimum size recommendations for invertebrate taxa with limited data?

In Chapter 5, I examined whether basic life-history principles could be adapted for use in data-limited invertebrate fisheries. Using inference from closely related taxa and limited catch information, I generated size limit recommendations that can help protect spawning-sized invertebrates. This chapter helps create conservation measures that are complementary to marine reserves.

The foundation of fisheries management—and largely, of conservation—is ensuring enough spawning output to support future generations. In data-rich stocks, where age structure is known (or estimated), fisheries models provide assessment and management recommendations to

conserve spawning potential (Hilborn et al., 2020; Worm and Branch, 2012). On Danajon Bank, most, if not all small-scale fisheries do not fit into this category—they are data-limited and the capacity of their target taxa to produce future generations is unknown. Invertebrate fisheries are further complicated by social dimensions in that extraction is principally conducted by women, children and the elderly—groups that typically fish in intertidal areas, primarily by gleaning (Kleiber et al., 2014).

In this chapter, I synthesized a set of steps for estimating spawning size and optimal size at capture in fished invertebrate taxa. I then examined gleaning fisheries data from the Danajon Bank to assess the depletion of spawners in these fisheries. My finding that most taxa are being fished before they reach maturity suggests a need for minimum size limits, among other management measures. My models suggest that such size limits could produce significant gains in abundance and fisheries yield for target species. Despite potential positive impacts of size limits, implementation may be compromised, both by invertebrate movement ecology and by social dynamics of people associated with this fishery. Because many mobile invertebrate species migrate to greater depths as they grow and age, setting a lower size limit for mobile taxa could severely limit the fishing opportunities for gleaners who do not have access to boats and deeper waters associated with larger animals. In this chapter I suggest that further work is required to understand the trade-offs associated with increasing the abundance of spawners while also respecting food security needs of marginalized fishers. For example, there may be options to close small sections of gleaning areas in conjunction with setting size limits in sub-tidal zones fished by skin-divers. On Danajon Bank, marine reserves are an established component of barangay and municipal-level conservation. Evaluating the plausibility of these trade-offs

between closed areas and size limits will require consultation with village groups and likely, significant local leadership.

6.3 Limitations

In exploring my research findings, I seek to avoid over-interpretation even while feeling pleased with what I was able to achieve. We are always limited in our data collection, especially when it involves night-time surveys of little known marine taxa in isolated areas of a foreign country, covering marine reserves that are already in place. I am aware of the limitations of my work and conscious that they constrain my results to some extent.

In a perfect world, one would seek to improve data gathering in the following ways:

- Larger sample sizes for day-night sampling comparison. The goal of my field work on the Danajon Bank was to rapidly census the inside and outside of ten marine reserves and a set of reference sites. When daytime sampling failed to yield satisfactory data, I quickly moved on to more effective night sampling. Given my time allowances in the field I was unable to add additional data points to the day-night comparison. Despite this low sample size in Chapter 2, the magnitude of the effect is notable.
- A before-after-control-impact (BACI) design. BACI design, while powerful, requires monitoring at reserve and reference areas before reserves are in place (Eberhardt, 1976). Given the known lags in time for populations to respond after reserve establishment (Lester et al., 2009; McClanahan and Graham, 2015) this design would have required several years of monitoring, and would not be realistic in the timelines of this research. Instead, a space-for-time approach allowed me to examine temporal trends.

- Finer scale taxonomic identification. Invertebrate species diversity is exceptionally high in the Central Philippines and many species remain undescribed. For example, a number of studies have documented invertebrate species new to science from the Central Philippines since I collected these data (e.g. Gosliner, 2015; Matsuda and Gosliner, 2018; Pola et al., 2019; Shipman and Gosliner, 2015). Given my tiny field team (one local assistant and me) and the length of my field season (four months), identifying each animal to the species level (or even the genus level in many cases) during surveys would have limited the scope of our census of invertebrate species across the ten reserves and three reference sites I studied.
- Increased sampling intensity at each site for increased power to detect in-out-reference differences.
- A longer time-series for invertebrate catch data, collected at very regular intervals for better life history estimation. Additional data could have shed more light on timing of spawning behavior, thus facilitating analysis on potential for seasonal closures of invertebrate fisheries.
- A stronger analysis of local socioeconomics. This thesis began strictly as an examination of biological differences between protected and non-protected areas. As the thesis developed it became clear to me that local socioeconomics play a central role in the pressures exerted on marine invertebrate taxa. Further work is required to understand the relationship between these taxa, and the often marginalized people who fish, consume and sell them.
- A stronger understanding of local contexts. As a foreigner, I arrived in Danajon Bank with my own set of judgements and biases. This region has its own rich set of societal

and cultural norms that I cannot begin to fully understand—particularly given my limited time in the region. These norms and values shape local relationships with natural resources and dictate the acceptability of various types of natural resource management. What management recommendations may sound acceptable to me as a foreigner and outsider may not be acceptable in the villages in which I worked. Management recommendations must fit within local contexts and norms which, as an outsider, I lack a strong understanding of.

- Lastly, conservation research is not complete without engagement with the communities where the research was conducted. I am deeply indebted to the communities that that allowed me to conduct this work and who provided me with critical data and insight. Prior to the current coronavirus pandemic, I planned to return to Danajon Bank in the summer of 2020 to report my findings back to the communities in which I worked. This reporting will happen when I can safely travel again to the Philippines. Reporting, however, is only the first step in a much longer process needed to generate conservation change. Longer term work will require consultation with barangay captains (mayors) and councils, community organizations, and municipal fisheries officers. These processes can take many years and I plan to be involved in these steps through continued engagement.

6.4 Recommendations

After decades-long global efforts from ecologists, civil society, governmental and intergovernmental organizations, wide-scale acceptance and implementation of MPAs crystalized in the 2000s and 2010s. The Convention on Biological Diversity Aichi Target 11 and UN Sustainable Development Goal 14 set important goals for MPA establishment. Global MPA

coverage now sits at 7.8% of ocean area—an eight-fold increase since 2000 (<http://mpaatlas.org>)—and MPA coverage continues to grow by 8% per year (Worm, 2017). The push to designating these protected areas has resulted in significant conservation gains in coverage and abundance, but left important taxa out of the equation. It is now time for ecologists and conservation practitioners to ensuring that MPA creation shows greater inclusiveness with regard to the taxa being protected and the fisheries that are dependent on those taxa. Marine invertebrates must be taken into account, as must the often marginalized fishers that rely upon them. Monitoring finfish and an overwhelmingly focus of resources on management for large-scale finfish fisheries is no longer good enough.

From this research, I have developed five recommendations for marine conservation researchers, practitioners, and fisheries managers.

1. Monitor for mobile invertebrate taxa at night when detection rates are higher.

Practitioners must tailor their survey methods to the ecology of the taxa of interest. This work indicates that adoption of daytime survey techniques may introduce unnecessary bias for estimating invertebrate diversity. This will help with detection and monitoring for status of invertebrate taxa that constitute an important segment of marine biodiversity and small-scale fisheries.

2. Treat invertebrate taxa as central to—and equals in—conservation and management assessment, planning, and action. MPA development focuses overwhelmingly on the response of fish to protection. With a few exceptions for species of high economic importance, most

scientists and managers overlook the invertebrates that form the foundations of many food webs and fisheries. As an overwhelming component of marine biodiversity and a critical source of food security, MPA planners must design MPAs that support invertebrates. Protected area monitoring should measure trends in invertebrates diversity and abundance and tailor MPA management to suit the life history of those taxa. Fisheries managers must pay close attention to the conservation challenges facing invertebrate taxa—whether it be loss of important habitat or overexploitation of particular taxa—and respond to these challenges.

3. Use marine reserves to protect invertebrate taxa, recognizing that not all will respond positively. Reserves work for many invertebrate taxa—particularly those important in fisheries. Marine reserves should be considered a key component in increasing invertebrate abundance for many taxa, both within their boundaries and in the areas nearby. Furthermore, reserves can help change the functional traits that invertebrate communities contribute to the broader system. Marine reserves and reserve networks should be seen as an important tool for conserving invertebrates and their critical life-history stages.

4. Ban destructive fishing gears and methods. An important finding in this thesis is the link between structurally complex habitats and higher invertebrate abundance. These complex habitats are critical for many components of invertebrate life-history. Many macro-invertebrates, both mobile and habitat forming, are limited in their ability to evade active gears. Bans on destructive fishing will help maintain the viability of habitats to support abundant invertebrate life. Fisheries, wherever possible, should endeavor to use gears that are more selective and do not contact bottom habitat.

5. Consider use of minimum size limits in invertebrate fisheries to protect spawning stock.

MPAs, while effective, should not be used in isolation to address all marine conservation challenges. My work showed that invertebrate growth overfishing is impacting both yield and reproductive output in local stocks. Minimum size limits, even if generated via life history estimates, should be considered as a complimentary action to fishing closures, provided they account for local fishing practices and species biology.

6.5 Future Work

Future invertebrate conservation work must address issues ranging from basic species biology through to international ocean policy. A multi-tiered conservation approach places a species' biology and the protection of the ecosystem on which it depends as central to preventing extinction (Vincent, 2008). Moving progressively outward through the layers of a conservation onion requires addressing the needs and securities of local people who depend on those taxa and ecosystems. Regional and national laws and governance structures make up the next layers, followed finally by global conservation policy agreements. In this thesis, I focus on species biology, habitats and the local ocean management structures—the inner layers of the conservation onion. In sections 6.3 and 6.4 of this chapter, I suggest additional data collection, analyses, and actions that could further support inner and middle layers of the invertebrate conservation onion. Address outer layers, requires national and global-scale exploration of policy dimensions. For example, a global synthesis of invertebrate-MPA responses is needed. This global perspective will be important for informing higher level MPA policy. For example, this type of analysis could address whether universal (or near-universal) patterns for MPA design could be applied to enhance response in invertebrate taxa.

At the global policy scale, work is needed to advance invertebrate conservation issues. Among the multilateral environmental agreements (MEAs), few mentions are made of invertebrate conservation issues. The Aichi Targets, a core set of goals associated with the Convention on Biological Diversity are undergoing a major update in 2020. The update, “A Post-2020 Global Biodiversity Framework” details a set of 2030 and 2050 biodiversity goals. Unfortunately, at the time of writing, zero draft text of the CBD Post-2020 goals does not include specific or measurable targets for addressing conservation of marine species, let alone marine invertebrate taxa. As other MEAs (Ramsar, CMS, CITES, etc.) undergo review and update, sufficient leadership could lead to opportunities for these bodies to develop policy language that specifically addresses invertebrate conservation. These policies could set standards for invertebrate planning in MPA design, or could devote text to controls on fishing practices that impact invertebrate taxa, for example active gears. There may also be opportunities to conserve invertebrate taxa through emerging treaties. For example, a proposed UN Treaty for marine life in the high seas could address invertebrate conservation issues in areas beyond coastal waters (Barbier et al., 2014).

All of this work is set in a global environmental of climate change and ocean acidification. Tropical invertebrates are vulnerable to both—warming seas may push many taxa beyond their thermal limits and declining pH will impact their ability to build shells or form reefs (Przeslawski et al., 2008). Significant effort has been invested in understanding how individual invertebrate taxa may fare in the coming decades (Chappon and Seuront, 2011; Harley and Rogers-Bennett, 2004; Lawrence and Soame, 2004; Prather et al., 2013). However, further work is needed to understand how or if protected areas and fisheries management can be used to buffer

the effects of a rapidly changing ocean on coral reef invertebrates (Côté and Darling, 2010; McClanahan et al., 2012).

6.6 Conclusion

This thesis contributes to a narrative of solutions and optimism for rebuilding marine populations and communities—even in the face of the many challenges confronting marine life. Marine conservation science is dominated by stories of pessimism and collapse in the face of significant global pressures and challenges (Myers and Worm, 2003; Pinsky et al., 2011; Worm et al., 2006). While documenting decline in marine animals serves as an important alarm bell for the risks of maintaining conservation status quo, there must be a shift in focus towards identifying and advancing solutions. This thesis shows that marine reserves can work for exploited coral reef invertebrates and their communities on Danajon Bank, especially in concert with minimum size limits, and could result in significant gains for coral reef invertebrate taxa. There is a growing body of work that suggests that “stacking of complementary actions” (e.g. MPAs, better fisheries assessment and management, restoration of critical habitats) can serve to repair the key processes (e.g. herbivory and larval recruitment) needed for rebuilding plant and animal populations (Duarte et al., 2020; Hughes et al., 2017; Sale et al., 2005; Shears and Babcock, 2003). It is my hope that this thesis adds to conservation biology’s collective list of solutions and helps spur actions needed to achieve meaningful conservation gains for invertebrates in the coming decades.

References

- Abesamis, R.A., Russ, G.R., 2005. Density-dependent spillover from a marine reserve: long-term evidence. *Ecol. Appl.* 15, 1798–1812.
- Adams, P.B., 1980. Life history patterns in marine fishes and their consequences for fisheries management. *Fish. Bull.* 78, 1–12.
- Agardy, T.M., 1994. Advances in marine conservation: the role of marine protected areas. *Trends Ecol. Evol.* 9, 267–270. [https://doi.org/doi:10.1016/0169-5347\(94\)90297-6](https://doi.org/doi:10.1016/0169-5347(94)90297-6)
- Agardy, T.M., Bridgewater, P., Crosby, M.P., Day, J., Dayton, P.K., Kenchington, R., Laffoley, D., McConney, P., Murray, P.A., Parks, J.E., Peau, L., 2003. Dangerous targets? Unresolved issues and ideological clashes around marine protected areas. *Aquat. Conserv. Freshw. Ecosyst.* 13, 353–367. <https://doi.org/10.1002/aqc.583>
- Allen, K.R., 1953. A Method for computing the Optimum Size-Limit for a Fishery. *Nature* 172, 210. <https://doi.org/10.1038/172210a0>
- Allison, G.W., Lubchenco, J., Carr, M.H., 1998. Marine reserves are necessary but not sufficient for marine conservation. *Ecol. Appl.* 8, S79–S92.
- Alvarez-Filip, L., Dulvy, N.K., Gill, J.A., Côté, I.M., Watkinson, A.R., 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proc. R. Soc. B Biol. Sci.* rspb20090339.
- Anderson, S.C., Flemming, J.M., Watson, R., Lotze, H.K., 2011. Rapid global expansion of invertebrate fisheries: trends, drivers, and ecosystem effects. *PLoS One* 6, e14735. <https://doi.org/10.1371/journal.pone.0014735>
- Andrew, N.L., Béné, C., Hall, S.J., Allison, E.H., Heck, S., Ratner, B.D., 2007. Diagnosis and management of small-scale fisheries in developing countries. *Fish Fish.* 8, 227–240.

