POTENTIAL VALUE OF GEAR-BASED MANAGEMENT FOR CORAL REEF FISHERIES AND CONSERVATION

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POTENTIAL VALUE OF GEAR-BASED MANAGEMENT FOR
CORAL REEF FISHERIES AND CONSERVATION

BY

PAUL G. CARVALHO

A DISSERTATION SUBMITTED IN PARTIAL FULFILLMENT OF THE
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ABSTRACT

Access to markets and globalization has fueled the expansion of fishing pressure in coral reef fisheries and has consequently led to overfishing on many reefs around the world. Overfishing has profound consequences for reef ecosystems and the people that rely on reef resources for nutrition and income. Collecting fisheries-dependent data required for traditional stock assessment methods that guide management is often infeasible for coral reefs due to the small-scale, dispersed, multi-species, and multi-gear nature of these fisheries. In addition, coral reefs are concentrated in developing countries that often have inadequate capacity for management and enforcement, which limits the effectiveness of the default management strategy for marine ecosystems around the world – marine protected areas. However, fishers on coral reefs use a variety of fishing gears and generally favor gear-restrictions over spatial closures. Thus, the aims of this dissertation were to investigate the effects of fishing pressure and habitat condition on reef fishes, quantify the selectivity of fishing gear types (i.e., hook-and-line, nets, and spears) for functional groups and size classes of reef fishes, and generate a fisheries model to observe population dynamics of reef fishes under various gear-restriction management scenarios.

Chapter 1 is an overall introduction for the dissertation that provides background information for Chapters 2, 3, and 4. The general importance and scale of coral reef fisheries globally is outlined, and detailed information on fisheries-independent indicators (specifically size-spectra) and gear-restriction management are provided in this chapter.

In Chapter 2, we investigate the effectiveness of a fisheries-independent indicator – size spectra slope – for detecting the effects of fishing and habitat condition on reef fishes. Size spectra slopes quantify the relationship between relative abundance and size of
organisms. Size spectra can be useful for the assessment of coral reef fishes because fish life-history characteristics are related to fish size and, thus, can represent the flow and distribution of energy through food webs. We quantified benthic composition and size spectra of coral reef fishes using underwater visual surveys across three regions of Indonesia. We found that total fish biomass (proxy for fishing pressure) was the best predictor of size spectra for reefs fishes. Also, we found an interaction effect between fishing pressure and structural complexity such that structural complexity decreased as fishing pressure increased. Thus, suggesting that fishing pressure was associated with habitat degradation. Biomass and structural complexity were also the best predictors of size spectra slopes when carnivores and herbivores were analyzed separately, but carnivores had a sharper decrease in size spectra (i.e., fewer small fish) as fish biomass decreased. Our results suggest that size spectra slopes could be an efficient method for assessing coral reef fish populations.

In Chapter 3, we quantify the selectivity of hook-and-line, net, and spear fishing in Wakatobi National Park in Southeast Sulawesi, Indonesia. We determined the catch composition using fisheries-dependent data, and developed selectivity indices by using the Manly-Chesson selectivity equation. The Manly-Chesson equation allowed us to calculate selectivity as fishes caught (fisheries-dependent data) in relation to fishes available (fisheries-independent data). We found that hook-and-line fishing heavily targeted piscivorous fishes, net fishing caught the most diversity and the smallest fishes, and spear fishing targeted herbivores (particularly browsers and grazers) and piscivores.

In Chapter 4, we constructed a fisheries model to simulate population dynamics of reef fishes under gear-restricted management. We used the fisheries-dependent
and independent data from Chapter 3 to determine the catchability of functional group-size class combinations by each gear type (i.e., hook-and-line, net, and spear). Our baseline management scenario included all gear types with effort equally distributed among gears, and subsequent scenarios included a full-factorial design of gear restrictions. We found that permitting only spear fishing maintained the highest total biomass compared with other management scenarios, and prohibiting only spear fishing (i.e., permitting hook-and-line and net fishing) maintained the lowest total biomass across the full range of fishing effort tested. However, permitting only hook-and-line fishing generated the highest overall catch and maintained higher biomass of most functional groups compared with other management scenarios. These findings were primarily due to the low catchability of planktivores by spears and relatively high catchability by hook-and-line fishing, as planktivores were the most abundant functional group. Thus, gear-based management may be capable of achieving conservation and fisheries objectives simultaneously.

Chapter 5 is a recapitulation of results for Chapters 2, 3, and 4. Also, limitations and caveats of each chapter are discussed. The chapter concludes with a discussion on the future directions for this research.
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PREFACE

This dissertation has been prepared in the manuscript format according to guidelines established by the Graduate School of the University of Rhode Island. Chapter two is under review in *Ecological Applications*, and Chapter four is under review in *Fish and Fisheries*. Chapter three has been formatted, but not yet submitted, for the journal *Coral Reefs*. 
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CHAPTER I: Introduction

Coral reef fisheries support the livelihoods of hundreds of millions of people in tropical and subtropical coastal communities globally (Teh, Teh, & Sumaila, 2013). Over 650 million people live within 100 km of coral reefs in approximately 100 countries and territories (Donner & Potere, 2007). Coral reef fisheries are small-scale in nature but generate an estimated 1.4 to 4.2 million tons of catch and about USD 6.8 billion annually (Burke, Reytar, Spalding, & Perry, 2011; Pauly et al., 2002). Thus, coral reefs play a vital role in food security and support poor and vulnerable communities around the world (Whittingham, Campbell, & Townsley, 2003).

A majority of coral reefs are located in developing countries with limited financial resources and technical expertise for managing fisheries and enforcing regulations (Donner & Potere, 2007). Consequently, overfishing is a pervasive issue and diminishes the ability of coral reefs to deliver ecosystem services to coastal communities (Pandolfi et al., 2003). An estimated 55% of coral reefs are considered threatened by overfishing (Burke et al., 2011). Coral reef fisheries are typically dispersed across small islands, catch hundreds of species, and use a variety of gear types (e.g., nets, hook-and-line, and spears), which complicates efforts to collect fishery-dependent data. The lack of biological data for many coral reef fishes precludes scientists and managers from using traditional fisheries stock assessment methods. However, studies have demonstrated the ability of fishery-independent indicators (e.g., mean size, size spectra) for assessing the health and productivity of reef fish populations (Nash, Bijoux, Robinson, Wilson, & Graham, 2016; Wilson et al., 2010).

Fishery-independent indicators that are size based can be particularly useful for
assessing coral reef fish communities because fish life-history characteristics (e.g., maturity, fecundity, and mortality) are inherently linked to fish size (Kerr & Dickie, 2001). Thus, size-based indicators can represent the distribution and flow of energy through an ecosystem (Jennings, 2005). Abundance size spectra are widely used indicators that quantify the relationship between organism size and relative abundance (Jennings & Mackinson, 2003). Abundance generally has a negative relationship with body size (length or mass) such that large organisms are less abundant than small organisms (Rice & Gislason, 1996). Previous studies have investigated the relative impacts of fishing pressure and habitat condition (e.g., coral cover, structural complexity, etc.) on the size spectra of coral reef fishes, but fish assemblages were aggregated regardless of taxonomic identify for these analyses (Wilson et al., 2010). Fishes with different feeding strategies (i.e., carnivores and herbivores), however, have intrinsically different body size-abundance relationships due to metabolic limitations and can have different responses to fishing pressure and habitat conditions (Treblilco, Baum, Salomon, & Dulvy, 2013).

We addressed this gap in Chapter 2 by quantifying the size spectra slopes for herbivorous and carnivorous coral reef fishes across three regions in Indonesia: Raja Ampat, Wakatobi, and Lombok. These sites represent a regional gradient in fishing pressure such that Raja Ampat experiences the lowest fishing pressure and Lombok experiences the highest fishing pressure. Our goals were to quantify the relationship between size spectra (independent variable) and fishing pressure and habitat condition (i.e., hard coral cover, algal cover, and structural complexity) for the entire fish community, and separately for carnivores and herbivores. The dispersed nature of fisheries landing sites prevented us from directly quantifying fishing pressure and, thus, we used fishable biomass
as a proxy at each study site. Fishable biomass is a commonly used proxy for fishing pressure on reef fisheries (McClanahan et al., 2011; McClanahan, Graham, MacNeil, & Cinner, 2015; Nash et al., 2016) and has been shown to be sensitive to metrics of fishing pressure (Cinner, McClanahan, Daw, et al., 2009; Cinner, Graham, Huchery, & MacNeil, 2013). In addition, we validated this assumption for our study by running a linear regression between total fish biomass and population gravity (a metric that considers human population density and distance to reef to describe human pressure; Cinner et al., 2018), and found a significant negative relationship. We predicted that fishing pressure would be the dominant explanatory variable of size spectra slopes for reef fishes and that carnivore size spectra would be impacted by fishing more than herbivores.

