An Assessment of Community-Managed Marine Reserves in the Central Philippines, and the Identification of Key Variables Impacting Reserve Success

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A thesis submitted in partial fulfilment of the requirements for the degree of Master of Science and the Diploma of Imperial College London
DERCLARATION OF OWN WORK

I declare that this thesis

An Assessment of Community-Managed Marine Reserves in the Central Philippines,
and the Identification of Key Variables Impacting Reserve Success

Is entirely my own work and that where the material could be construed as the
work of others it is fully cited and referenced, and/ or with appropriate
acknowledgement given.

Signature ………………………………

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Dr. Marcus Rowecliffe
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<tbody>
<tr>
<td>AIC</td>
<td>Akaike Information Criterion</td>
</tr>
<tr>
<td>AICc</td>
<td>Akaike Information Criterion corrected</td>
</tr>
<tr>
<td>BACIP</td>
<td>Before-After Control-Impact Paired</td>
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<tr>
<td>CI</td>
<td>95% Confidence Interval</td>
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<tr>
<td>GLM</td>
<td>General Linear Model</td>
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<td>GLMM</td>
<td>General Linear Mixed Model</td>
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<td>LM</td>
<td>Linear Model</td>
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<tr>
<td>RR</td>
<td>Response Ratio</td>
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<td>lnRR</td>
<td>Logged Response Ratio</td>
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<td>MPA</td>
<td>Marine Protected Areas</td>
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<td>NTR</td>
<td>No-take marine reserve</td>
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<tr>
<td>PA</td>
<td>Protected Area</td>
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<td>PSF</td>
<td>Project Seahorse Foundation for Marine Protection</td>
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<tr>
<td>RR</td>
<td>Response Ratio</td>
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<tr>
<td>RVI</td>
<td>Relative Variable Importance</td>
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<tr>
<td>SCUBA</td>
<td>Self Contained Underwater Breathing Apparatus</td>
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<td>UVC</td>
<td>Underwater Visual Census</td>
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ABSTRACT
Community-managed no-take marine reserves have been widely implemented as cost effective tools to conserve coral reef biodiversity. However, the effectiveness of marine reserves has been shown to be highly variable. There is a need to monitor and evaluate marine reserves in order to demonstrate the impacts of protection and explain the causes of heterogeneous reserve performance. This study uses underwater visual census (UVC) data of 22 fish families, within reserves and at control sites to evaluate eight community-managed marine reserves in the Danajon bank, Central Philippines. Results indicate that there were significantly more fish within reserves than at respective control sites for only two reserves, and that reserve effectiveness is contingent on high compliance with reserve regulations. The strongest responses to protection were seen by herbivorous (surgeonfish and damselfish) and predatory fish (groupers and lizardfish). Analysis of drivers found that compliance with reserve regulations, age and size of the reserve, and trophic group of the focal taxa, were all important variables impacting on reserve performance. These drivers were also shown to interact to influence reserve performance, with the impact of reserve age dependent on the trophic group of assessed taxa. Also, the impact of age and size were shown to vary between reserves with different levels of compliance. The evaluation of reserve performance is also complicated by the difficulty of matching reserves to appropriate control sites.
Acknowledgements

First and foremost I would like to say a huge thank you to my main supervisor Phil Molloy. If it wasn’t for his persistent encouragement and tireless patience this project would never have been possible. I am also grateful to the Project Seahorse Foundation for Marine Conservation, for the opportunity of this project.

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Of course I would not be anywhere without the love and support of my parents, who have fully encouraged me in all my endeavours.

Finally, a big thank you to all my Con-Sci compatriots, best of luck to you all.
1. Introduction

1.1. Coral Reefs Under Threat

Coral reefs are found throughout the shallow waters of over 100 countries in the world’s tropical regions (Spalding et al, 2001). They occupy a mere 0.1% of the world’s ocean floor, yet these ecosystems host a disproportionate amount of biodiversity, and are heralded among the most diverse and productive habitats on the planet (Odum and Odum 1955; Hughes et al. 2002). The biodiversity value of tropical reefs includes a vast array of ecosystem goods and services, such as seafood, coastal protection and cultural benefits. These services are critical to the social and economic welfare of millions of people inhabiting developing countries in the world’s tropical regions (Wilkinson 2008).

Unfortunately, a range of anthropogenic stressors imminently threaten these ecosystems and the livelihoods they support (Sebens, 1994; Bellwood et al, 2004; Jackson 2008). Coral abundance on the world’s reefs has been declining for several decades (Bruno and Selig, 2007; Alvarez et al, 2009; Paddack et al, 2009). An estimated 30% of the world’s reefs are now severely degraded (Wilkinson 2003) and coral reefs have been referred to as the most threatened ecosystems on the planet (Jackson 2008). Many reefs have undergone ecological transformations, widely known as ‘phase shifts’, where biomass and cover of benthic macro algae increases concurrently with coral loss (Bruno et al. 2009). Phase shifts therefore result in reef systems that are dominated by macro algae, and are associated with reduced reef complexity, declining fish abundance, and a loss of ecosystem services (Brock and Carpenter 2006).

1.2. Artisanal Coral Reef Fisheries – A Conservation Priority

Throughout the tropics, artisanal coral reef fisheries have long sustained maritime populations as vital, sources of protein and livelihood (Cesar et al. 2003). Such fisheries are small-scale in nature, yet they account for 25% of global fisheries catch, and constitute 50% of the fish used for direct human consumption (Mathew, 2001).
Small scale fisheries have undergone significant growth in recent history, fuelled by rapidly growing coastal populations (McManus, 2001) and the open access regime of coastal environments. It is estimated that global landings of coral reef fisheries are currently 64% higher than can be sustained (Newton et al., 2007). Overexploitation is therefore rife, and is widely acknowledged as the primary cause of reef fish population declines (Newton., 2007) as well as a principle threat to coral reef diversity, structure, function and resilience (Jackson et al., 2001).

Sustainable management is necessary to counter coral reef declines and to ensure fisheries yield their maximum socioeconomic returns (Cinner et al., 2009). However, the complexity of reef fisheries is thought to render conventional management methods largely ineffective or not applicable (Roberts and Polunin 1991). For example, reef fisheries involve impoverished communities, and consist of multiple gears, landing sites and target species. Implementing a conventional tool, such as quotas would be problematic; enforcement would have to span huge spatial scales and implementing fishing quotas on impoverished communities becomes a moral quagmire. Also, even if traditional fisheries management methods could be used for coral reef fisheries, their record of preventing overexploitation is less than impressive (Buckworth, 1998; Pauley et al. 2002; FAO, 2005)

1.3. The Role of Marine reserves

No-take marine reserves\(^1\) – areas of the ocean where all forms of resource extraction are permanently prohibited - are designed to provide protection to resident species and their biophysical environments (Halpern and Warner, 2002; Lubchenco et al., 2003). Within no-take marine reserves (henceforth marine reserves), populations of exploited species are allowed to recover while habitats modified by fishing can regenerate (Lester et al, 2009). Furthermore, reserves have benefits to fisheries through the spillover of adult fish to adjacent waters (Russ and Alcala, 1996; Roberts et al., 2001; Russ et al., 2003; Halpern et al., 2009; Stobar et al., 2009). In recent decades marine

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\(^1\) Not all marine reserves are no take, many allow resource extraction with certain caveats, such as gear limitations.
It should also be noted that the term marine reserve is considered synonymous with marine protected area (MPA).
reserves have become a widely advocated conservation tool and their use has proliferated around the world (Keleher et al., 1996; Mora et al., 2006; Wood, 2008), for example, more than 400 official no-take reserves have been established in the Philippines since the 1970s (Pajaro., 1999). Although, only an estimated 1.4% of the world’s coral reef area is contained within a no-take marine reserves (Mora, 2006)

Specifically, strong support has been voiced for community-managed marine reserves - reserves that are autonomously or collaboratively managed by local stakeholders (White et al., 2004). Such reserves are thought to be the most viable form of resource management on tropical reefs (Russ and Alcala, 2003), and a common theme in the coral reef literature is that for any type of management to be successful, it should be community managed (e.g. Kenchington, 1990; White et al., 1994). The primary tenet of community based management is that when people are well informed on the goals of the management, participate in the process that deems it necessary, and are involved in its implementation, they are more likely to comply with regulations (Johanes, 1978).

The advocacy for marine reserves stems from a number of studies demonstrating how species abundance, richness, biomass, size, and reproductive potential of marine organisms have benefited from protection (Halpern & Warner, 2002, Gell & Roberts 2003, Halpern &Warner, 2003, Claudet et al., 2008, Lester et al., 2009). However, some studies provide contradictory results, indicating that many reserves fail to produce tangible conservation benefits (McClanahan 1999; Christie et al 2003; Christie 2004), for example, McClanahan et al., (2006) demonstrate that out of eight reserves in Papa New Guinea and Indonesia, only one was successful at protecting reef fish. Also, a meta-analysis by Halpern and Warner (2002) found that the effect of reserves vary in both direction and magnitude, and comparative research conducted by Pollnac et al., (2001) documents large numbers of reserves as ineffective. This variation in reserve success presents a troubling scenario, illustrating that no-take reserves can be a highly effective conservation tools, but results are variable and reserves may be prone to high rates of failure.

Sources of heterogeneity in reserve effectiveness are hypothesised to stem from a number of different sources. These sources pertain to the characteristics of individual
reserves or to the focal taxa, such as: differences in size or age of reserves, differences in life history traits of target species, efficacy of reserve regulation enforcement, or a combination of these effects. Previous studies have explored potential sources of variation, for example, it has been empirically demonstrated that large sized reserves perform more effectively than small reserves (Claudet et al., 2008; Vandeperre, 2011). Other studies have come to conflicting conclusions about time since protection (Micheli et al., 2004; Russ and Alcala 2004; Molloy et al., 2009), while (although it may seem axiomatic) conclusive evidence has been provided about the role good enforcement of regulations plays in a successful marine reserve (Claudet et al. 2008; Claudet & Guidetti, 2010) The specific characteristics of fish species or families have also been considered. Studies have found that fish considered fishery targets show greater responses to protection than non-targets (Mosqueira et al., 2000; Cote et al., 2001; Floeter et al 2006). Also Micheli et al, (2004) shows that response to protection is correlated to trophic group, with predatory fish showing a greater response to protection than other groups.

A number of key drivers influencing response of fish to protection have therefore been discovered. However, there are potentially other variables impacting on the response of fish to protection, and the impact of interactions between these drivers seems to have been widely overlooked. Most importantly, the impact of these drivers at the level of small, community managed marine reserves is largely absent from the literature.

This situation underlines the overwhelming need to monitor and evaluate the world’s marine reserves, specifically community managed reserves. If we seek to develop the general theory of marine reserves and increase success rates, well designed monitoring and evaluation must be used to identify the extent to which existing reserves meet conservation aims and to gain insight into the sources of heterogeneity determining reserve success.
1.4. Study Focus: The Philippines

The coral reefs of the Philippines are famed for being at the centre of the most biodiverse marine region on the planet, harbouring more than 1700 reef fish species (Roberts, 2002; Carpenter, 2005) and containing approximately 9% of the world’s coral reef area (Spalding et al., 2001). Like many of the world’s reefs, overfishing, accompanied by a diverse array of compounding threats, including pollution, sedimentation and climate change, have left many of the Philippine’s reefs highly degraded (Christie, 2006). Only 3-5% of the archipelago’s reefs are thought to be in excellent condition (White, 2000) and the situation has been referred to as reaching crisis proportions (Christie et al., 2006).

In an effort to combat coral degradation and fisheries declines, the Philippines have significantly increased the amount of reefs protected by marine reserves in recent history (Pajaro, 1999). Evaluations have hailed some of these reserves as outstanding success stories (Alcala, 2001) but also, monumental failures have been documented (Crawford, 2000). The situation in the Philippines typifies global trends in coral reef health, reserve establishment, and reserve effectiveness variability. It can therefore be used as a model system to study the heterogeneity observed in community managed marine reserves.

1.5. Study aims and objectives

The main aim of this study is to use fish population count data from eight marine reserves in the Danajon bank, Central Philippines, in order to understand the impacts community-managed marine reserves have on economically and ecologically important fish populations.

