

2018

THE IMPACT OF FISHERIES MANAGEMENT ON CORAL REEF FISH COMMUNITIES AND LIFE-HISTORY CHARACTERISTICS

Diky Suganda
University of Rhode Island, superdiky.fisheries@gmail.com

Follow this and additional works at: <https://digitalcommons.uri.edu/theses>

Recommended Citation

Suganda, Diky, "THE IMPACT OF FISHERIES MANAGEMENT ON CORAL REEF FISH COMMUNITIES AND LIFE-HISTORY CHARACTERISTICS" (2018). *Open Access Master's Theses*. Paper 1288.
<https://digitalcommons.uri.edu/theses/1288>

This Thesis is brought to you for free and open access by DigitalCommons@URI. It has been accepted for inclusion in Open Access Master's Theses by an authorized administrator of DigitalCommons@URI. For more information, please contact digitalcommons@etal.uri.edu.

THE IMPACT OF FISHERIES MANAGEMENT ON CORAL
REEF FISH COMMUNITIES AND LIFE-HISTORY

CHARACTERISTICS

BY

DIKY SUGANDA

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE

REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

IN

BIOLOGICAL AND ENVIRONMENTAL SCIENCES

UNIVERSITY OF RHODE ISLAND

2018

MASTER OF SCIENCE THESIS

OF

DIKY SUGANDA

APPROVED:

Thesis Committee:

Major Professor Austin Humphries

Kathleen Castro

Jeremy Collie

Nasser H. Zawia
DEAN OF THE GRADUATE SCHOOL

UNIVERSITY OF RHODE ISLAND
2018

ABSTRACT

Indonesia's coral reefs support over half of all small-scale fishers globally and are thus an important economic and sociocultural resource. These coral reef fisheries, however, are threatened from a variety of stressors including overexploitation. No-take fisheries closures are thought to be a suitable management strategy in Indonesia that provide a refuge for fish species with different ecological and life-history characteristics. While examining such indicators is increasingly important to determine management efficacy, few have done so in Indonesia. I investigate community ecological and life-history responses to no-take fisheries closures using abundance data from 2009-2015 in three regions across Indonesia's Sunda Banda Seascape. Overall, fish biomass was 30% greater in no-take closures than fished reefs. The only functional groups to respond to management were corallivores and detritivores, and fished reefs had greater biomasses of these groups. No-take closures had fish communities with greater maximum lengths, longer life spans, slower growth rates, and higher mean trophic levels. Surprisingly, total fish biomass was not a good predictor for life history values or functional group biomass. These results indicate that non-target fish species may thrive in fished reefs where predators with slow life histories are reduced. Also, no-take closures in Indonesia's Sunda Banda Seascape are facilitating recovery of life-history characteristics and fish biomass but these impacts are not uniformly distributed across functional groups. My findings are of value to current ecosystem-based management objectives attempting to achieve broader conservation goals of maintaining ecological sustainability.

ACKNOWLEDGMENTS

The completion of this thesis would not have been possible without the guidance and support of many people. First, thank you Dr. Austin Humphries for the opportunity to learn about many different coral reef fish species, for his guidance and patience while working with me. My sincere gratitude to my committee members Prof. Jeremy Collie and Dr. Kathleen Castro for their advice.

I would like to thank my Indonesian friends and my lab mates in Rhode Island, for their companionship during my study. I would like to acknowledge the sources of my financial support: Bappenas (Pak Gellwynn) and Coremap DGCF MMAF in Jakarta. Last but not least, I would like to thank my lovely wife (Asriyani), my beautiful daughter (Aisha) and also my big family in Indonesia for their constant, continuing support so that my thesis came together.

PREFACE

This thesis is written in manuscript format and adheres to the guidelines of the Graduate School of the University of Rhode Island. The manuscript is formatted in accordance with the guidelines set forth for publication in *Fisheries Research*.

TABLE OF CONTENTS

ABSTRACT.....	ii
ACKNOWLEDGMENTS	iii
PREFACE	iv
TABLE OF CONTENTS.....	v
LIST OF TABLES	vi
LIST OF FIGURES	vii
MANUSCRIPT-1.....	1
1. Introduction	3
2. Materials and methods	6
2.1. Field methods	6
2.2 Data analyses	7
2.3. Statistical analyses	9
3. Results.....	9
3.1. Total fish biomass.....	9
3.2. Functional group biomass.....	10
3.3. Life-history characteristics	11
4. Discussion	12
5. Conclusions	16
6. References	17

LIST OF TABLES

TABLE	PAGE
Table 1. Mean biomass (kg/ha) of reef fish communities on fished reefs and no-take closures in three Sunda Banda Seascape regions	26
Table 2. Mean biomass (kg/ha) of reef fish families in fished reefs and no-take closures of the Sunda Banda Seascape.....	27
Table 3. Statistical results testing the impact of region, management, and their interaction on biomass of reef fish	28
Table 4. Mean values (kg/ha) and results from individual t-tests of mean functional group biomass from fished reefs versus no-take closures in the Sunda Banda Seascape	29
Table 5. Functional group classifications and life history values of the 25 most abundant reef fish in the Sunda Banda Seascape	30
Table 6. Mean values and results from individual t-tests of mean life-history characteristics from fished reefs versus no-take closures in the Sunda Banda Seascape	31

LIST OF FIGURES

FIGURE	PAGE
Fig. 1. Study sites within Indonesia’s Sunda Banda Seascape across the Wakatobi (a), Alor (b), and Koon-Kei (c) regions.....	32
Fig. 2. Relationship of mean (and standard error) functional group fish biomass (kg/ha) between fished reefs and no-take closures. Different letters above bars indicate statistical differences between management based on individual t-tests	33
Fig. 3. Relationship between log biomass and functional group biomass by management type (blue = fished reefs; orange = no-take closures).....	35
Fig. 4. Boxplot of median and quartile range of community-level mean maximum length (cm), life span (yrs), growth rate (cm/yr), and trophic level for fished reefs and no-take closures. Letters above boxplots indicate statistical differences between management based on individual t-tests	39
Fig. 5. Relationship between reef fish biomass (log) and functional group by management (blue = fished reefs; orange = no-take closures).....	40

Manuscript-1

Prepared for submission to *Fisheries Research*

The Impact of Fisheries Management on Coral Reef Fish Communities and Life-History Characteristics

Diky Suganda¹, Austin Humphries^{1,2}

¹ Department of Fisheries, Animal and Veterinary Sciences, University of Rhode Island, Kingston, RI, 02881 USA

² Graduate School of Oceanography, University of Rhode Island, Narragansett, RI, 02882 USA

Corresponding Author: Diky Suganda
Department of Fisheries, Animal and Veterinary
Sciences
University of Rhode Island
Kingston, RI 02881
Tel: 401-932-3665
Email: superdiky@my.uri.edu

Abstract

Indonesia's coral reefs support over half of all small-scale fishers globally and are thus an important economic and sociocultural resource. These coral reef fisheries, however, are threatened from a variety of stressors including overexploitation. No-take fisheries closures are thought to be a suitable management strategy in Indonesia that provide a refuge for fish species with different ecological and life-history characteristics. While examining such indicators is increasingly important to determine management efficacy, few have done so in Indonesia. We investigate community ecological and life-history responses to no-take fisheries closures using abundance data from 2009-2015 in three regions across Indonesia's Sunda Banda Seascape. Overall, fish biomass was 30% greater in no-take closures than fished reefs. The only functional groups to respond significantly to management were corallivores and detritivores, and fished reefs had greater biomasses of these groups. No-take closures had fish communities with greater maximum lengths, longer life spans, slower growth rates, and higher mean trophic levels. Surprisingly, total fish biomass was not a good predictor for life history values or functional group biomass, as none of these indicators responded to fish recovery. Our results indicate that non-target fish species may thrive in fished reefs where predators with slow life histories may be reduced. Also, no-take closures in Indonesia's Sunda Banda Seascape are facilitating recovery of life-history characteristics and fish biomass but these impacts are not uniformly distributed across functional groups. These findings are of value to current ecosystem-based management objectives attempting to achieve broader conservation goals of maintaining ecological sustainability.

1. Introduction

Coral reefs are an extremely important ecosystem because of biological, ecological, and socioeconomic reasons. They are one of the most biodiverse and productive ecosystems in the world, matching rainforests in their richness of life (Birkeland 1997). They constitute less than 0.1% of the ocean floor (Spalding et al. 2001) but support greater than 30% of all known fish species (Sorokin 2013). Coral reefs are critical for both economic security and food security because they sustain the lives of more than 130 million coastal communities and supply global markets, providing ecosystem services to coastal communities that include fisheries, aquaculture, tourism, coastal protection, and transport (Moberg & Folke 1999). Coral reefs, however, are sensitive to a myriad of natural and anthropogenic stressors, primarily through invasive species, climate change, pollution, and destructive fishing practices (Edinger 1998; McClanahan 2007, Wenger 2016). In particular, the impact of overfishing has been shown to severely damage coral reef fish community structure and functioning (Jennings & Kaiser 1998; Roberts 1995). These changes come as a result of a reduction in fish abundance, shifts in body size distribution, diversity, and biomass (Jennings et al. 1999; Graham et al. 2007; Worm et al. 2009; McClanahan & Humphries 2012).