Size spectra and other fisheries-independent indicators can be efficient and cost-effective methods for assessing coral reef fisheries and guiding managers in developing strategies to mitigate overfishing (Nash & Graham, 2016). Marine protected areas (MPAs) have become the default management option for curbing overfishing and the negative effects of various global (e.g., climate change) and local (i.e., coastal development) stressors in marine ecosystems globally. Approximately 5.3% of marine areas are designated as MPAs, and the Convention on Biological Diversity Aichi Targets 11 and International Union for the Conservation of Nature call for expanding protection to 10% and 30%, respectively (MPAtlas.org, 2020). The motivations for establishing MPAs, particularly no-take MPAs that prohibit all fishing activities indefinitely, are to eliminate direct human impacts on marine ecosystems (e.g., fishing and habitat degradation via destructive fishing) and protect species that promote healthy coral reefs through performing important ecological functions (Sala & Giakoumi, 2018). Well-enforced MPAs have
benefited marine ecosystems by increasing biomass and biodiversity (Gill et al., 2017; Lester et al., 2009); however, MPAs remain controversial for many coral reef fisheries because fishers are displaced from traditional fishing grounds, fishers often have few alternative livelihoods, and the act of fishing is tightly woven into cultural fabrics (Cinner, 2014). The disconnect between conservation and socio-economic objectives can lead to low compliance with regulations (Jupiter, Cohen, Weeks, Tawake, & Govan, 2014). Thus, alternative management strategies that are aligned with cultural and socio-economic contexts are needed for successful management and conservation of coral reefs.

Fishers on coral reefs use a myriad of fishing gears that can differentially impact reef fish populations and ecosystems (Mangi & Roberts, 2006; Mbaru, Graham, McClanahan, & Cinner, 2020). Thus, gear-based regulation presents an alternative management strategy for coral reef fisheries. Fishing communities have used customary gear-based management to restrict gear types (e.g., nets and hook-and-line) or gear specifications (i.e., mesh size and hook size) based on social and ecological conditions (McClanahan & Cinner, 2008). For example, communities in Melanesia have implemented bans on gillnets and spears (often banning night spearfishing for parrotfish) in response to declining fish stocks (Johannes, 2002). Although some fishers support gear-based management because these regulations can be easy to circumvent, studies typically find high compliance among fishers and increased fish biomass in response to gear restrictions (Campbell, Edgar, Stuart-Smith, Soler, & Bates, 2018; Cinner et al., 2005).

Fishing gears can exhibit selectivity for specific species, functional groups, and sizes of fish, which can have negative impacts on reef ecosystems (Cinner, McClanahan, Graham, et al., 2009). For example, fishing gears that heavily target herbivorous fishes can
reduce herbivory rates and, in some cases, allow algae to outcompete coral recruits (McClanahan & Cinner, 2008; Williams et al., 2019). Studies have analyzed selectivity through species or functional group composition of landings data (Cinner, McClanahan, Graham, et al., 2009; Mbaru et al., 2020). However, gear selectivity is appropriately measured as fishes caught in relation to fishes available in the environment. In Chapter 3 we aim to expand gear selectivity studies on coral reef fishes through quantifying gear selectivity with the Manly-Chesson selectivity index (Chesson, 1978; Manly, 1974) using fisheries-dependent and -independent data from Wakatobi National Park in Southeast Sulawesi, Indonesia.

Empirical studies that investigate fishing gear selectivity, such as Chapter 3, provide a starting point to develop gear-based management frameworks. However, fish population dynamics in response to specific gear-restrictions remain uncertain. In Chapter 4, we constructed a length-based, multispecies model to investigate fish population responses to gear restrictions at various levels of fishing intensity. We modeled hook-and-line, net, and spear fishing, which are gear types widely used on coral reefs around the world. The baseline model scenario permitted all fishing gears, and subsequent scenarios followed a full factorial design of prohibiting gears. This model will provide insight into the utility of gear restrictions on coral reefs fisheries and tradeoffs between conservation and socio-economic objectives.
References


Cinner, J. E., McClanahan, T. R., Graham, N. A. J., Pratchett, M. S., Wilson, S. K., &


CHAPTER II: Fishing and Habitat Condition Differentially Affect Size Spectra of Coral Reef Fishes

By

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In review in Ecological Applications

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Keywords: Coral reef fisheries, Size spectra, Fisheries management, Community ecology, Fisheries ecology, Ecosystem-based fisheries management, Ecosystem indicators, Indonesia
Abstract

Marine food webs are structured through a combination of top-down (e.g., fishing) and bottom-up (e.g., habitat condition) processes. In coral reef ecosystems, fish size is related to life-history characteristics and size-based indicators can represent the distribution and flow of energy through the food web. Thus, size spectra can be a useful tool for investigating the impacts of both fishing and habitat condition on the health and productivity of coral reef fisheries. Abundance size spectra are widely used and quantifies the relationship between organism size and relative abundance. Previous studies that have investigated the impacts of fishing and habitat condition together on the size distribution of coral reef fishes, however, have aggregated all fishes regardless of taxonomic identity. This leads to a poor understanding of how fishes with different feeding strategies, body size-abundance relationships, or catchability might be influenced by top-down and bottom-up drivers. To address this gap, we quantified benthic composition and size spectra slopes of coral reef fishes across three regions of Indonesia representing a gradient in fishing pressure and habitat condition. We show that fishing pressure is the dominant driver of size spectra slopes such that they become steeper as fishing pressure increases. This was due to the removal of large-bodied fishes and not the proliferation of small-bodied fishes. When considering fish functional groups separately, however, carnivore size spectra slopes were more heavily impacted by fishing than herbivores. Also, carnivore size spectra slopes were shallower at intermediate levels of hard coral cover (~ 50%). Herbivore size spectra slopes were significantly influenced by habitat and became shallower with increased structural complexity. Our results show that size spectra slopes can be used as an indicator of fishing pressure on coral reef fishes and that fishing pressure and habitat condition differentially
impact carnivores and herbivores. These findings suggest that protecting areas with intermediate levels of hard coral cover may help fisheries managers achieve conservation and fisheries objectives by maintaining healthy herbivore populations, which will support more productive carnivore populations that are targeted by fisheries.
**Introduction**

Coral reefs provide vital sources of nutrition and income for more than one billion people worldwide (UNEP, 2004). Most coral reefs are located in developing countries with limited resources for monitoring and enforcement (Johnson et al., 2013). Consequently, a majority of coral reef fisheries remain unassessed or are fished unsustainably (Costello et al., 2012; Newton, Côté, Pilling, Jennings, & Dulvy, 2007). Traditional stock assessment methods require extensive biological data and technical expertise (Walters & Martell, 2004), which are often unavailable for small-scale, dispersed, multi-gear and multi-species coral reef fisheries (Erisman, Apel, MacCall, Román, & Fujita, 2014; Sadovy & Domeier, 2005). However, fisheries-independent indicators can be cost-effective tools to monitor ecosystem health and assess the impacts of fishing and habitat condition on fisheries productivity (Mangi, Roberts, & Rodwell, 2007; Nash & Graham, 2016).

Size-based indicators can be particularly useful for coral reef fisheries because many life-history characteristics of fishes, such as age at maturity, fecundity, and natural mortality are size dependent (Kerr & Dickie, 2001). In addition, trophic positions of coral reef fishes have been shown to be positively correlated with body size due to ontogenetic diet shifts (de la Moriniere et al. 2003). Thus, size-based indicators can represent the distribution and flow of energy within a food web (Shin, Rochet, Jennings, Field, & Gislason, 2005). The abundance size spectrum is a commonly used size-based indicator that quantifies the relative abundance of organisms based on body size (length or mass) regardless of taxonomic identity (Boudreau & Dickie, 1992; Jennings & Mackinson, 2003). Abundance typically has a negative linear relationship with body size on logarithmic axes – as body size increases the abundance of organisms decreases geometrically (Rice &
Gislason, 1996). Size spectra have been used in temperate and tropical marine systems to examine the impacts of fishing (top-down process) and habitat condition (bottom-up process) on size distributions of fish assemblages (e.g., Blanchard et al. 2005, Wilson et al. 2010).

Coral reef food webs and ecosystems experience top-down control via predation and herbivory (Rasher, Hoey, & Hay, 2013, Roff et al., 2016). However, the effects of fishing pressure can overshadow the impacts of natural top-down processes and act as the primary mechanism structuring marine food webs (Smith, Hunter, & Smith, 2010). Top-down pressure from fishing can directly affect the size spectra of coral reef fishes by selectively removing large-bodied species (Graham, Dulvy, Jennings, & Polunin, 2005; Wilson et al., 2010). Also, the removal of large-bodied, carnivorous fishes can have indirect effects on size spectra through prey release, whereby smaller prey organisms proliferate in the absence of top-down control from predators (Dulvy, Polunin, Mill, & Graham, 2004). The effects of fishing, both direct and indirect, can be observed through comparing size spectra of fish communities that endure various levels of fishing pressure.