The objectives of the study are to:

a) Test the performance of community-managed marine reserves by comparing reef fish populations between protected and unprotected conditions.

b) Understand how the performance of community-managed reserves is affected by various reserve attributes.
c) Understand how characteristics of fish affect their response to protection by community-managed reserves.

d) Understand how these variables interact to impact community-managed reserve success.

To achieve its aim, this study will test a number of hypotheses:

H1: Reef fish populations will be higher within reserves compared to unprotected reference sites
H2: Larger reserves will have higher densities of fish than smaller reserves
H3: Older reserves will have higher densities of fish than newer reserves
H4: Reserves where regulations are respected and complied with will have higher fish densities when compared to reserves where regulations are not respected.
H5: High value fish families will show a larger increase in abundance within reserves than low value families.
H6: Families actively traded in the aquarium trade will show a larger increase in abundance within reserves than fish not traded.
H7: Families actively targeted by fishers will show greater increases in abundance within reserves than families not targeted
H8: Families belonging to a high trophic level will show greater increases in abundance within reserves than families belonging to low trophic group

2. Background

2.1. Assessing Impact of Marine Protected Areas

In recent history, the empirical evaluation of terrestrial and marine protected area performance has become an increasingly important priority in the field of conservation (Green 1997; MEA 2005; Ferraro & Pattanayak, 2006). However, protected areas can be established for a number of different objectives, meaning what constitutes conservation ‘success’ will vary between reserves. For example, evaluations may examine factors such as human impacts within reserves, e.g. deforestation, economic opportunities for people inhabiting areas adjacent to the
protected areas (PAs), while others focus on ecological outputs, such as the response of animal populations to protection.

In the case of community-managed marine reserves, one of their primary objectives is to maintain or restore marine biodiversity and ecosystem function (Halpern & Walner 2003; Beger et al., 2003). As reef fish are an exploited and key component of this biodiversity, assessments of reserves frequently use fish abundances.

2.2. Sampling Reef Fish Populations

UVC are regularly used to estimate abundances of coral-reef fishes, providing quick and inexpensive methods to collect community data (Willis, 2001). Trained observers record fish presence along transects and within a fixed water column. UVC is frequently the basis of empirical research behind marine reserve analysis, especially small, community-managed reserves on coral reefs (such as: Russ 2005; Samoilys et al., 2007). UVC data is however limited by the ability of observers to see and identify fish accurately under variable conditions (Samoilys & Carlos, 1997). Substantial bias may be caused by substandard monitoring, leading to false conclusions regarding the state of a given ecosystem (Samoilys & Carlos, 1997; Jennings & Polunin, 1995; Edgar, 2004). To avoid the potential bias involved in misidentification, many monitoring programmes monitor fish at the family level, such as the ubiquitous reef check (Hodgeson, 1999)

2.3. Control-Impact Studies

Control-impact assessments of protected area effectiveness typically contrast the intensity of human impacts, or biodiversity condition, inside a reserve with a control site - a site with unrestricted use that shares ecological similarities with the reserve (Skalski and Robson, 1992). A range of studies exist comparing different conservation interests inside and outside reserves, such as: deforestation rates (Oliveira et al., 2007), hunting pressure (Laurence et al., 2006), and abundances of focal taxa (Nardi, et al. 2004). Lower human impacts or higher abundances within reserves compared to the control conditions indicate that the reserve is having a positive conservation impact.

Control-impact assessments of fish abundance estimates are the most prevalent assessment technique used for marine reserves (Edgar et al., 2004). The dominance
of this technique is attributed to the ease and reduced time control-impact studies require, compared to alternative assessments that necessitate temporal repetition (Russ et al., 2005). Scepticism has however been raised about the reliability of inferences derived from control-impact evaluations. For example, Edgar et al, (2004) illustrate that single spatial comparisons can be significantly biased if selection of control sites areas are not appropriately matched to reserves, i.e. it can be impossible to separate natural spatial variation from reserve effects through spatial comparison alone. Although rare, comparative studies of control-impact and alternative evaluation methods have been performed, testing the credibility of inferences made from control-impact evaluations (see: Russ et al. 2005; Hawkings 2006). Conclusions indicate that useful inferences about reserve effectiveness can be made by control impact evaluation, provided studies are carefully designed - i.e. census techniques do not vary, and habitat of the reserve and control site are properly matched at the time of reserve establishment (Russ et al. 2005).

2.4. Before-After Control-Impact Paired (BACIP) experiments

Before-After Control-Impact (BACI) experiments combine long term monitoring with a control impact design and are considered as the strongest experimental design for reserve research and evaluation. They are more robust than a control-impact design (Russ 2002; Edgar et al., 2005) and quantify spatial and temporal variation in the same study, providing powerful tests of the hypothesised effects of marine reserves. Although, these studies are considered to be more demanding on resources and their implementation is therefore rare compared to control impact designs (Edgar et al., 2004).

2.5. Meta Analysis

Meta-analyses are a set of quantitative methods designed to summarise research findings of disparate studies, which may have used different designs or sample sizes to investigate a similar question (Hedges & Olkins, 1985). Such methods are frequently used in other disciplines (such as medicine; Fazey et al., 2004), but have recently been widely applied to summarise broad patterns of marine reserve effectiveness and to investigate trends (such as: Mosquera et al., 2000; Côté et al.,
Relevant aspects of the meta-analysis analytical framework to this study are briefly discussed below, for a detailed discussion of the meta-analysis process see Hedges and Olkin (1985).

A common metric, called ‘effect size’, is used in meta-analyses to express the outcomes from multiple studies (Hedges & Gurevitch, 1999). A wide variety of effect size metrics exist, and the choice of metric depends on the question posed by the study (Osenberg et al., 1999); for the meta analysis of marine reserves a commonly used effect size is the standardised difference between means of experimental and control groups (i.e. inside and outside reserves), known as Response Ratios (RR) (Hedges & Gurevitch, 1999; such as: Mosquera et al., 2000; Côté et al., 2001; Halpern & Warner 2002; Molloy et al 2009). Once the appropriate metric is decided, effect sizes can be weighted allowing the most robust studies to provide a greater contribution to the analysis. Robustness is usually based on (inversed) sample variances (Rosenberg et al., 2000) but alternative measures of robustness have been used. For example, to include studies that did not disclose sample variance Molloy et al, (2009) weights studies that surveyed greater areas as more robust.

Calculated effect sizes can then be divided into biologically meaningful subgroups, and compared using the statistic $Q_a$ (Hedges and Olkins 1985), a method analogous to an analysis of variance. These tests allow the identification of key variables that account for significant amounts of variance in effect size (Cooper and Hedges 1994)

Meta-analysis of marine reserves has been criticised due to the majority of studies they examine are control-impact designs (Edgar 2004). Results from meta-analysis would be more robust if they primarily considered outputs from BACIP experiments, however, as previously mentioned, these studies are few in number severely limiting the sample size. Also, a common issue with meta-analyses is they are vulnerable to publication bias, a situation when significant results are disproportionately published (Begg 1994). This could be the cause of a number of positive reviews of marine reserve effectiveness in meta-analyses that do not account for it (such as Mosqueira et al., 2000; Côté et al., 2001), however more recent studies have accounted for this.
problem (such as: Molloy et al., 2009) by examining normal quantile plots (Wang & Bushman 1998).

2.6. Statistical Techniques and Key Variables

A number of key drivers influencing the response of fish to protection have been demonstrated using meta-analytical techniques (statistic $Q_B$), for example, Cote et al, (2001) found that targeted fish species respond better to protection while Mosqueira et al.(2000) shows that large bodied fish benefit more from protection than smaller fish. However, limitations meant that these studies only tested a small array of non-interacting variables. Generalized Linear Mixed Effects Models (GLMMs) represent a flexible statistical approach, which has become exceedingly popular for analysing ecological data in the last decade (Bolker et al., 2009). Their use of random effects allows for non-independent data, particular important when analysing monitoring data, where temporal or spatial sampling repetition is involved. GLMMs are now increasing used to model the variation in fish density between protected and unprotected conditions. They can be used to simultaneously test the impact of a suite of interacting variables on reserve performance. For example Claudet et al, (2008) simultaneously tests for how reserve size, buffer zone size, age and proximity to nearest reserve, impact on reserve success. Also, Claudet et al, (2010) tests a number biological traits specific to fish species, such as: maximum size, home, range and, depth range.

2.7. Study Location - The Danajon bank

The Danajon bank reef system consists of three large reefs spanning approximately 130 kilometres along the northern coastline of Bohol Island, central Philippines (Fig 2.1; Pichon 1977). The reef system is considered an area of international significance due to its high biodiversity value and its rare double barrier reef formation - one of only three double barriers in the indo-pacific (Pichon 1977). On a local scale, the rich diversity of marine life is vitally important to maritime populations that inhabit the shores and islands of the Danajon bank (Christie et al., 2006). Few economic developments exist in the region, and small scale subsistence reef fisheries are crucial
for the provision of livelihoods and direct food consumption. Unfortunately, the reef system of the Danajon bank faces a multitude of natural and anthropogenic threats that contribute to reef degradation (Armada et al., 2009).

![Map detailing the position of the Danajon Bank, and Bohol Island, Central Philippines. Note the double barrier reef formation running across the top segment of the image.](image)

2.7.1 Threats to the Danajon Bank

Poor fishing practice - such as overfishing and destructive fishing - are currently regarded as urgent matters for coastal management in the Philippines, (Green et al., 2000; Christie et al., 2006; Armada et al., 2009) and destructive fishing is considered as the largest contributor to reef deterioration (Burke et al., 2002)

The high density of fishers within the Danajon bank, has subjected the area to overexploitation, largely through unsustainable, destructive, and illegal fishing methods. Destructive fishing practice and the associated deterioration of the Danajon bank can be traced back to the 1950s, when destructive fishing methods such as blasting became rampant (Aumentado, 2001). The active use of dynamite for fishing and cyanide for collection of fish for the aquarium trade is a common occurrence today (Christie et al., 2006). Both fishing methods have been recognised by local
fishers as among the top three issues impacting the marine environment (Armada et al. 2004). In addition, poverty and human population growth exacerbate the threats imposed by poor fishing techniques. The coastal areas of the Danajon Bank have an average of 505 people/km² compared to 282 people km² for the province of Bohol (ADB et al. 2003). The majority of the inhabitants of this densely populated region are believed to live below the poverty line (Green et al. 2002). Low income and a lack of alternative livelihoods renders people unable to exit the fishery, therefore as stocks decline fishers are driven to catch smaller fish and use more efficient but destructive gears - a situation known as Malthusian overfishing (Pauley et al., 1989).

2.7.2. Previous Marine Reserve Assessments on Danajon Bank

Samoilys et al, (2007) provides a previous evaluation of a subset of sites examined in this study. Results indicate that reserves are overall successful, with two reserves showing significant positive increases in fish numbers when compared to control sites. This previous study used a BACIP design and could therefore be considered to provide more robust estimates of individual fish families to protection. However, with Samoilys et al, (2007) it must be noted that it was significantly limited in the way inferences were made about the impact of compliance on reserve success. Similarities and differences between results of each study will be contrasted throughout the discussion.

A number of studies have also correlated the success of marine protected areas to a range of socio-economic variables. For example, using survey and interview data from communities in the Danajon bank, Christie et al, (2009) found variables such as community population size, remoteness, and perceived punishment for violation of reserve regulations, all exhibited relationships with reserve success.

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2 Original definition of Malthusian overfishing, given by Pauley et al., (1989):
“Malthusian overfishing occurs when poor fishermen, faced with declining catches and lacking any other alternative initiate wholesale resource destruction in their effort to maintain their incomes. This may involve in order of seriousness, and generally in temporal sequence: (1) use of gears and mesh sizes not sanctioned by the government; (2) use of gears not sanctioned within the fisherfolk communities and/or catching of fish reserved for a certain segment of the community; (3) use of gears that destroy the resource base; and (4) use of gears, such as dynamite or sodium cyanide that do all of the above and even endanger the fisherfolks themselves.”
3. Methods

3.1. Methodological framework

Underwater Visual Census (UVC) data were used to investigate the impact of community-managed marine reserves on economically important fish families, and explore sources of variation impacting reserve success. Following a meta-analysis framework, and to facilitate more flexible data analysis, count data were converted to an effect size metric - a measure of relative difference between fish abundance inside and outside a reserve. Differences in performance among reserves and in responses among families were explained using key variables that capture potential drivers at the reserve and fish levels. Reserve and fish family variables were then combined with effect size data and the impact of key variables quantified using a combination of univariate and multivariate analysis. For multivariate analyses a general linear mixed effect models were used to provide the basis of parameter estimation, and an information theoretic framework was used to provide the basis for model selection. This methodology allowed the identification of key drivers of fish responses to protection, and for the discovery of obscure but important trends that could have been overlooked by a more basic analytical approach.