Indonesian coral reefs cover 32,000 km² or about 18% of the world's coral reef area, which is the second largest in the world after the Great Barrier Reef in Australia (Nontji 2002). Indonesia's Sunda Banda Seascape (SBS) has been designated as the second most important marine ecological region in Indonesia in terms of its biodiversity (Wang et al. 2015). The SBS is 151 million hectares that stretches from Bali to Nusa Tenggara and Maluku Tenggara, as well as the southern and eastern sides of Sulawesi. The SBS

provides habitat for 76% of known coral species globally, and over 3000 fish species (Veron et al. 2009). These coral reefs, however, are at constant risk of degradation due to natural and anthropogenic stressors. A recent study by the Indonesian government suggests that less than 7% of coral reefs in the SBS are in ‘excellent’ condition (76-100 percent of live coral cover), and 35% are functionally obsolete (Giyanto et al. 2017).

Fisheries management and harvest tools, such as gear restrictions, periodically harvested closures, and Marine Protected Areas (MPA) have been implemented to protect coral reef fisheries from decline and collapse (Friedlander 2015). MPAs, for example, have been widely promoted as strategy for an ecosystem approach to fisheries management (Hastings & Botsford 1999; Claudet et al. 2006), potentially benefiting both fisheries and conservation objectives (Claudet et al. 2010, Rodrigues et al. 2004). Evidence supporting these claims, however, is limited; managing for coral reef fisheries production along with biodiversity conservation remains as a major challenge (Balmford et al. 2005). While such MPAs provide a refuge to a variety of fish species (Di Lorenzo et al. 2016), they may not provide protection to fish with different life-history and ecological characteristics. Furthermore, the efficacy of MPAs to increase fish biomass and diversity has been proven to be dictated by the ability of management to enforce regulations (Gill et al. 2017). This presents particular problems for Indonesia where MPAs are often touted as a panacea for management solutions but capacity to enforce them is low.

Ecosystem functionality highlights feeding functional groups and multiple processes involved in the transfer of energy and matter over time and space (Reiss et al. 2009). Trophic guilds (i.e., feeding functional groups) have thus become important tools

in providing a better understanding of the structure and functioning of fish assemblages (Mathieson et al. 2000). Feeding functional group affects distribution, abundance, and demographics of the fish community. These processes can be dynamic, changing population productivity and trophic structure at ecological or evolutionary time scales (Brodeur et al. 2017). Viewing ecosystems through this functional group lens is particularly well-suited for coral reef systems that are incredibly diverse. It is important in coral reefs to enable description of community-level feeding patterns and determine how habitat is influenced by fish functional groups and which species or taxa are critical in maintaining an ecosystem (Edwards et al. 2014).

Patterns of recovery are controlled by ecological organization principles such as competition and predator-prey interactions (McClanahan et al. 2007). For example, species with life-history characteristics that support fast growth and short generation times can maintain populations and production under high fishing mortality, but they are expected to experience genetic change under new conditions and associated selection pressures (McClanahan & Graham 2015). The opposite is true with fishes characterized by slow growth rates and low natural mortality and protection from fishing can take a long time to recover such life histories (McClanahan & Humphries 2012). These trade-offs are poorly understood in diverse coral reef fish communities. Thus, in order for fisheries management to be successful at maintaining not only fisheries-specific goods and services from coral reefs but also the portfolio of characteristics necessary to support resilience and tourism, such life-history characteristics should be examined (Taylor et al. 2014).

Classical fisheries management relies on life-history characteristics such as growth, reproduction, and longevity as the basis for key indicators of productivity and maximum sustainable yield (Walters & Martell 2004). In coral reef systems that lack data, less attention has been given to life-history characteristics which are also important in evaluations of the increasing frequency and magnitude of anthropogenic and climate stressors (McClanahan & Humphries 2012). This study is intended to provide a greater understanding of how fisheries management impacts fish communities by comparing ecological indicators between fished reefs and no-take fisheries closures. Specifically, we investigated the efficacy of no-take closures in protecting or recovering coral reef fish assemblages and traits, thus bolstering ecosystem functioning. Utilizing a large dataset of coral reef fish abundances, we evaluated changes in biomass, functional groups, as well as key life-history characteristics of coral reef fish communities of the Sunda Banda Seascape in Indonesia. We hypothesized that reef fish communities would shift towards larger, slower growing fish in no-take closures, and community biomass would be higher in these closures, particularly for piscivores and herbivores that are target species.

2. Materials and Methods

2.1. Field Methods

Abundance data for fish were collected by the non-governmental organization World Wildlife Fund (WWF) within the three regions in the Sunda Banda Seascape (SBS; Fig. 1). Regions studied included Wakatobi, Alor Timur, Koon-Kei, and data were collected between 2009 and 2015. Individual sampling sites were classified as

either being a fished reef, where fishing activities were open to everyone, or no-take closures where fishing activities were prohibited and enforced. If enforcement capabilities of local authorities were unknown or in question, the data were not used in analyses.

At sampling sites, species, size, and number of fish found in 5 x 50 meters belt transects were recorded and tabulated using underwater visual census (UVC; English et al. 1994; Samoilys & Carlos 2000). Three to five replicates were carried out for each site. In order to minimize any biases during UVC, divers were trained prior to the field sampling on species identification and all trained divers swam slowly (approximately 30 minutes per transect) with an average depth of 10 meters. Coral boulders within transects were circumnavigated in order to count and identify reef fish hidden from view. Fish smaller than 10 cm were excluded to reduce errors in density comparisons. Large transect widths and lengths were selected to reduce inconsistency between transects, to include species at low densities, and to minimize flight distance effects observed in certain species (Bellwood & Alcala 1988).

2.2. *Data analyses*

Estimated fish size and count data were converted into biomass using species-specific length-weight relationships (Letourneur et al. 1998; Froese & Pauly 2012; McClanahan et al. 2015) where:

$$W = aL^b$$

a and b are growth coefficients retrieved from FishBase and L is total length (cm). We then converted each 250 m² transect to kilograms per hectare (kg/ha) to be consistent with the literature.

We determined each individual's functional group at the genus-level based on diet and foraging strategies (Wilson et al. 2008; Froese & Pauly 2012). We obtained these classifications from FishBase and categorized each individual as one of the followings: corallivore, detritivore, grazer, invertivore, piscivore, planktivore, and scraper. Grazers and scrapers are both types of herbivores but were not lumped together for our analyses because they have been shown to have differential effects on reef functioning and structure (Humphries et al. 2015).

Life history characteristics of individual species included in this study were maximum length, growth rate, and life span. We retrieved species-level values for these using FishBase (www.fishbase.org). Non-existing life-history parameters of certain species were estimated from studies of the closest genus or family level. Maximum length represents the greatest size ever reported for that particular species. Intrinsic growth rate is an estimate of the growth of individuals in size or length for a given time period as a fraction of the population at the beginning of a time period. Life span is the approximate maximum age that fish of a given population would reach. Trophic level of a species is a unitless metric which represents its position in the food chain and it is estimated based on diet composition. For example, a high trophic level value such as 4 may represent a piscivorous species (e.g., apex predators such as sharks), and conversely, a low trophic level value may represent an herbivorous fish species. Community-level weighted averages for life histories and trophic level (resulting in 'mean trophic level') were calculated for each year (k) as:

$$LH = \frac{\sum i Y_i LH}{\sum Y_i}$$

where Y_i is the biomass of species i (per transect), and LH is the life-history characteristic of interest (McClanahan & Humphries 2012).

2.3. Statistical analyses

We used a linear mixed effects model to determine if region, management, or their interaction influenced fish biomass. To account for site-level differences within each region ($n = 3$), site was included in the model as an orthogonal nested random effect. Biomass was not normally distributed (determined using a Kolmogorov-Smirnov test), and thus a log-transformation was necessary. We used an alpha value of 0.05 for statistical significance. We used individual t-tests to compare functional group biomass of fishes between fished reefs and no-take closures for corallivores, detritivores, grazers, invertivores, piscivores, planktivores, and scrapers. We also used individual t-tests to compare life-history characteristics of maximum length, growth rate, life span, or trophic level between management zones. Last, we used linear regression to explore relationships between the recovery of fish biomass on reefs and functional group biomass as well as individual life-history characteristics.

3. Results

The dataset ended up consisting of 193 unique sites: Wakatobi contained the most sites ($n = 126$), followed by Alor ($n = 47$), and Koon-Kei ($n = 20$; Fig. 1). A total of 9,899 individuals were included, belonging to 293 species, 77 genera, and 24 families.

3.1. Total fish biomass

Mean biomass of reef fish in the no-take closures was 30% greater than biomass on fished reefs (Table 1). The difference was the most prevalent in Alor, where biomass in

the no-take closures was 86% greater than that in the fished reefs. Similarly, although smaller, there was 14% increase of reef fish biomass in Wakatabi's no-take closures compared to its fished reef areas. On the contrary, Koon-Kei acted differently, where reef fish biomass in no-take closure (401 kg/ha) was found to be 5% lower than the biomass in fished reef (424 kg/ha).

Based on their high abundance, Acanthuridae was the most dominant family in the Sunda Banda Seascape, followed by Scaridae, and Lutjanidae (Table 2). All of these families had greater than 200 kg/ha on both fished reefs and no-take closures. After these top 3 families, there were numerous less abundant families with biomass levels below 100 kg/ha, such as: Haemulidae, Serranidae, Lethrinidae, Siganidae, Holocentridae. The families of Pomacentridae, Tetradontidae, and Zanclidae were found only in fished reefs but not in no-take closures.