Bottom-up processes also affect coral reef food webs and ecosystems. For example, structural complexity of reef building corals provides prey refugia for small-bodied fishes to avoid predation (Hixon & Beets, 1993; Rogers, Blanchard, & Mumby, 2014). Structural complexity and low macroalgal cover have also been shown to mediate herbivorous fish populations that crop algae from reefs, such as acanthurids and siganids (Robinson et al., 2020). Therefore, degraded reefs with low structural complexity can limit prey refugia or food sources and reduce the abundance of small-bodied reef fishes, which results in shallower size spectra (Alvarez-Filip, Gill, & Dulvy, 2011; Rogers et al., 2014; Wilson et
al., 2010). Thus, top-down fishing impacts and bottom-up habitat destruction can cause harm to fishes along the entire size spectrum and severely compromise biological processes and functions carried out by fishes on coral reefs (e.g., predation and herbivory).

Previous studies that have examined fish size spectra slopes in response to fishing and habitat condition aggregated individuals from the entire assemblage, thus overlooking potentially important changes for organisms that respond differently to these explanatory variables, such as carnivores and herbivores (Blanchard et al., 2009). For example, fishes that feed at the same trophic level (e.g., herbivores) are expected to exhibit abundance–body size relationships in accordance with the energetic equivalence hypothesis such that abundance scales with body mass ($M$) as $M^{0.75}$ (Trebilco, Baum, Salomon, & Dulvy, 2013). In contrast, the abundance–body size relationship for fishes that feed across trophic levels (e.g., carnivores) is expected to be constrained by inefficient energy transfer such that abundance scales with body mass as $M^1$ (Trebilco et al., 2013). Robinson and Baum (2016) investigated the size spectra of carnivores and herbivores on relatively undisturbed coral reefs around Kiritimati Island and found that carnivore size spectra slopes were indeed steeper than those of herbivores. Here, we build on these findings by investigating the size spectra slopes of carnivorous and herbivorous reef fishes across a gradient of fishing pressure and various habitat conditions. Our goal is to determine how the influences of fishing and habitat condition change when fish assemblages are divided into groups that have different feeding strategies, abundance–body size relationships, and are targeted differently in the fishery. We hypothesize that fishing will be the dominant explanatory variable of fish size spectra slopes when all species are aggregated. Also, we predict that fishing will have a greater impact on size spectra slopes of carnivores than herbivores due
to the high value and desirability of large-bodied piscivores in coral reef fisheries.

Methods

Study sites

We conducted fish and benthic surveys at 57 sites across Indonesia: 20 sites in Raja Ampat, 19 sites in Wakatobi Marine National Park, and 18 sites in Lombok (Fig. 1). Raja Ampat is located in West Papua in Eastern Indonesia, the center of the Coral Triangle (Fig. 1b), and contains coral reefs with exceptional biodiversity that support both fishing and tourism industries (Allen & Erdmann, 2009; Veron et al., 2009). Many coral reefs in Raja Ampat are remote and away from major human development. Raja Ampat regency has established six locally managed Marine Protected Areas (MPAs), with assistance from Conservation International and The Nature Conservancy, to promote conservation and tourism (Atmodjo et al. 2017; Fig. 1c). Wakatobi Marine National Park (hereafter referred to as Wakatobi) is located south-west of Raja Ampat in Southeast Sulawesi and covers 13,900 km² (Clifton, 2013). Wakatobi has a human population of about 100,000 that is dependent on fisheries and agricultural industries (Clifton, 2013). Unlike the locally managed MPAs of Raja Ampat, Wakatobi management remains centralized by the Indonesia government and is regulated by the Ministry of Forestry (Clifton, 2013). Lombok is located to the east of Bali (Fig. 1d) and has a population of ~ 3 million people. Fishing is one of the primary forms of livelihood in Lombok. We excluded management status of each site from our analyses because enforcement of fishing closures was very weak.

Data collection

Fish and benthic communities were surveyed using underwater visual census
(UVC) along shallow reef slopes (3 – 10 m deep). Raja Ampat was surveyed in January 2018, Wakatobi in May 2018, and Lombok in July 2018. Three to six 5 × 50 m belt transects were conducted at each site. Diurnal, noncryptic fishes were identified to the lowest taxonomic level possible and sizes were estimated to the nearest cm. Prior to data collection, observers calibrate size estimates by estimating various lengths of PVC pipe underwater. Large, flighty fishes (e.g., lutjanids) were surveyed before small, territorial fishes (e.g., pomacentrids) to minimize bias against fishes that tend to flee in the presence of divers. The point-intercept method was used to survey benthic communities at 0.5 m intervals along the same transects as fish surveys, and benthic substrate was identified by life-form category (Table S1). Structural complexity was represented by a five-point visual scale (1 being a flat area with no vertical relief to 5 being the most complex vertical structure with caves and overhangs) and recorded at 10 m intervals along each belt transect (Polunin & Roberts, 1993).

Mass of individual fishes were calculated using the standard length-weight conversion equation (from cm to g), \[ W = \alpha L^\beta, \] and the \( \alpha \) and \( \beta \) parameters were obtained from FishBase (Froese & Pauly, 2020). In addition, fish functional groups were identified from diet and published literature (Froese & Pauly, 2020; MacNeil et al., 2015). Fishes were designated as carnivores, herbivores, or placed into an “other” category and excluded from the carnivore versus herbivore analyses.

**Fishing intensity**

Fish biomass density (kg/ha) was used as a proxy for fishing intensity at each site, such that high fish biomass indicates low fishing pressure and low fish biomass indicates high fishing pressure. Fish biomass is widely used as a proxy for fishing pressure (e.g.,...
McClanahan et al. 2011, 2015, Nash et al. 2016) as studies have found negative relationships between fish biomass and human population density and other metrics for fishing pressure in coral reef fisheries (Campbell et al., 2020; Cinner et al., 2009; Cinner, Graham, Huchery, & MacNeil, 2013; Gorospe et al., 2018). To validate the relationship between fish biomass and fishing intensity, we performed an analysis of fish biomass density in relation to human population gravity, a metric of fishing intensity that considers human population density and distance to reef (Cinner et al. 2018; Fig. S1).

**Estimating size spectra slopes**

Previous studies that have investigated the influence of fishing pressure on size spectra slopes of coral reef fish communities used linear regression for binned abundance data (using arbitrary bin sizes) on a logarithmic scale (Graham et al., 2005; Wilson et al., 2010). However, Edwards et al. (2017) used simulated data to show that linear regression of log-transformed and binned abundance data yield biased results with wide confidence intervals. Edwards et al. (2017) found that linear regression on logarithmic axes was analogous to treating abundance and body-size data as a probability distribution (i.e., power-law distribution; \( f(x) = Cx^b \)), which can be fit to data using likelihood methods. Thus, the bounded power-law distribution, more specifically the abundance density function (Edwards et al., 2017), was used here to estimate the size spectra slopes \( (b) \):

\[
N(x) = nx^b \left( \frac{b+1}{x_{max}^{b+1} - x_{min}^{b+1}} \right),
\]

where \( n \) is the number of individuals, \( x \) is fish mass (kg), \( x_{max} \) is the maximum mass of fish at 65 cm, and \( x_{min} \) is the minimum mass of fish at 10 cm. The maximum and minimum lengths indicate fish sizes that can be surveyed effectively using the UVC belt transect method (Ackerman & Bellwood, 2000; Kulbicki, 1998). A steeper size spectrum slope (i.e.,
more negative $b$) indicates fewer large-bodied and/or more small-bodied fishes.

Size spectra slopes were estimated for each region (Raja Ampat, Wakatobi and Lombok) and each survey site within regions. We used generalized additive models (GAMs) to determine the impact of fishing pressure (fish biomass density) and habitat condition (hard coral cover, algal cover, and structural complexity) on size spectra slopes at each site (mgcv R package, Wood 2011). GAMs were used to allow for non-linear relationships between size spectra and predictor variables, and the number of basis functions was set to $k = 3$ to prevent overfitting (Zuur, Ieno, & Walker, 2009). We used residual plots to check model assumptions (Figs. S2-S4). In addition, the absolute values of estimated size spectra slopes were used to allow for a gamma log-link model. We tested for concurvity (non-linear covariance) between predictor variables. Concurvity values range from 0 to 1, with 0 indicating that there is no problem with covariance between predictor variables. This analysis revealed that structural complexity covaried with hard coral cover (Fig. S5) and total fishable biomass (i.e., carnivores and herbivores; Fig. S6). Thus, we included interaction terms in the global model structure ($|b| ~ s(\text{biomass}, k = 3) + s(\text{hard coral cover}, k = 3) + s(\text{algal cover}, k = 3) + s(\text{structural complexity}, k = 3) + te(\text{biomass, structural complexity}) + te(\text{hard coral, structural complexity})$). We tested a full factorial combination of predictor variables using the MuMIn package (Barton, 2013) in R (Table S2). Akaike’s Information Criteria (AICc) corrected for small sample sizes was used for model comparisons. We assigned weights (inverse variance) to size spectra slopes to account for uncertainty in slope estimates.