3.2. Study Sites

This study focuses on eight community-managed marine reserves in the Danajon bank, central Philippines. Focal reserves are located between the northern coast of Bohol Island and the outer reef of the Danajon Bank (Fig 3.1). Sites were primarily patch reefs located 0 -1000m from shore. Reserves were irregular in shape and varied, in age (8 to 15 years), and size (from 10.5 to 50 ha)

All reserves were established by local communities and are managed by community based organisations and committees. The NGO Project Seahorse Foundation for Marine Conservation (PSF) provides varying levels of support, and previous studies reveal that management effectiveness and stakeholder support vary highly between sites (Panes 2006; Yasué et al 2006)
Fig 3.1. - Map of Bohol, Central Philippines, displaying location of reserves (aka MPA site) and control sites. Shallow depth ≤10m is indicated by grey pixels.
Table 3.1– Marine reserve characteristics, detailing the governing Municipality, the GPS coordinates, the Total Area of the reserve, the year it was established and the compliance rating of the marine reserve:

<table>
<thead>
<tr>
<th>Marine Reserve</th>
<th>Asinan</th>
<th>Bantiguian</th>
<th>Batasan</th>
<th>Bilangbilangan</th>
<th>Handumon</th>
<th>Jandayan Norte</th>
<th>Pandanon</th>
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<tr>
<td>Municipality</td>
<td>Buenavista</td>
<td>Saguise</td>
<td>Tubigon</td>
<td>Tubigon</td>
<td>Getafe</td>
<td>Getafe</td>
<td>Getafe</td>
<td>Bien Unido</td>
</tr>
<tr>
<td>Lat/ long Coords</td>
<td>$10^\circ 06' 22'' N$</td>
<td>$10^\circ 08.954' N$</td>
<td>$10.0040 N$</td>
<td>$9.98820 N$</td>
<td>$10^\circ 10.321' N$</td>
<td>$10.10393 N$</td>
<td>$10^\circ 11.242' N$</td>
<td>$10^\circ 11.38.2' N$</td>
</tr>
<tr>
<td>Total Area (ha.)</td>
<td>50</td>
<td>10.6</td>
<td>123.58588 E</td>
<td>123.87830 E</td>
<td>10.5</td>
<td>50</td>
<td>24.86</td>
<td>37.8</td>
</tr>
<tr>
<td>Compliance Rating</td>
<td>High</td>
<td>High</td>
<td>High</td>
<td>Low</td>
<td>High</td>
<td>Low</td>
<td>Low</td>
<td>Low</td>
</tr>
</tbody>
</table>
Data collection

3.3.1. Evaluation/Monitoring Design
The monitoring programme for the focal marine reserves is a quasi-experimental, matched design. Each reserve is paired with a distant control site as similar as possible in biogeographic and ecological characteristics. Control sites are intended - as far as possible - to differ from the marine reserve only by the fact they are not protected from fishing. Thus, fish populations from matched control sites can be monitored and compared to populations within marine reserves, providing insight into the counterfactual outcome of protection, i.e. what would happen in the absence of protection.

Two categories of treatment were defined and monitored for this study, (1) Inside, within the marine reserve, (2) Control, distant matched reference sites open to fishing. This study can be viewed as unbalanced as some control sites were matched to more than one reserve. Monitoring was undertaken through a partnership between the local non-governmental organisation, PSF and local communities.

3.3.2. Fish Surveys

Four 50m x 5m permanently positioned transects were monitored at each site and treatment. Fish populations were surveyed using self contained underwater breathing apparatus (SCUBA) and standard UVC protocols (Samoilys et al., 1997). Teams consisting of a biologist and a trained volunteer, conducted each transect by swimming slowly along the line, recording all fish observed within the transect boundary during a 15 min time period. To maximise accuracy, transient fish species were recorded first, followed by less mobile territorial species (Hill and Wilkinson, 2004). Attention was taken not to double count fish that crossed the central transect line during the survey. Fish were recorded to family level due to the difficulty associated with identifying all fish species. Two depth levels were monitored and a total of 22 fish families (Table 3.2.) were surveyed in this study.
Table 3.2. Fish Families Surveyed in this Study. Fish family names are presented alongside their common name (Lieske & Myers, 1994), trophic level based on broad dietary information from fishbase (Top, mid or low-trophic), their status as fishery Targets for food, status in the live fish Aquarium trade, collected (Y) or non-collected (N), and relative financial value. For a full explanation of classification see Table 3.3.

<table>
<thead>
<tr>
<th>Family</th>
<th>Common Name</th>
<th>Trophic Group</th>
<th>Target</th>
<th>Aquarium</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthuridae</td>
<td>Surgeonfish</td>
<td>Low-trophic</td>
<td>Target</td>
<td>Y</td>
<td>Medium</td>
</tr>
<tr>
<td>Balistidae</td>
<td>Triggerfish</td>
<td>Mid-trophic</td>
<td>Non-target</td>
<td>Y</td>
<td>Medium</td>
</tr>
<tr>
<td>Caesionidae</td>
<td>Fusilier</td>
<td>Mid-trophic</td>
<td>Target</td>
<td>N</td>
<td>Low</td>
</tr>
<tr>
<td>Carangidae</td>
<td>Trevally (Jack)</td>
<td>Top-trophic</td>
<td>Target</td>
<td>N</td>
<td>High</td>
</tr>
<tr>
<td>Chaetodontidae</td>
<td>Butterflyfish</td>
<td>Mid-trophic</td>
<td>Non-target</td>
<td>Y</td>
<td>Low</td>
</tr>
<tr>
<td>Cirrhitidae</td>
<td>Hawkfish</td>
<td>Mid-trophic</td>
<td>Non-target</td>
<td>N</td>
<td>Low</td>
</tr>
<tr>
<td>Haemulidae</td>
<td>Sweetlips</td>
<td>Top-trophic</td>
<td>Target</td>
<td>N</td>
<td>High</td>
</tr>
<tr>
<td>Holocentridae</td>
<td>Soldierfish</td>
<td>Mid-trophic</td>
<td>Non-target</td>
<td>N</td>
<td>Medium</td>
</tr>
<tr>
<td>Labridae</td>
<td>Wrasse</td>
<td>Mid-trophic</td>
<td>Non-target</td>
<td>N</td>
<td>Medium</td>
</tr>
<tr>
<td>Lethrinidae</td>
<td>Emperor</td>
<td>Top-trophic</td>
<td>Target</td>
<td>N</td>
<td>High</td>
</tr>
<tr>
<td>Lutjanidae</td>
<td>Snapper</td>
<td>Top-trophic</td>
<td>Target</td>
<td>N</td>
<td>High</td>
</tr>
<tr>
<td>Mullidae</td>
<td>Goatfish</td>
<td>Mid-trophic</td>
<td>Target</td>
<td>N</td>
<td>Medium</td>
</tr>
<tr>
<td>Nemipteridae</td>
<td>Bream</td>
<td>Top-trophic</td>
<td>Target</td>
<td>N</td>
<td>High</td>
</tr>
<tr>
<td>Pinguipenidae</td>
<td>Sandperch</td>
<td>Mid-trophic</td>
<td>Non-target</td>
<td>N</td>
<td>Low</td>
</tr>
<tr>
<td>Pomacanthidae</td>
<td>Angelfish</td>
<td>Low-trophic</td>
<td>Non-target</td>
<td>Y</td>
<td>Low</td>
</tr>
<tr>
<td>Pomacentridae</td>
<td>Damselfish</td>
<td>Low-trophic</td>
<td>Non-target</td>
<td>Y</td>
<td>Low</td>
</tr>
<tr>
<td>Scaridae</td>
<td>Parrotfish</td>
<td>Low-trophic</td>
<td>Target</td>
<td>N</td>
<td>Medium</td>
</tr>
<tr>
<td>Scorpaenidae</td>
<td>Scorpionfish</td>
<td>Mid-trophic</td>
<td>Non-target</td>
<td>Y</td>
<td>Low</td>
</tr>
<tr>
<td>Serranidae</td>
<td>Groupers</td>
<td>Top-trophic</td>
<td>Target</td>
<td>Y</td>
<td>High</td>
</tr>
<tr>
<td>Siganidae</td>
<td>Rabbitfish</td>
<td>Low-trophic</td>
<td>Target</td>
<td>N</td>
<td>Medium</td>
</tr>
<tr>
<td>Synodontidae</td>
<td>Lizardfish</td>
<td>Low-trophic</td>
<td>Non-target</td>
<td>N</td>
<td>Low</td>
</tr>
<tr>
<td>Zanclidae</td>
<td>Moorish Idol</td>
<td>Low-trophic</td>
<td>Non-target</td>
<td>Y</td>
<td>Low</td>
</tr>
</tbody>
</table>
3.4. Data Processing and Management

3.4.1. Fish Count Data

For analysis UVC counts were averaged to give a mean fish abundance per 250m², for each family, at each site. Data were pooled across transect depths as preliminary data analysis revealed they did not contribute to the variation among sites. Fish belonging to the Pinguipenidae family were not observed in a single transect and were completely removed from the study. Data was not pooled across seasons as early data exploration revealed apparent trends.

3.4.2. Response Ratios

Borrowing from a meta-analysis framework, an effect size metric was calculated for each family in each reserve in order to model differences between protected and unprotected conditions (Hedges and Gurevitch 1999). The particular effect size used in this study was the natural logarithm of the response ratio (\( \ln(RR) \)), calculated as \( \ln(Xi/Xr) \), where Xi is mean density of a family inside the reserve while Xr is the mean density of the family at the appropriate reference site i.e. the control site or the outside site (section 3.3.1) (Mosquera et al. 2000; Molloy et al, 2009). This metric provides an intuitive metric for analysis as it quantifies the proportionate change that results from experimental manipulation, i.e. values greater than 0 signify a greater abundance inside the reserve when compared to the reference site and values below zero signify a greater abundance in the reference site than in the reserve (Molloy et al 2009). The natural logarithm of the ratio (\( \ln(RR) \)) was used instead of a ratio (RR) as it linearises the metric - i.e. changes in the denominator and numerator are treated equally - giving preferred sampling distributions (Hedges et al. 1999; Rosenberg et al. 2000).

In order to include cases where fish families were absent from either the reserve or the reference site, a small constant value of 0.0001 was added to all raw abundance estimates, following Molloy et al, (2009). Trials performed by Molloy et al, (2008) - adding a range of constant and percentage values to total abundance estimates - indicate that the addition of a constant value of 0.0001 to abundance estimates had the
smallest impact on overall lnRR. Without this step large amounts of important information would have been discarded from the analysis.

Response ratios for these cases where fish are absent from one of the two treatments produce extreme lnRR values relative to those where fish are observed in both. Resulting lnRR values are therefore extreme in comparison to lnRR values where fish are observed at both treatments. To understand the impact of these extreme values on the analysis, the analytical process was repeated using data without these values. Results from this alternative analysis can be found in appendix … and the implications are discussed in the final section.

Under meta-analysis protocols, effect sizes are commonly weighted to ensure greater contributions from the most robust studies. In this study sampling for each reserve was performed using the same protocols and by the same monitoring team. It was therefore deemed unnecessary to weight effect sizes.

Averaged fish counts for each family within each site and treatment were converted to response ratios using the following equation:

$$\lnRR[f,s] = \frac{(\bar{x}[f,s] + 0.0001)}{\bar{x}[f,s] + 0.0001}$$

Where lnRR[f,s] stands for the logged response ratio for family ‘f’ at site ‘s’. \(\bar{x}[f,s]\) stands for the overall mean count inside a reserve, of fish family ‘f’ at site ‘s’. \(\bar{x}[f,s]\) is the overall mean count of fish family ‘f’ at site ‘s’ for the appropriate reference site.