There was a significant effect of management on the overall biomass of fish in the Sunda Banda Seascape ($p = 0.023$), whereas region had no significant effect (Table 3). Also, there was no significant interaction between region and management for biomass.

3.2. *Functional group biomass*

Based on total functional group biomass, no-take closures were dominated by grazers (1067 kg/ha), piscivores (495 kg/ha), and scrapers (454 kg/ha; Fig. 2). There were very few corallivores (7 kg/ha) or detritivores (37 kg/ha) in no-take closures, whereas their existence was abundant in fished reefs. Comparisons of individual functional groups revealed that corallivore and detritivore were significantly different between management zones ($p < 0.05$), with both being higher in fished reefs (Table 4). The biomass of grazers, invertivores, piscivores, planktivores, and scrapers found in

fished reefs were comparable to that in no-take closures ($p > 0.05$). As fish biomass increased across the sites, functional group biomass did not respond predictably (Fig. 3). No linear regressions had an R^2 value greater than 0.15 and none were statistically significant. Although, there were trends of an inverse relationship between total biomass and functional group biomass for corallivores, detritivores, invertivores, and planktivores.

3.3. *Life-history characteristics*

We found that *Bolbometopon muricatum*, *Naso hexacanthus* and *Lutjanus bohar* had the highest maximum length values of all species in the dataset: 130 cm, 100 cm and 90 cm, respectively (Table 5). Life spans of reef fish were highly varied, ranging from the shortest of 2 years (*Cephalopholis urodeta*) to the longest-lived species of 31.8 years (*Lutjanus bohar*). On the contrary, these two fish were found as the fastest and slowest growth rate species, respectively. Meanwhile, feeding functional groups of dominant reef fish were grazer, piscivore, invertivore, and scraper. The species with the highest trophic level (TL) found in the study sites was *Cephalopholis argus*, belonging to piscivore group with TL value of 4.9; all piscivores had trophic level values above 3.9. Herbivores were represented as either grazers or scrapers and they all had trophic levels between 2 and 3. Planktivores and invertivores occupied trophic levels between those of the herbivores and piscivores, around 3. There were only two detritivores in the top 25 species and they have a low trophic level of 2, similar to that of some herbivores.

Management had a significant effect on each life-history characteristic (Fig. 4). Individual t-tests showed that no-take closures had fish communities with greater maximum lengths, lower growth rates, greater life spans, and higher mean trophic levels

(Table 6). The maximum length for fished reefs was 47.2 cm compared to 55 cm in no-take closures. The mean trophic levels were both below 3, however, the no-take closures were greater at 2.83 versus 2.69 in the fished reefs. Life span was 11.2 years in the closures and only 9.3 years in the fished reefs.

Linear regressions indicated that while there were increasing trends of maximum length and life span of reef fish in both management areas as total biomass increased, these were not significant or very predictive ($R^2 < 0.1$; Fig. 5). Trophic level showed no sign of increase or decrease with fish biomass on reefs, regardless of management. In addition, growth rates decreased slightly along the fish biomass gradient.

4. Discussion

Our primary hypotheses in this study were supported but with some important nuances. No-take fisheries closures in Indonesia's Sunda Banda Seascape were an effective management strategy to increase total fish biomass, but this was spread rather indiscriminately across functional groups. In other words, target groups such as piscivores and scrapers showed no statistically significant differences between fished and protected reefs. Community life histories changed as expected towards larger, slower growing and long-lived fauna in the no-take closures. Our results agree with life-history theory and a number of previous studies that measure fish abundance and biomass responses to management (e.g., Halpern & Warner 2002; Rakitin & Kramer 1996; Russ & Alcala 1996; Watson et al. 1996; Jennings & Kaiser 1998; and McClanahan & Humphries 2012). What is less clear is why functional groups did not

respond as strongly to management and why our indicators were not strongly correlated on a continuous gradient with biomass.

One of our sites, Koon-Kei, had fish biomass on fished reefs that was slightly higher than the biomass in no-take closures. In this case, level of protection did not necessarily associate with an increase in biomass. However, McClanahan et al. (2008) and Claudet et al. (2008) found that size and age of no-take closures can also influence fish communities. The no-take closures in Koon-Kei were established in 2012, or three years before the sampling was conducted in 2015. Some studies suggested that fish density and species richness increasing after three years of protection (Halpern & Warner 2002, Russ et al. 2005). We also note that fishing is not the lone factor responsible to fish biomass but there are other aspects such as habitat and environmental parameters which create sub-regions within the SBS (Rochet & Trenkel 2003). For instance, Wang et al. (2015) delineated the SBS based on environmental conditions such as temperature, currents, and primary productivity, and Koon-Kei was in a different class than Wakatobi and Alor. Furthermore, Tegner (1993) and Armstrong et al. (1993) indicated that no-take closures performed poorly when they were located in unfavorable habitats or contained an insufficient portion of critical habitats. A number of these factors may help explain why this region did not show the same trends as the other, but we do not have sufficient data to tease apart these mechanisms.

The coral reef fish communities in the SBS were multispecies and spanned a broad trophic spectrum from detritivore to apex predators (piscivore). We found that Acanthuridae, Scaridae, Lutjanidae and Haemulidae were the dominant families in both management regimes. This result, along with the fact that the associated functional

groups also had similar compositions in both management regimes, was somewhat surprising. However, non-selective fishing has been shown to have an equal impact across all families and functional groups for fisheries in Kenya (McClanahan 1995). Our study also revealed that lower trophic level fish were more abundant in fished reef area, suggesting that these fish is non-targeted by the fishers or their predators have been removed (e.g., Botsford 1997; Hall 1999). Chaetodontidae are also highly dependent on coral cover, so habitat quality and quantity may be interacting to influence these findings (Coker et al. 2014).

Our study revealed that all life-history characteristics showed a predictable and significant response to management. No-take closures contained fish communities that had greater maximum lengths, slower growth rates, and longer life spans. The result conformed with our central hypothesis and previous studies (e.g., McClanahan et al. 2014). Trophic level was also greater in the no-take closures, which has been shown to be highly variable and even lower because of a dominance of herbivores that are slow to recover (McClanahan & Humphries 2012).

Growth rate is a plastic trait which can vary in response to environmental conditions such as food availability (Overholtz 1989; Lorenzen & Enberg 2002) and water temperature (Jorgensen 1992; Brander 1995; Daufresne et al. 2009). Our study showed that growth rate was slower in no-take closure compared to fished reef, indicating that no-take closure provided a better environment for bigger reef fish to grow and to live longer. In contrast, higher growth rates in fished reefs indicate that fish can mature faster, turning over faster and providing increases in fisheries production that is resilient to high fishing pressure.

Most fisheries preferentially target larger species and individuals (Jennings & Polunin 1997). However, we also noted that coral reef fisheries in Indonesia are characterized by artisanal fishers where the fishers do not necessarily only target specific species and sizes to meet their daily consumption. It is important to protect large, old, and mature fish from fishing as these have greater reproductive potential than the younger ones (Birkeland & Dayton 2005). Our findings revealed that fish found in no-take closure had higher life span and maximum length compared to that in fished reef, suggesting that a more mature and larger fish are abundant and the management can be successful for bolstering recruitment in surrounding areas.

Our study also showed that lower trophic level species were almost non-existent in no-take closure. This result indicated that protected areas favored higher trophic level species. We also noted that piscivory is considered as the main process of energy transfer in coral reef ecosystems (Parish et al. 1986; Hixon 1991). Therefore, this result indicates that piscivory may be contributing to a rapid decrease of these prey species (low trophic level) in the no-take closure area and future analyses should investigate size-spectra as another indicator for management efficacy. On the flip side of this, we found a very high proportion of lower trophic level species such as corallivores and detritivores on fished reefs. These functional groups were fast growing species and have relatively low contribution to fisheries yield in the SBS.

We recognize our findings have some limitations to consider. For instance, using global databases such as FishBase in this study may introduce bias in the analysis of fish life-history characteristics. This is because those data are not geographically specific to Indonesia and some of the values were obtained from studies in the Caribbean

or when species were not available, the next closest relative. However, due to limited data available in Indonesia for the myriad of coral reef fish species, we have to assume that the data from those previous studies are better than any other alternative at this time. In addition to this is the issue of covariates driving fish community composition outside of fishing pressure. We previously discussed things like habitat quality and quantity, as well as environmental characteristics, but enforcement has been shown to be the strongest predictor of fish biomass on a global scale (Gill et al. 2017). We addressed this issue by removing any data from no-take closures where it was not clear how well it was managed by communicating with WWF and the field team that collected the data. We have no way of knowing these values for our dataset and therefore have to treat all no-take closures as equal even though we acknowledge the bias this may introduce.

5. Conclusions

This study demonstrated that fishing activity affected the biomass and community level life-history characteristics of reef fish in Sunda Banda Seascape (SBS) of Indonesia. Our findings corroborate other study by Davis & Dodrill (1989) that no-take closure produced positive results for some species and functional groups, but not others. Although community biomass did not increase in all three regions with no-take closures or across all functional groups, closures did provide protection for larger, slower growing high trophic level species. Non-target fish species may thrive in fished reefs where predators with slow life histories may be reduced. Future research should look to incorporate things like habitat, enforcement and environmental conditions to test whether these have greater impacts on fish community characteristics than fishing.

To safeguard sustainable coral reef fisheries in the SBS, we suggest no-take closures should continue to established but to also look for alternative strategies that may provide complimentary benefits for functional groups and fish life histories. Such adaptive management strategies might include things like a gear restriction or temporal closures in heavily fished areas. These strategies may improve coral reef fish resilience to interacting effects of fishing and climate.