- Anticamara, J.A., Zeller, D., Vincent, A.C.J., 2010. Spatial and temporal variation of abundance, biomass and diversity within marine reserves in the Philippines. *Divers. Distrib.* 16, 529–536.
- Ashworth, J.S., Ormond, R.F.G., Sturrock, H.T., 2004. Effects of reef-top gathering and fishing on invertebrate abundance across take and no-take zones. *J. Exp. Mar. Bio. Ecol.* 303, 221–242.
- Babcock, R.C., Kelly, S., Shears, N.T., Walker, J.W., Willis, T.J., 1999. Changes in community structure in temperate marine reserves. *Mar. Ecol. Prog. Ser.* 189, 125–134.
- Babcock, R.C., Shears, N.T., Alcala, A.C., Barrett, N.S., Edgar, G.J., Lafferty, K.D., McClanahan, T.R., Russ, G.R., 2010. Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *Proc. Natl. Acad. Sci.* 107, 18256–18261.
<https://doi.org/10.1073/pnas.0908012107>
- Barbier, E.B., Moreno-Mateos, D., Rogers, A.D., Aronson, J., Pendleton, L., Danovaro, R., Henry, L.-A., Morato, T., Ardron, J., Van Dover, C.L., 2014. Ecology: Protect the deep sea. *Nature* 505, 475–477.
- Bartoń, K., 2015. MuMIn: Multi-model inference. R package version 1.15.6. *Compr. R Arch. Netw.* (CRAN), Vienna, Austria.
- Bates, D., Maechler, M., Bolker, B.M., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* <https://doi.org/10.18637/jss.v067.i01>
- Batoy, C.B., Pilapil, B.C., Sarmago, J.F., 1988. Size composition, distribution, length-weight relationship and natural food of the blue crab, *Portunus pelagicus* (L.) in selected coastal waters in Leyte and vicinity, Philippines. *Ann. Trop. Res.*
- Baum, J.K., Worm, B., 2009. Cascading top-down effects of changing oceanic predator

- abundances. *J. Anim. Ecol.* 78, 699–714. <https://doi.org/10.1111/j.1365-2656.2009.01531.x>
- Bell, J.D., Kronen, M., Vunisea, A., Nash, W.J., Keeble, G., Demmke, A., Pontifex, S., Andréfouët, S., 2009. Planning the use of fish for food security in the Pacific. *Mar. Policy* 33, 64–76.
- Benbow, S., Humber, F., Oliver, T.A., Oleson, K.L.L., Raberinary, D., Nadon, M., Ratsimbazafy, H., Harris, A., 2014. Lessons learnt from experimental temporary octopus fishing closures in south-west Madagascar: benefits of concurrent closures. *African J. Mar. Sci.* 36, 31–37.
- Béné, C., 2006. Small-scale fisheries: assessing their contribution to rural livelihoods in developing countries. *FAO Fish. Circ.* 1008, 46.
- Bengtsson, J., 1998. Which species? What kind of diversity? Which ecosystem function? Some problems in studies of relations between biodiversity and ecosystem function. *Appl. Soil Ecol.* 10, 191–199.
- Benzoni, F., Ashworth, J.S., Addamo, A.M., Stefani, F., Mabrouk, A., Galli, P., 2006. Artisanal fisheries and no-take zones in Nabq, Egypt: Effects on molluscs and reef top benthic assemblages, in: *Proceedings of the 10th International Coral Reefs Symposium, Okinawa, Japan*. pp. 1362–1367.
- Berkes, F., 2001. Managing small-scale fisheries: alternative directions and methods. IDRC.
- Berkes, F., Folke, C., Colding, J., 2000. Linking social and ecological systems: management practices and social mechanisms for building resilience. Cambridge University Press.
- Berkes, F., Hughes, T.P., Steneck, R.S., Wilson, J.A., Bellwood, D.R., Crona, B., Folke, C., Gunderson, L.H., Leslie, H.M., Norberg, J., Nystrom, M., Olsson, P., Osterblom, H., Scheffer, M., Worm, B., 2006. Globalization, roving bandits, and marine resources. *Science*

- (80-). 311, 1557–1558. <https://doi.org/10.1126/science.1122804>
- Bertrand, Y., Pleijel, F., Rouse, G.W., 2006. Taxonomic surrogacy in biodiversity assessments, and the meaning of Linnaean ranks. *Syst. Biodivers.* 4, 149–159.
- Beverton, R.J.H., Holt, S.J., 1957. *On the Dynamics of Exploited Fish Populations*. Springer.
- Boersma, P.D.D., Parrish, J.K., 1999. Limiting abuse: marine protected areas, a limited solution. *Ecol. Econ.* 31, 287–304. [https://doi.org/10.1016/S0921-8009\(99\)00085-3](https://doi.org/10.1016/S0921-8009(99)00085-3)
- Bohnsack, J.A., 1998. Application of marine reserves to reef fisheries management. *Aust. J. Ecol.* 23, 298–304.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.-S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* <https://doi.org/10.1016/j.tree.2008.10.008>
- Boonzaier, L., Pauly, D., 2016. Marine protection targets: an updated assessment of global progress. *Oryx* 50, 27–35.
- Bremner, J., Frid, C.L.J., Rogers, S.I., 2003a. Assessing marine ecosystem health: the long-term effects of fishing on functional biodiversity in North Sea benthos. *Aquat. Ecosyst. Health Manag.* 6, 131–137.
- Bremner, J., Rogers, S.I., Frid, C.L.J., 2006a. Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). *Ecol. Indic.* 6, 609–622. <https://doi.org/http://dx.doi.org/10.1016/j.ecolind.2005.08.026>
- Bremner, J., Rogers, S.I., Frid, C.L.J., 2006b. Matching biological traits to environmental conditions in marine benthic ecosystems. *J. Mar. Syst.* 60, 302–316.
- Bremner, J., Rogers, S.I., Frid, C.L.J., 2003b. Assessing functional diversity in marine benthic ecosystems: a comparison of approaches. *Mar. Ecol. Prog. Ser.* 254, 11–25.

- Brotz, L., Cheung, W.W.L., Kleisner, K., Pakhomov, E., Pauly, D., 2012. Increasing jellyfish populations: trends in Large Marine Ecosystems. *Hydrobiologia* 690, 3–20.
- Buxton, C.D., Hartmann, K., Kearney, R., Gardner, C., 2014. When Is Spillover from Marine Reserves Likely to Benefit Fisheries? *PLoS One* 9, e107032.
<https://doi.org/10.1371/journal.pone.0107032>
- Campbell, A., 2000. Northern abalone: Using an invertebrate to focus marine conservation ideas and values. Canadian Stock Assessment Secretariat.
- Canion, C.R., Heck Jr, K.L., 2009. Effect of habitat complexity on predation success: re-evaluating the current paradigm in seagrass beds. *Mar. Ecol. Prog. Ser.* 393, 37–46.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., 2012. Biodiversity loss and its impact on humanity. *Nature* 486, 59–67.
- Cardoso, P., Borges, P.A.V., Triantis, K.A., Ferrández, M.A., Martín, J.L., 2011a. Adapting the IUCN Red List criteria for invertebrates. *Biol. Conserv.* 144, 2432–2440.
<https://doi.org/10.1016/j.biocon.2011.06.020>
- Cardoso, P., Borges, P.A. V, Triantis, K.A., Ferrández, M.A., Martín, J.L., 2012. The underrepresentation and misrepresentation of invertebrates in the IUCN Red List. *Biol. Conserv.* 149, 147–148.
- Cardoso, P., Erwin, T.L., Borges, P.A. V, New, T.R., 2011b. The seven impediments in invertebrate conservation and how to overcome them. *Biol. Conserv.* 144, 2647–2655.
- Cariglia, N., Wilson, S.K., Graham, N.A.J., Fisher, R., Robinson, J., Aumeeruddy, R., Quatre, R., Polunin, N.V.C., 2013. Sea cucumbers in the Seychelles: effects of marine protected areas on high-value species. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 23, 418–428.

<https://doi.org/10.1002/aqc.2316>

- Carpenter, K.E., Springer, V.G., 2005. The center of the center of marine shore fish biodiversity: the Philippine Islands. *Environ. Biol. Fishes* 72, 467–480. <https://doi.org/10.1007/s10641-004-3154-4>
- Carruthers, T.R., Punt, A.E., Walters, C.J., MacCall, A., McAllister, M.K., Dick, E.J., Cope, J., 2014. Evaluating methods for setting catch limits in data-limited fisheries. *Fish. Res.* 153, 48–68.
- Castella, E., Speight, M.C.D., 1996. Knowledge representation using fuzzy coded variables: an example based on the use of Syrphidae (Insecta, Diptera) in the assessment of riverine wetlands. *Ecol. Modell.* 85, 13–25.
- Castilla, J.C., Duran, L.R., 1985. Human exclusion from the rocky intertidal zone of central Chile: the effects on *Concholepas concholepas* (Gastropoda). *Oikos* 391–399.
- Castro, P., 1988. Animal symbioses in coral reef communities: a review. *Symbiosis*.
- CBD, 2012. Quick Guide to Target 11 of the Aichi Biodiversity Targets [WWW Document]. URL <http://www.cbd.int/doc/strategic-plan/targets/T11-quick-guide-en.pdf> (accessed 9.25.15).
- Cesar, C.P., Frid, C.L.J., 2009. Effects of experimental small-scale cockle (*Cerastoderma edule* L.) fishing on ecosystem function. *Mar. Ecol.* 30, 123–137.
- Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., Ellison, A.M., 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecol. Monogr.* 84, 45–67.
- Chappon, C., Seuront, L., 2011. Behavioral thermoregulation in a tropical gastropod: links to climate change scenarios. *Glob. Chang. Biol.* 17, 1740–1749.

- Chevene, F., Doleadec, S., Chessel, D., 1994. A fuzzy coding approach for the analysis of long-term ecological data. *Freshw. Biol.* 31, 295–309. <https://doi.org/10.1111/j.1365-2427.1994.tb01742.x>
- Christie, P., Armada, N.B., White, A.T., Gulayan, A.M., Dios, H.H.Y. de, 2006. Coastal environmental and fisheries profile of Danajon Bank, Bohol, Philippines.
- Cinner, J.E., 2009. Poverty and the use of destructive fishing gear near east African marine protected areas. *Environ. Conserv.* 321–326.
- Clarke, K., Gorley, R., 2015. PRIMER v7: User Manual/Tutorial. PRIMER-E, Plymouth.
- Clarke, K., Gorley, R., 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth.
- Clarke, K.R., Green, R.H., 1988. Statistical design and analysis for a "biological effects" study. *Mar. Ecol. Prog. Ser.* 46, 213–226.
- Claudet, J., Pelletier, D., Jouvenel, J.-Y., Bachet, F., Galzin, R., 2006. Assessing the effects of marine protected area (MPA) on a reef fish assemblage in a northwestern Mediterranean marine reserve: Identifying community-based indicators. *Biol. Conserv.* 130, 349–369. [https://doi.org/https://doi.org/10.1016/j.biocon.2005.12.030](https://doi.org/10.1016/j.biocon.2005.12.030)
- Coleman, M.A., Bates, A.E., Stuart-Smith, R.D., Malcolm, H.A., Harasti, D., Jordan, A., Knott, N.A., Edgar, G.J., Kelaher, B.P., 2015. Functional traits reveal early responses in marine reserves following protection from fishing. *Divers. Distrib.* 21, 876–887.
- Collen, B., Bohn, M., Kemp, R., Baillie, J.E.M., 2012. Spineless: status and trends of the world's invertebrates, Zoological Society of London, United Kingdom. London, UK.
- Collen, B., Ram, M., Zamin, T., McRae, L., 2008. The Tropical Biodiversity Data Gap: Addressing Disparity in Global Monitoring. *Trop. Conserv. Sci.* 1, 75–88. <https://doi.org/10.1177/194008290800100202>

- Collie, J.S., Hall, S.J., Kaiser, M.J., Poiner, I.R., 2000. A quantitative analysis of fishing impacts on shelf-sea benthos. *J. Anim. Ecol.* 69, 785–798.
- Colloca, F., Cardinale, M., Maynou, F., Giannoulaki, M., Scarcella, G., Jenko, K., Bellido, J.M., Fiorentino, F., 2013. Rebuilding Mediterranean fisheries: a new paradigm for ecological sustainability. *Fish Fish.* 14, 89–109.
- Copes, P., 1986. A critical review of the individual quota as a device in fisheries management. *Land Econ.* 62, 278–291.
- Costello, C., Ovando, D., Hilborn, R., Gaines, S.D., Deschenes, O., Lester, S.E., 2012. Status and Solutions for the World's Unassessed Fisheries. *Science* (80-.). 338, 517 LP-520.
- Côté, I.M., Darling, E.S., 2010. Rethinking Ecosystem Resilience in the Face of Climate Change. *PLOS Biol.* 8, e1000438.
- Côté, I.M., Mosqueira, I., Reynolds, J.D., 2001. Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis. *J. Fish Biol.* 59, 178–189.
- Dalzell, P., Adams, T.J.H., Polunin, N.V.C., 1996. Coastal Fisheries of the South Pacific Islands. *Oceanogr. Mar. Biol. An Annu. Rev. UCL Press. London* 34, 395–531.
- Darling, E.S., Alvarez-Filip, L., Oliver, T.A., McClanahan, T.R., Côté, I.M., 2012. Evaluating life-history strategies of reef corals from species traits. *Ecol. Lett.* 15, 1378–1386.
<https://doi.org/https://doi.org/10.1111/j.1461-0248.2012.01861.x>
- Davis, G.E., Haaker, P.L., Richards, D. V, 1996. Status and Trends of White Abalone at the California Channel Islands. *Trans. Am. Fish. Soc.* 125, 42–48. [https://doi.org/10.1577/1548-8659\(1996\)125<0042:SATOWA>2.3.CO;2](https://doi.org/10.1577/1548-8659(1996)125<0042:SATOWA>2.3.CO;2)
- de Bakker, D.M., van Duyl, F.C., Bak, R.P.M., Nugues, M.M., Nieuwland, G., Meesters, E.H., 2017. 40 Years of benthic community change on the Caribbean reefs of Curaçao and

Bonaire: the rise of slimy cyanobacterial mats. *Coral Reefs* 1–13.

<https://doi.org/10.1007/s00338-016-1534-9>

- Di Franco, A., Thiriet, P., Di Carlo, G., Dimitriadis, C., Francour, P., Gutiérrez, N.L., Jeudy de Grissac, A., Koutsoubas, D., Milazzo, M., Otero, M. del M., Piante, C., Plass-Johnson, J., Sainz-Trapaga, S., Santarossa, L., Tudela, S., Guidetti, P., 2016. Five key attributes can increase marine protected areas performance for small-scale fisheries management. *Sci. Rep.* 6, 38135.
- Di Lorenzo, M., Guidetti, P., Di Franco, A., Calò, A., Claudet, J., 2020. Assessing spillover from marine protected areas and its drivers: A meta-analytical approach. *Fish Fish.* 21, 906–915.
- Diaz, S., Cabido, M., 2001. Vive la difference: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.* 16, 646–655.
- Donaldson, M., Burnett, N., Braun, D., Suski, C., Hinch, S., Cooke, S., Kerr, J., 2016. Taxonomic bias and international biodiversity conservation research. *FACETS* 1, 105–113.
- Donaldson, W.E., Donaldson, W.K., 1992. A review of the history and justification for size limits in Alaskan king, Tanner, and snow crab fisheries. Alaska Department of Fish and Game, Division of Commercial Fisheries.
- Duarte, C.M., Agusti, S., Barbier, E., Britten, G.L., Castilla, J.C., Gattuso, J.-P., Fulweiler, R.W., Hughes, T.P., Knowlton, N., Lovelock, C.E., Lotze, H.K., Predragovic, M., Poloczanska, E., Roberts, C., Worm, B., 2020. Rebuilding marine life. *Nature* 580, 39–51.
- <https://doi.org/10.1038/s41586-020-2146-7>
- Dulvy, N.K., Baum, J.K., Clarke, S., Compagno, L.J. V, Cortés, E., Domingo, A., Fordham, S., Fowler, S., Francis, M.P., Gibson, C., Martínez, J., Musick, J.A., Soldo, A., Stevens, J.D., Valenti, S., 2008. You can swim but you can't hide: the global status and conservation of

- oceanic pelagic sharks and rays. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 18, 459–482.
- <https://doi.org/10.1002/aqc.975>
- Dulvy, N.K., Sadovy, Y., Reynolds, J.D., 2003. Extinction vulnerability in marine populations. *Fish Fish.* 4, 25–64.
- Dumas, P., Ham, J., Kaku, R., William, A., Kaltavara, J., Gereva, S., Léopold, M., 2017. *Tectus* (Trochus) niloticus search for suitable habitats can cause equivocal benefits of protection in village-based marine reserves. *PLoS One* 12, e0176922.
- Dumas, P., Jimenez, H., Peignon, C., Wantiez, L., Adjeroud, M., 2013. Small-scale habitat structure modulates the effects of no-take marine reserves for coral reef macroinvertebrates. *PLoS One* 8, e58998.
- Eberhardt, L.L., 1976. Quantitative ecology and impact assessment. *J. Environ. Manage.*
- Eddy, T.D., Lotze, H.K., Fulton, E.A., Coll, M., Ainsworth, C.H., Araújo, J.N., Bulman, C.M., Bundy, A., Christensen, V., Field, J.C., 2017. Ecosystem effects of invertebrate fisheries. *Fish Fish.* 18, 40–53.
- Edgar, G.J., Barrett, N.S., 2012. An assessment of population responses of common inshore fishes and invertebrates following declaration of five Australian marine protected areas. *Environ. Conserv.* 39, 271.
- Edgar, G.J., Barrett, N.S., 1999. Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. *J. Exp. Mar. Bio. Ecol.* 242, 107–144.
- Edgar, G.J., Russ, G.R., Babcock, R.C., 2007. Marine protected areas. *Mar. Ecol.* 533–555.
- Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T.F., Berkhout, J., 2014. Global conservation outcomes depend on marine protected areas with five key features. *Nature* 506, 216–220.