3.5. Univariate Data Analysis

3.5.1. Overall Response of Fish Families to Protection
An overall grand estimate of the response of fish to protection (lnRR) was obtained and its significance from zero i.e. equal abundances inside and outside the reserve tested by running an intercept only general linear model.
3.5.2 Individual Reserve Performance

\( \ln RR[f,s] \) values were used to generate overall \( \ln RR \) means and standard error estimates for each site (\( \ln RR[s] \)). 95% confidence intervals (CI) for each mean were then calculated by multiplying the standard error by 1.96 (Zar, 1984). CIs were then visually compared to zero, as this point represents equal fish abundances inside reserves and at the reference site. CIs that did not overlap zero indicated an overall significant impact (Zar, 1984) of protection on fish families within the reserve.

3.5.3 Overall response of individual fish families

The previous process was then repeated to give an overall mean response ratio and CIs for each fish family (\( \ln RR[f] \)). Comparing confidence intervals to zero allowed inferences to be made about the overall response of individual families to protection.

3.5.4 Variables influencing reserve success

To investigate heterogeneity in reserve success, eight variables were modelled, each individually hypothesised to influence reserve success. How these variables are classified is explained in tables 3.1 alongside their hypotheses.

To examine support for the above hypotheses, and due to interactions preventing the interpretation of main effects (van de Pol & Wright 2009), each explanatory variable was modelled against \( \ln RR \) values individually, using general linear mixed effects models. Similar to the analysis of overall reserve and family response ratios (section 3.5.1), each level within a categorical variable was primarily examined in relation to zero allowing the response of fish classified within that level to be estimated. Levels for individual variables were then compared to each other, testing for significant differences in response of fish between the levels. General linear mixed models were used due to their ability to cope with non-independent observations via the inclusion of random effects. In this study, observations within reserves and within families were non-independent and were therefore included as crossed random effects (Baayen 2008) for all models created.
Table 3.2 Reserve and fish family level variables hypothesised to impact the response of fish to protection. Variables are presented alongside explanations of their measurement or classification, the source behind the classification, a hypothesis on how the variable will impact on the response of fish to protection, and references for the hypotheses.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Hypothesis</th>
<th>Measurement or Classification</th>
<th>Source</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reserve Level</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Variables</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Compliance</td>
<td>lnRR will be significantly more positive in high compliance rated reserves compared to low rated reserves due to lower fishing pressure within high compliance reserves</td>
<td>Two level factor: Compliance High or Low. High rated reserves indicate high adherence to reserve regulations. Low rating indicates regulations are potentially violated.</td>
<td>Reserve classification based on a number of quantitative indicators and interviews. Original methods of the CCEF* Foundation MPA report guide</td>
<td>Guidetti et al. 2008</td>
</tr>
<tr>
<td>Age</td>
<td>lnRR will increase with reserve age as fish abundances should accumulate as time elapses</td>
<td>Time elapsed since protection began, age in years.</td>
<td>Ages based on long term monitoring information obtained from Project Seahorse.</td>
<td>Myers et al. 1997; Jennings 2001; Claudet et al., 2008</td>
</tr>
<tr>
<td>Size</td>
<td>InRR will increase with reserve size as larger reserves may allow a greater fraction of mobile fish species to remain protected</td>
<td>Size of marine reserve in hectares (ha).</td>
<td>Sizes taken from mapping surveys performed by project seahorse.</td>
<td>Jennings, 2001; Apostolaki et al. 2003; Claudet et al. 2008</td>
</tr>
<tr>
<td>Fish Level</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Variables</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trophic</td>
<td>Top-trophic fish will have significantly more positive lnRR values than lower trophic groups, as top fish are more vulnerable to fishing pressure due to their slower life histories</td>
<td>Three levels: low, mid or Top. families were assigned to one of three categories: low (trophic level 2-3), medium (trophic level 3-4) or high (trophic level &gt;4)</td>
<td>Families assigned to trophic groups based on broadscale dietary information from fishbase.</td>
<td>Pauly et al. 2004; Micheli et al. 2004</td>
</tr>
<tr>
<td>Aquarium</td>
<td>lnRR values will be significantly more positive for fish traded in the live ornamental fish than non-traded fish as higher harvesting pressure on ornamental species will mean a greater response to protection</td>
<td>Two levels: Yes or No indicating if the fish family is a target of the live ornamental fish trade</td>
<td>Groupings based on information from fishbase and confirmed by Project Seahorse partners in the Philippines</td>
<td>Friedlander 2001</td>
</tr>
<tr>
<td>Value</td>
<td>lnRR values for high value fish will be significantly more positive when compared to lower value fish as higher fishing pressure on high value fish will mean a greater response when protected</td>
<td>Three levels: Low, Medium or High, shows relative market value of fish families</td>
<td>Information based on a previous studies by Samoilys et al (2007) Confirmed by PSF partner in the Philippines</td>
<td>Samoilys et al., 2007 Confirmed by PSF partner in the Philippines</td>
</tr>
<tr>
<td>Target</td>
<td>lnRR values will be significantly more positive for target species than non-target species due to the higher fishing pressure on target species they will have a greater response to protection.</td>
<td>Two levels: Target or Non-target, indicates if fish are target food fish or not</td>
<td>Target status of fish families following previous studies by Christie et al (2006) and Molloy et al (2010)</td>
<td>Mosqueira et al., 2000; Christie et al (2006) Molloy et al (2010)</td>
</tr>
</tbody>
</table>
3.6. Multivariate Analysis

3.6.1. Model Creation

Following the information theoretic approach (Burnham & Anderson, 2002), a set of general linear mixed models were created to investigate the interactions between variables and to determine which variables have the largest impact on the response of fish to protection. Models with single terms were initially produced to represent each original hypothesis (Table 3.1). Variables were however deemed likely to act in concert and/or synergistically. For example, the hypotheses for trophic and age could simultaneously occur, but also, they could interact if the impact of reserve age is different for fish of alternative trophic levels. Models were therefore created to test combinations of the original hypotheses and biologically plausible interactions between them. Interactions were limited to two way interactions due to difficulty associated with developing formal hypotheses for more complex interactions. (For full model list see appendix 1)

3.6.2 Model Standardisation

To aid in the interpretation of model coefficients and to improve model fit (Gelman & Hill, 2006), continuous variables (reserve size and age) were centered and standardised by subtracting the mean and dividing by two standard deviations. This set the intercept to the mean, which in turn allowed inferences to be made at points within a meaningful range of the parameters (Gelman and Hill, 2006; Schielzeth, 2010), and also assigned these predictor variables to a common scale (Gelman 2008).

3.6.3. Model ranking

To account for model uncertainty, models were fitted using maximum likelihood and compared on the basis of their AICc values. AICc is a variant of the Akaike information criterion (AIC), which can be calculated using the following formula - $2\ln(L)+2K$, where $L$ is the model likelihood and $K$ is the number of parameters in a model. AIC and related information criteria (IC) use deviance as a measure of fit and penalise models with more parameters (i.e. more complex models are penalised)
(Bolker et al. 2009). AIC was designed to provide an unbiased estimator of the Kullback-Leibler information of a fitted model (Akaike, 1973). AICc is a corrected variant of AIC, designed to account for small sample sizes (Bedrick and Tsai, 1994); it remains the most widely used information criterion (Grueber et al., 2011).

A top model set was then delineated from the complete set of hypothesised models. Models with substantial support (i.e., $\Delta$AICc $\leq$ 2) (Burnham and Anderson, 2002) were thought to explain (as well as possible) the variation in fish family responses to protection and were included in the top model set. A higher cut off point was not defined as this could have led to the inclusion of models with poor weights. This is not recommended due to parameter estimates from these models being potentially spurious (Burnham and Anderson 2002).

### 3.6.4 Model averaging and Inference

An AIC model-averaging approach was used to account for model selection uncertainty, calculating robust parameter estimates across all models in the top model set (Burnham and Anderson 2002). Before model averaging, top models were refitted using restricted maximum likelihood (REML), as REML estimates of standard deviations for the random effects are generally less biased than the alternative maximum likelihood estimates (Bolker et al., 2008).

Inferences about the importance of hypothesised sources of variation in reserve effectiveness were based on the following two outputs from model averaging following methods used in Connors (2012):

1. The relative variable importance (RVI) of individual variables, indicating the total Akaike model weight of the models the variable features in (Burnham and Anderson 2002). The most important variables will feature in all models and therefore have an RVI of one. Variables that are the least important will be absent from the final model set and therefore have no RVI value.

2. The sign magnitude and uncertainty in the multimodel averaged parameter estimates representing each hypothesis in standard deviation units.
All analyses were conducted using the statistical software “R” (R development core team 2012). The “lme4” package was used to run GLMM, the ARM package was used to perform model standardisation and “MuMin” was used to conduct model ranking and averaging.

4. Results

4.1. Overall response to protection: Inside Reserves VS Control

Overall, there were significantly more fish within reserve boundaries than at distant control sites (lnRR = 1.000, SE = 0.2549, P < 0.001). The back-transformed overall response ratio (RR = 2.72) reveals that fish were 172% more abundant within reserves than at control sites.

4.2. Overall Response of Reserves

Two reserves – Asinan and Handumon - harboured significantly more fish than their distant control sites (Fig 4.1.) lnRR[s] values for all other reserves were not significantly different from zero, indicating that fish densities within these reserves were not significantly different from densities in control conditions.

4.3. Overall Response of Fish Families to Protection

Four fish families - Acanthuridae, Serranidae, Pomacentridae and Synodontidae - significantly benefited from protection (Fig 4.2.) Other fish families showed no significant response to protection, relative to distant control sites.

4.4. Fish Family and Reserve Level Variables

Fish families within High compliance reserves responded significantly and positively to protection while fish families within low compliance reserves exhibit a positive yet non-significant response (Table 4.1.). However, comparing overall response ratios of fish within different compliance rated reserves reveals no significant difference between the two groups (Table 4.2.) Analysis of trophic groups reveals a significant and positive response of both low-trophic and top trophic level fish to protection.
Mid-trophic groups exhibited positive responses but were not significant (Table 4.1.). Comparisons among levels revealed no significant differences (Table 4.2). The

![Graph showing mean response of fish families to protection within individual reserves.](image)

**Fig 4.1.** \( \ln(\text{RR}) \) values showing the mean response of fish families to protection within individual reserves. \( \ln(\text{RR}) \) estimates are presented with 95% Confidence intervals (CI). Values with confidence intervals not overlapping zero are deemed significant. Sample size for each site = 42.

The overall response of fish to protection during the dry season was positive and significant (Table 4.1.) Fish families observed during the wet season did not have a significant response to protection (Table 4.1.) and comparisons between seasons did not show significant differences (Table 4.2.). Fish families considered as a target food fish showed a significant and positive response to protection. Non-target fish families showed a positive and non-significant response to protection (Table 4.1.) and targeted
fish families did not indicate a significant difference in response to protection when compared to non-target fish families (Table 4.2.). Families known to be collected and not collected in the live fish trade did not show a significant response to protection (Table 4.1.) No significant difference in response existed between fish families

More outside Marine Reserve

More Inside Marine Reserve

![Diagram showing the mean response of fish families to protection over all reserves.](image)

Fig 4.2. \( \ln RR[f] \) values showing the mean response of fish families to protection over all reserves. \( \ln RR[f] \) estimates are presented with 95% Confidence intervals (CI). Values that do not overlap 0 with their confidence intervals are deemed significant. Only four fish families exhibit significant and positive responses: Acanthuridae, Synodontidae, Pomacentridae, and Serranidae. Sample for each site = 16

belonging to these two groups (Table 4.2.). Fish families identified of low, medium and high value in local markets all exhibited positive but non-significant responses to
No significant differences were present between these groups (Table 4.2.). The overall response of fish families to protection did not vary with reserve age ($\beta = 0.6424$, SE 1.0643, D = 1978, n 336) or with reserve size ($\beta = 1.6287$, SE 0.8713, D = 1975, n = 336).

### Table 4.1. Impact of Variables on Fish Family Response to Protection

Response ratios (lnRR) for individual variable levels are displayed alongside standard error estimates SE, model deviance, and sample size (n) for each level. Levels that display significant lnRR values (an estimate twice the standard error from zero) represent a significant difference between fish abundances within the reserve and control conditions.