Separate size spectra slopes were estimated for carnivores and herbivores for all regions combined and at the site level. GAMs were used to test the effects of fishing
pressure and habitat condition on carnivore and herbivore size spectra slopes. Biomass represented separate carnivore and herbivore biomass values rather than total site biomass. Models with total site biomass as a predictor variable were examined, but separate biomass values for carnivores and herbivores provided better model fits. We used the concurvity function in the mgcv package in R to test for covariance between herbivore and carnivore biomass and the other predictor variables. Structural complexity was correlated with carnivore biomass and hard coral cover. For the herbivore GAM, only hard coral cover covaried with structural complexity. Thus, interaction terms were included in the carnivore and herbivore GAMs (see Tables S3-S4 for global model structure). We repeated all of the above analyses using binned likelihood estimation methods for size spectra that account for uncertainty in fish mass after converting from length (Edwards, Robinson, Blanchard, Baum, & Plank, 2020) and our results remained the same.

**Results**

Our study regions represented a gradient in fishing pressure where Raja Ampat had the lowest pressure (i.e., highest mean biomass density) and Lombok had the highest (Fig. S1). Fish biomass was negatively, and significantly (p < 0.001, $R^2 = 0.29$), related to human population gravity (Fig. S1), a measure of fishing intensity (Cinner et al., 2018). The estimated size spectra slopes reflected this gradient in fishing pressure and slopes were significantly different between regions (Fig. 2). Raja Ampat had the shallowest size spectrum slope ($b = -1.58 \pm 0.02$ 95% CI), followed by Wakatobi ($b = -1.71 \pm 0.03$ 95% CI), and Lombok ($b = -2 \pm 0.02$ 95% CI). Shallower size spectra slopes indicate more large-bodied fishes and/or less small-bodied fishes present. Raja Ampat had significantly greater
average density of large- \((x \geq 1.2 \text{ kg})\) and medium-bodied fishes \((0.2 \text{ kg} \leq x < 1.2 \text{ kg})\) and slightly fewer small fishes \((x < 0.2 \text{ kg})\) compared with Wakatobi and Lombok (Fig. S7). However, we did not find significant differences in biomass density for large, medium or small fishes between Wakatobi and Lombok (Fig. S7).

Fishing pressure (i.e., fish biomass density in kg/ha) was the best predictor of size spectra slopes at each study site (Fig. 3, Table S2). The model with the lowest AICc value included fishing pressure and hard coral cover. However, hard coral cover was not a significant predictor and, thus, was dropped from the model and the difference in AICc values between the two models was 0.04 (Table S2). At sites with high fishing pressure, size spectra were steep \((b = -2.08\) at 110 kg/ha), and spectra became shallower (i.e., less negative) nonlinearly as fishing pressure decreased, reaching an asymptote \((b = -1.35)\), or possibly declining, for sites with fish biomass \(\geq 1,500\) kg/ha (Fig. 3). Habitat condition variables (hard coral cover, algae cover, and structural complexity) were not significant predictors of size spectra for the entire fish assemblage regardless of functional group (Table S2).

We found that the estimated size spectrum for carnivores aggregated across all study sites was steeper \((b = -1.98 \pm 0.03)\) than herbivores \((b = -1.55 \pm 0.02);\) Fig. 4). For carnivores, the best fit model included fishing pressure (i.e., carnivore biomass), structural complexity, and an interaction between fishing pressure and structural complexity (Table S3). We found that size spectra slopes were steepest at high fishing pressure and low structural complexity \((b = -2.74\) at 36.70 kg/ha) and became shallower as fishing pressure decreased and structural complexity increased (Fig. 5). The best fit model for herbivores included fishing pressure (i.e., herbivore biomass) and structural complexity (Table S4).
The predicted herbivore size spectrum slope at high fishing pressure (50.26 kg/ha) and low structural complexity was \( b = -1.66 \) and became shallower with decreasing fishing pressure and increasing structural complexity (Fig. 6). Size spectra slopes for herbivores increased nearly linearly and reached a predicted slope of \( b = -0.81 \) at 1430 kg/ha and high structural complexity (Fig. 6). The change in predicted size spectra slopes for herbivores from sites with high to low fishing pressure (\( b = -1.66 \) to \(-0.81\) from 50 to 1,430 kg/ha, respectively) was less than the change in size spectra slopes for carnivores (\( b = -2.78 \) to \(-1.08\) from 37 kg/ha 803 kg/ha, respectively; Figs. 5 and 6).

**Discussion**

We show that size spectra slopes can be used as indicators of fishing pressure in coral reef fisheries. In this study we provide evidence that fishing has a substantial impact on the size spectra of coral reef fishes – size spectra slopes became steeper as fish biomass decreased (i.e., fishing pressure increased). This result corroborates findings from other studies that investigated the relationship between spatial and temporal differences in fishing pressure and size spectra slopes of coral reef fishes (Graham et al., 2005; Wilson et al., 2010). Steeper size spectra slopes were likely a consequence of coral reef fishers selectively removing large-bodied individuals (Dulvy et al., 2004; Graham, Evans, & Russ, 2003). Indeed, Raja Ampat had the lowest fishing pressure, shallowest size spectra, and significantly higher biomass of large- (\( x \geq 1.2 \) kg) and medium-bodied fishes (\( 1.2 \) kg \(< x \leq 0.2 \) kg) than Wakatobi and Lombok (Fig. S7). The biomass density of small fishes was not different across regions, which suggest that prey release is not contributing to region-scale differences in size spectra (Dulvy et al., 2004).
Habitat condition has been shown to affect the size distribution of coral reef fishes through bottom-up processes (Alvarez-Filip et al., 2011; Rogers et al., 2014). However, we found that algal cover, hard coral cover, and structural complexity were not significant predictors of size spectra slopes for the entire fish assemblage. This suggests that fishing, a top-down process, had a greater impact on size spectra of all coral reef fishes across Indonesia. A country wide assessment of coral reef fishes in Indonesia also found that top-down drivers of fishing pressure were better predictors of fish communities than bottom-up drivers (Campbell et al. 2020). In addition, Wilson et al. (2010) found that fishing pressure was a better predictor of size spectra than habitat condition in Fiji. However, the effects of fishing pressure on size spectra decreased, and the effects of habitat increased, in Fiji due to a decrease in fishing pressure and increased habitat degradation from an outbreak of crown-of-thorns starfish between 2000-2006 (Wilson et al. 2010). Therefore, the relative impacts of fishing and habitat likely depend on the magnitudes of disturbance in a particular area and the timing of these disturbances. Fisheries managers can attribute habitat conditions to the size distribution of coral reef fish populations inside well-enforced no-take MPAs (Alvarez-Filip et al., 2011; Rogers et al., 2014), but managers must interpret size spectra slopes with caution if the relative levels of fishing pressure and habitat degradation are uncertain, as both can affect size spectra.

To the best of our knowledge, we provide the first analysis of carnivore and herbivore size spectra in response to fishing and habitat condition on coral reefs. We found that carnivores had steeper size spectra than herbivores when data were aggregated across all study regions and across a gradient of fishing pressure. Our results align with findings from relatively undisturbed coral reefs in Kiritimati Island, an atoll in the Line Islands,
where carnivores had steeper slopes than herbivores and trophic position scaled positively with body size (Robinson & Baum, 2016). Our results also support ecological theory, which predicts that carnivores will have steeper size spectra than herbivores because herbivores acquire energy at the same trophic level (i.e., energetic equivalence hypothesis), while carnivores consume prey across trophic levels and abundance-body size relationships are constrained by inefficient energy transfer (Brown & Gillooly, 2003; Trebilco et al., 2013).

Our estimated size spectra for carnivores, when data were aggregated across regions \( (b = -1.98 \pm 0.03) \), agreed with ecological theory, which predicts \( b \sim -2 \) (Brown & Gillooly, 2003; Reuman, Mulder, Raffaelli, & Cohen, 2008; Robinson & Baum, 2016). However, our estimated size spectra for herbivores \( (b = -1.55 \pm 0.02) \) was shallower than predicted, \( b \sim -1.75 \) (Brown & Gillooly, 2003; Reuman et al., 2008; Robinson & Baum, 2016). Although our estimated size spectra for carnivores agreed with theoretical values, we expected size spectra slopes for carnivores and herbivores to be steeper than predicted by theory due to the effects of fishing pressure and removal of large fishes in Wakatobi and Lombok. The difference between expected and estimated values may be due to the limitations of underwater visual census (UVC) methods for surveying fish populations. We only included fishes > 10 cm because fish below this size are inadequately sampled by UVC (Ackerman & Bellwood, 2000; Kulbicki, 1998). Also, we only included non-cryptic, diurnally active fish species, as nocturnal and cryptic species are difficult for divers to detect. Another limitation of UVC is observer bias; however, we analyzed differences in estimated size spectra by divers and the results were robust to these differences (Fig. S6). Although it is probable that our estimated size spectra would be steeper if all species and
all sizes could be sampled effectively, biases and surveyed species were consistent across study sites, and thus unlikely to change the major findings of this study.