- Fanshawe, S., Vanblaricom, G.R., Shelly, A.A., 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. *Conserv. Biol.* 17, 273–283.
- FAO, 2014. The State of World Fisheries and Aquaculture. Food Agric. Organ. United Nations Rome, 243.
- Francis, F.T., Filbee-Dexter, K., Yan, H.F., Côté, I.M., 2019. Invertebrate herbivores: Overlooked allies in the recovery of degraded coral reefs? *Glob. Ecol. Conserv.* 17, e00593. [https://doi.org/https://doi.org/10.1016/j.gecco.2019.e00593](https://doi.org/10.1016/j.gecco.2019.e00593)
- Freeman, D.J., MacDiarmid, A.B., Taylor, R.B., Davidson, R.J., Grace, R. V, Haggitt, T.I.M.R., Kelly, S., Shears, N.T., 2012. Trajectories of spiny lobster *Jasus edwardsii* recovery in New Zealand marine reserves: is settlement a driver? *Environ. Conserv.* 1, 1–10.
- Frid, C.L.J., Paramor, O.A.L., Brockington, S., Bremner, J., 2008. Incorporating ecological functioning into the designation and management of marine protected areas, in: *Challenges to Marine Ecosystems*. Springer, pp. 69–79.
- Fröcklin, S., de la Torre-Castro, M., Håkansson, E., Carlsson, A., Magnusson, M., Jiddawi, N.S., 2014. Towards improved management of tropical invertebrate fisheries: Including time series and gender. *PLoS One* 9, e91161.
- Froese, R., Binohlan, C., 2003. Simple methods to obtain preliminary growth estimates for fishes. *J. Appl. Ichthyol.* 19, 376–379. <https://doi.org/10.1111/j.1439-0426.2003.00490.x>
- Froese, R., Binohlan, C., 2000. Empirical relationships to estimate asymptotic length, length at first maturity and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. *J. Fish Biol.* 56, 758–773.
- Froese, R., Pauly, D., 2017. FishBase 2017, version (march, 2017). World Wide Web Electron.

Publ. Home page <http://www.fishbase.org>.

Froese, R., Pauly, D., Winker, H., Coro, G., Demirel, N., Tsikliras, A.C., Dimarchopoulou, D.,

Scarcella, G., Probst, W.N., Dureuil, M., 2018. A new approach for estimating stock status from length frequency data. *ICES J. Mar. Sci.* 75, 2004–2015.

<https://doi.org/10.1093/icesjms/fsy078>

Froese, R., Stern-Piriot, A., Winker, H., Gascuel, D., 2008. Size matters: How single-species management can contribute to ecosystem-based fisheries management. *Fish. Res.* 92, 231–241. <https://doi.org/10.1016/j.fishres.2008.01.005>

Froese, R., Winker, H., Coro, G., Demirel, N., Tsikliras, A.C., Dimarchopoulou, D., Scarcella, G., Probst, W.N., Dureuil, M., Pauly, D., 2019. On the pile-up effect and priors for Linf and M/K: response to a comment by Hordyk et al. on “A new approach for estimating stock status from length frequency data.” *ICES J. Mar. Sci.* 76, 461–465.

Froese, R., Winker, H., Gascuel, D., Sumaila, U.R., Pauly, D., 2016. Minimizing the impact of fishing. *Fish Fish.* 17, 785–802.

Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., Slade, E.M., Steffan-Dewenter, I., Emmerson, M., Potts, S.G., Tschardt, T., Weisser, W., Bommarco, R., 2015. Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proc. R. Soc. B Biol. Sci.* 282.

Gaines, S.D., White, C., Carr, M.H., Palumbi, S.R., 2010. Designing marine reserve networks for both conservation and fisheries management. *Proc. Natl. Acad. Sci.* 107, 18286–18293. <https://doi.org/10.1073/pnas.0906473107>

García-Rubies, A., Hereu, B., Zabala, M., 2013. Long-term recovery patterns and limited spillover of large predatory fish in a Mediterranean MPA. *PLoS One* 8.

- Gell, F.R., Roberts, C.M., 2003. Benefits beyond boundaries: the fishery effects of marine reserves. *Trends Ecol. Evol.* 18, 448–455.
- Gibson, R., Atkinson, R., Gordon, J., Smith, I., Hughes, D., 2011. Coral-associated invertebrates: diversity, ecological importance and vulnerability to disturbance. *Ocean. Mar. Biol.* 49, 43–104.
- Gill, D.A., Mascia, M.B., Ahmadi, G.N., Glew, L., Lester, S.E., Barnes, M., Craigie, I., Darling, E.S., Free, C.M., Geldmann, J., Holst, S., Jensen, O.P., White, A.T., Basurto, X., Coad, L., Gates, R.D., Guannel, G., Mumby, P.J., Thomas, H., Whitmee, S., Woodley, S., Fox, H.E., 2017. Capacity shortfalls hinder the performance of marine protected areas globally. *Nature* 543, 665–669.
- Giller, P.S., Hillebrand, H., Berninger, U., O Gessner, M., Hawkins, S., Inchausti, P., Inglis, C., Leslie, H., Malmqvist, B., T Monaghan, M., 2004. Biodiversity effects on ecosystem functioning: emerging issues and their experimental test in aquatic environments. *Oikos* 104, 423–436.
- Gillespie, K.M., Vincent, A.C.J., 2019. Tropical invertebrate response to marine reserves varies with protection duration, habitat type, and exploitation history. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 29, 511–520. <https://doi.org/10.1002/aqc.3019>
- Goñi, R., Adlerstein, S., Alvarez-Berastegui, D., Forcada, A., Reñones, O., Criquet, G., Polti, S., Cadiou, G., Valle, C., Lenfant, P., 2008. Spillover from six western Mediterranean marine protected areas: evidence from artisanal fisheries. *Mar. Ecol. Prog. Ser.* 366, 159–174.
- Goodyear, C.P., 1993. Spawning stock biomass per recruit in fisheries management: foundation and current use. *Can. Spec. Publ. Fish. Aquat. Sci.* 120, 67–81.
- Gosliner, T., 2015. Three new species of aglajid Cephalaspidean mollusks from the tropical

- Indo-pacific of the Verde Island passage. *Proc. Calif. Acad. Sci.* 6, 191–205.
- Graham, N.A.J., Nash, K.L., 2013. The importance of structural complexity in coral reef ecosystems. *Coral Reefs* 32, 315–326. <https://doi.org/10.1007/s00338-012-0984-y>
- Grorud-Colvert, K., Claudet, J., Tissot, B.N., Caselle, J.E., Carr, M.H., Day, J.C., Friedlander, A.M., Lester, S.E., de Loma, T.L., Malone, D., Walsh, W.J., 2014. Marine Protected Area Networks: Assessing Whether the Whole Is Greater than the Sum of Its Parts. *PLoS One* 9, e102298.
- Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. *J. Evol. Biol.* 24, 699–711.
- Hall, M.O., Bell, S.S., 1988. Response of small motile epifauna to complexity of epiphytic algae on seagrass blades. *J. Mar. Res.* 46, 613–630.
- Hall, S.J., Mainprize, B., 2004. Towards ecosystem-based fisheries management. *Fish Fish.* 5, 1–20.
- Halpern, B.S., 2003. The impact of marine reserves: do reserves work and does reserve size matter? *Ecol. Appl.* 13, 117–137.
- Halpern, B.S., Warner, R.R., 2003. Matching marine reserve design to reserve objectives. *Proc. R. Soc. B Biol. Sci.* 270, 1871.
- Halpern, B.S., Warner, R.R., 2002. Marine reserves have rapid and lasting effects. *Ecol. Lett.* 5, 361–366.
- Harborne, A.R., Mumby, P.J., Ferrari, R., 2012. The effectiveness of different meso-scale rugosity metrics for predicting intra-habitat variation in coral-reef fish assemblages. *Environ. Biol. fishes* 94, 431–442.
- Harley, C.D.G., Rogers-Bennett, L., 2004. The potential synergistic effects of climate change

- and fishing pressure on exploited invertebrates on rocky intertidal shores. *Calif. Coop. Ocean. Fish. Investig. Rep.* 45, 98.
- Harper, S., Adshade, M., Lam, V.W.Y., Pauly, D., Sumaila, U.R., 2020. Valuing invisible catches: Estimating the global contribution by women to small-scale marine capture fisheries production. *PLoS One* 15, e0228912.
- Harper, S., Zeller, D., Hauzer, M., Pauly, D., Sumaila, U.R., 2013. Women and fisheries: Contribution to food security and local economies. *Mar. Policy* 39, 56–63.
- Heck, K.L., Hays, G., Orth, R.J., 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. *Mar. Ecol. Prog. Ser.* 253, 123–136.
<https://doi.org/10.3354/meps253123>
- Heslinga, G.A., Orak, O., Ngiramengior, M., 1984. Coral reef sanctuaries for trochus shells. *Mar. Fish. Rev.* 46, 73–80.
- Hilborn, R., 2010. Pretty good yield and exploited fishes. *Mar. Policy* 34, 193–196.
- Hilborn, R., Amoroso, R.O., Anderson, C.M., Baum, J.K., Branch, T.A., Costello, C., de Moor, C.L., Faraj, A., Hively, D., Jensen, O.P., 2020. Effective fisheries management instrumental in improving fish stock status. *Proc. Natl. Acad. Sci.*
- Hilborn, R., Stokes, K., Maguire, J.J., Smith, T., Botsford, L.W., Mangel, M., Orensanz, J., Parma, A., Rice, J., Bell, J., 2004. When can marine reserves improve fisheries management? *Ocean Coast. Manag.* 47, 197–205.
- Hobday, A.J., Tegner, M.J., Haaker, P.L., 2000. Over-exploitation of a broadcast spawning marine invertebrate: decline of the white abalone. *Rev. Fish Biol. Fish.* 10, 493–514.
- Hodgson, G., Stepath, C.M., Seas, S.O., 1998. Using Reef Check for long-term coral reef monitoring in Hawaii, in: *Proceedings of the Hawaii Coral Reef Monitoring Workshop-A*

- Tool for Management. East–West Center Honolulu, HI.
- Holland, D.S., 2002. Integrating marine protected areas into models for fishery assessment and management. *Nat. Resour. Model.* 15, 369–386.
- Holt, S.J., 2014. The graceful sigmoid: Johan Hjort’s contribution to the theory of rational fishing. *ICES J. Mar. Sci.* 71, 2008–2011.
- Holt, S.J., 1958. The evaluation of fisheries resources by the dynamic analysis of stocks, and notes on the time factors involved. *ICNAF Spec. Publ.* 1, 77–95.
- Hordyk, A., Ono, K., Sainsbury, K., Loneragan, N., Prince, J., 2014a. Some explorations of the life history ratios to describe length composition, spawning-per-recruit, and the spawning potential ratio. *ICES J. Mar. Sci.* 72, 204–216.
- Hordyk, A., Ono, K., Valencia, S., Loneragan, N., Prince, J., 2014b. A novel length-based empirical estimation method of spawning potential ratio (SPR), and tests of its performance, for small-scale, data-poor fisheries. *ICES J. Mar. Sci.* 72, 217–231.
- Hordyk, A.R., Loneragan, N.R., Prince, J.D., 2015. An evaluation of an iterative harvest strategy for data-poor fisheries using the length-based spawning potential ratio assessment methodology. *Fish. Res.* 171, 20–32.
[https://doi.org/https://doi.org/10.1016/j.fishres.2014.12.018](https://doi.org/10.1016/j.fishres.2014.12.018)
- Hordyk, A.R., Ono, K., Prince, J.D., Walters, C.J., 2016. A simple length-structured model based on life history ratios and incorporating size-dependent selectivity: application to spawning potential ratios for data-poor stocks. *Can. J. Fish. Aquat. Sci.* 73, 1787–1799.
<https://doi.org/10.1139/cjfas-2015-0422>
- Hsieh, T.C., Ma, K.H., Chao, A., 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods Ecol. Evol.* 7, 1451–1456.

- Hughes, J.J., Ward, D., 1993. Predation risk and distance to cover affect foraging behaviour in Namib Desert gerbils. *Anim. Behav.* 46, 1243–1245.
- Hughes, T.P., Barnes, M.L., Bellwood, D.R., Cinner, J.E., Cumming, G.S., Jackson, J.B.C., Kleypas, J., Van De Leemput, I.A., Lough, J.M., Morrison, T.H., 2017. Coral reefs in the Anthropocene. *Nature* 546, 82–90.
- Hughes, T.P., Bellwood, D.R., Folke, C., Steneck, R.S., Wilson, J., 2005. New paradigms for supporting the resilience of marine ecosystems. *Trends Ecol. Evol.* 20, 380–386.
- Idjadi, J.A., Edmunds, P.J., 2006. Scleractinian corals as facilitators for other invertebrates on a Caribbean reef. *Mar. Ecol. Prog. Ser.* 319, 117–127.
- IUCN, 2017. The IUCN Red List of Threatened Species. Version 2017-1 [WWW Document]. IUCN Red List Threat. Species. Version 2017-1. URL <http://www.iucnredlist.org> (accessed 10.13.17).
- Jackson, J., Donovan, M., Cramer, K., Lam, V., 2014. Status and trends of Caribbean coral reefs: 1970-2012. Global Coral Reef Monitoring Network.
- Jacquet, J., Pauly, D., 2008. Funding priorities: big barriers to small-scale fisheries. *Conserv. Biol.* 22, 832–835.
- Jamieson, G.S., 1993. Marine invertebrate conservation: evaluation of fisheries over-exploitation concerns. *Am. Zool.* 33, 551–567.
- Jensen, A.L., 1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. *Can. J. Fish. Aquat. Sci.* 53, 820–822.
- Jimenez, H., Dumas, P., Bigot, L., Amouroux, J.M., Ferraris, J., 2010. Taxonomic resolution needed to describe invertebrate assemblages and to detect harvesting effects on coral reef ecosystems. *Mar. Ecol. Prog. Ser.* 406, 211–222.