<table>
<thead>
<tr>
<th>Variable</th>
<th>lnRR</th>
<th>SE</th>
<th>D</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Compliance</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Compliance A</td>
<td>1.8089</td>
<td>0.6172</td>
<td>1975</td>
<td>168</td>
</tr>
<tr>
<td>Compliance B</td>
<td>0.1917</td>
<td>0.6172</td>
<td>1975</td>
<td>168</td>
</tr>
<tr>
<td>Trophic</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low-trophic</td>
<td>1.4804</td>
<td>0.6456</td>
<td>1974</td>
<td>96</td>
</tr>
<tr>
<td>Mid-trophic</td>
<td>0.4408</td>
<td>0.6014</td>
<td>1974</td>
<td>128</td>
</tr>
<tr>
<td>Top-trophic</td>
<td>1.2282</td>
<td>0.6207</td>
<td>1974</td>
<td>112</td>
</tr>
<tr>
<td>Season</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dry</td>
<td>1.1905</td>
<td>0.5688</td>
<td>1978</td>
<td>168</td>
</tr>
<tr>
<td>Wet</td>
<td>0.8101</td>
<td>0.5688</td>
<td>1978</td>
<td>168</td>
</tr>
<tr>
<td>Aquarium</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Traded</td>
<td>1.1020</td>
<td>0.6165</td>
<td>1978</td>
<td>128</td>
</tr>
<tr>
<td>Non-traded</td>
<td>0.9377</td>
<td>0.5562</td>
<td>1978</td>
<td>208</td>
</tr>
<tr>
<td>Target</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Target</td>
<td>1.1573</td>
<td>0.5726</td>
<td>1978</td>
<td>176</td>
</tr>
<tr>
<td>Non-target</td>
<td>0.8276</td>
<td>0.5839</td>
<td>1978</td>
<td>160</td>
</tr>
<tr>
<td>Value</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low-value</td>
<td>0.9077</td>
<td>0.6242</td>
<td>1978</td>
<td>128</td>
</tr>
<tr>
<td>Mid-value</td>
<td>1.1404</td>
<td>0.6460</td>
<td>1978</td>
<td>112</td>
</tr>
<tr>
<td>High-value</td>
<td>0.9603</td>
<td>0.6739</td>
<td>1978</td>
<td>96</td>
</tr>
</tbody>
</table>
4.5. Interactions among Variables and Relative Variable Importance

General linear mixed models were used to gain insights into which of the hypothesised descriptor variables (Section 3.5.3.) has the biggest impact on fish family response to protection and how these descriptors interact. To account for model uncertainty a top model set was generated (Table 4.3.) consisting of models with substantial support based on AICc ($\Delta$AICc < 2).

4.1. Model averaged coefficients

Trophic Level and Compliance

Analysis of relative variable importance (RVI) indices shows that the predictors compliance, age, size, trophic, compliance:size, compliance: age and trophic:age are the most important predictors of fish abundances within reserves relative to control

<table>
<thead>
<tr>
<th>Variable</th>
<th>$\Delta$lnRR</th>
<th>SE</th>
<th>D</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Compliance</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>High Compliance / Low Compliance</td>
<td>-1.6173</td>
<td>0.8729</td>
<td>1975</td>
<td>336</td>
</tr>
<tr>
<td>Trophic</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low-trophic / Mid-trophic</td>
<td>-1.0396</td>
<td>0.6215</td>
<td>1974</td>
<td>240</td>
</tr>
<tr>
<td>Low-trophic / Top-trophic</td>
<td>-0.2522</td>
<td>0.6404</td>
<td>1974</td>
<td>208</td>
</tr>
<tr>
<td>Mid-trophic/ Top-trophic</td>
<td>0.7874</td>
<td>0.5965</td>
<td>1974</td>
<td>224</td>
</tr>
<tr>
<td>Season</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dry / Wet</td>
<td>-0.3084</td>
<td>0.4923</td>
<td>1978</td>
<td>336</td>
</tr>
<tr>
<td>Aquarium</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Traded / Non-traded</td>
<td>-0.1643</td>
<td>0.5451</td>
<td>1978</td>
<td>336</td>
</tr>
<tr>
<td>Target</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Target / Non-target</td>
<td>0.3297</td>
<td>0.5259</td>
<td>1978</td>
<td>336</td>
</tr>
<tr>
<td>Value</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low-value/ Mid-value</td>
<td>0.2327</td>
<td>0.644</td>
<td>1978</td>
<td>240</td>
</tr>
<tr>
<td>Low-value/ Top-value</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mid-value/Top-value</td>
<td>-0.1801</td>
<td>0.6923</td>
<td>1978</td>
<td>208</td>
</tr>
</tbody>
</table>

Table 4.2. Comparison of fish responses to protection between levels of categorical variables. Differences in lnRR values between levels are given as $\Delta$lnRR, also standard error estimates (SE), model deviance estimates (D), and sample size (n) are given. All estimates where obtained from univariate analyses using linear mixed effects models and site and family as crossed random effects. As above, significant differences are $\Delta$lnRR estimates more than twice the standard error from zero.
areas. In contrast, aquarium, value, target and season are shown to explain little variation in the response of fish families to protection (Table 4.4.).

**Table 4.3.** Model selection statistics for hypotheses explaining variation in fish family responses to protection. Hypotheses shown are within two AICc units of the top model, ordered by ΔAICc. Also shown are the log likelihoods, differences from the best model AICc (ΔAICc), and Akaike model weights renormalized for the top model set (wi). All interactions include lower order main effects (e.g., “Compliance * size” represents a model that includes an interaction between Compliance and Size as well as single variables for Compliance and Size), as well as crossed random effects for Reserve, and Family.

<table>
<thead>
<tr>
<th>#</th>
<th>Hypothesis Inside Reserves vs. Control Sites</th>
<th>logLik</th>
<th>ΔAICc</th>
<th>wi</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>(Compliance*Size) + (Age * Trophic)</td>
<td>-974.72</td>
<td>0</td>
<td>0.30</td>
</tr>
<tr>
<td>2</td>
<td>(Compliance *Size) + Trophic + Age</td>
<td>-978.54</td>
<td>1.18</td>
<td>0.16</td>
</tr>
<tr>
<td>3</td>
<td>(Compliance*Size) + (Trophic *Age) + Season</td>
<td>-975.34</td>
<td>1.24</td>
<td>0.16</td>
</tr>
<tr>
<td>4</td>
<td>(Compliance<em>Size) + (Compliance</em>Age) + Trophic</td>
<td>-977.62</td>
<td>1.49</td>
<td>0.14</td>
</tr>
<tr>
<td>5</td>
<td>(Compliance<em>Size) + (Age</em>Size) + (Trophic *Age)</td>
<td>-975.64</td>
<td>1.85</td>
<td>0.12</td>
</tr>
<tr>
<td>6</td>
<td>(Compliance<em>Size) + (Trophic</em>Age) + Aquarium</td>
<td>-975.65</td>
<td>1.86</td>
<td>0.12</td>
</tr>
</tbody>
</table>

Averaged coefficient estimates (Table 4.4.) indicate that the response of low-trophic species to protection is positive in both high compliance and low compliance rated marine reserves. Top-trophic fish demonstrate a positive response to protection in both compliance ratings while mid-trophic fish show positive responses within high compliance rated reserves, and negative responses within low compliance rated reserves.

A negative relationship between reserve age and the response of low-trophic fish families to protection indicates that low-trophic fish show a greater response to protection (>lnRR) in younger reserves compared to older reserves. The high RVI of the interaction term trophic:age indicates the impact of age varies among trophic groups. Age slopes for mid-trophic and top-trophic fish show that the effect of age on response to protection is still negative in both groups but to a lesser extent.
The interaction between reserve compliance rating and reserve age featured in two of the six top models and shows the impact of reserve age on fish family response to protection is more positive in low-compliance rated reserves than in compliance-A rated reserves.

The main effect of Size was considered as an important variable as it featured in all top models and had an RVI of 1. The averaged coefficient estimate indicates that fish within larger marine reserves have a more positive response to protection than fish within smaller reserves (Table 4.4). This effect is only for high-compliance reserves as a size compliance interaction exists.

The interaction between Size and Compliance reveals that the affect of size in low-compliance reserves is strongly negative in comparison to high-compliance reserves. This interaction indicates that as the size of marine reserves increase the response of fish to protection decreases in reserves rated as low compliance. The interaction of age and size was shows a slight decrease in the affect of size as reserves get older. The small magnitude, large standard error and low RVI show the impact of this interaction to be of negligible influence of the response of fish families to protection.

### Table 4.4. Multimodel averaged parameter estimates standard errors (SE), and relative variable importance (RVI) of parameters featured in the top model set (Table 4.8). Continuous variables were estimated in standard deviation units (SDU) to allow meaningful comparisons between independent variables on different numerical scales.

<table>
<thead>
<tr>
<th>Coefficient Estimate</th>
<th>SE</th>
<th>RVI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Compliance A</td>
<td>2.2069</td>
<td>0.5179</td>
</tr>
<tr>
<td>Compliance B</td>
<td>0.3488</td>
<td>0.9284</td>
</tr>
<tr>
<td>Mid-Trophic</td>
<td>-1.0378</td>
<td>0.5729</td>
</tr>
<tr>
<td>Top-Trophic</td>
<td>-0.2490</td>
<td>0.6190</td>
</tr>
<tr>
<td>Age</td>
<td>-2.7987</td>
<td>1.1764</td>
</tr>
<tr>
<td>Size</td>
<td>3.5054</td>
<td>0.8456</td>
</tr>
<tr>
<td>Compliance B * Age</td>
<td>2.1218</td>
<td>1.5578</td>
</tr>
<tr>
<td>Compliance B * Size</td>
<td>-4.5536</td>
<td>1.3578</td>
</tr>
<tr>
<td>Mid-Trophic * Age</td>
<td>1.7289</td>
<td>1.1423</td>
</tr>
<tr>
<td>Top-Trophic * Age</td>
<td>2.9317</td>
<td>1.2280</td>
</tr>
<tr>
<td>SeasonW</td>
<td>-0.3804</td>
<td>0.4812</td>
</tr>
<tr>
<td>Age * Size</td>
<td>-0.1130</td>
<td>1.0465</td>
</tr>
<tr>
<td>Aquarium N</td>
<td>2.1899</td>
<td>0.5750</td>
</tr>
<tr>
<td>Aquarium Y</td>
<td>2.1531</td>
<td>0.5397</td>
</tr>
</tbody>
</table>
Seasonal differences in the response of fish families to protection show a small negative difference of the response of families observed during the wet season when compared to fish families observed to the dry season. The main effect Aquarium was present in only a single model of the top model set and demonstrates a positive response of low-trophic level families that are both collected and not collected for the live fish trade. Examining the response of fish families collected for the Aquarium trade for other trophic levels reveals a positive but weaker response for top-trophic, and mid-trophic groups.

Variables not included in the final model set included Target and Value. Their exclusion deems them unimportant descriptors of fish family response to protection.

5. Discussion

Using a control-impact design, this study provides empirical evidence that community-managed marine reserves convey an overall benefit to fish populations while identifying important variables and interactions that influence the response of reef fish families to protection. This thesis identifies the need to explain variation in reserve success, particularly in the case of community-managed marine reserves, and advances on previous studies by formally testing the impact of a suite of variables on reserve success. This study demonstrates that the compliance rating, age and size of the reserve are important predictors in fish response to protection as well as the trophic grouping of the fish taxa itself. These variables were also shown to have synergistic and antagonistic effects, indicating that the success of community-managed reserves is dependent on a complicated suite of interacting variables.

5.1. Impact of Compliance

For marine reserves to achieve their objectives it is obvious that compliance with their regulations is essential. It may therefore seem unnecessary to state that no-take reserves are only successful when fishing within their boundaries is prevented, but rarely do reserve evaluations actually examine compliance and enforcement characteristics (such as, Claudet et al 2008; Molloy et al 2009). When reserve studies have examined compliance and enforcement, they have been significantly correlated...
with increases in fish abundance (Walmsley & White, 2003; Maliao, 2004; Guidetti et al., 2008). Overall results from this study support these previous findings, as reserves with superior compliance have a positive and significant impact on fish populations while reserves with inferior compliance have a non-significant impact. Inspection of individual reserves reveals that only two high-compliance rated sites, Asinan, and Handumon exhibit significant and positive overall responses. This result confirms previous evaluations by Samoilys (2007), which documents a positive performance at both sites.