6. References

- Armstrong, D. A., Wainwright, T. C., Jensen, G. C., Dinnel, P. A., and Andersen, H. B. Taking refuge from by-catch issues: red king crab (*Paralithodes camtschaticus*) and trawl fisheries in the Eastern Bering Sea. *Canadian Journal of Fisheries and Aquatic Sciences*, no. 50 (1993): 1993–2000.
- Balmford, Andrew, Peter Crane, Andy Dobson, Rhys E. Green, and Georgina M. Mace. "The 2010 challenge: data availability, information needs and extraterrestrial insights." *Philosophical Transactions of the Royal Society B: Biological Sciences* 360, no. 1454 (2005): 221-228.
- Bellwood, D. R., and A. C. Alcala. "The effect of a minimum length specification on visual estimates of density and biomass of coral reef fishes." *Coral reefs* 7, no. 1 (1988): 23-27.
- Birkeland, Charles. *Life and death of coral reefs*. Springer Science & Business Media, 1997.
- Birkeland, Charles, and Paul K. Dayton. "The importance in fishery management of leaving the big ones." *Trends in Ecology & Evolution* 20, no. 7 (2005): 356-358.

- Botsford, Louis W., Juan Carlos Castilla, and Charles H. Peterson. "The management of fisheries and marine ecosystems." *Science* 277, no. 5325 (1997): 509-515.
- Brander, K. M. "The effect of temperature on growth of Atlantic cod (*Gadus morhua* L.)." *ICES Journal of Marine Science* 52, no. 1 (1995): 1-10.
- Brodeur, Richard D., Brian E. Smith, Richard S. McBride, Ron Heintz, and Ed Farley. "New perspectives on the feeding ecology and trophic dynamics of fishes." *Environmental Biology of Fishes* 100, no. 4 (2017): 293-297.
- Claudet, Joachim, Dominique Pelletier, J-Y. Jouvenel, F. Bachet, and R. Galzin. "Assessing the effects of marine protected area (MPA) on a reef fish assemblage in a northwestern Mediterranean marine reserve: Identifying community-based indicators." *Biological conservation* 130, no. 3 (2006): 349-369.
- Claudet, Joachim, Craig W. Osenberg, Lisandro Benedetti-Cecchi, Paolo Domenici, José-Antonio García-Charton, Ángel Pérez-Ruzafa, Fabio Badalamenti et al. "Marine reserves: size and age do matter." *Ecology letters* 11, no. 5 (2008): 481-489.
- Claudet, Joachim, C. W. Osenberg, Paolo Domenici, Fabio Badalamenti, Marco Milazzo, Jesús Manuel Falcón, Iacopo Bertocci et al. "Marine reserves: fish life history and ecological traits matter." *Ecological applications* 20, no. 3 (2010): 830-839.
- Coker, Darren J., Shaun K. Wilson, and Morgan S. Pratchett. "Importance of live coral habitat for reef fishes." *Reviews in Fish Biology and Fisheries* 24, no. 1 (2014): 89-126.

- Daufresne, Martin, Kathrin Lengfellner, and Ulrich Sommer. "Global warming benefits the small in aquatic ecosystems." *Proceedings of the National Academy of Sciences* 106, no. 31 (2009): 12788-12793.
- Davis, Gary E., and Jon W. Dodrill. "Recreational fishery and population dynamics of spiny lobsters, *Panulirus argus*, in Florida Bay, Everglades National Park, 1977–1980." *Bulletin of Marine Science* 44, no. 1 (1989): 78-88.
- Di Lorenzo, Manfredi, Joachim Claudet, and Paolo Guidetti. "Spillover from marine protected areas to adjacent fisheries has an ecological and a fishery component." *Journal for Nature Conservation* 32 (2016): 62-66.
- Edinger, Evan N., Jamaluddin Jompa, Gino V. Limmon, Wisnu Widjatmoko, and Michael J. Risk. "Reef degradation and coral biodiversity in Indonesia: effects of land-based pollution, destructive fishing practices and changes over time." *Marine Pollution Bulletin* 36, no. 8 (1998): 617-630.
- Edwards C.B., Friedlander A.M., Green A.G., Hardt M.J., Sala E., Sweatman H.P., Williams I.D., Zgliczynski B., Sandin S.A. and Smith J.E. Global assessment of the status of coral reef herbivorous fishes: evidence for fishing effects. *Proceedings of the Royal Society Biological Sciences* no. 281(2014): 20131835.
- English, Susan S., Clive CR Wilkinson, and Valonna V. Baker. *Survey manual for tropical marine resources*. Australian Institute of Marine Science, 1997.
- Friedlander, Alan M. "21 A perspective on the management of coral reef fisheries." *Ecology of fishes on coral reefs* (2015): 208.

- Froese, Rainer, and Daniel Pauly. "Fishbase (www database)." *World Wide Web Electronic Publications*. Available at: <http://www.fishbase.org> (accessed June 2012) (2012).
- Gill, David A., Michael B. Mascia, Gabby N. Ahmadi, Louise Glew, Sarah E. Lester, Megan Barnes, Ian Craigie et al. "Capacity shortfalls hinder the performance of marine protected areas globally." *Nature* 543, no. 7647 (2017): 665.
- Giyanto et al. Status Terumbu Karang Indonesia. COREMAP CTI. Jakarta: Puslit Oseanografi – LIPI, 2017.
- Graham, Nicholas AJ, Shaun K. Wilson, Simon Jennings, Nicholas VC Polunin, J. A. N. Robinson, Jude P. Bijoux, and Tim M. Daw. "Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems." *Conservation biology* 21, no. 5 (2007): 1291-1300.
- Hall, Stephen J. *The effects of fishing on marine ecosystems and communities*. Blackwell Science Ltd, 1999.
- Halpern, Benjamin S., and Robert R. Warner. "Marine reserves have rapid and lasting effects." *Ecology letters* 5, no. 3 (2002): 361-366.
- Hastings, Alan, and Louis W. Botsford. "Equivalence in yield from marine reserves and traditional fisheries management." *Science* 284, no. 5419 (1999): 1537-1538.
- Hixon, M. "Tropical and temperate reef fishes: comparison of community structures." *The ecology of fishes on coral reefs* (1991): 509-563.
- Humphries, Austin T., Christopher D. McQuaid, and Tim R. McClanahan. "Context-Dependent Diversity-Effects of Seaweed Consumption on Coral Reefs in Kenya." *PloS one* 10, no. 12 (2015): e0144204.

- Jennings, S., and N. V. C. Polunin. "Impacts of predator depletion by fishing on the biomass and diversity of non-target reef fish communities." *Coral reefs* 16, no. 2 (1997): 71-82.
- Jennings, Simon, and Michel J. Kaiser. "The effects of fishing on marine ecosystems." In *Advances in marine biology*, vol. 34, pp. 201-352. Academic Press, 1998.
- Jennings, Simon, Simon Greenstreet, and John Reynolds. "Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories." *Journal of Animal Ecology* 68, no. 3 (1999): 617-627.
- Jørgensen, Terje. "Long-term changes in growth of North-east Arctic cod (*Gadus morhua*) and some environmental influences." *ICES Journal of Marine Science* 49, no. 3 (1992): 263-278.
- Letourneur, Y., Michel Kulbicki, and P. Labrosse. "Length-weight relationship of fishes from coral reefs and lagoons of New Caledonia: an update." *Naga, the ICLARM Quarterly* 21, no. 4 (1998): 39-46.
- Lorenzen, Kai, and Katja Enberg. "Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons." *Proceedings of the Royal Society of London B: Biological Sciences* 269, no. 1486 (2002): 49-54.
- Mathieson, S., André Cattrijsse, M. J. Costa, Pilar Drake, M. Elliott, J. Gardner, and J. Marchand. "Fish assemblages of European tidal marshes: a comparison based on species, families and functional guilds." *Marine Ecology Progress Series* 204 (2000): 225-242.

- McClanahan, T. R. "A coral reef ecosystem-fisheries model: impacts of fishing intensity and catch selection on reef structure and processes." *Ecological Modelling* 80, no. 1 (1995): 1-19.
- McClanahan, Tim R., Nicholas AJ Graham, Jacquelyn M. Calnan, and M. Aaron MacNeil. "Toward pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya." *Ecological applications* 17, no. 4 (2007): 1055-1067.
- McClanahan, T. R., M. Ateweberhan, N. A. J. Graham, S. K. Wilson, C. Ruiz Sebastián, Mireille MM Guillaume, and J. Henrich Bruggemann. "Western Indian Ocean coral communities: bleaching responses and susceptibility to extinction." *Marine Ecology Progress Series* 337 (2007): 1-13.
- McClanahan, Tim R., Nicholas AJ Graham, Shaun K. Wilson, Yves Letourneur, and Rebecca Fisher. "Effects of fisheries closure size, age, and history of compliance on coral reef fish communities in the western Indian Ocean." *Marine Ecology Progress Series* 396 (2009): 99-109.
- McClanahan, T. R., and A. T. Humphries. "Differential and slow life-history responses of fishes to coral reef closures." *Marine Ecology Progress Series* 469 (2012): 121-131.
- McClanahan, T. R., and N. A. J. Graham. "Marine reserve recovery rates towards a baseline are slower for reef fish community life histories than biomass." *Proc. R. Soc. B* 282, no. 1821 (2015): 20151938.
- McClanahan, T. R., N. A. J. Graham, M. A. MacNeil, and J. E. Cinner. "Biomass-based targets and the management of multispecies coral reef fisheries." *Conservation Biology* 29, no. 2 (2015): 409-417.