- Jimenez, H., Dumas, P., Bigot, L., Ferraris, J., 2015. Harvesting effects on tropical invertebrate assemblages in New Caledonia. *Fish. Res.* 167, 75–81.
- Jimenez, H., Dumas, P., Mouillot, D., Bigot, L., Ferraris, J., 2015. Harvesting effects on functional structure and composition of tropical invertebrate assemblages. *ICES J. Mar. Sci. J. du Cons.* <https://doi.org/10.1093/icesjms/fsv179>
- Johannes, R.E., 2002. The renaissance of community-based marine resource management in Oceania. *Annu. Rev. Ecol. Syst.* 33, 317–340.
- Johannes, R.E., 1998. The case for data-less marine resource management: examples from tropical nearshore finfisheries. *Trends Ecol. Evol.* 13, 243–246.
- Kaiser, M.J., 2005. Are marine protected areas a red herring or fisheries panacea? *Can. J. Fish. Aquat. Sci.* 62, 1194–1199.
- Kellner, K.F., Swihart, R.K., 2014. Accounting for Imperfect Detection in Ecology: A Quantitative Review. *PLoS One* 9, e111436.
- Kéry, M., Schmidt, B., 2008. Imperfect detection and its consequences for monitoring for conservation. *Community Ecol.* 9, 207–216.
- Kindsvater, H.K., Mangel, M., Reynolds, J.D., Dulvy, N.K., 2016. Ten principles from evolutionary ecology essential for effective marine conservation. *Ecol. Evol.* 6, 2125–2138. <https://doi.org/10.1002/ece3.2012>
- Klain, S.C., Chan, K.M.A., 2012. Navigating coastal values: participatory mapping of ecosystem services for spatial planning. *Ecol. Econ.* 82, 104–113.
- Kleiber, D., Harris, L.M., Vincent, A.C.J., 2015. Gender and small-scale fisheries: a case for counting women and beyond. *Fish Fish.* <https://doi.org/10.1111/faf.12075>
- Kleiber, D., Harris, L.M., Vincent, A.C.J., Rochet, M.-J., 2014. Improving fisheries estimates by

- including women's catch in the Central Philippines. *Can. J. Fish. Aquat. Sci.* 71, 656–664.
<https://doi.org/10.1139/cjfas-2013-0177>
- Knowlton, N., Jackson, J.B.C., 2008. Shifting baselines, local impacts, and global change on coral reefs. *Plos Biol.* 6, e54.
- Kough, A.S., Belak, C.A., Paris, C.B., Lundy, A., Cronin, H., Gnanalingam, G., Hagedorn, S., Skubel, R., Weiler, A.C., Stoner, A.W., 2019. Ecological spillover from a marine protected area replenishes an over-exploited population across an island chain. *Conserv. Sci. Pract.* 1, e17.
- La Peyre, M.K., Humphries, A.T., Casas, S.M., La Peyre, J.F., 2014. Temporal variation in development of ecosystem services from oyster reef restoration. *Ecol. Eng.* 63, 34–44.
- Lasiak, T.A., Field, J.G., 1995. Community-level attributes of exploited and non-exploited rocky infratidal macrofaunal assemblages in Transkei. *J. Exp. Mar. Bio. Ecol.* 185, 33–53.
- Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.* 16, 545–556.
<https://doi.org/10.1046/j.1365-2435.2002.00664.x>
- Lawrence, A.J., Soame, J.M., 2004. The effects of climate change on the reproduction of coastal invertebrates. *Ibis (Lond. 1859)*. 146, 29–39.
- Le Port, A., Montgomery, J.C., Smith, A.N.H., Croucher, A.E., McLeod, I.M., Lavery, S.D., 2017. Temperate marine protected area provides recruitment subsidies to local fisheries. *Proc. R. Soc. B Biol. Sci.* 284, 20171300.
- Leenhardt, P., Cazalet, B., Salvat, B., Claudet, J., Feral, F., 2013. The rise of large-scale marine protected areas: Conservation or geopolitics? *Ocean Coast. Manag.* 85, 112–118.
- Lenihan, H.S., Gallagher, J.P., Peters, J.R., Stier, A.C., Hofmeister, J.K.K., Reed, D.C., 2021.

- Evidence that spillover from Marine Protected Areas benefits the spiny lobster (*Panulirus interruptus*) fishery in southern California. *Sci. Rep.* 11, 1–9.
- Lester, S.E., Halpern, B.S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B.I., Gaines, S.D., Aíramé, S., Warner, R.R., 2009. Biological effects within no-take marine reserves: a global synthesis. *Mar. Ecol. Prog. Ser.* 384, 33–46.
- Levin, S.A., Lubchenco, J., 2008. Resilience, robustness, and marine ecosystem-based management. *Bioscience* 58, 27–32.
- Lewis, J.B., 1958. The biology of the tropical sea urchin *Tripneustes esculentus* Leske in Barbados, British West Indies. *Can. J. Zool.* 36, 607–621.
- Lubchenco, J., Gaines, S.D., 1981. A unified approach to marine plant-herbivore interactions. I. Populations and communities. *Annu. Rev. Ecol. Syst.* 12, 405–437.
- Luckhurst, B.E., Luckhurst, K., 1978. Analysis of the influence of substrate variables on coral reef fish communities. *Mar. Biol.* 49, 317–323. <https://doi.org/10.1007/BF00455026>
- Lundquist, C.J., Granek, E.F., 2005. Strategies for successful marine conservation: integrating socioeconomic, political, and scientific factors. *Conserv. Biol.* 19, 1771–1778.
- MacKenzie, D.I., 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, San Diego, California, USA.
- Mangi, S.C., Roberts, C.M., 2006. Quantifying the environmental impacts of artisanal fishing gear on Kenya's coral reef ecosystems. *Mar. Pollut. Bull.* 52, 1646–1660.
- Manríquez, P.H., Castilla, J.C., 2001. Significance of marine protected areas in central Chile as seeding grounds for the gastropod *Concholepas concholepas*. *Mar. Ecol. Prog. Ser.* 215, 201–211.
- Martell, S., Froese, R., 2013. A simple method for estimating MSY from catch and resilience.

- Fish Fish. 14, 504–514.
- Matsuda, S.B., Gosliner, T.M., 2018. Glossing over cryptic species: Descriptions of four new species of *Glossodoris* and three new species of *Doriprismatica* (Nudibranchia: Chromodorididae). *Zootaxa* 4444, 501–529.
- McClanahan, T.R., 2014. Recovery of functional groups and trophic relationships in tropical fisheries closures. *Mar. Ecol. Prog. Ser.* 497, 13–23. <https://doi.org/10.3354/meps10605>
- McClanahan, T.R., 1994. Kenyan coral reef lagoon fish: effects of fishing, substrate complexity, and sea urchins. *Coral Reefs* 13, 231–241. <https://doi.org/10.1007/BF00303637>
- McClanahan, T.R., Donner, S.D., Maynard, J.A., MacNeil, M.A., Graham, N.A.J., Maina, J., Baker, A.C., Alemu I., J.B., Beger, M., Campbell, S.J., Darling, E.S., Eakin, C.M., Heron, S.F., Jupiter, S.D., Lundquist, C.J., McLeod, E., Mumby, P.J., Paddock, M.J., Selig, E.R., van Woesik, R., 2012. Prioritizing Key Resilience Indicators to Support Coral Reef Management in a Changing Climate. *PLoS One* 7, e42884.
- McClanahan, T.R., Graham, N.A.J., 2015. Marine reserve recovery rates towards a baseline are slower for reef fish community life histories than biomass. *Proc. R. Soc. London B Biol. Sci.* 282.
- McClanahan, T.R., Mangi, S., 2000. Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. *Ecol. Appl.* 10, 1792–1805.
- McClanahan, T.R., Shafir, S.H., 1990. Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. *Oecologia* 83, 362–370.
- McCook, L., Jompa, J., Diaz-Pulido, G., 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral reefs* 19, 400–417.
- McFarland, W.N., 1986. Light in the Sea—Correlations with Behaviors of Fishes and

- Invertebrates. *Integr. Comp. Biol.* 26, 389–401. <https://doi.org/10.1093/icb/26.2.389>
- McMahan, M.D., Brady, D.C., Cowan, D.F., Grabowski, J.H., Sherwood, G.D., Jech, J.M., 2013. Using acoustic telemetry to observe the effects of a groundfish predator (Atlantic cod, *Gadus morhua*) on movement of the American lobster (*Homarus americanus*) 1. *Can. J. Fish. Aquat. Sci.* 70, 1625–1634.
- McManus, J.W., Reyes Jr, R.B., Nanola Jr, C.L., 1997. Effects of some destructive fishing methods on coral cover and potential rates of recovery. *Environ. Manage.* 21, 69–78.
- Micheli, F., Benedetti-Cecchi, L., Gambaccini, S., Bertocci, I., Borsini, C., Osio, G.C., Romano, F., 2005. Cascading human impacts, marine protected areas, and the structure of Mediterranean reef assemblages. *Ecol. Monogr.* 75, 81–102.
- Mills, D.J., Westlund, L., de Graaf, G., Kura, Y., Willman, R., Kelleher, K., 2011. Under-reported and undervalued: small-scale fisheries in the developing world. *Small-scale Fish. Manag. Fram. approaches Dev. world.* CAB Int. Oxfordsh. 1–15.
- Miloslavich, P., Bax, N.J., Simmons, S.E., Klein, E., Appeltans, W., Aburto-Oropeza, O., Andersen Garcia, M., Batten, S.D., Benedetti-Cecchi, L., Checkley Jr, D.M., 2018. Essential ocean variables for global sustained observations of biodiversity and ecosystem changes. *Glob. Chang. Biol.* 24, 2416–2433.
- Moberg, F., Folke, C., 1999. Ecological goods and services of coral reef ecosystems. *Ecol. Econ.* 29, 215–233.
- Mobrand, L.E., Barr, J., Blankenship, L., Campton, D.E., Evelyn, T.T.P., Flagg, T.A., Mahnken, C.V.W., Seeb, L.W., Seidel, P.R., Smoker, W.W., 2005. Hatchery reform in Washington state: Principles and emerging issues. *Fisheries* 30, 11–23.
- Moreno, C.A., Lunecke, K.M., Lépez, M.I., 1986. The response of an intertidal *Concholepas*

- concholepas (Gastropoda) population to protection from man in southern Chile and the effects on benthic sessile assemblages. *Oikos* 359–364.
- Mosquera, I., Côté, I.M., Jennings, S., Reynolds, J.D., 2000. Conservation benefits of marine reserves for fish populations. *Anim. Conserv.* 3, 321–332.
- Muallil, R.N., Mamauag, S.S., Cabral, R.B., Celeste-Dizon, E.O., Aliño, P.M., 2014. Status, trends and challenges in the sustainability of small-scale fisheries in the Philippines: Insights from FISHDA (Fishing Industries' Support in Handling Decisions Application) model. *Mar. Policy* 44, 212–221. <https://doi.org/10.1016/j.marpol.2013.08.026>
- Mumby, P.J., Dahlgren, C.P., Harborne, A.R., Kappel, C. V, Micheli, F., Brumbaugh, D.R., Holmes, K.E., Mendes, J.M., Broad, K., Sanchirico, J.N., 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* (80-.). 311, 98–101.
- Munday, P.L., 2004. Habitat loss, resource specialization, and extinction on coral reefs. *Glob. Chang. Biol.* 10, 1642–1647.
- Myers, R.A., Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423, 280–283.
- Naeem, S., 2004. How biodiversity loss affects the health of ecosystems.
- Nañola, C.L., Aliño, P.M., Carpenter, K.E., 2011. Exploitation-related reef fish species richness depletion in the epicenter of marine biodiversity. *Environ. Biol. Fishes* 90, 405–420.
- Nash, W.J., 1993. Biology and fishery management of trochus (*Trochus niloticus* L.). *Nearshore Mar. Resour. South Pacific*.
- Newell, R.I.E., 1988. Ecological changes in Chesapeake Bay: are they the result of overharvesting the American oyster, *Crassostrea virginica*. *Underst. estuary Adv. Chesap. Bay Res.* 129, 536–546.

- Nonacs, P., Dill, L.M., 1990. Mortality risk vs. food quality trade-offs in a common currency: ant patch preferences. *Ecology* 71, 1886–1892.
- Obura, D.O., 2005. Resilience and climate change: lessons from coral reefs and bleaching in the Western Indian Ocean. *Estuar. Coast. Shelf Sci.* 63, 353–372.
<https://doi.org/https://doi.org/10.1016/j.ecss.2004.11.010>
- Ogden, J.C., Lobel, P.S., 1978. The role of herbivorous fishes and urchins in coral reef communities. *Environ. Biol. Fishes* 3, 49–63. <https://doi.org/10.1007/BF00006308>
- Olsgard, F., Somerfield, P.J., 2000. Surrogates in marine benthic investigations-which taxonomic unit to target? *J. Aquat. Ecosyst. Stress Recover.* 7, 25–42.
- Orth, R.J., Heck, K.L., van Montfrans, J., 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. *Estuaries and Coasts* 7, 339–350.
- Orth, R.J., Van Montfrans, J., 1984. Epiphyte-seagrass relationships with an emphasis on the role of micrograzing: a review. *Aquat. Bot.* 18, 43–69.
- Palomares, M.L.D., Pauly, D., 2017. SeaLifeBase [WWW Document]. URL
<https://www.sealifebase.org>
- Palomares, M.L.D., Pauly, D., 2014. Philippine Marine Fisheries Catches: A Bottom-up Reconstruction, 1950-2010. *Fish. Cent. Res. Reports* 22, 171p.
- Palumbi, S.R., 2003. Population genetics, demographic connectivity, and the design of marine reserves. *Ecol. Appl.* 13, 146–158. [https://doi.org/10.1890/1051-0761\(2003\)013\[0146:PGDCAT\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2003)013[0146:PGDCAT]2.0.CO;2)
- Pardo, S.A., Kindsvater, H.K., Reynolds, J.D., Dulvy, N.K., 2016. Maximum intrinsic rate of population increase in sharks, rays, and chimaeras: the importance of survival to maturity.

- Can. J. Fish. Aquat. Sci. 73, 1159–1163.
- Pauly, D., 2019. A précis of Gill-Oxygen Limitation Theory (GOLT), with some Emphasis on the Eastern Mediterranean. *Mediterr. Mar. Sci.*
- Pauly, D., 1998. Beyond our original horizons: the tropicalization of Beverton and Holt. *Rev. fish Biol. Fish.* 8, 307–334.
- Pauly, D., 1984. Fish population dynamics in tropical waters: a manual for use with programmable calculators. *WorldFish.*
- Pauly, D., 1983. Some simple methods for the assessment of tropical fish stocks. *FAO Fish. Tech. Pap., Food & Agriculture Org.* 234, 52p.
- Pauly, D., 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *ICES J. Mar. Sci.* 39, 175–192.
- Pauly, D., Calumpong, H., 1984. Growth, reproduction and mortality of the sea hare *Dolabella auricularia* (Gastropoda: Aplysiidae) in the Central Visayas, Philippines. *Mar. Biol.* 79, 289–293. <https://doi.org/10.1007/BF00393260>
- Pauly, D., Cheung, W.W.L., 2018. Sound physiological knowledge and principles in modeling shrinking of fishes under climate change. *Glob. Chang. Biol.* 24, e15–e26.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres Jr, F., 1998. Fishing down marine food webs. *Science* (80-.). 279, 860–863.
- Pauly, D., Zeller, D., 2016. Catch reconstructions reveal that global marine fisheries catches are higher than reported and declining. *Nat. Commun.* 7, ncomms10244.
- Pereira, H.M., Cooper, H.D., 2006. Towards the global monitoring of biodiversity change. *Trends Ecol. Evol.* 21, 123–129.
- Perry, R.I., Walters, C.J., Boutillier, J.A., 1999. A framework for providing scientific advice for

- the management of new and developing invertebrate fisheries. *Rev. fish Biol. Fish.* 9, 125–150.
- Pikitch, E.K., Santora, C., Babcock, E.A., Bakun, A., Bonfil, R., Conover, D.O., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E.D., Link, J., Livingston, P.A., Mangel, M., McAllister, M.K., Pope, J., Sainsbury, K.J., 2004. Ecosystem-based fishery management. *Science* (80-.). 305, 346–347.
- Pinnegar, J.K., Polunin, N.V.C., Francour, P., Badalamenti, F., Chemello, R., Harmelin-Vivien, M.L., Hereu, B., Milazzo, M., Zabala, M., D’Anna, G., Pipitone, C., 2000. Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. *Environ. Conserv.* 27, 179–200.
- Pinsky, M.L., Jensen, O.P., Ricard, D., Palumbi, S.R., 2011. Unexpected patterns of fisheries collapse in the world’s oceans. *Proc. Natl. Acad. Sci.* 108, 8317–8322.
- Pola, M., Hallas, J.M., Gosliner, T.M., 2019. Welcome back Janolidae and Antiopella: Improving the understanding of Janolidae and Madrellidae (Cladobranchia, Heterobranchia) with description of four new species. *J. Zool. Syst. Evol. Res.* 57, 345–368.
- Pons, M., Kell, L., Rudd, M.B., Cope, J.M., Lucena Frédou, F., 2019. Performance of length-based data-limited methods in a multifleet context: application to small tunas, mackerels, and bonitos in the Atlantic Ocean. *ICES J. Mar. Sci.*
- Posey, M., Powell, C., Cahoon, L., Lindquist, D., 1995. Top down vs. bottom up control of benthic community composition on an intertidal tideflat. *J. Exp. Mar. Bio. Ecol.* 185, 19–31. [https://doi.org/10.1016/0022-0981\(94\)00127-Y](https://doi.org/10.1016/0022-0981(94)00127-Y)
- Powell, A., Smith, D.J., Hepburn, L.J., Jones, T., Berman, J., Jompa, J., Bell, J.J., 2014. Reduced Diversity and High Sponge Abundance on a Sedimented Indo-Pacific Reef System:

- Implications for Future Changes in Environmental Quality. PLoS One 9, e85253.
<https://doi.org/10.1371/journal.pone.0085253>
- Prather, C.M., Pelini, S.L., Laws, A., Rivest, E., Woltz, M., Bloch, C.P., Del Toro, I., Ho, C., Kominoski, J., Newbold, T.A.S., 2013. Invertebrates, ecosystem services and climate change. *Biol. Rev.* 88, 327–348.
- Prince, J., Hordyk, A., 2019. What to do when you have almost nothing: A simple quantitative prescription for managing extremely data-poor fisheries. *Fish Fish.* 20, 224–238.
- Prince, J., Hordyk, A., Valencia, S.R., Loneragan, N., Sainsbury, K., 2015a. Revisiting the concept of Beverton---Holt life-history invariants with the aim of informing data-poor fisheries assessment. *ICES J. Mar. Sci.* 72, 194–203.
- Prince, J., Victor, S., Kloulchad, V., Hordyk, A., 2015b. Length based SPR assessment of eleven Indo-Pacific coral reef fish populations in Palau. *Fish. Res.* 171, 42–58.
- Przeslawski, R., Ahyong, S., Byrne, M., Woerheide, G., Hutchings, P.A.T., 2008. Beyond corals and fish: the effects of climate change on noncoral benthic invertebrates of tropical reefs. *Glob. Chang. Biol.* 14, 2773–2795.
- QGIS Development Team, 2014. QGIS Geographic Information System.
- R Core Team, 2017. R: A language and environment for statistical computing.
- Rhyne, A., Rotjan, R., Bruckner, A., Tlusty, M., 2009. Crawling to collapse: ecologically unsound ornamental invertebrate fisheries. PLoS One 4, e8413.
- Ricard, D., Minto, C., Jensen, O.P., Baum, J.K., 2012. Examining the knowledge base and status of commercially exploited marine species with the RAM Legacy Stock Assessment Database. *Fish Fish.* 13, 380–398.
- Ripple, W.J., Beschta, R.L., 2006. Linking a cougar decline, trophic cascade, and catastrophic

- regime shift in Zion National Park. *Biol. Conserv.* 133, 397–408.
- Roberts, C.M., Bohnsack, J.A., Gell, F., Hawkins, J.P., Goodridge, R., 2001. Effects of marine reserves on adjacent fisheries. *Science* (80-.). 294, 1920–1923.
- Rudd, M.B., Thorson, J.T., 2017. Accounting for variable recruitment and fishing mortality in length-based stock assessments for data-limited fisheries. *Can. J. Fish. Aquat. Sci.* 75, 1019–1035.
- Russ, G.R., Alcala, A.C., 1996. Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. *Mar. Ecol. Prog. Ser.* 132, 1–9.
- Russ, G.R., Alcala, A.C., Maypa, A.P., Calumpong, H.P., White, A.T., 2004. Marine reserve benefits local fisheries. *Ecol. Appl.* 14, 597–606. <https://doi.org/10.1890/03-5076>
- Sadovy, Y., 2005. Trouble on the reef: the imperative for managing vulnerable and valuable fisheries. *Fish Fish.* 6, 167–185.
- Sainsbury, K.J., Campbell, R.A., Lindholm, R., Whitelaw, A.W., 1997. Experimental management of an Australian multispecies fishery: examining the possibility of trawl-induced habitat modification. *Glob. trends Fish. Manag.* 20, 107–112.
- Sala, E., Aburto-Oropeza, O., Paredes, G., Parra, I., Barrera, J.C., Dayton, P.K., 2002. A General Model for Designing Networks of Marine Reserves. *Science* (80-.). 298, 1991 LP-1993.
- Sale, P.F., 1991. Habitat structure and recruitment in coral reef fishes, in: *Habitat Structure*. Springer, pp. 197–210.
- Sale, P.F., Cowen, R.K., Danilowicz, B.S., Jones, G.P., Kritzer, J.P., Lindeman, K.C., Planes, S., Polunin, N.V.C., Russ, G.R., Sadovy, Y.J., Steneck, R.S., 2005. Critical science gaps impede use of no-take fishery reserves. *Trends Ecol. Evol.* 20, 74–80. <https://doi.org/https://doi.org/10.1016/j.tree.2004.11.007>

- Salomon, A.K., Tanape Sr, N.M., Huntington, H.P., 2007. Serial depletion of marine invertebrates leads to the decline of a strongly interacting grazer. *Ecol. Appl.* 17, 1752–1770.
- Samoilys, M.A., Martin-Smith, K.M., Giles, B.G., Cabrera, B., Anticamara, J.A., Brunio, E.O., Vincent, A.C.J., 2007. Effectiveness of five small Philippines' coral reef reserves for fish populations depends on site-specific factors, particularly enforcement history. *Biol. Conserv.* 136, 584–601. <https://doi.org/10.1016/j.biocon.2007.01.003>
- Selgrath, J.C., Gergel, S.E., Vincent, A.C.J., Thurstan, H. editor: R., 2017. Incorporating spatial dynamics greatly increases estimates of long-term fishing effort: a participatory mapping approach. *ICES J. Mar. Sci.* 75, 210–220.
- Shanks, A.L., 2009. Pelagic larval duration and dispersal distance revisited. *Biol. Bull.* 216, 373–385.
- Shears, N.T., Babcock, R.C., 2003. Continuing trophic cascade effects after 25 years of no-take marine reserve protection. *Mar. Ecol. Prog. Ser.* 246, 1–16.
- Shears, N.T., Babcock, R.C., 2002. Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia* 132, 131–142.
- Shears, N.T., Grace, R. V, Usmar, N.R., Kerr, V., Babcock, R.C., 2006. Long-term trends in lobster populations in a partially protected vs. no-take Marine Park. *Biol. Conserv.* 132, 222–231.
- Shipman, C., Gosliner, T., 2015. Molecular and morphological systematics of *Doto* Oken, 1851 (Gastropoda: Heterobranchia), with descriptions of five new species and a new genus. *Zootaxa* 3973, 57–101.
- Sloan, N.A., 2004. Northern abalone: Using an invertebrate to focus marine conservation ideas

- and values. *Coast. Manag.* 32, 129–143.
- Stoner, A.W., 1980. The role of seagrass biomass in the organization of benthic macrofaunal assemblages. *Bull. Mar. Sci.* 30, 537–551.
- Stoner, A.W., Davis, M.H., Booker, C.J., 2012. Abundance and population structure of queen conch inside and outside a marine protected area: repeat surveys show significant declines. *Mar. Ecol. Prog. Ser.* 460, 101–114.
- Terrados, J., Borum, J., 2004. Why are seagrasses important?-Goods and services provided by seagrass meadows. *Eur. seagrasses an Introd. to Monit. Manag.* 8–10.
- Thorson, J.T., Munch, S.B., Cope, J.M., Jin, G., 2017. Predicting life history parameters for all fishes worldwide. *Ecol. Appl.* 27, 2262–2276. <https://doi.org/10.1002/eap.1606>
- Tillin, H.M., Hiddink, J.G., Jennings, S., Kaiser, M.J., 2006. Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Mar. Ecol. Prog. Ser.* 318, 31–45.
- Travis, J., Coleman, F.C., Auster, P.J., Cury, P.M., Estes, J.A., Orensanz, J., Peterson, C.H., Power, M.E., Steneck, R.S., Wootton, J.T., 2013. Integrating the invisible fabric of nature into fisheries management. *Proc. Natl. Acad. Sci.* <https://doi.org/10.1073/pnas.1305853111>
- Vanderklift, M.A., Ward, T.J., Phillips, J.C., 1998. Use of assemblages derived from different taxonomic levels to select areas for conserving marine biodiversity. *Biol. Conserv.* 86, 307–315.
- Vincent, A.C.J., 2008. Keynote: Reconciling Fisheries with Conservation on Coral Reefs: The World as an Onion, in: *American Fisheries Society Symposium. American Fisheries Society*, p. 1435.
- Vytopil, E., Willis, B., 2001. Epifaunal community structure in *Acropora* spp.(Scleractinia) on

- the Great Barrier Reef: implications of coral morphology and habitat complexity. *Coral Reefs* 20, 281–288.
- Walsh, J.J., Dieterle, D.A., Lenos, J., 2001. A numerical analysis of carbon dynamics of the Southern Ocean phytoplankton community: the roles of light and grazing in effecting both sequestration of atmospheric CO₂ and food availability to larval krill. *Deep Sea Res. Part I Oceanogr. Res. Pap.* 48, 1–48.
- Ware, D.M., Thomson, R.E., 2005. Bottom-up ecosystem trophic dynamics determine fish production in the Northeast Pacific. *Science* 308, 1280–4.
<https://doi.org/10.1126/science.1109049>
- Weeks, R., Russ, G.R., Alcala, A.C., White, A.T., 2010. Effectiveness of marine protected areas in the Philippines for biodiversity conservation. *Conserv. Biol.* 24, 531–540.
- White, A.T., Aliño, P.M., Cros, A., Fatan, N.A., Green, A.L., Teoh, S.J., Laroya, L., Peterson, N., Tan, S., Tighe, S., 2014. Marine protected areas in the coral triangle: progress, issues, and options. *Coast. Manag.* 42, 87–106.
- White, A.T., Aliño, P.M., Meneses, A.B.T., 2006. Creating and managing marine protected areas in the Philippines. *Fisheries Improved for Sustainable Harvest Project*.
- White, A.T., Courtney, C.A., Salamanca, A., 2002. Experience with Marine Protected Area Planning and Management in the Philippines. *Coast. Manag.* 30, 1–26.
<https://doi.org/10.1080/08920750252692599>
- Williams, B.K., Nichols, J.D., Conroy, M.J., 2002. Analysis and management of animal populations. Academic Press, San Diego, California, USA.
- Williams, E.H., Shertzer, K.W., 2003. Implications of life-history invariants for biological reference points used in fishery management. *Can. J. Fish. Aquat. Sci.* 60, 710–720.

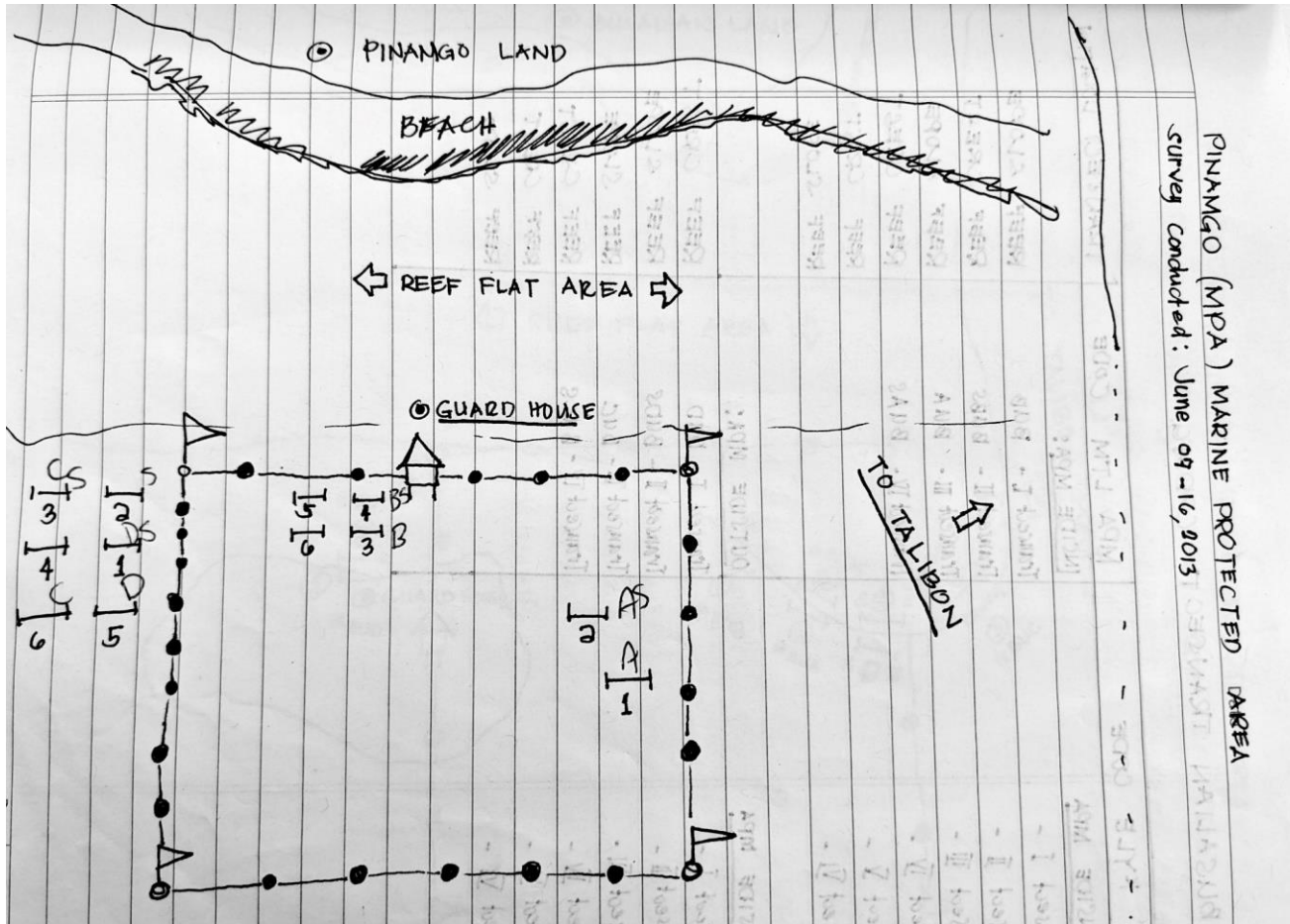
- World Bank, FAO, WorldFish Center, 2012. The hidden harvests: the global contribution of capture fisheries. Washington, DC (USA) International Bank for Reconstruction and Development ..., Washington, D.C.
- Worm, B., 2017. Marine conservation: how to heal an ocean. *Nature* 543, 630–631.
- Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J., Watson, R., 2006. Impacts of Biodiversity Loss on Ocean Ecosystem Services. *Science* (80-.). 314, 787–790. <https://doi.org/10.1126/science.1132294>
- Worm, B., Branch, T.A., 2012. The future of fish. *Trends Ecol. Evol.* 27, 594–599. <https://doi.org/http://dx.doi.org/10.1016/j.tree.2012.07.005>
- Yasue, M., Kaufman, L., Vincent, A.C.J., 2010. Assessing ecological changes in and around marine reserves using community perceptions and biological surveys. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 20, 407–418. <https://doi.org/10.1002/aqc.1090>
- Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R. Springer-Verlag, New York.
- Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1, 3–14.