Model averaging results support these results, specifying compliance as an important descriptor when examining variation in the response of fish to protection. These results corroborate a number of studies, recommending that compliance with regulations should always be considered in studies that evaluate reserve effectiveness (Claudet & Guidetti, 2010). More importantly, if new reserves are to be successful in conserving biodiversity, it is essential that mechanisms and funding are in place to ensure compliance with reserve regulations (McClanahan et al., 2006; Samoilys 2007).

5.2. Response of Low-trophic Fish

Among trophic groups, the strongest overall response to protection was exhibited by low-trophic fish. This result disagrees with the hypothesised response and is unexpected due to two prevalent theories that should simultaneously reduce the response of low-trophic fish to protection. 1) Increased numbers of low-trophic fish are expected when top-trophic, predatory fish numbers are reduced (Jennings and Polunin, 1997; Dulvy et al., 2004). Therefore, control sites which are vulnerable to overfishing would be expected to be dominated by low trophic-fish. 2) Marine reserves are commonly predicted to cause top-down trophic cascades, where low-trophic species suffer reduced numbers after protection due to increased numbers of predatory species (Dulvy et al. 2004; Micheli et al. 2004; Baskett et al. 2007; Mumby & Stenek, 2008). However, proliferations of low-trophic fish in response to reduced predatory abundance are equivocal (Jennings & Polunin, 1996). Also, responses of low-trophic species to protection are considered to be unpredictable, depending on complex interactions between community dynamics (Baskett et al. 2007), habitat
Given the complexity and debate surrounding the response of low-trophic fish to protection, it is difficult to draw conclusions behind the reasons for this relative large increase.

Two low-trophic families - Acanthuridae and Pomacentridae (Surgeonfish and Damselfish) - showed significantly more fish within reserves, supporting previous studies demonstrating positive responses of these families to protection. (Russ & Alcala 1998; Ashworth & Ormond, 2005; Abesamis et al., 2006). Acanthurids showed the greatest response to protection which can be partially attributed to their extreme scarcity at control sites. Their absence at unprotected sites was expected as Acanthurids are considered vulnerable to overfishing owing to their life history traits, such as: relatively long life spans, medium to low natural mortality, and medium recruitment rate (Jennings et al, 1999; Russ and Alcala 1998).

Acanthurids are considered important grazers (herbivores), vital to maintain reefs in a coral-dominated state through their consumption of algae (Glynn 1990; McCook et al., 2007). Mumby et al, (2007) demonstrate that reduced fishing pressure and weak predator-prey interactions can significantly increase grazer populations. The mechanism behind this increase was attributed to size-escape, a situation where fish species become too large to be consumed by predatory species (Jones 1993; Mumby et al 2006; McClanahan, 2008). Acanthuridae are considered medium bodied fish (Russ and Alcala 1998), therefore it is possible that size escape could occur dependent on the size and species of predatory fish present. Future studies examining body size of predatory and lower trophic species, accompanied by research into site specific food web dynamics could be used to unearth if body-size escape is occurring.

This situation highlights the complexity behind fish responses to protection within marine reserves. To help disentangle these complexities detailed studies of fish densities at the species level could help to decipher the causation of the observed increases in Acanthurids, and low-trophic fish in general.

5.3. Response of Predatory Fish

The overall positive and significant response of top-trophic level fish families supports previous studies demonstrating abundance increases of predatory fish in
response to protection (Russ & Alcala 2004; Russ, 2005; Ormond, 2005). Top trophic species are though to respond well to protection as they are highly vulnerable to fishing pressure due to their larger sizes and long maturation periods (Micheli 2004). Of the top-trophic fish families, both Serranidae and Synodontidae showed the greatest response. Serranids are considered important biological indicators for overfishing, cyanide fishing, and blastfishing (Hodgson 1999), all of which threaten the Danajon bank ecosystem (Christie 2006). The overall response of this important reef health indicator could be used as evidence that within study reserves overfishing, blastfishing and cyanide fishing are reduced when compared to matched control sites, however, other families also considered as indicators for reef health, destructive fishing and overexploitation, such as, Chaetodontidae and Haemulidae, (Hodgson 1999) did not show significant responses to protection.

Results from model averaged coefficients show that top-trophic fish responded strongly and positively within high compliance reserves, whereas a negative but much smaller magnitude of response was evident for low-compliance reserves. Top-trophic fish are usually large in size and are primary targets for artisanal fishers. Some top-trophic families are also regarded as more vulnerable to exploitation due to their slow life histories - such as groupers (Jennings et al., 1999) – and fishing pressure has been demonstrated to reduce numbers of top-trophic fish before lower trophic-groups (Pauley et al 1998). Given that top-trophic fish are highly prized, it is plausible that efficient protection of high-compliance reserves and a degree of illegal fishing within low-compliance reserves could cause this heterogeneous response in predatory fish. As coastal populations continue to increase and reef fisheries decline, it is plausible that more people will violate the regulations of low compliance reserves, potentially causing this dichotomy to worsen. Continued monitoring will allow the detection of these trends however efforts should be made to ensure the highest possible compliance at all sites.

5.4. Impact of Age

Previous studies have struggled to empirically demonstrate that increased fish abundances are correlated with reserve age (Micheli et al 2004; Russ and Alcala 2004; Molloy et al., 2009), however, this study indicates that the impact of reserve
age on community managed reserves may be more complex than previously identified. Interactions between age and other variables were deemed of high importance by model averaging. Such interactions have been hypothesised, but not unequivocally demonstrated by previous work. For example, potentially fast reproducing low-trophic fish are hypothesised to show larger increases in new reserves, while relatively slow maturing and reproducing top-trophic species are thought to take longer to noticeably respond to protection (Jennings 2001; Russ and Alcala 2003). As reserves age, trophic cascades could also potentially complicate the effect of age, as increased abundances of predatory fish are hypothesised to cause declines in prey species (Sandin et al., 2008). This study gives support to some aspects of these theories, showing that low-trophic fish tend to have the most positive responses in young reserves. However, if increased predator abundance in older reserves was responsible for the observed reduction of low-trophic fish, a positive impact of age would also be expected for top-trophic fish.

An interaction between compliance and age indicates the impact of age is substantially more positive within low-compliance reserves when compared to high compliance rated reserves; although this is accompanied by a large SE estimate. Increasing the number of reserves studied and the range of reserve ages studied could allow more accurate inferences to be made about the impact of reserve age.

5.5. Size

This study indicates that the impact of reserve size is important, but also complicated by interactions with other variables. Theoretical and empirical studies predict that larger reserves are more effective for conservation purposes than small reserves (Hastings & Botsford 2003; Roberts et al., 2003; Claudet et al., 2008). However results from this study show that the impact of size on relatively small (≤1km²) community-managed reserves is not as straight forward, being strongly negative in low-compliance reserves compared to high compliance reserves. This result highlights that even at the small scales of community managed reserves, larger reserves could illicit a greater response of fish to protection than smaller reserves, but only if adequate compliance and enforcement are present. It also emphasises the importance of considering reserve compliance for future studies assessing the impact.
of reserve size. If possible extending this study to include a larger range of marine reserve sizes would allow more robust conclusions to be made about the overall impact of reserve size.

An age size effect was included in the model averaged coefficients, however, the small size of the estimate, large standard error and low RVI indicates that it is not as important as other variables when investigating variation in fish responses to protection.

5.6. Coral Reef Health Indicators

Chaetodontidae (butterflyfish) are considered important reef health indicators and were one of only three fish families found to have a negative response to protection. Chaetodontids are highly dependent on live coral habitat and their numbers are often used as a proxy for coral reef health (Hourigan et al 1988, Hodgson 1999; Linton & Warner 2003). Recent studies have demonstrated that densities of Chaetodontids significantly decline in conjunction with loss of hard coral (Pratchet et al., 2006). Large negative responses for these families were observed within the reserves Jandan Norte and Pandanon. Both reserves had low compliance ratings and a possible explanation for the negative responses of these families is the encroachment of fishers, preventing significant hard coral recovery. Although, it should be noted that the use of Chaetodontids as proxies for coral health has limitations (Öhman et al. 1998; McClanahan and Arthur, 2001; Williamson et al. 2004) To draw conclusions further studies would be required investigating the efficacy of reserve protection and performing benthic surveys to quantify trends in hard coral cover (for method see: Hill & Wilkinson, 2004) at both reserves and control sites.

5.7. Alternative Analysis

Repeating the analytical steps of this study using data that excluded extreme values (section 3.4.2) corroborated many of the trends identified using the original approach, but also revealed some differences. For the alternative analysis, 56 positive InRR values were removed and 30 negative InRR values out of a total of 336 InRR
values. The larger number of positive lnRR values could potentially bias the original study in the direction of positive responses to protection.

Overall there was still a positive and significant increase of fish within reserves however the percentage estimate of fish abundance increase was reduced to 35%. As this estimate does not included instances where fish are present inside the reserve but not at the reference site, it is likely to underestimate the number of fish within reserves. Overall, Asinan and Handumon remained the best performing reserves supporting earlier analysis.

Acanthuridae was still found to have a positive and significant response to protection, but alternative analysis revealed significant responses of fish families not seen in the original analysis (appendix 2, section 1.2 ) It is likely that these responses were masked in the original analysis by inflated lnRR values for families that were absent in reference/MPA sites. Patterns in the response of different trophic groups were identical to those in the original analysis, however, these trends were no longer significant. Both age and size still showed positive impacts on response but slopes were now deemed significant, implying that these relationships are genuine. Univariate analysis for all other variables yielded the same responses in both direction and significance when compared to initial analysis.

Multivariate analysis supported previous findings: compliance, size and age were still found to significantly impact on lnRR; however, the variable *fisheries value* was also included in the top model instead of trophic. Both value and trophic group are highly correlated variables. Therefore, it is likely both variables explain similar variance in the data.

5.8. Study Limitations and Areas of Future Research

In this study, general linear mixed effects models functioned as a powerful tool allowing the detection of trends that could have been overlooked by basic analysis. Their characteristics make them extremely useful when evaluating marine reserves (ability to deal with non-independent data), however, their use in the field of
community-managed marine evaluation will likely be limited due to a lack of capacity of local institutions. To help locally based reserve managers exploit these tools communities could establish relationships with institutions - such as universities – that could provide the necessary expertise.

5.8.1. The Limitations of Control Impact Designs

Control-impact experiments can bias results if original conditions within reserves are not well matched to the control sites (Edgar, 2004). However, original conditions of control sites are rarely known and the retrospective designation of sites is complicated by sources of inter-site variation such as: physiochemical conditions, biogeography and disturbance history (Samoilys et al., 2007). This is an issue for these study sites, nevertheless, by matching reserves as well as possible with unprotected areas this study was able to disentangle some factors influencing reserve success with a degree of confidence. A future study, conducting social studies to gain knowledge about the original conditions of the featured sites would allow more accurate inferences to be made in the future.

5.8.3. Future Work: Socio-economic Descriptors

As previously mentioned (section 2.6.), reserve success has been found to be correlated with certain socio-economic variables (Pollnac et al., 2001; Christie 2009). Although not examined here, it is possible that these variables could be included in a future study, allowing more robust examination of the underlying trends responsible for heterogeneity in marine reserve success.

5.8.4. Future Work and Recommendations

This study was designed to complement a more detailed study evaluating both temporal and spatial variation. Examining changes at multiple sites over time will provide a more powerful test to determine the relative performance of marine reserves and disentangle the impact of variables on reserve success. By conducting both a control-impact and BACIP, conclusions about the utility of using control impact designs to evaluate marine reserves could be made. Such conclusions would be welcome additions to the scarce literature comparing these two methods (section 2.3.). As mentioned throughout the discussion, species level monitoring could be used to
disentangle and quantify the impact of key descriptors more accurately however the cost associated with such a monitoring programme is likely prohibitive.