- Moberg, Fredrik, and Carl Folke. "Ecological goods and services of coral reef ecosystems." *Ecological economics* 29, no. 2 (1999): 215-233.
- Nontji, Anugerah. "Coral reefs of Indonesia: past, present and future." In *Proceedings of the Ninth International Coral Reef Symposium, Bali, 23-27 October 2000*, vol. 1, pp. 17-27. 2002.
- Overholtz, W. J. "Density-dependent growth in the Northwest Atlantic stock of Atlantic mackerel (*Scomber scombrus*)." *J. Northw. Atl. Fish. Sci* 9 (1989): 115-121.
- Parrish, James D., James E. Norris, Michael W. Callahan, Janice K. Callahan, Eric J. Magarifuji, and Robert E. Schroeder. "Piscivory in a coral reef fish community." In *Contemporary studies on fish feeding: the proceedings of GUTSHOP'84*, pp. 285-298. Springer, Dordrecht, 1986.
- Rakitin, Ana, and Donald L. Kramer. "Effect of a marine reserve on the distribution of coral reef fishes in Barbados." *Marine Ecology Progress Series* (1996): 97-113.
- Reiss, Julia, Jon R. Bridle, Jose M. Montoya, and Guy Woodward. "Emerging horizons in biodiversity and ecosystem functioning research." *Trends in ecology & evolution* 24, no. 9 (2009): 505-514.
- Roberts, Callum M. "Effects of fishing on the ecosystem structure of coral reefs." *Conservation Biology* 9, no. 5 (1995): 988-995.
- Rochet, Marie-Joëlle, and Verena M. Trenkel. "Which community indicators can measure the impact of fishing? A review and proposals." *Canadian Journal of Fisheries and Aquatic Sciences* 60, no. 1 (2003): 86-99.
- Rodrigues, Ana SL, H. Resit Akcakaya, Sandy J. Andelman, Mohamed I. Bakarr, Luigi Boitani, Thomas M. Brooks, Janice S. Chanson et al. "Global gap analysis:

- priority regions for expanding the global protected-area network." *AIBS Bulletin* 54, no. 12 (2004): 1092-1100.
- Russ, Garry R., and Angel C. Alcala. "Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines." *Marine Ecology Progress Series* (1996): 1-9.
- Samoilys, Melita A., and Gary Carlos. "Determining methods of underwater visual census for estimating the abundance of coral reef fishes." *Environmental Biology of Fishes* 57, no. 3 (2000): 289-304.
- Spalding, Mark, Mark D. Spalding, Corinna Ravilious, and Edmund Peter Green. *World atlas of coral reefs*. Univ of California Press, 2001.
- Sorokin, Yuri I. *Coral reef ecology*. Vol. 102. Springer Science & Business Media, 2013.
- Taylor, Brett M., Peter Houk, Garry R. Russ, and J. Howard Choat. "Life histories predict vulnerability to overexploitation in parrotfishes." *Coral Reefs* 33, no. 4 (2014): 869-878.
- Tegner, M. J. Southern California abalones: can stocks be rebuilt using marine refugia? *Canadian Journal of Fisheries and Aquatic Sciences* no. 50. (1993): 2010–2018.
- Veron, J. E. N., Lyndon M. Devantier, Emre Turak, Alison L. Green, Stuart Kininmonth, Mary Stafford-Smith, and Nate Peterson. "Delineating the coral triangle." *Galaxea, Journal of Coral Reef Studies* 11, no. 2 (2009): 91-100.
- Walters, Carl J., and Steven JD Martell. *Fisheries ecology and management*. Princeton University Press, 2004.

- Wang, Mingshu, Gabby N. Ahmadia, Iliana Chollett, Charles Huang, Helen Fox, Anton Wijonarno, and Marguerite Madden. "Delineating biophysical environments of the Sunda Banda Seascape, Indonesia." *International journal of environmental research and public health* 12, no. 2 (2015): 1069-1082.
- Watson, Maggie, Dave Righton, Tim Austin, and Rupert Ormond. "The effects of fishing on coral reef fish abundance and diversity." *Journal of the Marine Biological Association of the United Kingdom* 76, no. 1 (1996): 229-233.
- Wenger, Amelia S., David H. Williamson, Eduardo T. da Silva, Daniela M. Ceccarelli, Nicola K. Browne, Caroline Petus, and Michelle J. Devlin. "Effects of reduced water quality on coral reefs in and out of no-take marine reserves." *Conservation Biology* 30, no. 1 (2016): 142-153.
- Wilson, Shaun K., Scott C. Burgess, Alistair J. Cheal, Mike Emslie, Rebecca Fisher, Ian Miller, Nicholas VC Polunin, and Hugh Sweatman. "Habitat utilization by coral reef fish: implications for specialists vs. generalists in a changing environment." *Journal of Animal Ecology* 77, no. 2 (2008): 220-228.
- Worm, Boris, Ray Hilborn, Julia K. Baum, Trevor A. Branch, Jeremy S. Collie, Christopher Costello, Michael J. Fogarty et al. "Rebuilding global fisheries." *Science* 325, no. 5940 (2009): 578-585.

Tables

Table 1

Mean biomass (kg/ha) of reef fish communities on fished reefs and no-take closures in three Sunda Banda Seascape regions.

Region (Year of MPA established)	MPA area (ha)	Mean Biomass (kg/ha)		Management Impact
		Fished Reef	No-take Closure	
Alor (2002)	21.85	356	664	+86.6%
Koon-Kei (2012)	150	424	401	-5.4%
Wakatobi (1996)	1,390,000	496	565	+13.9%
	Total	435	564	+29.7%

Table 2

Mean biomass (kg/ha) of reef fish families in fished reefs and no-take closures of the Sunda Banda Seascape.

Family	Mean Biomass (kg/ha)	
	Fished Reef	No-take Closure
Acanthuridae	666.2	735.2
Scaridae	395.4	454.2
Lutjanidae	237.5	333.6
Haemulidae	62.4	67.3
Serranidae	62.4	98.2
Lethrinidae	49.8	44.1
Siganidae	44.8	37.3
Holocentridae	28.5	2.6
Chaetodontidae	27.7	7.1
Mullidae	24.7	5.4
Nemipteridae	17.0	7.2
Pomacanthidae	11.3	4.4
Ephippidae	10.5	2.1
Balistidae	10.1	0.5
Kyphosidae	8.0	5.4
Pomacentridae	8.0	0
Labridae	7.3	9.7
Tetraodontidae	0.4	0
Zanclidae	0.4	0
Pempheridae	0.4	1.3
Sphyraenidae	0.2	12.5

Table 3

Statistical results testing the impact of region, management, and their interaction on biomass of reef fish.

Effect	numDF	denDF	F-value	<i>p-value</i>
Region	2	105	2.12	0.125
Management	1	105	5.55	0.023
Region * Management	2	105	0.91	0.406

Table 4

Mean values (kg/ha) and results from individual t-tests of mean functional group biomass from fished reefs versus no-take closures in the Sunda Banda Seascape.

Functional Group	Fished Reef	No-take Closure	df	t-value	p-value
Corallivore	25.33	6.97	186.9	3.43	< 0.001
Detritivore	104.89	37.31	189.9	3.30	< 0.01
Grazer	965.32	1,067.02	153.2	-0.58	0.468
Invertivore	75.88	77.96	144.3	-0.11	0.913
Piscivore	390.91	495.44	171.7	-1.28	0.204
Planktivore	94.21	75.59	110.4	0.09	0.924
Scraper	395.39	454.20	117.7	-0.76	0.448

Table 5

Functional group classifications and life history values of the 25 most dominant reef fish in the Sunda Banda Seascape.

Family	Species	Functional Group	Max Length (cm)	Life Span (year)	Growth Rate (cm / year)	Trophic Level
Acanthuridae	<i>Acanthurus leucocheilus</i>	Grazer	45.00	10.60	0.27	2.00
Acanthuridae	<i>Acanthurus mata</i>	Grazer	50.00	12.90	0.22	2.50
Acanthuridae	<i>Acanthurus nigrofuscus</i>	Grazer	38.00	4.00	0.70	2.00
Acanthuridae	<i>Acanthurus olivaceus</i>	Grazer	35.00	2.70	1.06	2.30
Acanthuridae	<i>Acanthurus pyroferus</i>	Grazer	29.00	6.70	0.42	2.00
Acanthuridae	<i>Acanthurus spp.</i>	Grazer	40.72	7.42	0.49	2.21
Scaridae	<i>Bolbometopon muricatum</i>	Scraper	130.00	28.80	0.10	2.70
Serranidae	<i>Cephalopholis argus</i>	Piscivore	60.00	15.90	0.18	4.50
Serranidae	<i>Cephalopholis urodeta</i>	Piscivore	28.00	2.00	1.40	4.00
Acanthuridae	<i>Ctenochaetus binotatus</i>	Detritivore	22.00	4.50	0.63	2.00
Acanthuridae	<i>Ctenochaetus striatus</i>	Detritivore	26.00	3.50	0.80	2.00
Lutjanidae	<i>Lutjanus bohar</i>	Piscivore	90.00	31.80	0.09	4.30
Lutjanidae	<i>Lutjanus gibbus</i>	Piscivore	50.00	9.20	0.31	4.10
Lutjanidae	<i>Lutjanus kasmira</i>	Piscivore	40.00	13.60	0.21	3.90
Lutjanidae	<i>Macolor macularis</i>	Piscivore	60.00	11.50	0.25	4.00
Lutjanidae	<i>Macolor niger</i>	Piscivore	75.00	13.70	0.21	4.00
Lethrinidae	<i>Monotaxis grandoculis</i>	Invertivore	60.00	13.00	0.22	3.40
Acanthuridae	<i>Naso annulatus</i>	Grazer	100.00	13.70	0.21	2.10
Acanthuridae	<i>Naso hexacanthus</i>	Planktivore	75.00	13.00	0.22	3.10
Acanthuridae	<i>Naso lituratus</i>	Grazer	46.00	8.10	0.35	2.30
Acanthuridae	<i>Naso lopezi</i>	Planktivore	60.00	13.60	0.21	2.90
Acanthuridae	<i>Naso spp.</i>	Grazer	59.67	11.66	0.29	2.49
Haemulidae	<i>Plectorhinchus chaetodonoides</i>	Invertivore	72.00	17.90	0.16	3.80
Haemulidae	<i>Plectorhinchus lineatus</i>	Invertivore	72.00	9.60	0.30	3.90
Scaridae	<i>Scarus spp.</i>	Scraper	45.89	7.59	0.47	2.00