Appendix: Supporting Material for Chapter 3

A.1 Invertebrate families († indicates superfamily) sampled in this study and their respective densities inside and outside of reserves and at distant fished sites

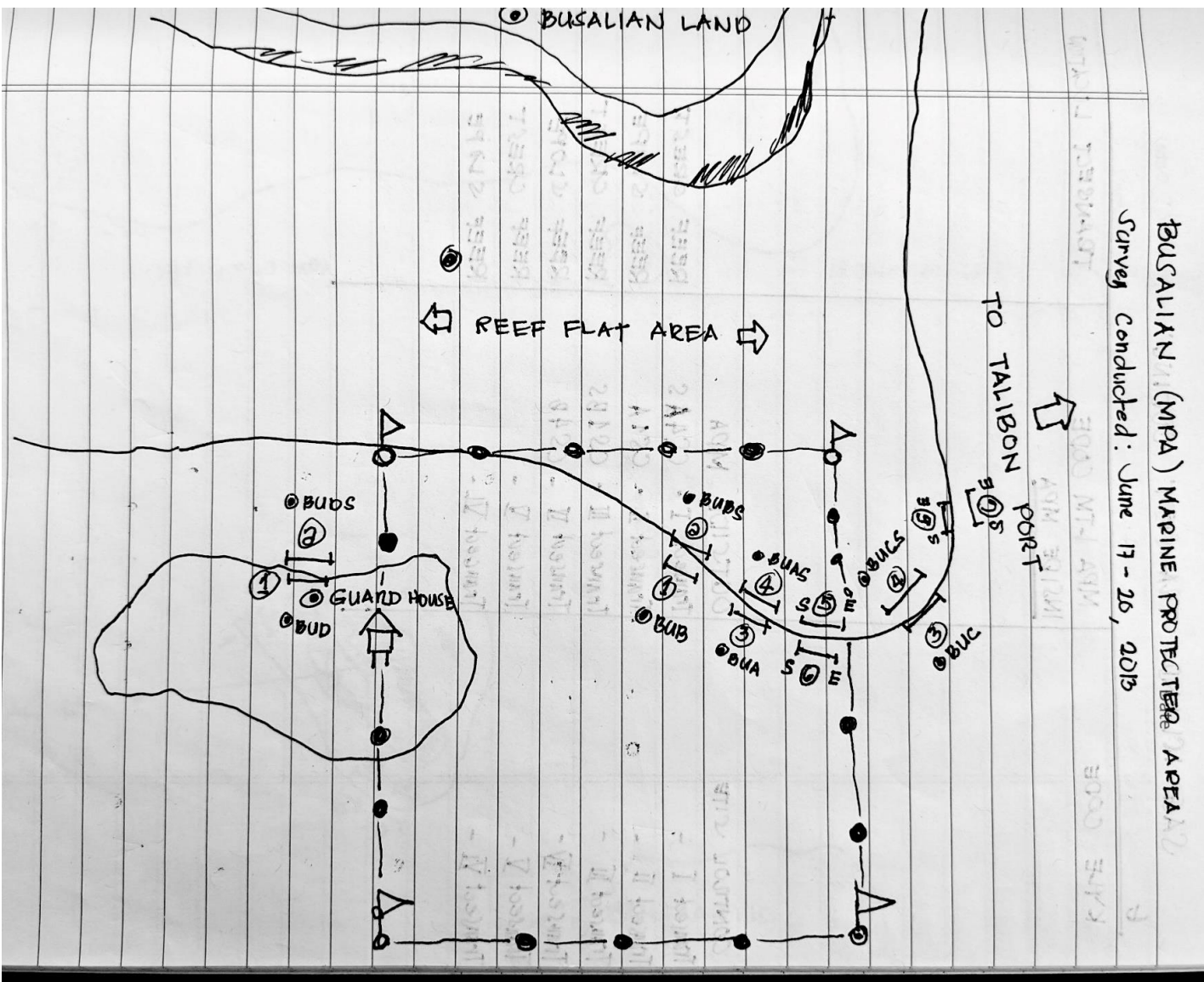
Phylum	Family	Density (per m ²)			Phylum	Family	Density (per m ²)		
		In	Out	Ref			In	Out	Ref
Annelida	Sabellidae	0.30289	0.22500	0.23444	Mollusca	Cassidae	0.00011	0.00000	0.00000
	Serpulidae	0.00011	0.00044	0.00000		Chromodorididae	0.00067	0.00033	0.00000
Arthropoda	Calappidae	0.00022	0.00089	0.00111		Conidae	0.00044	0.00089	0.00000
	Diogenidae	0.00056	0.00067	0.00074		Cypraeidae	0.00922	0.00856	0.00704
	Dromiidae	0.00044	0.00078	0.00037		Discodorididae	0.00044	0.00089	0.00000
	Ethusidae	0.00000	0.00011	0.00000		Fasciolaridae	0.00033	0.00011	0.00000
	Hippolytidae	0.55356	0.48078	0.37926		Gryphaeidae	0.00322	0.00211	0.00370
	Inachidae	0.00000	0.00056	0.00000		Haliotidae	0.00089	0.00133	0.00037
	Majidae	0.00589	0.01089	0.00741		Hexabranhidae	0.00000	0.00011	0.00000
	Majoidea	0.00033	0.00078	0.00037		Limidae	0.00000	0.00011	0.00000
	Paguroidea†	0.04989	0.02833	0.02185		Loliginidae	0.00022	0.00111	0.00074
	Parthenopidae	0.00011	0.00000	0.00001		Malleidae	0.14900	0.28311	0.22407
	Penaeidae	0.02333	0.02689	0.01741		Muricidae	0.04133	0.03644	0.03481
	Portunidae	0.10122	0.10844	0.07630		Mytilidae	0.13922	0.08644	0.04889
	Scyllaridae	0.00311	0.00367	0.00185		Naticidae	0.00022	0.00022	0.00000
Echinodermata	Stenopodidae†	0.01011	0.01211	0.01111		Octopodidae	0.00011	0.00011	0.00000
	Xanthidae	0.07989	0.07444	0.05148		Ostreidae	0.05278	0.03467	0.05185
	Acanthasteridae	0.00256	0.00178	0.00148		Pectinidae	0.07144	0.06178	0.07074
	Amphiuridae	0.01722	0.01544	0.02000		Phyllidiidae	0.00089	0.00089	0.00259
	Asteropseidae	0.00133	0.00078	0.00074		Pinnidae	0.00400	0.00356	0.00444
	Comasteridae	0.04467	0.05689	0.23333		Plakobranhidae	0.00067	0.00056	0.00037
	Cucumariidae	0.00000	0.00011	0.00000		Pleurobranchidae	0.00011	0.00000	0.00000
	Diadematidae	0.02767	0.08011	0.04926		Polyceridae	0.00011	0.00000	0.00000
	Echinometridae	0.00933	0.00844	0.00259		Pteriidae	0.00233	0.00189	0.00037
	Eurypatagidae	0.00011	0.00000	0.00000		Ranellidae	0.00011	0.00011	0.00000
	Gorgonocephalidae	0.00011	0.00011	0.00037		Sepiidae	0.00344	0.00511	0.00593
	Holothuriidae	0.01344	0.01578	0.01889		Sepiolidae	0.00000	0.00011	0.00000
	Mithrodiidae	0.00044	0.00000	0.00000		Spondylidae	0.03500	0.03078	0.03074
	Ophiocomidae	0.09622	0.17689	0.32037		Strombidae	0.00067	0.00078	0.00000
	Oreasteridae	0.00289	0.00278	0.00333		Tonnidae	0.00022	0.00000	0.00000
	Stichopodidae	0.00278	0.00167	0.00185		Trochidae	0.00167	0.00167	0.00111
Mollusca	Synaptidae	0.02000	0.03444	0.03741		Turbinidae	0.00900	0.00744	0.00296
	Temnopleuridae	0.00000	0.00011	0.00074		Velutinidae	0.00211	0.00178	0.00000
	Aplysiidae	0.00056	0.00056	0.00074		Vermetidae	0.30922	0.32056	0.18074
	Arcidae	0.67422	0.45100	0.75037		Volutidae	0.00089	0.00089	0.00037
	Cardiidae	0.00189	0.00144	0.00074	Platyhelminthes	Pseudocerotidae	0.00667	0.00689	0.00296

A.2 Sample site maps (not to scale), hand drawn by research assistant Geralde Sucano: Pinamgo MPA, Busalian MPA, Sag distant fished site, Cataban MPA, Handuman MPA, Jandayan Norte MPA, Putik distant fished site, Batasan MPA, Bilang-bilangan MPA, Matabao MPA, Ubayon distant fished site, Tugas MPA, Bantiguian MPA