5.9. Conclusion

In conclusion, this study provides support for previous assessments of the beneficial impact of community managed marine reserves on fish communities in the central Philippines. It has also shown that reserve effectiveness is dependent on a suite of interacting variables, particularly, compliance with reserve regulations, age and size of the reserve, and the trophic group of focal taxa. Although these variables have been previously identified to impact on reserve success, they have rarely been considered in the specific context of community managed marine reserves, and interactions between them may have been largely overlooked in previous reserve studies as a result of basic analysis. I therefore urge they are considered in future, not only in studies that seek to explain variation in reserve success but also when establishing new reserves. This study also provides evidence in favour of the continued establishment of community managed marine reserves in the Danajon bank, but only with the appropriate support to sustain high compliance with reserve regulations.
REFERENCES


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Pomeroy, R. S. (1994) *Community management and common property of coastal fisheries in Asia and the Pacific: concepts, methods and experiences*.


Appendix 1 Final model list

# Focus on main effects with no interaction terms
lme1<-standardize(lmer(RR.In.Con ~ 1 + Aquarium + Compliance + Season + Trophic + Age + Size + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme2<-standardize(lmer(RR.In.Con ~ 1 + Aquarium + Compliance + Season + Trophic + Age + Size + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme3<-standardize(lmer(RR.In.Con ~ 1 + Aquarium + Compliance + Season + Age + Size + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme4<-standardize(lmer(RR.In.Con ~ 1 + Aquarium + Compliance + Trophic + Age + Size + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme5<-standardize(lmer(RR.In.Con ~ 1 + Aquarium + Season + Trophic + Age + Size + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme6<-standardize(lmer(RR.In.Con ~ 1 + Compliance + Season + Trophic + Age + Size + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme7<-standardize(lmer(RR.In.Con ~ 1 + Compliance + Trophic + Age + Size + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme8<-lmer(RR.In.Con ~ 1 + Compliance + Trophic + (1 | Site) + (1 | Family), REML=FALSE, data = Fish)
lme9<-standardize(lmer(RR.In.Con ~ 1 + Compliance + Trophic + Age + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme10<-standardize(lmer(RR.In.Con ~ 1 + Trophic + Age + Size + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme11<-standardize(lmer(RR.In.Con ~ 1 + Trophic + Age + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme12<-standardize(lmer(RR.In.Con ~ 1 + Trophic + Size + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme13<-standardize(lmer(RR.In.Con ~ 1 + Age + Size + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme14<-standardize(lmer(RR.In.Con ~ 1 + Compliance + Age + Size + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme15<-standardize(lmer(RR.In.Con ~ 1 + Compliance + Age + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme16<-lmer(RR.In.Con ~ 1 + Aquarium + (1 | Site) + (1 | Family), REML=FALSE, data = Fish)
lme17<-lmer(RR.In.Con ~ 1 + Season + (1 | Site) + (1 | Family), REML=FALSE, data = Fish)
lme18<-lmer(RR.In.Con ~ 1 + Trophic + (1 | Site) + (1 | Family), REML=FALSE, data = Fish)
lme19<-standardize(lmer(RR.In.Con ~ 1 + Age + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme20<-standardize(lmer(RR.In.Con ~ 1 + Size + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme21<-lmer(RR.In.Con ~ 1 + Target + (1 | Site) + (1 | Family), REML=FALSE, data = Fish)

# Three interactions all input variables
lme22<- standardize(lmer(RR.In.Con ~ 1 + Compliance + Trophic + Age + Size + Season + Aquarium + Compliance: Aquarium + Size: Aquarium + Trophic: Aquarium + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme23<- standardize(lmer(RR.In.Con ~ -1 + Compliance + Trophic + Age + Size + Aquarium + Season + Compliance:Size + Compliance:Aquarium + Compliance:Trophic + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme24<- standardize(lmer(RR.In.Con ~ -1 + Compliance + Trophic + Age + Size + Aquarium + Season + Compliance:Trophic + Size:Trophic + Age:Trophic + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme25<- standardize(lmer(RR.In.Con ~ -1 + Compliance + Trophic + Age + Size + Aquarium + Season + Compliance:Size + Size:Age + Size:Trophic + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme26<- standardize(lmer(RR.In.Con ~ -1 + Compliance + Trophic + Age + Size + Aquarium + Season + Compliance:Size + Compliance:Aquarium + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")

#Two interactions all input variables
lme27<- standardize(lmer(RR.In.Con ~ -1 + Compliance + Trophic + Age + Size + Aquarium + Season + Age:Aquarium + Trophic:Aquarium + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme28<- standardize(lmer(RR.In.Con ~ -1 + Compliance + Trophic + Age + Size + Aquarium + Season + Compliance:Size + Compliance:Aquarium + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme29<- standardize(lmer(RR.In.Con ~ -1 + Compliance + Trophic + Age + Size + Aquarium + Season + Compliance:Trophic + Size:Trophic + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme30<- standardize(lmer(RR.In.Con ~ -1 + Compliance + Trophic + Age + Size + Aquarium + Season + Size:Trophic + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme31<- standardize(lmer(RR.In.Con ~ -1 + Compliance + Trophic + Age + Size + Aquarium + Season + Compliance:Age + Size:Age + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme32<- standardize(lmer(RR.In.Con ~ -1 + Compliance + Trophic + Age + Size + Aquarium + Season + Compliance:Age + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme33<- standardize(lmer(RR.In.Con ~ -1 + Compliance + Trophic + Age + Size + Aquarium + Season + Size:Trophic + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")

#One interaction term all input variables
lme34<- standardize(lmer(RR.In.Con ~ -1 + Compliance + Trophic + Age + Size + Aquarium + Season + Compliance:Trophic + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme35<- standardize(lmer(RR.In.Con ~ -1 + Compliance + Trophic + Age + Size + Aquarium + Season + Compliance:Size + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme36<- standardize(lmer(RR.In.Con ~ -1 + Compliance + Trophic + Age + Size + Aquarium + Season + Size:Trophic + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme37<- standardize(lmer(RR.In.Con ~ -1 + Compliance + Trophic + Age + Size + Aquarium + Season + Age:Trophic + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme38<- standardize(lmer(RR.In.Con ~ -1 + Compliance + Trophic + Age + Size + Aquarium + Season + Size:Age + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme39<- standardize(lmer(RR.In.Con ~ -1 + Compliance + Trophic + Age + Size + Aquarium + Season + Aquarium:Age + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
\textbf{#Remove main effects while keeping the interactions}

\textbf{#Remove season}
\begin{verbatim}
lme40<- standardize(lmer(RR.In.Con ~ -1 + Compliance + Trophic + Age + Size + Season + Aquarium + Aquarium:Trophic + (1|Site) + (1|Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
\end{verbatim}

\begin{verbatim}
lme41<-standardize(lmer(RR.In.Con ~ -1 + Aquarium + Compliance + Trophic + Age + Size + Compliance:Size + Trophic:Age + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
nme42<-lmer(RR.In.Con ~ -1 + Aquarium + Compliance + Trophic + (1 | Site) + (1 | Family), REML=FALSE, data = Fish)
\end{verbatim}

\begin{verbatim}
lme43<-standardize(lmer(RR.In.Con ~ -1 + Aquarium + Compliance + Trophic + Age + Size + Compliance:Size + Trophic:Age + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme44<-standardize(lmer(RR.In.Con ~ -1 + Aquarium + Age + Size + Compliance:Age + Compliance:Size + Trophic:Age + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme45<-standardize(lmer(RR.In.Con ~ -1 + Aquarium + Compliance + Trophic + Age + Size + Aquarium:Age + Compliance:Size + Trophic:Age + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme46<-standardize(lmer(RR.In.Con ~ -1 + Aquarium + Compliance + Trophic + Age + Size + Compliance:Size + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme47<-standardize(lmer(RR.In.Con ~ -1 + Aquarium + Compliance + Season + Trophic + Age + Size + Compliance:Size + Trophic:Age +(1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
\end{verbatim}

\begin{verbatim}
lme48<-standardize(lmer(RR.In.Con ~ -1 + Compliance + Season + Trophic + Age + Size + Compliance:Size + Trophic:Age + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme49<-standardize(lmer(RR.In.Con ~ -1 + Compliance + Season + Trophic + Age + Size + Compliance:Size + Trophic:Age + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme50<-standardize(lmer(RR.In.Con ~ -1 + Compliance + Season + Trophic + Age + Size + Compliance:Size + Trophic:Age + Age:Size + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme51<-standardize(lmer(RR.In.Con ~ -1 + Compliance + Season + Trophic + Age + Size + Compliance:Size + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
\end{verbatim}

\begin{verbatim}
lme52<-standardize(lmer(RR.In.Con ~ -1 + Compliance + Trophic + Age + Size + Compliance:Size + Trophic:Age + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme53<-standardize(lmer(RR.In.Con ~ -1 + Compliance + Trophic + Age + Size + Compliance:Size + Trophic:Age + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme54<-standardize(lmer(RR.In.Con ~ -1 + Compliance + Trophic + Age + Size + Compliance:Size + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme55<-standardize(lmer(RR.In.Con ~ -1 + Compliance + Trophic + Age + Size + Compliance:Size + Trophic:Age + Age:Size + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme56<-standardize(lmer(RR.In.Con ~ -1 + Compliance + Trophic + Age + Size + Compliance:Age + Age:Size + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
lme57<-standardize(lmer(RR.In.Con ~ -1 + Compliance + Trophic + Age + Size + Compliance:Trophic + Trophic:Age + (1 | Site) + (1 | Family), REML=FALSE, data = Fish),binary.inputs = "leave.alone")
\end{verbatim}

\# Remove season and aquarium
lme58 <- standardize(lmer(RR.In.Con ~ -1 + Compliance + Trophic + Age + Size + Compliance:Size + Age:Size + (1 | Site) + (1 | Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme59 <- standardize(lmer(RR.In.Con ~ -1 + Compliance + Trophic + Age + Size + Compliance:Trophic + Compliance:Age + Compliance:Size + Trophic:Age + (1 | Site) + (1 | Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme60 <- standardize(lmer(RR.In.Con ~ -1 + Compliance + Trophic + Age + Size + Compliance:Trophic + Compliance:Compliance:Size + (1 | Site) + (1 | Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")

####Replace trophic with target
lme61 <- standardize(lmer(RR.In.Con ~ -1 + Compliance + Target + Age + Size + Aquarium + Season + Compliance:Size + Compliance:Age + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme62 <- standardize(lmer(RR.In.Con ~ -1 + Compliance + Target + Age + Size + Aquarium + Season + Compliance:Size + Compliance:Target + Size:Target + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme63 <- standardize(lmer(RR.In.Con ~ -1 + Compliance + Target + Size + Aquarium + Season + Compliance:Size + Compliance:Target + Size:Target + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")