Fishing pressure and structural complexity were included in the best fit models for carnivores and herbivores. However, Fishing pressure of carnivores and structural complexity were correlated and, thus, the interaction was included in the best fit mode (Table S2). The degree of change in size spectra slopes for carnivores from low to high fishing pressure was greater than herbivores, which is likely a result of fishers targeting large-bodied piscivores (Mora, 2015). The effects of fishing on these species can be apparent even at low levels of fishing pressure (Roberts, 1995). Carnivore size spectra slopes were shallowest at low fishing pressure and high structural complexity (Fig. 5), which suggest that fishing pressure potentially causes habitat degradation. Fishing gears can have negative impacts on coral reef structural complexity, and fishers in Wakatobi and Lombok use gear types associated with direct physical reef degradation, such as nets and spears (Mangi & Roberts, 2006), as well as cyanide and dynamite (Pet-Soede, van Densen, Pet, & Machiels, 2001).

Herbivore size spectra slopes had a positive, nearly linear, relationship with fishing pressure and structural complexity (Fig. 6). In this case, we found that herbivore biomass was not correlated with structural complexity and, thus, did not include an interaction effect. Structural complexity can affect predator-prey interactions and competition among prey species for refugia (Syms and Jones 2000). Previous studies have found nonlinearities in size spectra slopes that were linked to the provisioning of prey refugia, which influences mortality and growth rates differentially across the size spectrum (Rogers et al. 2014). Our results suggest that fishing pressure and structural complexities are dominant drivers of
size spectra slopes for carnivores and herbivores across our study sites (Alvarez-Filip et al., 2011; Rogers et al., 2014).

We show that fishing pressure has a negative effect on size spectra of coral reef fishes by removing large- and medium-bodied fishes. Also, we present novel evidence that fishing pressure has a greater impact on size spectra of carnivores than herbivores on coral reefs. Our results indicate that management of coral reef fisheries should focus on regulating fishing pressure, particularly for fishing gears that cause physical damage to coral reefs and reduce structural complexity. Future studies on size spectra slopes could focus on developing reference points and thresholds as more studies use the MLE method outlined in Edwards et al. (2017, 2020) and more estimates of size spectra slopes for coral reef fishes become available. Size spectra will be an important tool for coral reef conservation and fisheries management because it is an efficient method of assessing top-down and bottom-up impacts on communities without the need for species-level identification, something that is difficult in tropical ecosystems worldwide.
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Figure II-1. Map of Indonesia and 57 survey sites. Country map (a) and underwater visual census sites in Raja Ampat (n = 20; b), Wakatobi (n = 19; c) and Lombok (n = 18; d).
Figure II-2. Rank frequency plot for size spectra. Fitted using maximum likelihood estimation of a bounded power-law distribution (equation 1) for Raja Ampat (a; $b = -1.58 \pm 0.02$ 95% CI; a), Wakatobi (b, $b = -1.71 \pm 0.03$ 95% CI; b) and Lombok (c, $b = -2 \pm 0.02$ 95% CI; c).
Figure II-3. Size spectra in relation to biomass. Fitted size spectra ($b$) in relation to biomass density (kg/ha) for each study site ($n = 57$). A generalized additive model was used to fit the relationship between size spectra and biomass. Shapes indicate the region of each study site, and the shaded area indicates 95% confidence intervals.
Figure II-4. Rank frequency plot for carnivore and herbivore size spectra. Size spectra for carnivores ($b = -1.98 \pm 0.03$; a) and herbivores ($b = -1.55 \pm 0.02$; b) were fitted using maximum likelihood estimation of a bounded power-law distribution. Data are aggregated across all study sites ($n = 57$) and regions (Raja Ampat, Wakatobi and Lombok).
Figure II-5. Size spectra slopes of carnivores in relation to biomass and structural complexity, and correlation between biomass and structural complexity. Size spectra slopes \( b \) of carnivores in relation to biomass density (kg/ha; a) and structural complexity (b), and correlation between predictor variables (c). Markers represents study sites \( (n = 57) \), and shapes indicate region of each study site (Raja Ampat, Wakatobi and Lombok). The shaded regions indicate 95% C.I.
Figure II-6. Size spectra slopes of herbivores in relation to biomass and structural complexity. Size spectra ($b$) of herbivores in relation to biomass density (kg/ha; a) and structural complexity (five-point visual scale where 1 and 5 represent least and most complex, respectively; b). Markers represent study sites ($n = 57$), and shapes indicate region of each study site (Raja Ampat, Wakatobi and Lombok). Shaded regions indicate 95% C.I.
Supplementary Information

Supplementary Table S1. Benthic life-form categories used for point-intercept surveys.

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**Supplementary Table S2.** Model selection table for GAM (\(|b| \sim s(\text{algal cover}, k = 3) + s(\text{hard coral cover}, k = 3) + s(\text{biomass}, k = 3) + s(\text{structural complexity}, k = 3) + \text{te(\text{hard coral cover, structural complexity}) + te(\text{biomass, structural complexity})})\). The tensor product smooth (te) indicates non-linear interactions. The “+” indicates predictors included in each model.

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**Supplementary Table S4.** Model selection table for GAM (\(\sim s\text{(algal cover, } k = 3) + s\text{(hard coral cover, } k = 3) + s\text{(herbivore biomass, } k = 3) + s\text{(structural complexity, } k = 3)\)). Response variable is size spectra of herbivores at each site.

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**Supplementary Figure S1.** Biomass density (kg/ha) in relation to population gravity (Cinner et al. 2018) at each study site. Colors indicate region of each study site. Linear relationship between biomass and population gravity was significant ($p < 0.001$, 0.29).
Supplementary Figure S2. Model checking plots for Generalized Additive Model (~s(biomass, k = 3)) where the response variable (size spectra slopes) follows a gamma distribution with a log link.
Supplementary Figure S3. Model checking plots for Generalized Additive Model
\((-s(\text{biomass}, k = 3) + s(\text{structural complexity}, k = 3) + \text{te(\text{biomass}, \text{structural complexity}}))\)
where the response variable (size spectra slopes of carnivores) follows a gamma
distribution with a log link.
Supplementary Figure S4. Model checking plots for Generalized Additive Model (~s(biomass, k = 3) + s(structural complexity)) where the response variable (size spectra slopes of herbivores) follows a gamma distribution with a log link.
Supplementary Figure S5. Hard coral cover (percent cover) in relation to structural complexity. Each marker represents a single study site and shapes indicate region each study site. The model was fitted using a generalized additive model (p < 0.001, $R^2 = 0.27$).
Supplementary Figure S6. Fish biomass density (kg/ha) in relation to mean structural complexity at each survey site. Each marker represents a study site and shapes indicates region of each study site. The nonlinear relationship between biomass density and structural complexity was significant ($p < 0.001, R^2 = 0.18$).
Supplementary Figure S7. Biomass density (kg/ha) of large- \((x \geq 1.2 \text{ kg})\), medium- \((1.2 \text{ kg} < x \leq 0.2 \text{ kg})\), and small-sized \((x < 0.2 \text{ kg})\) fishes by region. Bars indicate standard error.
Supplementary Figure S8. Size spectra estimates for carnivores and herbivores by each observer (PC = P. Carvalho, FS = F. Setiawan, PS = P. Santoso) and region (indicated by shape).
CHAPTER III: Fishing Gear Selectivity in Coral Reef Fisheries

By

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\textbf{Keywords:} Coral reefs, Ecosystem-based management, Fisheries ecology, Gear-based management, gear selectivity, Indonesia
Abstract

Overfishing is a pervasive problem on coral reefs, which threatens ecosystems and the livelihoods of millions of fishers globally. Gear-based management can provide conservation benefits to coral reefs by maintaining greater fish biomass than open access areas, and fishers often express more support for gear-based management than spatial closures. However, few studies have investigated the differential impacts of fishing gears on reef fishes. Here, we explore the selectivity of hook-and-line, nets, and spears on reef fishes in Wakatobi National Park, Indonesia. We quantified the functional group and size class composition of each fishing gear and generate gear selectivity values for coral reefs based on fishes caught (fisheries-dependent data) in relation to fishes available for capture (fisheries-independent data). Fishing gear and location were significant predictors of functional groups and size classes in the catch, and there is some evidence of overlap in functional groups targeted by the different gears. Hook-and-line fishing targeted large and piscivorous fishes, net fishing targeted the most diversity and small fishes, and spear fishing targeted herbivores and some piscivores. Net fishing seemed to be the least sustainable gear, but hook-and-line and spear fishing also had some negative impacts. Also, the large proportion of herbivores in overall catch indicates the maturity of the Wakatobi coral reef fishery. Gear selectivity information provided here can help to adaptively manage coral reef fisheries. However, our results suggest that long-term sustainability of coral reefs will require additional management measures, such as effort restrictions or biomass targets.
Introduction

Coral reef fisheries are small-scale in nature but support the livelihoods of six million fishers globally (Teh, Teh, & Sumaila, 2013). Fishers on coral reefs use a variety of gear types to catch multiple species, often with little to no bycatch, which stymies traditional stock assessment and single-species management approaches (Peterman, 2004). Consequently, many coral reef fisheries have reduced biomass of fishes to less than half the expected biomass in the absence of fishing (~ 1,000 kg ha$^{-1}$ for unfished populations of diurnally active fishes), reduced biodiversity, altered species compositions, and modified the size distributions of target species (Campbell et al., 2020; Graham, Dulvy, Jennings, & Polunin, 2005; MacNeil et al., 2015). These effects from fishing can impair ecological processes necessary to prevent phase shifts from coral to macroalgal dominance and recover from disturbance events, such as coral bleaching (Hughes et al., 2007).