Table 6

Mean values and results from individual t-tests of mean life-history characteristics from fished reefs versus no-take closures in the Sunda Banda Seascape.

Life-history Characteristic	Fished Reef	No-take Closure	df	t-value	p-value
Max length (cm)	47.2	55.0	149.8	-5.06	> 0.001
Growth rate (cm/yr)	0.47	0.40	188.7	-5.11	> 0.001
Life span (yr)	9.3	11.2	164.8	-5.37	> 0.001
Trophic level	2.69	2.83	163.0	-2.94	> 0.01

Figures

Fig. 1. Study sites within Indonesia's Sunda Banda Seascape across the Wakatobi (a), Alor (b), and Koon-Kei (c) regions.

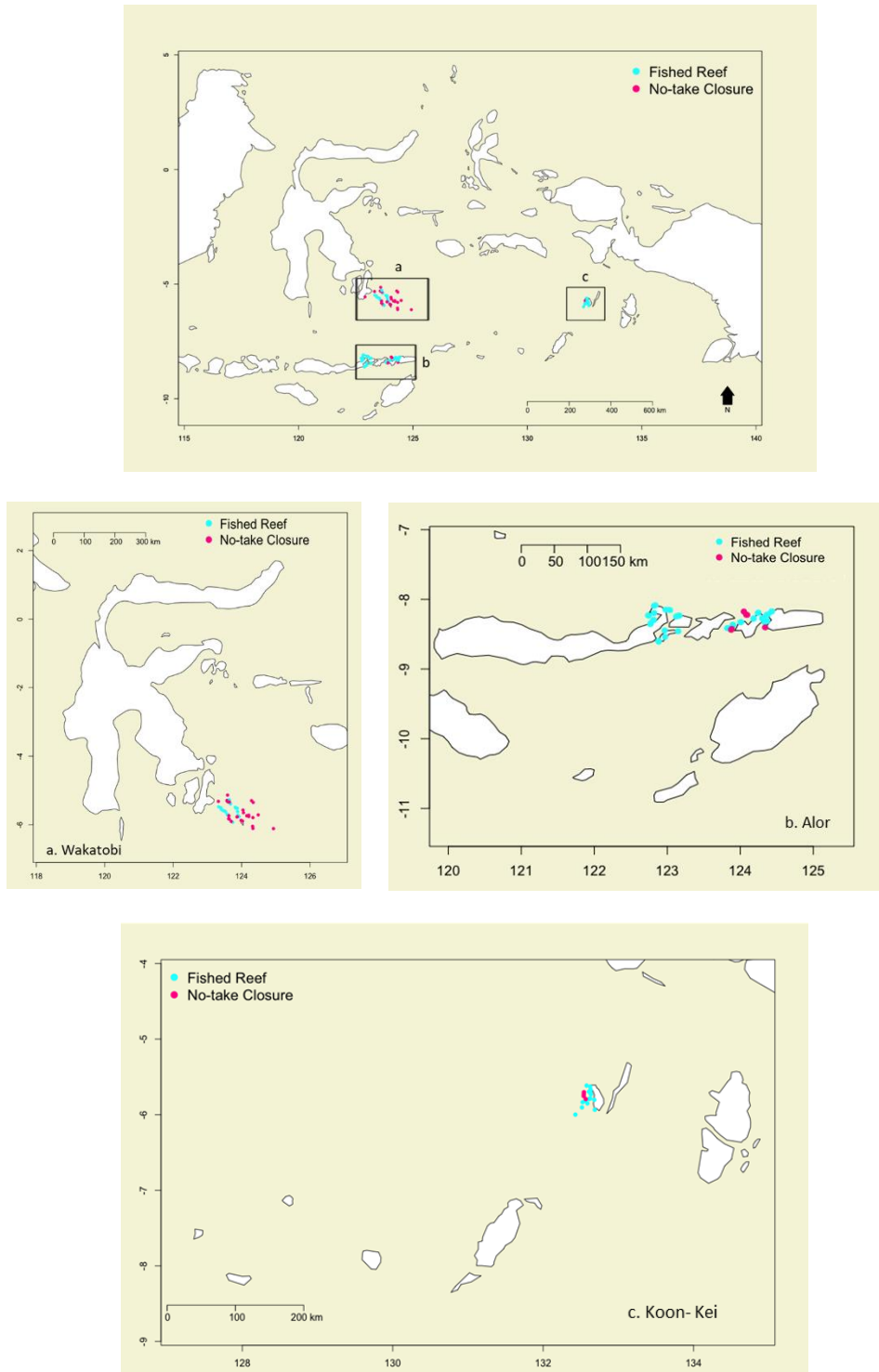
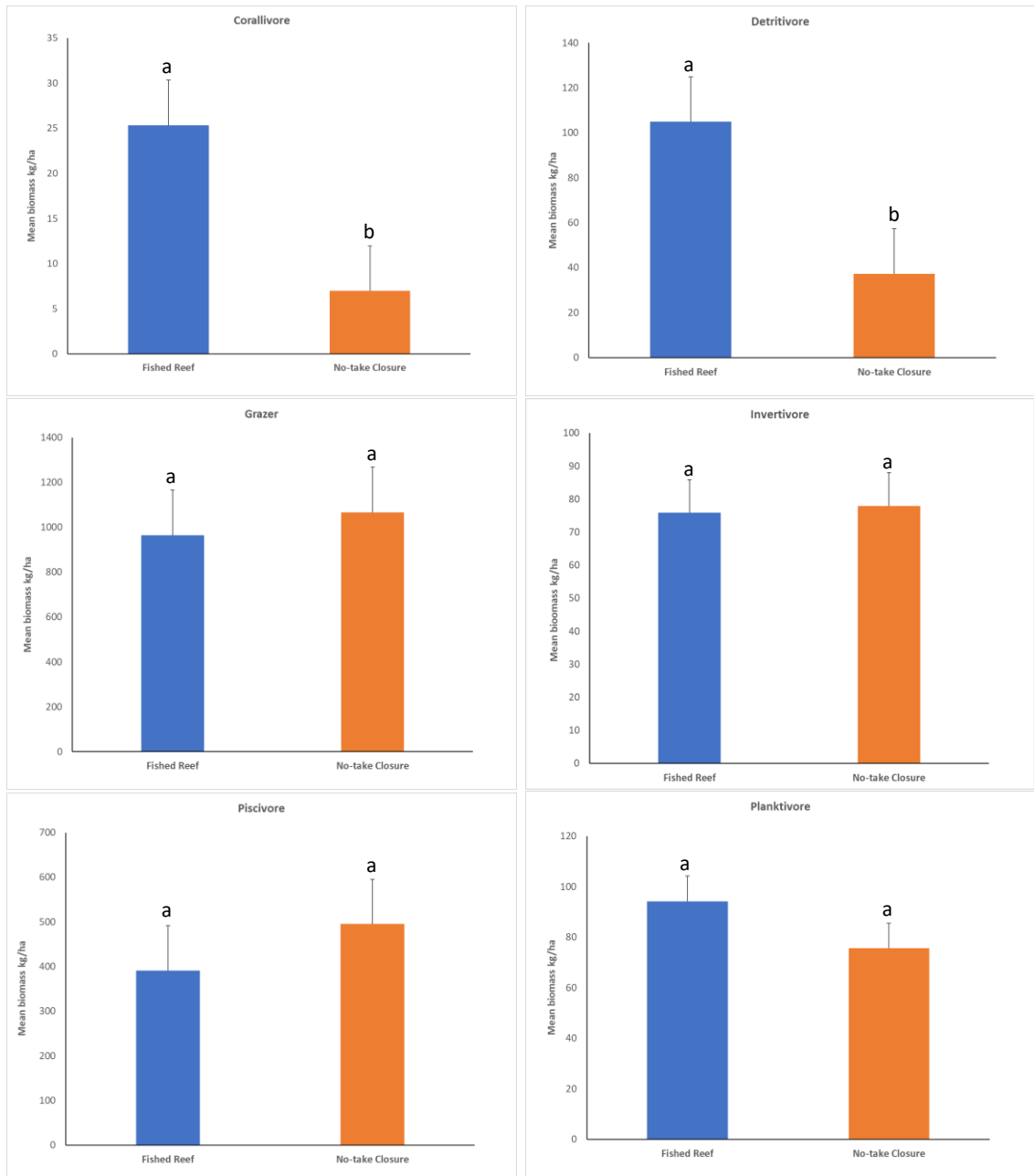


Fig. 2. Relationship of mean (and standard error) functional group fish biomass (kg/ha) between fished reefs and no-take closures. Different letters above bars indicate statistical differences between management based on individual t-tests.