#remove trophic interactions
lme64 <- standardize(lmer(RR.In.Con ~ -1 + Compliance + Target + Age + Size + Season + Aquarium + Compliance:Target + Size:Target + Age:Target + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme65 <- standardize(lmer(RR.In.Con ~ -1 + Compliance + Target + Age + Size + Season + Aquarium + Compliance:Target + Size:Target + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme66 <- standardize(lmer(RR.In.Con ~ -1 + Compliance + Target + Age + Size + Season + Aquarium + Compliance:Target + Size:Target + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme67 <- standardize(lmer(RR.In.Con ~ -1 + Target + Age + Size + Season + Aquarium + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme68 <- standardize(lmer(RR.In.Con ~ -1 + Compliance + Target + Age + Size + Season + Aquarium + Size:Target + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme69 <- standardize(lmer(RR.In.Con ~ -1 + Compliance + Target + Age + Size + Season + Aquarium + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme70 <- lmer(RR.In.Con ~ -1 + Target + Aquarium + (1|Site) + (1|Family), REML=FALSE, data = Fish)
lme71 <- standardize(lmer(RR.In.Con ~ -1 + Compliance + Target + Age + Size + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme72 <- standardize(lmer(RR.In.Con ~ -1 + Compliance + Target + Age + Aquarium + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme73 <- lmer(RR.In.Con ~ -1 + Compliance + Target + (1|Site) + (1|Family), REML=FALSE, data = Fish)
lme74 <- lmer(RR.In.Con ~ -1 + Target + Compliance + Compliance:Target + (1|Site) + (1|Family), REML=FALSE, data = Fish)
# Include Value

lme75 <- standardize(lmer(RR.In.Con ~ -1 + Compliance + Value + Age + Size + Season + Aquarium + Compliance:Value + Age:Value + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme76 <- standardize(lmer(RR.In.Con ~ -1 + Value + Age + Size + Season + Aquarium + Size:Value + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme77 <- standardize(lmer(RR.In.Con ~ -1 + Compliance + Trophic + Age + Size + Compliance:Age + Trophic:Age + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme78 <- standardize(lmer(RR.In.Con ~ -1 + Compliance + Value + Age + Size + Season + Aquarium + Compliance:Value + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme79 <- standardize(lmer(RR.In.Con ~ -1 + Compliance + Value + Age + Size + Season + Aquarium + Size:Value + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme80 <- standardize(lmer(RR.In.Con ~ -1 + Value + Age + Size + Season + Aquarium + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme81 <- standardize(lmer(RR.In.Con ~ -1 + Compliance + Value + Age + Size + Aquarium + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme82 <- standardize(lmer(RR.In.Con ~ -1 + Compliance + Value + Size + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme83 <- standardize(lmer(RR.In.Con ~ -1 + Compliance + Value + Age + Aquarium + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme84 <- lmer(RR.In.Con ~ -1 + Compliance + Value + (1|Site) + (1|Family), REML=FALSE, data = Fish)
lme85 <- lmer(RR.In.Con ~ -1 + Value + Compliance + Compliance:Value + (1|Site) + (1|Family), REML=FALSE, data = Fish)
lme86 <- lmer(RR.In.Con ~ -1 + Value + (1|Site) + (1|Family), REML=FALSE, data = Fish)
lme87 <- standardize(lmer(RR.In.Con ~ -1 + Compliance + Age + Size + Value + Compliance:Size + Value:Size + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme88 <- standardize(lmer(RR.In.Con ~ -1 + Compliance + Age + Value + Compliance:Size + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")

# Remove compliance

lme89 <- standardize(lmer(RR.In.Con ~ -1 + Trophic + Age + Size + Trophic:Age + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme90 <- standardize(lmer(RR.In.Con ~ -1 + Trophic + Age + Size + Target + Target:Size + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme91 <- standardize(lmer(RR.In.Con ~ -1 + Trophic + Age + Size + Aquarium + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme92 <- standardize(lmer(RR.In.Con ~ -1 + Trophic + Age + Size + Trophic:Size + Trophic:Age + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme93 <- standardize(lmer(RR.In.Con ~ -1 + Compliance + Value + Age + Size + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme94 <- standardize(lmer(RR.In.Con ~ -1 + Compliance + Value + Age + Size + Aquarium + Value:Aquarium + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme95 <- standardize(lmer(RR.In.Con ~ -1 + Value + Age + Size + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme96 <- standardize(lmer(RR.In.Con ~ -1 + Value + Age + Size + Aquarium + Value:Aquarium + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme97 <- standardize(lmer(RR.In.Con ~ -1 + Value + Age + Size + (1|Site) + (1|Family), REML=FALSE, data = Fish), binary.inputs = "leave.alone")
lme.null <- lmer(RR.In.Con ~ 1 + (1|Site) + (1|Family), REML=FALSE, data = Fish)
7. Appendix 2 - Alternative analysis
As explained in the methods (section 3.4.2) analyses were repeated excluding response ratios that represent infinite differences. These results are not considered the main focus of the study and differences between the main and alternative analysis are fully contrasted in the discussion.

**Overall response**
Overall response ratios indicate significantly more fish within reserve boundaries than at distant control sites ($\lnRR = 0.31, \ SE = 0.077, P < 0.001$). Backtransformation reveals fish are 35% more abundant within reserves than at control sites.

**Reserve performance**
Asinan and Handumon were both found to have significantly more fish within their boundaries than their distant control sites (Table 4.1.)

Four fish families – Acanthuridae, Caesionidae, Pomacentridae and Serranidae – responded positively and significantly to protection while only Mullidae responded significantly and negatively. These findings are one of the major differences between the first and second phases of analysis.

**Univariate Analysis**
**Trophic Group**
Responses of fish within trophic groups demonstrated positive responses for all groups with low-trophic fish showing the largest response followed by top and mid-trophic. However, trophic groups did not exhibit significant responses to protection and differences between trophic groups were not significant.

**Compliance**
High compliance rated reserves showed a significant and positive response to protection while low-compliance rated reserves had a positive and non-significant response. (Table 4.6.). Comparing overall response ratios of fish within different compliance rated reserves once again reveals no significant difference between the two groups (Table 4.7.)
Target
Target and non-target fish showed positive, non-significant responses to protection with no significant difference detected between groups.

Aquarium
Fish collected for the live fish trade showed a positive and significant response to protection. No significant response was present for non-collected families. Also, no significant difference was shown to exist between groups.

Value
Low, medium and high value fish showed positive but non-significant response to protection. All levels did not significantly differ from each other.

Seasons
Fish observed during the dry season showed a positive and significant increase in densities within reserves compared to controls. Wet season observations did not show a significant response and no significant difference could be distinguished between the two groups.

Age and Size
The overall response of fish families to protection showed a small positive significant increase with reserve age \((\beta = 0.02714, \text{SE} 0.01285, \text{D} = 802, n = 253)\). With the overall response to reserve size showing a similar trend \((\beta = 0.011152, \text{SE} 0.004353, \text{D} = 800, n = 253)\)
Table 7.1. Results of univariate analysis. Positive results indicate more fish found within reserve boundaries than at matched control sites. Significant results are indicated by estimates being 2 SE from zero.

<table>
<thead>
<tr>
<th>Variable</th>
<th>lnRR</th>
<th>SE</th>
<th>D</th>
</tr>
</thead>
<tbody>
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<td>Compliance</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Compliance A</td>
<td>0.4898</td>
<td>0.1935</td>
<td>800</td>
</tr>
<tr>
<td>Compliance B</td>
<td>0.1480</td>
<td>0.1935</td>
<td>800</td>
</tr>
<tr>
<td>Trophic</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low-trophic</td>
<td>0.4162</td>
<td>0.2443</td>
<td>802</td>
</tr>
<tr>
<td>Mid-trophic</td>
<td>0.2108</td>
<td>0.2329</td>
<td>802</td>
</tr>
<tr>
<td>Top-trophic</td>
<td>0.3520</td>
<td>0.2606</td>
<td>802</td>
</tr>
<tr>
<td>Season</td>
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</tr>
<tr>
<td>Dry</td>
<td>0.4088</td>
<td>0.1750</td>
<td>800</td>
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<tr>
<td>Wet</td>
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<td>0.1785</td>
<td>800</td>
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<tr>
<td>Traded</td>
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<td>801</td>
</tr>
<tr>
<td>Non-traded</td>
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<td>0.1884</td>
<td>801</td>
</tr>
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<td>1978</td>
</tr>
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<td>Non-target</td>
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<tr>
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<td>Mid-value</td>
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<tr>
<td>High-value</td>
<td>0.3519</td>
<td>0.2601</td>
<td>802.3</td>
</tr>
</tbody>
</table>

Table 7.2. Comparison of fish responses to protection between levels of categorical variables. Differences in lnRR values between levels are given as ΔlnRR, also standard error estimates (SE), model deviance estimates (D). All estimates where obtained from univariate analyses using linear mixed effects models and site and family as crossed random effects. As above, significant differences are ΔlnRR estimates more than twice the standard error from zero.

<table>
<thead>
<tr>
<th>Variable</th>
<th>ΔlnRR</th>
<th>se</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>Compliance</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Compliance-A / Compliance-B</td>
<td>-0.3418</td>
<td>0.2331</td>
<td>800</td>
</tr>
<tr>
<td>Trophic</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low-trophic / Mid-trophic</td>
<td>-0.2055</td>
<td>0.30367</td>
<td>802</td>
</tr>
<tr>
<td>Low-trophic / Top-trophic</td>
<td>-0.0642</td>
<td>0.32544</td>
<td>802</td>
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<tr>
<td>Mid-trophic/ Top-trophic</td>
<td>0.14124</td>
<td>0.31692</td>
<td>802</td>
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<tr>
<td>Season</td>
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<td></td>
</tr>
<tr>
<td>Dry / Wet</td>
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<td>0.1406</td>
<td>800</td>
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<tr>
<td>Aquarium</td>
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<td>Traded / Non-traded</td>
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<td>801</td>
</tr>
<tr>
<td>Target</td>
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<td></td>
<td></td>
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<tr>
<td>Target / Non-target</td>
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<td>0.25291</td>
<td>802</td>
</tr>
</tbody>
</table>
Model ranking

Ranking hypothesised models by AIC revealed that the top model was a far superior fit to alternative models as shown by the $\Delta$AIC of model #2 (Table 7.3).

Table 7.3. Hypotheses shown are the top models ordered by $\Delta$AICc. Also shown are the log likelihoods, differences from the best model AICc ($\Delta$AICc), and Akaike model weights ($w$). All interactions include lower order main effects (e.g., “Compliance * size” represents a model that includes an interaction between Compliance and Size as well as single variables for Compliance and Size), as well as crossed random effects for Reserve, and Family. This table illustrates the superior fit of model 1 in comparison to the second model.

<table>
<thead>
<tr>
<th>#</th>
<th>Hypothesis Inside Reserves vs. Control Sites</th>
<th>logLik</th>
<th>$\Delta$AIC</th>
<th>$w$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>(Compliance<em>Size) + (Value</em> Size) + Age</td>
<td>-389.620</td>
<td>0</td>
<td>0.35</td>
</tr>
<tr>
<td>2</td>
<td>(Compliance *Size) + Trophic + Age</td>
<td>-393.759</td>
<td>3.89</td>
<td>0.05</td>
</tr>
</tbody>
</table>

Inference of relationships between variables was therefore taken from coefficients of the top model as model averaging was deemed unnecessary.

Table 7.4. Fixed effect parameter estimates, standard errors and indicator of significance. Estimates are generated from the top model ranked by AICc (Table 4.12.) . Significant results are indicated by estimates being 2 xSE from zero and are marked by a '*' in the 'Significance' column for clarity.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Coefficient Estimate</th>
<th>SE</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Compliance A</td>
<td>0.4926</td>
<td>0.2175</td>
<td>*</td>
</tr>
<tr>
<td>Compliance B</td>
<td>0.0914</td>
<td>0.2219</td>
<td></td>
</tr>
<tr>
<td>Medium Value</td>
<td>-0.2107</td>
<td>0.3031</td>
<td></td>
</tr>
<tr>
<td>High Value</td>
<td>-0.0405</td>
<td>0.3139</td>
<td></td>
</tr>
<tr>
<td>Age</td>
<td>-0.4321</td>
<td>0.1994</td>
<td>*</td>
</tr>
<tr>
<td>Size</td>
<td>0.7375</td>
<td>0.2809</td>
<td>*</td>
</tr>
<tr>
<td>Compliance * Size</td>
<td>-1.356</td>
<td>0.3794</td>
<td>*</td>
</tr>
<tr>
<td>Medium Value *Size</td>
<td>-0.3728</td>
<td>0.3345</td>
<td></td>
</tr>
<tr>
<td>High Value* Size</td>
<td>0.6632</td>
<td>0.3402</td>
<td></td>
</tr>
</tbody>
</table>
**Model Coefficients**

Model coefficients indicate that low value fish have a positive, significant response to protection in high-compliance reserves while they have less positive and non-significant response in low-compliance reserves. Medium value fish respond positively within high-compliance reserves while they show a negative response in low-compliance reserves; both responses are non-significant. High value fish have a positive non-significant response in both high and low compliance reserves; the magnitude of response is smaller in low-compliance reserves.

**Age**

As reserves get older, the response of fish to protection declines, as indicated by the negative and significant slope for all fish (Table 7.4)

**Size**

The presence of the size value interaction indicates that fish assigned to different categories of value respond disparately as reserve size increases or decreases. High value fish have the strongest positive response, followed by low value fish; both responses are significant. The impact of increasing reserve size is also positive for Medium value fish but is non-significant. The interaction between compliance and size indicates that within low compliance rated reserves fish respond significantly more negatively to increasing reserve size.