The most prevalent management option used to mitigate overfishing and other anthropogenic stressors on coral reefs is to establish no-take Marine Protected Areas (MPAs), which prohibit fishing activities (Mumby & Steneck, 2008). Theoretical and empirical research have demonstrated that well-enforced no-take MPAs can increase fish biomass and diversity (Gill et al., 2017; Lester et al., 2009), but coral reefs are disproportionately concentrated in developing countries that lack the resources for monitoring ecosystem health or enforcing spatial management regulations (Donner & Potere, 2007). Also, many communities rely heavily on coral reef resources and, thus, the exclusion of people from traditional fishing grounds is often seen as unethical and leads to low compliance and support from local communities (Hicks & McClanahan, 2012; McClanahan & Abunge, 2016, 2018). Therefore, other management approaches will be
necessary to improve coral reef health, promote sustainable resource use, and garner more support from fishers and coastal communities in coral reef ecosystems.

In many areas, coral reef fishers have expressed greater support for gear-based restrictions than no-take MPAs, and gear-restricted areas have been shown to produce greater fish biomass than open-access areas (Campbell et al., 2020; McClanahan, Maina, & Davies, 2005). Fishing gears used on coral reefs (e.g., hook-and-line, spears, and nets) exhibit selectivity for particular fishes, which can be specific to size, species, functional group, or any combination of these attributes and lead to different consequences for coral reef ecosystems (Cinner et al., 2009; Mbaru, Graham, McClanahan, & Cinner, 2020; McClanahan & Mangi, 2004). For example, a fishing gear that selectively catches herbivorous fishes can reduce herbivory rates and, in some cases, subsequently allow algae to outcompete corals (Cinner et al., 2009; Williams et al., 2019). Understanding the interactions between fishing gears and fishes is imperative for the development of adaptive ecosystem-based fisheries management that can maintain ecological functions in coral reef ecosystems while also balancing social dynamics (Cinner et al., 2009; Mbaru et al., 2020).

Previous studies have found hook-and-line fishing catches primarily piscivores, nets catch a high diversity of species, and herbivores are targeted by spear fishers in mature fisheries, but target piscivores in less mature fisheries (McClanahan & Cinner, 2008; Sluka & Sullivan, 1996). In addition, a study on coral reef fisheries in Kenya found that fishing gears catch a wide range of functional entities (unique combinations of fish traits including body size, diet, and behavior) and eliminating certain fishing gears will protect rare functional entities, but reduced fishing effort overall is necessary to protect the most heavily fished functional entities (Mbaru et al., 2020). While these studies provide valuable
information for management, a more detailed understanding of fishing gear selectivity requires a comparison of fisheries catch (fisheries-dependent data) in relation to fish available for capture (fisheries-independent data). For example, a fishing gear that catches 20% herbivores when herbivores compose 40% of available fish on a reef should have a different measure of selectivity from a gear that catches the same percent on a reef where herbivores compose 80% of available fish. Such information will provide a more detailed understanding of the interactions between fishing gears and reef fishes and assist managers with the development of adaptive management regulations.

Here we assess gear selectivity in the multi-species, multi-gear coral reef fishery in Wakatobi National Park located in Southeast Sulawesi, Eastern Indonesia (Fig. 1). Our goals were to investigate catch composition for functional groups and size classes using fisheries-dependent data and generate gear selectivity values by using the Manly-Chesson index (Chesson, 1978; Manly, 1974), which considers fish caught (fisheries-dependent data) in relation to fish available on reefs (fisheries-independent data).

Methods

Study site

This study was conducted in Wakatobi National Park (hereafter referred to as Wakatobi) in Southeast Sulawesi, Eastern Indonesia (Fig. 1). Wakatobi is the third largest Marine Protected Area (MPA) in Indonesia (covering 13,900 km²) and comprises four main islands: Wangi-Wangi, Kaledupa, Tomia, and Binongko. In addition, there are two large atolls (Kapota Atoll and Kaledupa Atoll) to the west of the main islands that are frequented by fishers (Fig. 1; von Heland & Clifton 2015). Wakatobi is a multi-use MPA and, thus,
fishing occurs within the boundaries. Although there are no-take zones within MPA boundaries, local fishing communities are unfamiliar with regulations and resist to cooperate with law enforcement agencies (Elliott, Mitchell, Wiltshire, Manan, & Wismer, 2001). The National Park Authority is situated within the Indonesian Ministry of Forestry, but local offices of the World Wildlife Fund and The Nature Conservancy provide support for research, surveillance, and management decisions (von Heland & Clifton, 2015). Wakatobi was an ideal location for this study because of the well-established multi-species, multi-gear coral reef fishery and because the majority of fishes caught throughout the park are landed and sold in Mola Village on Wangi-Wangi (Fig. 1).

**Landings data collection (fisheries-dependent data)**

Landings data were collected from January to December 2018 (with the exception of May). Overall, 284 landings surveys were conducted over 92 days of sampling. Fishers were selected opportunistically as they arrived in Mola Village to sell or trade their catch. Landings were sampled only for fishers targeting shallow coral reefs (rather than pelagic fishers), and fishing operations ranged from a single fisher in a canoe to 14 people on a two-ton vessel. Collecting data on total landings for a single trip was often unfeasible because fishers did not want to be delayed when selling or trading their catch. Thus, a randomized sub-sample of the total catch was recorded along with the weight of the total catch. Fishes were identified to genus, or species if possible, and total length was measured to the nearest centimeter. We also recorded the fishing grounds visited and fishing gear used.

Three main fishing gears were recorded for our landings data: hook-and-line, spears, and nets. Fishers used small (1 – 2 cm) hooks and monofilament lines from small
vessels, and a maximum of three fishers were present on a hook-and-line fishing trip. Spear guns (here referred to as spears) used in Wakatobi were about one meter long, with wooden stocks and propelled by a single band of rubber tubing. Spear fishing trips included as many as six fishers on a single boat. Nets were about 75 × 3 m with 6.4 cm mesh size, and sometimes multiple nets were tied together and deployed on shallow reef slopes. Fishers in Wakatobi used drive-in gill-net fishing methods, where fishers deploy gill-nets then scare fishes into the nets. Net fishing trips required more people than the other fishing gears. The number of species recorded for each gear in relation to the number of individuals sampled was used to ensure that our data included the full range of fishes targeted by each gear type (Fig. S1). Trap fishing and fence (semi-permanent structures on reef flats that direct fish into holding pens) fishing are also commonly used in Wakatobi (Exton et al., 2019); however, our surveys did not identify catch from these gear types.

**Underwater visual census (fisheries-independent data)**

Underwater visual census (UVC) for fish was conducted along shallow (3 – 10 m) reef slopes (n = 19; Fig. 1) to remain consistent with areas visited by fishers targeting reef fishes. At each site, three 50 × 5 m belt transects were completed, and each transect was separated by at least 15 m. Fishes were identified to genus, and species if possible, to remain consistent with landings identifications. Total lengths of fish were estimated to the nearest centimeter. Large, flighty fishes were surveyed on the first pass of the belt transect to reduce bias against species that tend to flee the survey area in the presence of divers (Kulbicki, 1998). Smaller fishes were surveyed on the second pass of the belt transect. Only diurnal, noncryptic species were included in this analysis, as nocturnal and cryptic species can be difficult for divers to survey. Fishes were categorized by functional groups
according to primary literature (MacNeil et al., 2015) and FishBase (Froese & Pauly, 2020).

**Analysis**

Catch composition was analyzed by examining the proportion of total landings for species and genera that composed 95% of the catch. In addition, catch composition of each fishing gear was assessed by comparing the percentage of functional groups and size classes recorded in landings. The correlations between fishing gears with functional groups and size classes were visually analyzed using correspondence analysis. Multinominal and ordinal logistic regression models were used to determine the effects of gear type and fishing ground on catching functional groups (multinominal) and size classes (ordinal) and calculate the probability of capture as a function of gear and fishing ground (Figure 1). The size-distributions of fishes, and mean size, caught by each gear type were examined through density distributions. For the top five species and genera landed, we generated length-frequency distributions and the biomass-weighted mean length at maturity using FishBase (Froese & Pauly, 2020).