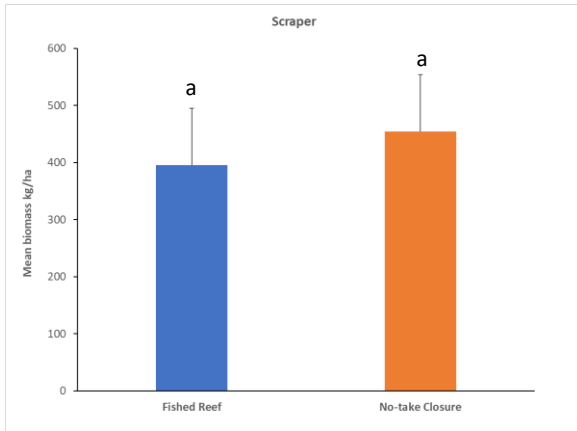
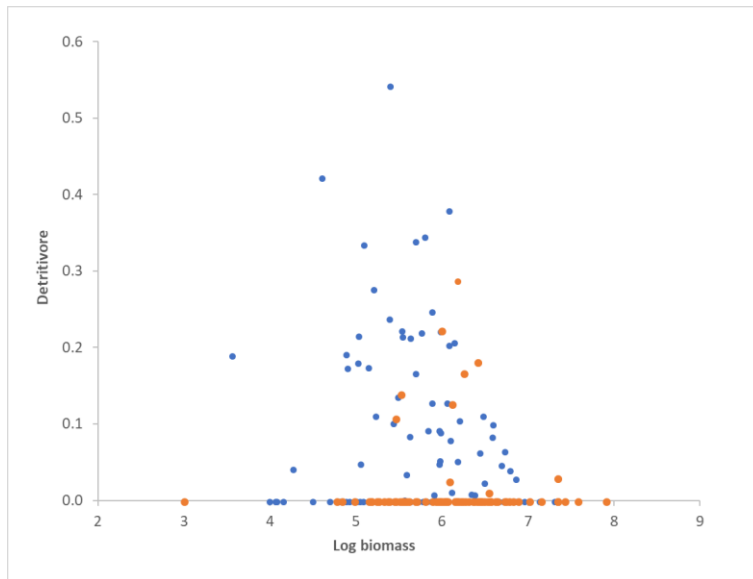
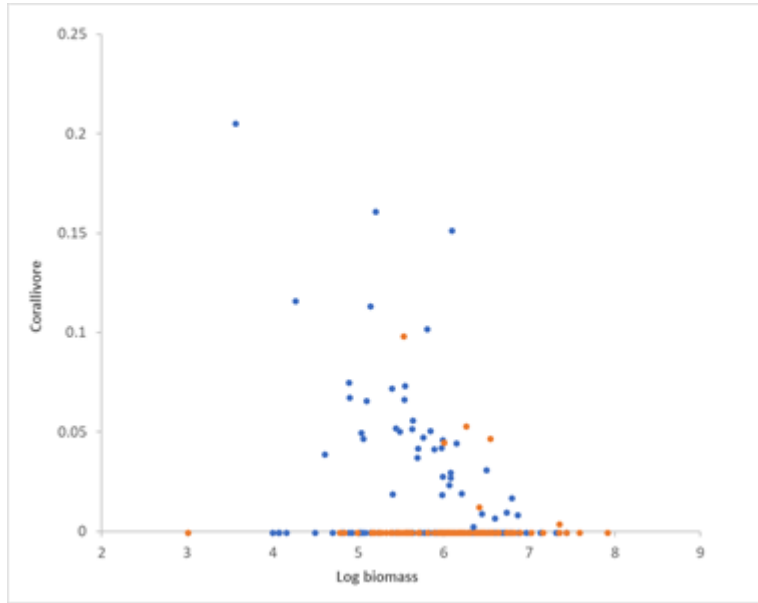
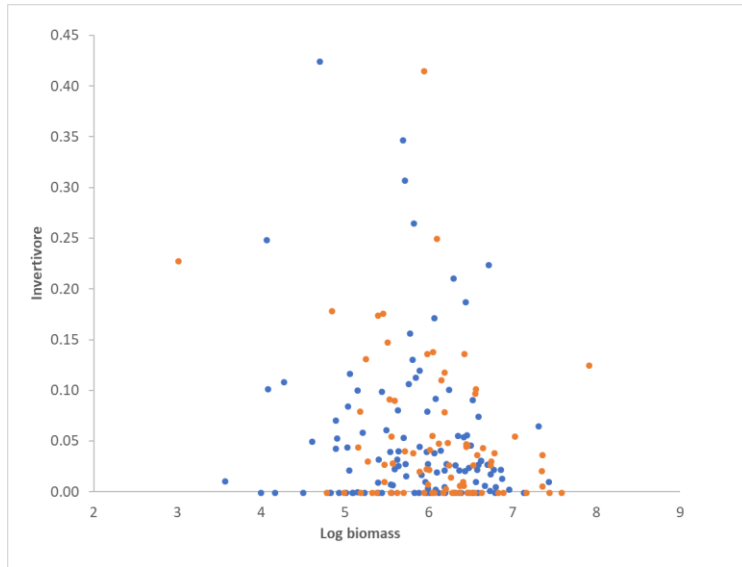
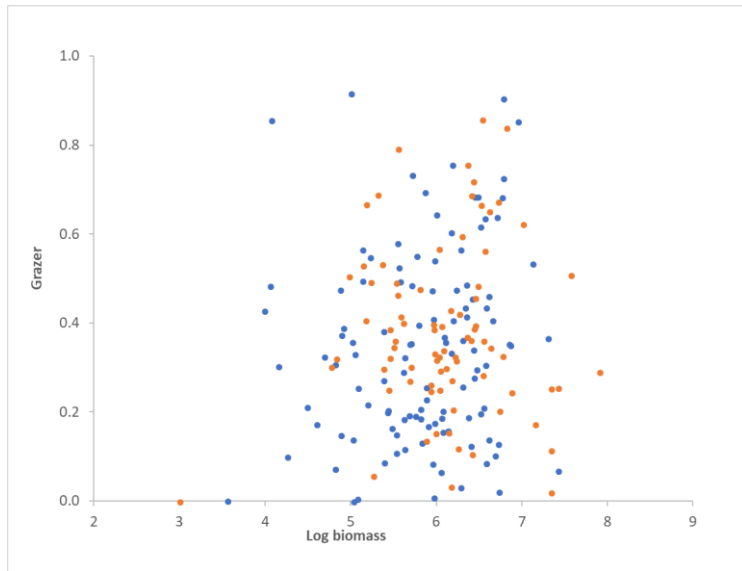
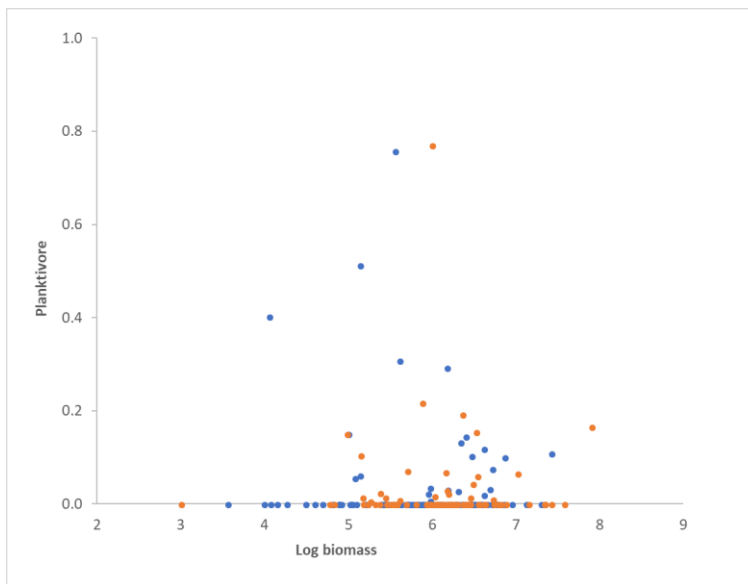
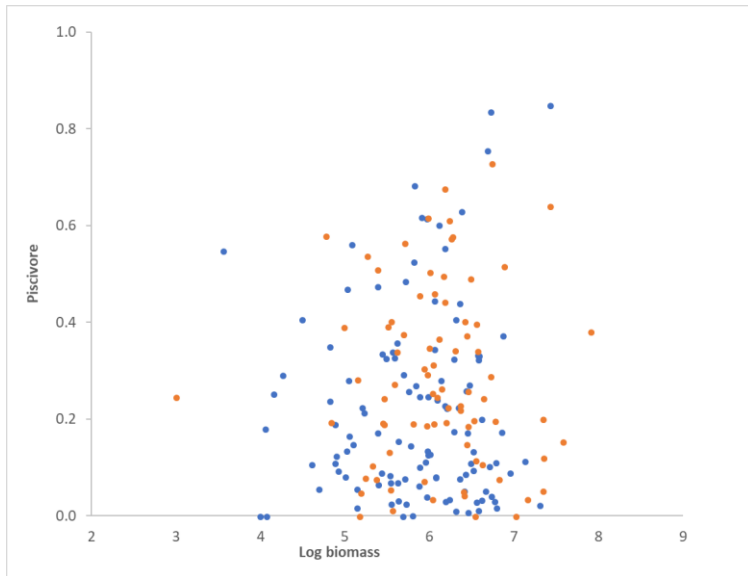


Fig. 3. Relationship between log biomass and functional group biomass by management type (blue = fished reefs; orange = no-take closures).