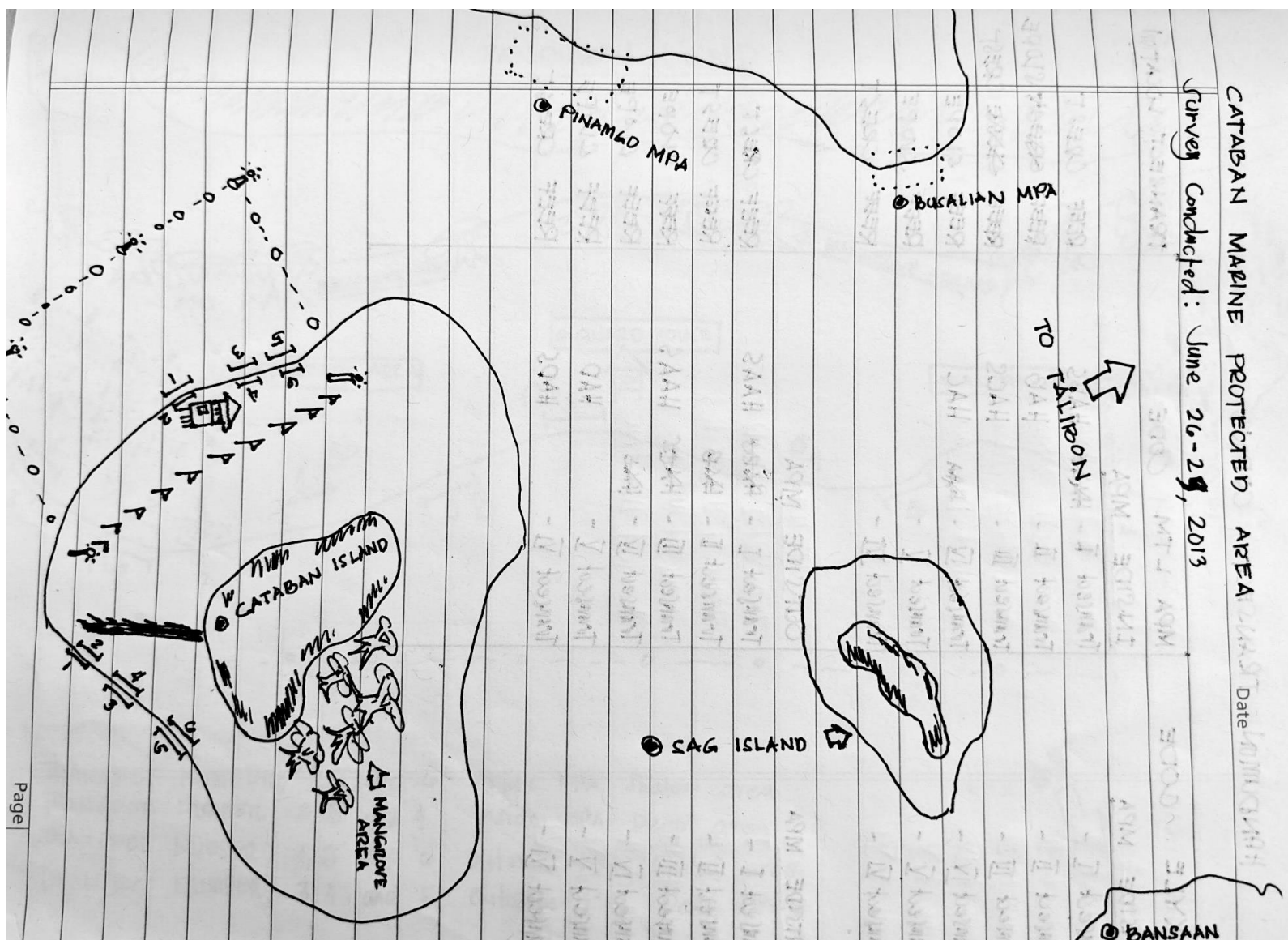


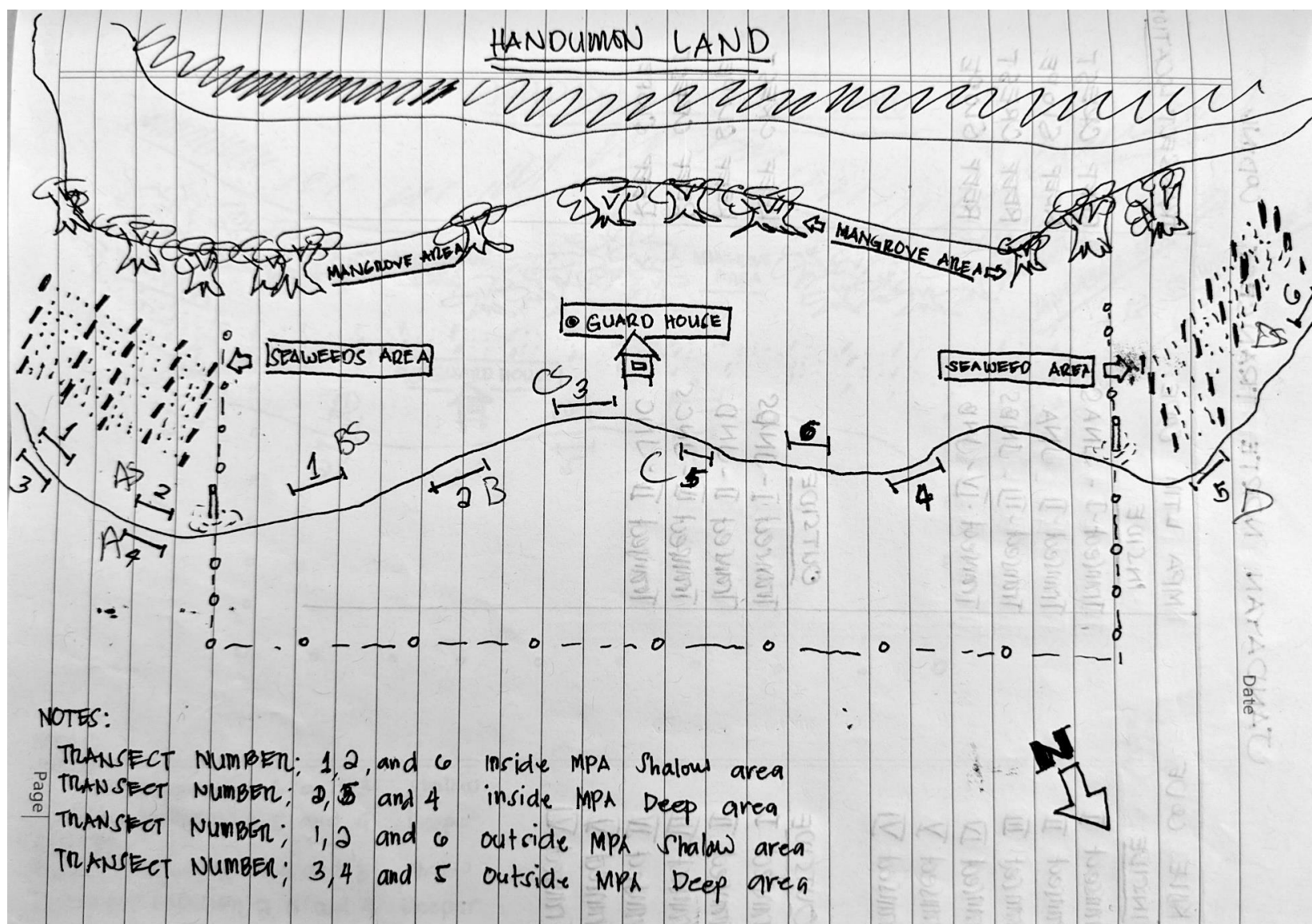
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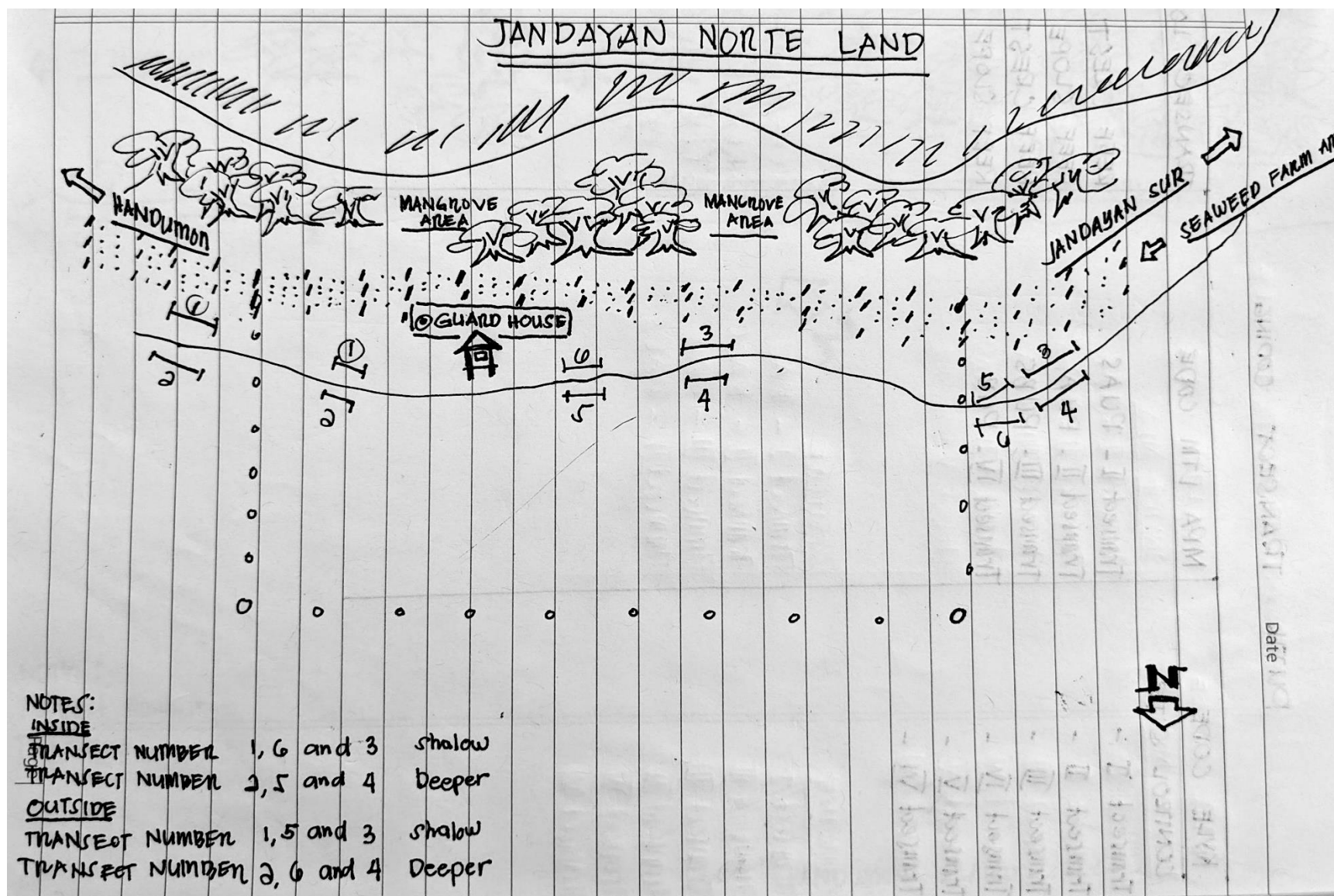
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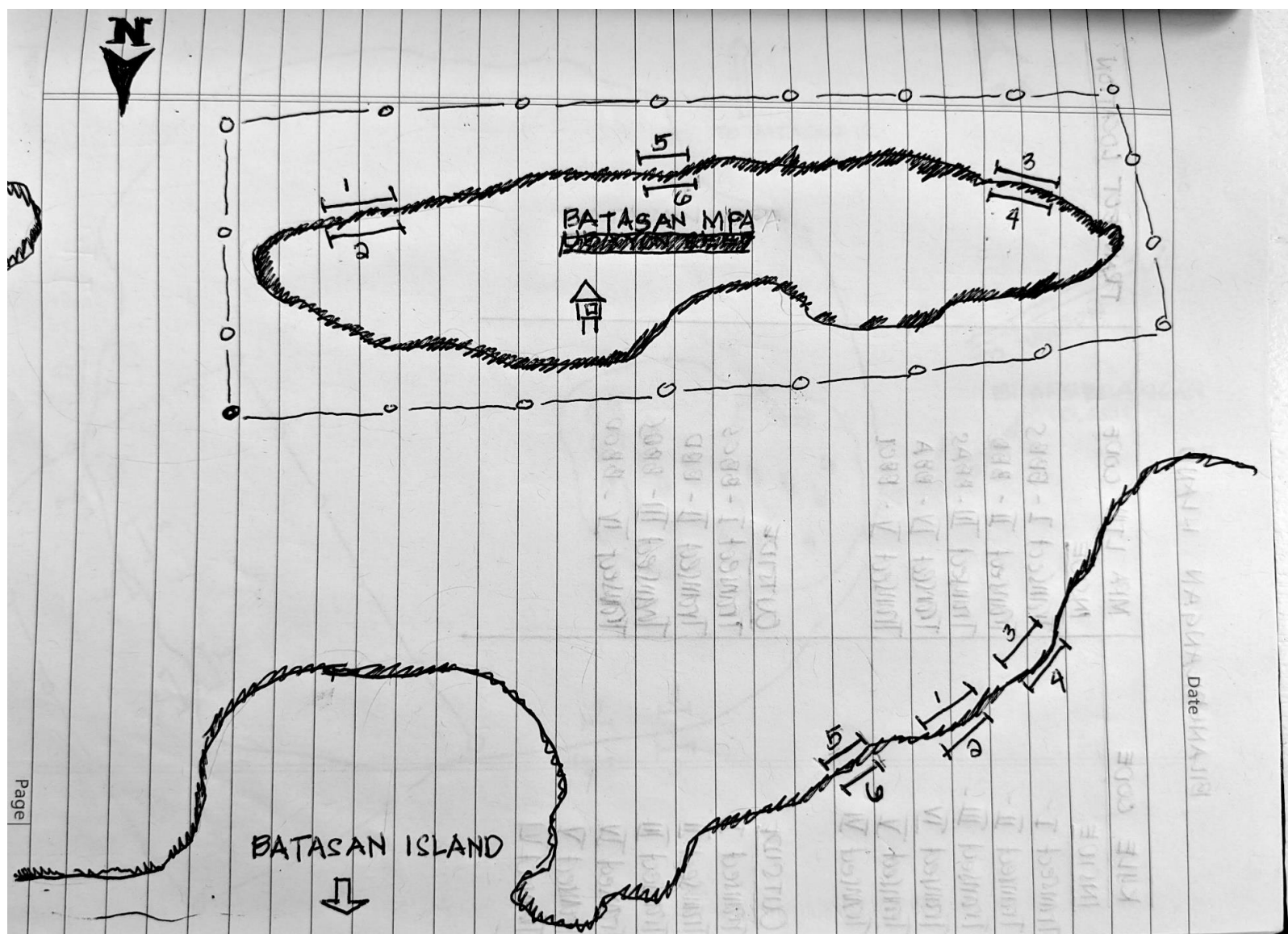