The Manly-Chesson index was used to quantify fishing gear selectivity (Chesson, 1978; Manly, 1974):

$$\gamma_i = \frac{(r_i/A_i)}{\left(\sum_{i=1}^{K} r_i/A_i\right)},$$

where $r_i$ is the mean proportion of fish landed from functional group or size class $i$ (per fishing trip), $A_i$ is the mean proportion of fish recorded from UVC, $K$ is the total number of functional groups ($K = 11$) or size classes ($K = 6$), and $\gamma_i$ is the gear selectivity index. Selectivity indices ($\gamma$) are measures of divergence between the proportion of group $i$ in the landings and the proportion observed in UVC, thus values indicate relative gear selectivity for each functional group and size class and are normalized such that $\Sigma \gamma_i = 1$ (Chesson,
1978; Manly, 1974). Gear selectivity indices were calculated only for fishes that were effectively observed through UVC. Thus, we excluded fishes <10 cm (Ackerman & Bellwood, 2000) and very “shy” and “flighty” fishes (e.g., families Carangidae and Lethrinidae) from the selectivity analysis.

**Results**

Over the one-year sample period, we recorded 13,446 fishes landed from 238 fishing trips. Approximately 115 species of coral reef fishes were recorded in our observations of nets, spears, and hook-and-line fishing in Wakatobi. In addition, 95% of landings was composed of 49 species (Fig. 2). The top 50% was composed of approximately six species identified as pisci-invertivores, macro-invertivores, grazers and excavator/scrapers (Fig. 2). We found that gear type and fishing ground were significant predictors of catching functional groups and size classes (Table 1).

We recorded the least number of trips for hook-and-line fishing (n = 42) and the least landings recorded (968 individuals) among fishing gears. Hook-and-line fishing caught a greater proportion of piscivores and pisci-invertivores than net and spear fishing (Fig. 3a). Only ~16% of fishes landed from hook-and-line trips came from non-predatory functional groups. The top five species caught by hook-and-line fishing came from Lethinidae, Serranidae, and Lutjanidae families (Fig. S2). The correspondence analysis supports these findings and shows a close association between hook-and-line fishing and piscivores and pisci-invertivores (Fig. 4a). Hook-and-line fishing caught a greater proportion of fishes between 1 – 10 cm, but also more fishes between 51 – 60 cm than net and spear fishing (Figs. 3b and 4b). The average size of fishes caught by hook-and-line
fishing was 20 cm (Fig. S3). In addition, multinomial logistic regression models show that piscivores and pisci-invertivores have the greatest probability of capture by hook-and-line fishing (Fig. 5). However, piscivores have the greatest probability of being caught at Kaledupa Atoll, and pisci-invertivores have the greatest probability of being caught at Kapota Island (Fig. 5). Hook-and-line fishing had the lowest probability of capturing browsers, excavator/scrapers, grazers, and macro-invertivores (Fig. 5). Ordinal logistic regression demonstrates that fishes between 11 – 20 cm had the highest probability of being captured at Kapota and Wangi-Wangi Islands for all gear types, but hook-and-line fishing had a greater probability of capturing fishes >20 cm than net fishing at Kaledupa Atoll and Kapota Atoll (Fig. 6).

A total of $n = 61$ trips was recorded for spearfishing, which included ~2,500 individual fishes. Spear and net fishing had considerable overlap in the proportion of functional groups targeted (Fig. 3a). However, correspondence analysis revealed that grazer and excavators/scrapers were more closely associated with spears than nets (Fig. 4a). The top species and genera caught by spear fishing included *Siganus spp.*, *Scarus spp.*, *Parupeneus spp.*, and *Lethrinus ornatus* (Fig. S4). Multinomial logistic regression models demonstrate that spear fishing had the greatest probability of capturing grazers, but spear fishing also had a high probability of catching pisci-invertivores relative to other functional groups (Fig. 5). Correspondence analysis indicates that spear fishing was associated with fishes in the medium to large size range (21 – 50 cm), but <1% of the fish landed from spear fishing trips were >40 cm (Figs. 3b and 4b). At Kaledupa Atoll and Kapota Atoll, spear fishing had the highest probability of capturing fishes ≥21 cm (Fig 6). Also, spear fishing had the greatest mean size of fish caught, which was at 22 cm (Fig. S3).
Net fishing was the predominant gear type used in the Wakatobi coral reef fishery. Landings data included $n = 135$ fishing trips and ~10,000 individual fishes from net fishing. Correspondence analysis shows that net fishing caught the greatest diversity of functional groups (Fig. 4b), and the top species and genera caught by nets included *L. ornatus, Siganus spp.*, *Parupeneus spp.*, and *Chlorurus spp.* (Fig. S5). Also, net fishing had the highest probability of catching browsers, detritivores, macro- and micro-invertivores, planktivores and spongivores (Fig. 5). Net fishing primarily targeted fishes in the 11 – 20 cm range (Fig. 3b and 4b) and had a higher probability of capturing fishes <21 cm relative to other gear types (Figs. 6).

The above analyses show that hook-and-line fishing had the least overlap in functional groups captured with other gear types, and that spear and net fishing overlapped most for excavators/scrapers. The probability of capture for excavators/scrapers was also related to fishing ground such that there was a very low probability of capturing excavators/scrapers at Wangi-Wangi and Kapota Island (Fig. 5). Also, ordinal logistic regression demonstrates that smaller fishes have a greater probability of capture at Wangi-Wangi and Kapota Island than the atolls, while larger fishes ($\geq 21$ cm) have a higher probability of being caught on the atolls (Fig. 6).

We generated length-frequency distributions for the top five species and genera caught in Wakatobi. We found that a majority of fishes caught were smaller than estimated length at maturity for *L. ornatus* (84% juveniles; Fig. S6), *Siganus spp.* (63% juveniles; Fig. S7), *Parupeneus spp.* (72% juveniles; Fig. S8), and *Scarus spp.* (51% juveniles; Fig. S9). However, most *Chlorurus spp.* caught were mature (46% juveniles; Fig. S10).

For the Manly-Chesson selectivity index, hook-and-line fishing had the greatest
selectivity values for piscivores ($\gamma = 0.839$) and pisci-invertivores ($\gamma = 0.103$; Table 2). Excavators/scrapers had the third highest selectivity for hook-and-line fishing ($\gamma = 0.026$), but was lower than net and spear fishing (Table 2). Also, hook-and-line fishing had zero selectivity for browsers, corallivores, and spongivores (Table 2). Hook-and-line fishing had the highest selectivity for fishes between 51 – 60 cm ($\gamma = 0.467$) and lowest selectivity values for size classes between 11 – 30 cm ($\gamma_{11-20cm} = 0.032$ and $\gamma_{21-30cm} = 0.150$) compared with other fishing gears (Table 3). Browsers had the highest selectivity value for net fishing ($\gamma = 0.458$), followed by grazers and piscivores ($\gamma = 0.158$ and 0.115, respectively; Table 2). Also, net fishing had the highest selectivity values for detritivores, macro- and micro-invertivores, and planktivores, although these selectivity values were relatively low (Table 2). Net fishing had the highest selectivity for fishes between 11 – 20 cm among gear types ($\gamma = 0.228$; Table 3). Piscivores had the highest selectivity for spear fishing ($\gamma = 0.375$) relative to other functional groups caught by spears, but selectivity was lower than line fishing (Table 2). Spear fishing had the highest selectivity for excavators/scrapers, grazers, and spongivores relative to other gear types (Table 2). In addition, spear fishing had the highest selectivity for fishes between 21 – 30 cm and 41 – 50 cm ($\gamma = 0.366$ and 0.407, respectively) compared with other gear types, and the lowest probability of catching fishes between 51 – 60 cm (Table 3).

Discussion

Our results demonstrate the diversity and maturity of the coral reef fishery of Wakatobi. Fishers predominantly used nets on coral reefs, and we found some evidence of overlap in target species among gear types. Selectivity and target fishes of spear fishing
overlapped with nets and hook-and-line fishing; however, overlap between nets and hook-
and-line fishing only included the emperor species *Lethrinus ornatus*, which was the most
heavily fished species in Wakatobi. Overall, catch composition from all gear types may
reflect the maturity of the Wakatobi fishery because herbivores made up a large proportion
of the catch (~43%) and average length was relatively small (~20 cm). In less mature
fisheries, large-bodied, carnivorous species are expected to compose a greater proportion
of the catch (Jennings & Polunin, 1997; McClanahan & Mangi, 2004).