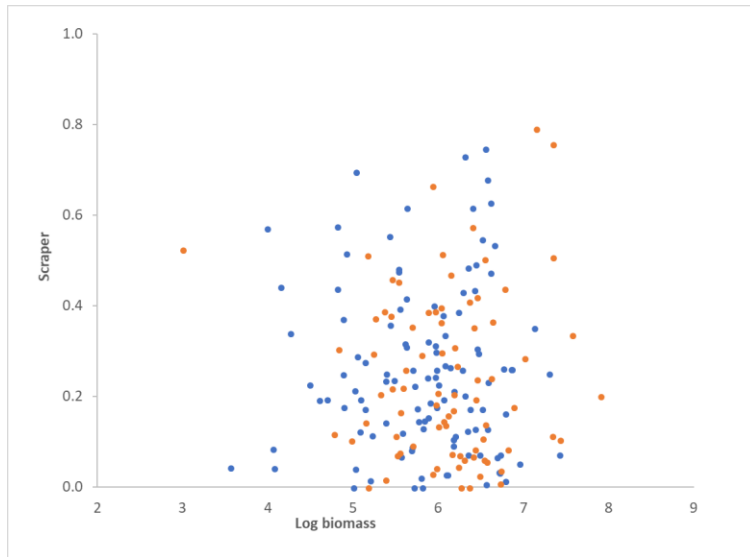
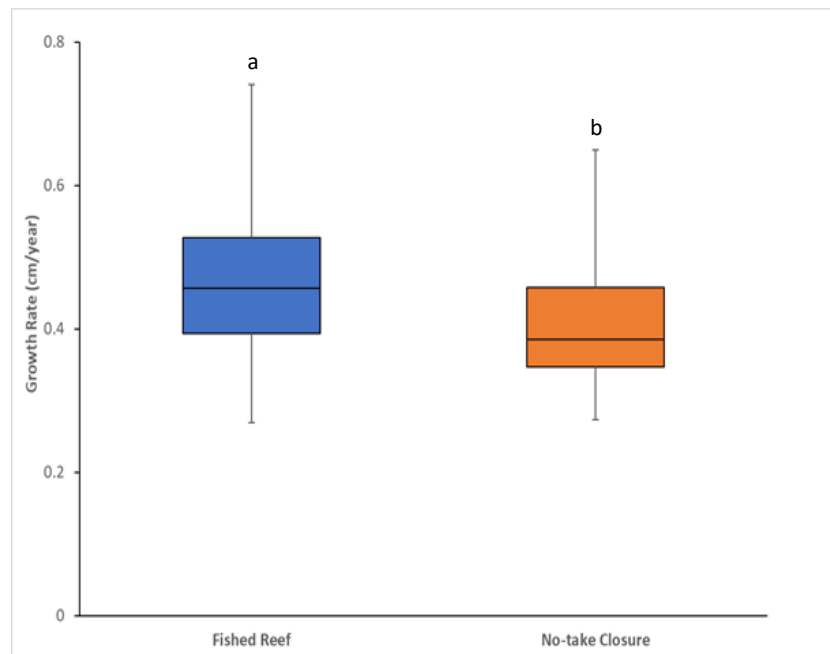
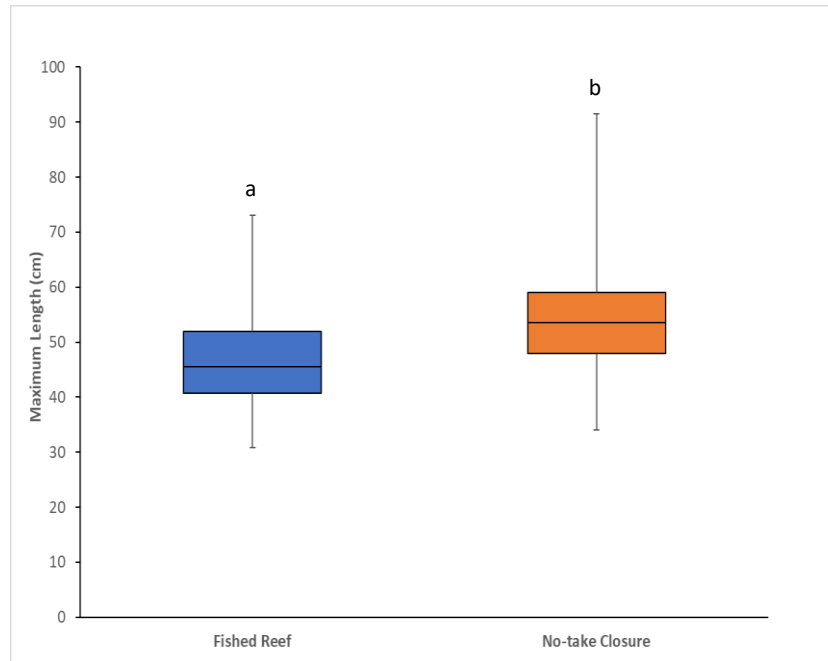


Fig. 4. Boxplot of median and quartile range of community-level mean maximum length (cm), life span (yrs), growth rate (cm/yr), and trophic level for fished reefs and no-take closures. Letters above boxplots indicate statistical differences between management based on individual t-tests.



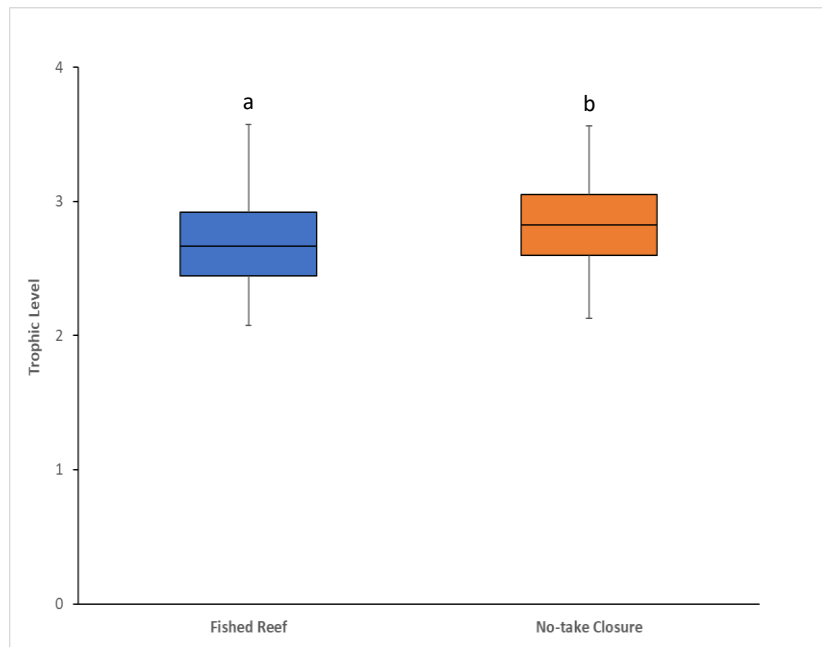
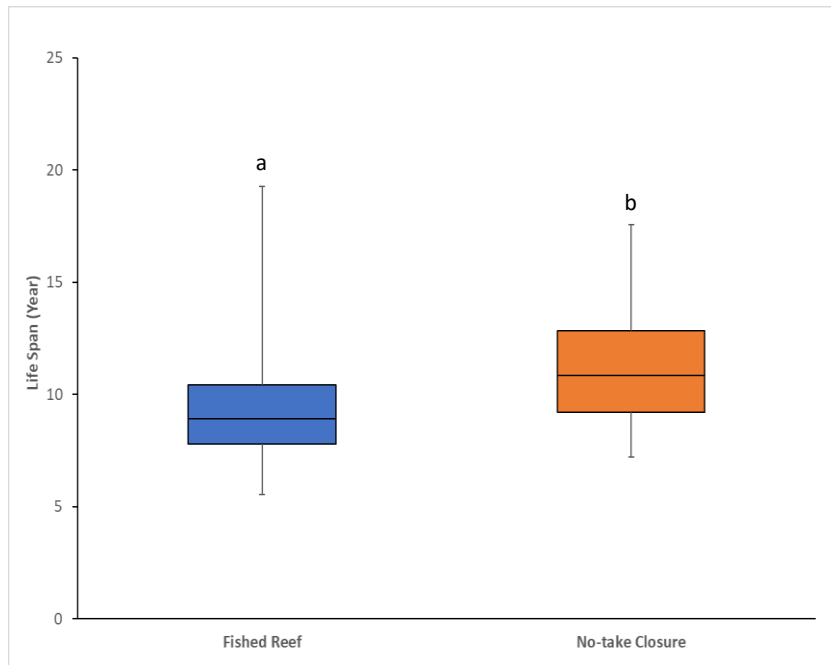


Fig. 5. Relationship between reef fish biomass (log) and functional group by management (blue = fished reefs; orange = no-take closures).