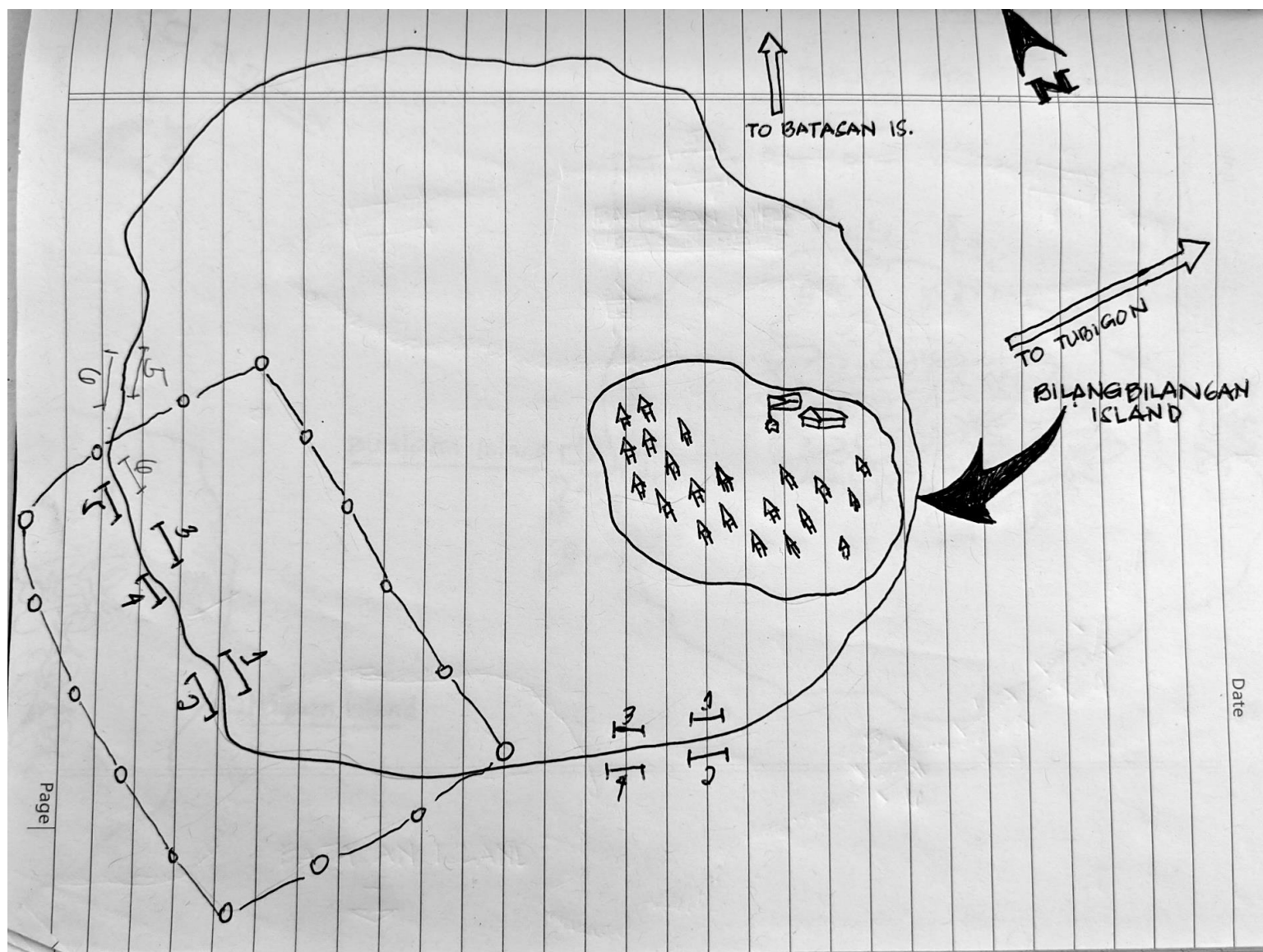


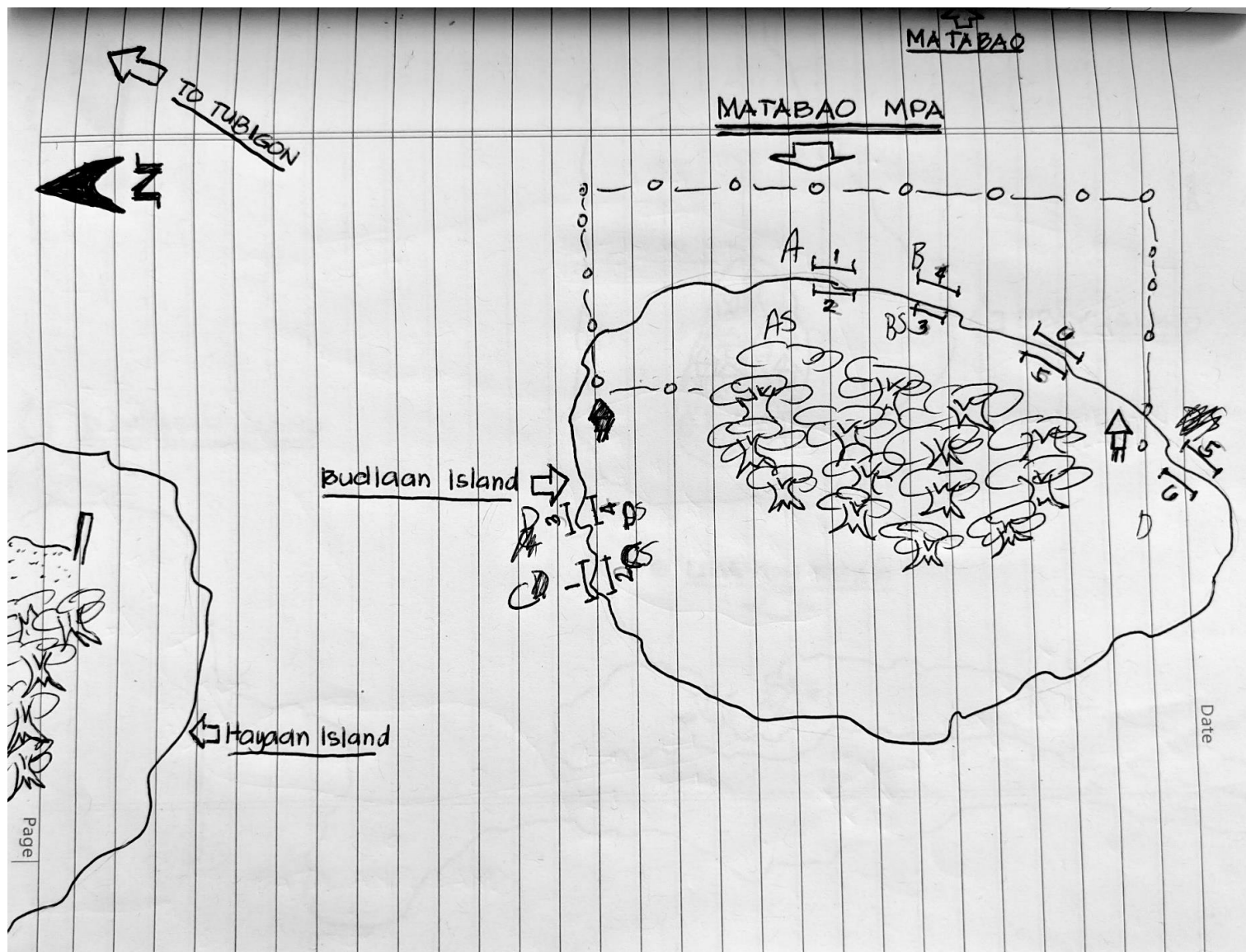




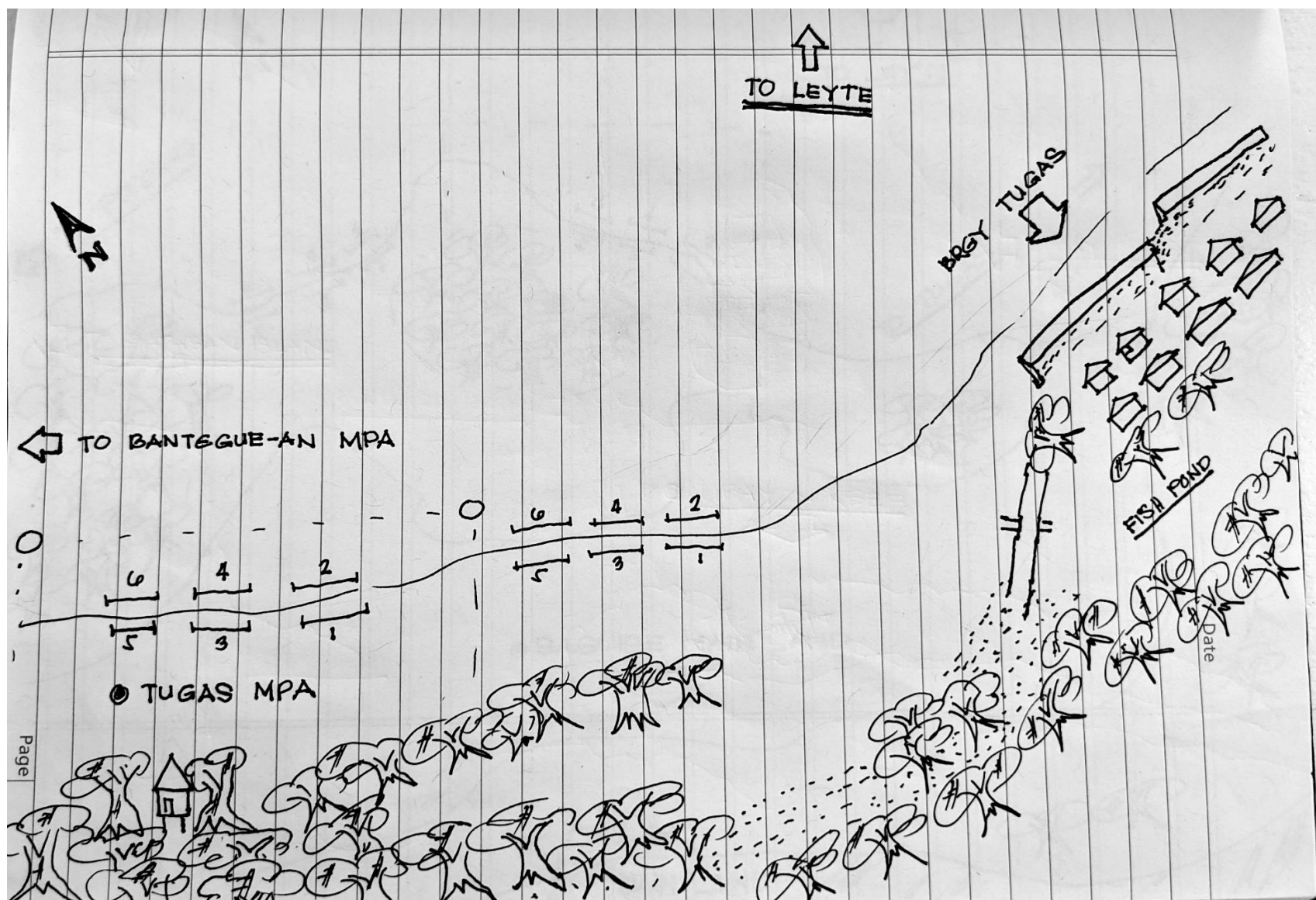


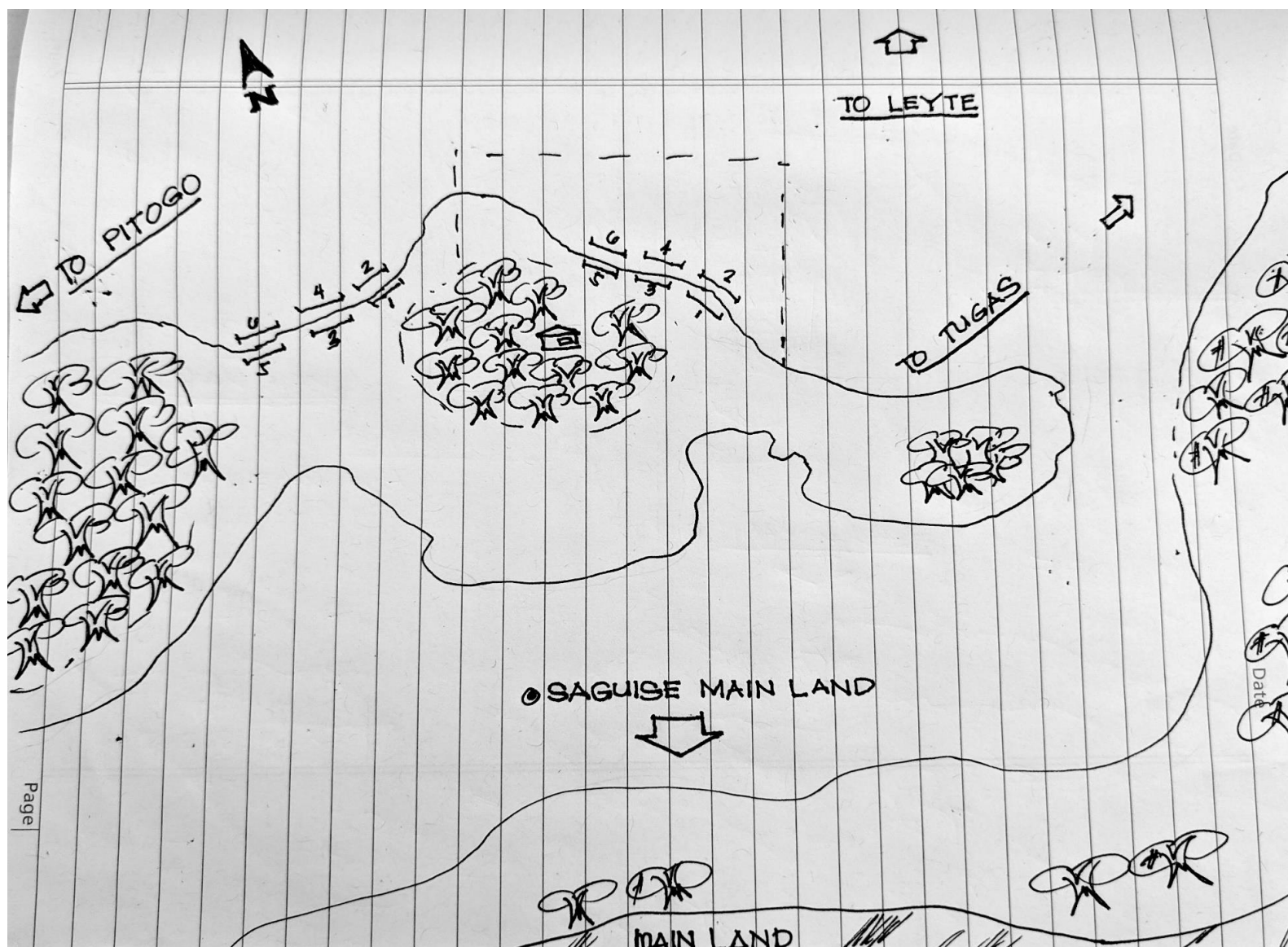












A.3 CCEF MPA management scoring criteria

Level	Question	Criteria
1	a	MPA concept accepted
	b	Site surveyed using standard/accepted methods with baseline assessment complete, preferably conducted in a participatory process
	c	Site selected
	d	Education program raising awareness about MPA functions and benefits started
	e	Management body membership tentatively determined
	f	Preliminary management plan drafted
2	a	Community acceptance gained and documented
	b	Ordinance passed and approved by municipal council
	c	Management body formally organized and recognized
	d	Management plan adopted by community and LGU or PAMB
	e	Management activities started
	f	Biophysical monitoring includes local participation
	g	IEC activities conducted to raise understanding on MPA rules and regulations
	h	Anchor buoys, marker buoys and/or boundary markers installed
	i	MPA rules and guidelines posted at strategic locations
	j	MPA outpost or other structures constructed
3	a	Education program sustained public awareness and compliance
	b	Regular biophysical monitoring measuring habitat conditions and changes conducted
	c	Collaborative patrolling and surveillance conducted by mandated enforcement group and local community volunteers
	d	MPA billboard signs, boundary markers and anchor buoys maintained
	e	Management body active
	f	Budget from local government or from other sources allocated and is accessible for MPA management
	g	Fishing effectively stopped inside sanctuary zone
	h	Illegal and destructive fishing reduced outside of MPA
4	a	MPA management plan updated in a participatory process
	b	Annual biophysical monitoring and feedback of results supervised by the managing body and implemented for 2 years or more
	c	Budget from government or from other sources allocated and was accessed for 2 or more consecutive years
	d	Management body trained and capacitated to run MPA independently
	e	Enforcement system fully operational
	f	Illegal and destructive activities stopped inside and within the vicinity of MPA

	g	Environment-friendly enterprise and/or user fees collected as a sustainable financing strategy
5	a	Information and education program on MPAs maintained over the years
	b	Ordinance passed by the provincial Council giving MPA stronger political support
	c	Management plan refined for adaptive management
	d	Management plan incorporated in the LGU development plan
	e	Evaluation of impacts on ecology and socioeconomics conducted and feedback of results completed
	f	Revenues from enterprise and/or user fees sustained and accounted for
	g	Management body capacitated for financial management and fund sourcing
	h	MPA emphasizes on public education and is being used as study tour site; residents advocate for MPA
	i	Expansion strategies or enhancement programs initiated

A.4 Candidate models used for estimating effects of variables on all invertebrate taxa. + indicates a positive effect.

Model rank	QAICc	Δ QAICc	ω	Reserve variables		Habitat variables		Fish variables		
				Protection status x reserve age	Distance from mainland	Rugosity	Live coral cover	Low-trophic fish abundance	Mid-trophic fish abundance	Top-trophic fish abundance
1	1360.6	0	0.149			0.423	0.456	0.281		
2	1361.7	1.11	0.085		0.221	0.408	0.440	0.247		
3	1362.0	1.39	0.074	+	0.570	0.378	0.490			
4	1362.4	1.80	0.061			0.437	0.443	0.274		-0.064
5	1362.5	1.87	0.059			0.412	0.455	0.265	0.068	
6	1362.6	2.03	0.054	+	0.580	0.356	0.481		0.131	
7	1363.0	2.46	0.044	+	0.421	0.382	0.476	0.159		
8	1363.2	2.64	0.040	+		0.411	0.469	0.270		
9	1363.2	2.66	0.039		0.324	0.405	0.445			
10	1363.4	2.83	0.036			0.422	0.471			
11	1363.4	2.86	0.036		0.242	0.395	0.437	0.226	0.080	
12	1363.6	3.00	0.033		0.223	0.422	0.428	0.242		-0.062
13	1364.2	3.62	0.024		0.342	0.387	0.440		0.118	
14	1364.2	3.62	0.024			0.426	0.440	0.256	0.075	-0.070
15	1364.3	3.67	0.024	+	0.568	0.388	0.481			-0.039
16	1364.3	3.76	0.023	+	0.463	0.362	0.473	0.124	0.110	
17	1364.5	3.93	0.021			0.404	0.466		0.111	

A.5 Candidate models used for estimating effects of variables on unexploited invertebrate taxa. + indicates a positive effect.

Model rank	QAICc	Δ QAICc	ω	Reserve variables		Habitat variables		Fish variables		
				Protection status x reserve age	Distance from mainland	Rugosity	Live coral cover	Low-trophic fish abundance	Mid-trophic fish abundance	Top-trophic fish abundance
1	1346.6	0	0.237			0.423	0.520	0.359		
2	1348.0	1.36	0.120		0.214	0.405	0.500	0.318		
3	1348.8	2.16	0.080			0.416	0.519	0.348	0.047	
4	1348.9	2.24	0.078			0.429	0.514	0.356		-0.029
5	1350.1	3.45	0.042	+	0.641	0.378	0.550			
6	1350.1	3.47	0.042		0.231	0.395	0.497	0.302	0.062	
7	1350.3	3.66	0.038		0.214	0.411	0.495	0.316		-0.027
8	1350.3	3.71	0.037		0.347	0.404	0.505			
9	1350.4	3.82	0.035			0.425	0.541			

A.6 Candidate models used for estimating effects of variables on exploited invertebrate taxa. + indicates a positive effect.

Model rank	QAICc	Δ QAICc	ω	Reserve variables		Habitat variables		Fish variables		
				Protection status x reserve age	Distance from mainland	Rugosity	Live coral cover	Low-trophic fish abundance	Mid-trophic fish abundance	Top-trophic fish abundance
1	1033.2	0	0.096	+		0.461				
2	1033.3	0.09	0.092	+		0.391	0.185			
3	1034.6	1.47	0.046	+		0.475				-0.094
4	1034.8	1.63	0.042	+		0.403	0.197	-0.109		
5	1034.8	1.63	0.042	+		0.444			0.090	
6	1034.9	1.78	0.039	+		0.473		-0.089		
7	1035.1	1.98	0.036	+		0.380	0.177		0.077	
8	1035.3	2.15	0.033	+		0.407	0.166			-0.061
9	1035.5	2.33	0.030	+	0.031	0.456				
10	1035.6	2.46	0.028	+	0.040	0.384	0.186			
11	1035.7	2.51	0.027			0.492				
12	1036.0	2.86	0.023			0.430	0.165			
13	1036.2	3.08	0.021	+		0.456		-0.119	0.115	
14	1036.3	3.09	0.020	+		0.489		-0.107		-0.105
15	1036.3	3.13	0.020	+		0.458			0.092	-0.096
16	1036.3	3.13	0.020			0.509				-0.127
17	1036.3	3.17	0.020	+		0.389	0.189	-0.135	0.104	
18	1036.3	3.19	0.020	+	0.219	0.375	0.212	-0.188		
19	1036.8	3.61	0.016	+		0.421	0.176	-0.119		-0.071
20	1036.8	3.65	0.015	+	0.170	0.455		-0.149		
21	1037.0	3.87	0.014	+	0.024	0.471				-0.094
22	1037.1	3.95	0.013		0.167	0.468				

A.7 Candidate models used for estimating effects of habitat variables on all invertebrate taxa

Model rank	QAICc	Δ QAICc	ω	Algae	Branching coral	Dead coral	Encrusting coral	Massive coral	Seagrass	Soft coral
1	1787.8	0	0.226	0.247	0.691			0.351	0.365	
2	1788.6	0.84	0.149	0.222	0.646	-0.095		0.329	0.349	
3	1788.8	1.04	0.134	0.263	0.703		0.101	0.348	0.368	
4	1789.4	1.69	0.097	0.237	0.656	-0.102	0.110	0.325	0.352	
5	1790	2.21	0.075	0.256	0.696			0.355	0.367	0.019
6	1790.9	3.12	0.047		0.579	-0.128		0.235	0.363	
7	1790.9	3.12	0.047	0.219	0.644	-0.096		0.327	0.349	-0.006
8	1790.9	3.15	0.047	0.283	0.713		0.109	0.357	0.374	0.039
9	1791.3	3.52	0.039		0.632			0.250	0.387	
10	1791.7	3.99	0.031	0.245	0.661	-0.099	0.113	0.329	0.354	0.014

A.8 Candidate models used for estimating effects of habitat variables on unexploited invertebrate taxa

Model rank	QAICc	Δ QAICc	ω	Algae	Branching coral	Dead coral	Encrusting coral	Massive coral	Seagrass	Soft coral
1	1765.5	0	0.203	0.289	0.707	-0.144		0.419	0.361	
2	1765.5	0.04	0.199	0.330	0.777			0.454	0.385	
3	1766.4	0.91	0.129	0.307	0.718	-0.153	0.127	0.415	0.364	
4	1766.7	1.23	0.11	0.348	0.790		0.111	0.452	0.389	
5	1767.6	2.09	0.071	0.263	0.691	-0.154		0.406	0.353	-0.048
6	1767.8	2.29	0.065	0.325	0.774			0.452	0.383	-0.010
7	1768.7	3.18	0.041	0.293	0.709	-0.158	0.122	0.408	0.360	-0.026
8	1768.8	3.29	0.039		0.617	-0.190		0.295	0.377	
9	1769	3.51	0.035	0.355	0.793		0.114	0.454	0.391	0.012
10	1769	3.55	0.034		0.594	-0.206		0.288	0.350	-0.140

A.9 Candidate models used for estimating effects of habitat variables on exploited invertebrate taxa

Model rank	QAICc	Δ QAICc	ω	Algae	Branching coral	Dead coral	Encrusting coral	Massive coral	Seagrass	Soft coral
1	1375	0	0.106		0.409	0.160			0.283	
2	1375.6	0.61	0.078		0.345				0.249	
3	1376	0.99	0.065		0.413	0.146	0.120		0.289	
4	1376	1	0.064		0.428	0.174			0.304	0.110
5	1376.1	1.04	0.063		0.357		0.143		0.258	
6	1376.6	1.61	0.047		0.436	0.159	0.139		0.314	0.127
7	1377.1	2.04	0.038		0.356				0.264	0.086
8	1377.1	2.06	0.038		0.414	0.164		0.037	0.288	
9	1377.1	2.06	0.038		0.372		0.162		0.277	0.110
10	1377.2	2.19	0.035	0.019	0.413	0.163			0.281	
11	1377.8	2.74	0.027		0.347			0.021	0.251	
12	1377.8	2.79	0.026	-0.007	0.344				0.250	
13	1377.9	2.93	0.025	0.068	0.449	0.185			0.301	0.130
14	1378	3	0.024		0.435	0.180		0.046	0.311	0.114
15	1378	3.01	0.023	0.115	0.473	0.174	0.166		0.311	0.165
16	1378.1	3.09	0.023	0.044	0.424	0.150	0.128		0.284	
17	1378.2	3.18	0.022		0.416	0.149	0.116	0.023	0.291	
18	1378.2	3.21	0.021	0.026	0.363		0.149		0.255	
19	1378.3	3.25	0.021		0.358		0.142	0.006	0.259	
20	1378.8	3.78	0.016		0.441	0.164	0.135	0.031	0.319	0.130
21	1378.9	3.87	0.015	0.080	0.395		0.184		0.273	0.135