Hook-and-line fishing demonstrated high selectivity for piscivores and pisci-
invertivores because fishers typically used baited hooks that attract these functional groups.
This finding agrees with similar studies, and the small range of functional groups targeted
by hook-and-line fishing indicates that fewer ecological functions are disrupted compared
with other gear types (Cinner et al., 2009; Humphries et al., 2019; Mbaru et al., 2020).
Correspondence analysis and Manly-Chesson selectivity values indicate that hook-and-line
fishing exhibited high selectivity for large fishes (51 – 60 cm) in relation to size classes
available. Although line fishing appears to be a sustainable fishing method due to narrow
selectivity of functional groups, selectivity for relatively large sizes, low overlap with other
fishing gears, and light fishing pressure, many species targeted by hook-and-line fishing
were large-bodied, slow growing, and intrinsically vulnerable to fishing (e.g., species in
Serranidae and Lutjanidae families; Abesamis, Green, Russ, & Jadloc, 2014). Thus,
increased effort for hook-and-line fishing can have cascading effects on reef fish
communities through the removal of high trophic level species (Dulvy, Freckleton, &
Polunin, 2004; Hixon, 2015). The main advantage of hook-and-line fishing is that it causes
less physical damage to reef structure than net and spear fishing (Mangi & Roberts, 2006).
Net fishing caught the most biomass of fish and targeted the greatest diversity of functional groups compared hook-and-line and spear fishing. Thus, net fishing can disrupt a variety of ecological functions on coral reefs (Cinner et al., 2009; Mbaru et al., 2020). Nets and hook-and-line fishing overlapped in the most heavily fished species, *L. ornatus*, but nets caught more small-bodied fishes (11 – 20 cm) than hook-and-line fishing. Therefore, nets and hook-and-line fishing compete for shared resources, but nets seem to preemptively remove smaller individuals that otherwise would be available to hook-and-line fishing if they had the opportunity to grow larger. Multinomial logistic regression and Manly-Chesson selectivity values show some overlap and competition between nets and spears for excavators/scrapers and grazers at similar sizes, yet nets extracted greater biomass and potentially jeopardize resources used by spear fishers. Net fishing has also been shown to be destructive to coral reefs via entanglement and fishers trampling reefs while scaring fishes into nets (Mangi & Roberts, 2006). High fishing effort for nets, high diversity of catch, overlap in target species with other gears, and targeting of smaller sized fishes suggest that net fishing at the current level is unsustainable and can degrade coral reefs through physical damage and disrupt an array of ecological processes (Mangi & Roberts, 2006; Mbaru et al., 2020; McClanahan & Cinner, 2008).

We found some overlap in selectivity between spears and hook-and-line fishing. While spears landed mostly excavators/scrapers and grazers, correspondence analysis and Manly-Chesson selectivity values indicate that spears also selectively targeted some piscivores and pisci-invertivores in relation to available functional groups. Spears had higher selectivity values for smaller-bodied fishes (21 – 30 cm) compared with hook-and-line fishing and, thus, preemptively remove target species. Although spear fishing had a
high selectivity value for piscivores, the proportion of non-carnivorous fishes recorded in landings (~48%) for spears reflect the maturity of the Wakatobi coral reef fishery, as spears generally catch higher proportions of carnivores in less mature fisheries (Pet-Soede, van Densen, Pet, & Machiels, 2001; Sluka & Sullivan, 1996). Given the selectivity for piscivores and the large proportion of herbivores in landings, spears can potentially induce cascading effects. For example, spears can reduce herbivory rates through the removal of excavators/scrapers and grazers, which, in some instances, play important functional roles by removing algae that compete with corals, particularly at early life stages of corals, and thereby contributing to the persistence of coral reefs (Williams et al., 2019). Alternatively, spear fishing can cause prey release by removing high trophic levels species and (Pinnegar et al., 2000). In addition, spear fishing has been shown to be destructive to reef structure due to direct physical contact between fishers and reefs (Mangi & Roberts, 2006).

Multinomial and ordinal logistic regressions showed that the probability of capture was dependent on gear type and location of fishing activities. We found that fishing at Wangi-Wangi and Kapota Island, locations nearest to large human populations, had significantly lower probabilities of catching excavators/scrapers for all gear types. In addition, all gears had a greater probability of capturing small-bodied fishes (11 – 20 cm) at these sites. The differences between fishing grounds suggest that probability of capture of certain functional groups and size classes is dependent on the availability of fishes in a particular area (Kuparinen, Kuikka, & Merilä, 2009). Our selectivity values, calculated using the Manly-Chesson equation, consider fish available in the environment and, thus, provide more detailed selectivity information than only considering fisheries-dependent data. In addition, Wangi-Wangi had the greatest human population in relation to other
islands, as it is the administrative center and access point to other islands in the National Park. Thus, Wangi-wangi, and nearby Kapota Island, had greater human population densities in close proximity to fishing grounds than other islands in Wakatobi, which is a proxy for human pressure such as fishing (Cinner et al., 2018). This suggests that future research could investigate the feasibility of using human population gravity as an indicator of relative sizes and functional groups in reef fisheries catch.

This study quantifies fishing gear selectivity using fisheries-dependent and -independent data on coral reefs. However, surveying fishes through underwater visual census (UVC) has limitations (Samoilys & Carlos, 2000). For example, species within the families Carangidae and Lethrinidae (typically piscivores and pisci-invertivores) are particularly “shy” in the presence of divers and, thus, are underestimated through UVC (Jennings & Polunin, 1995). Therefore, we removed these species from the Manly-Chesson selectivity analysis. Consequently, underestimated relative proportions of piscivores and pisci-invertivores available in the environment lead to inflated selectivity indices of these functional groups. Future research could investigate differences in selectivity values generated by other fisheries-independent survey methods, such as baited remote underwater stereo-video systems (Schramm et al., 2020).

Small average size of fishes in the catch in Wakatobi (~20 cm) and the paucity of large fishes suggest growth overfishing is occurring, where fishes are unable to attain a size that results in optimal yield (McManus, 1997). For example, the average size of L. ornatus in the catch was ~18 cm, but the estimated optimal length is ~24 cm (Froese & Pauly, 2020). In addition, most individuals caught from the top species and genera were smaller than length at maturity. Extracting individuals before they reach maturity can lead to
recruitment overfishing where the spawning stock biomass is reduced such that recruitment declines (Abesamis et al., 2014). Indeed, previous studies have documented declines in stock abundances in Wakatobi (Exton, 2010). Managers may consider implementing effort limitations or gear modifications for net fishing to reduce the chance of growth and recruitment overfishing because nets caught the greatest biomass, and at smaller sizes on average, than other gear types (Hicks & McClanahan, 2012). There is also some indication of Malthusian overfishing in Wakatobi based on the magnitude of net and fence fishing and reported use of blast and cyanide fishing, the latter two are typically associated with non-residents of Wakatobi (Exton et al., 2019; von Heland & Clifton, 2015). Fence fishing in Wakatobi is particularly concerning because habitats on reef flats are destroyed, catch includes up to 500 species, and a high proportion of the catch includes juvenile fishes (Exton et al., 2019).

Our results support the adaptive management framework outlined in McClanahan and Cinner (2008), which suggests reducing hook-and-line fishing when the abundance or biomass of predators is low, reducing nets when coral cover or diversity is low, and reducing spear fishing when herbivore abundance or biomass is low and when algal cover is high. However, we add that spear fishing also be reduced if spear fishers exhibit high selectivity for predators and their abundance or biomass is low (Table 4). Consistency between this study and McClanahan and Cinner (2008) in Papua New Guinea imply that this heuristic management guide could be used for coral reef fisheries outside of these study locations. However, gear-restrictions alone are likely insufficient measures for reaching sustainable resource use in coral reef fisheries (Tuda, Wolff, & Breckwoldt, 2016).

In Indonesia, gear-restrictions have been shown to support greater biomass than
open-access areas, and no-take MPAs failed to provide additional conservation gains due to weak enforcement (Campbell et al., 2020). The Wakatobi National Park authorities can use the adaptive framework presented here (Table 4) and in McClanahan and Cinner (2008); however, there are additional social and cultural factors to consider when implementing gear-restrictions and additional management regulations to improve fisheries sustainability. For example, the Bajau community in Wakatobi is an ethnic minority and heavily dependent on marine resources, yet they often are excluded from management discussions (von Heland & Clifton, 2015). In addition, Wakatobi has a rapidly expanding tourism industry. Although fishers and other community members recognize the economic importance of tourism, the ecological effects of tourism on reefs remain uncertain in Wakatobi (von Heland & Clifton, 2015). Gear-based management will likely improve the Wakatobi fishery, but effective ecosystem-based fisheries management will require stronger co-management, stakeholder engagement, monitoring ecosystem response to ocean activities other than fishing, and consideration of additional management measures, such as effort restrictions or biomass targets (Campbell et al., 2020; Graham et al., 2017; MacNeil et al., 2015).
Acknowledgements

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References


Figures and Tables

Table III-1. Multinomial and ordinal logistic regression. Model output for predicting catch of functional groups and size classes, respectively.

<table>
<thead>
<tr>
<th>Predictor variables</th>
<th>d.f.</th>
<th>Likelihood ratio</th>
<th>p</th>
</tr>
</thead>
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<td>Multinomial model</td>
<td></td>
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<td></td>
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<tr>
<td>Gear</td>
<td>18</td>
<td>1853.8</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Fishing ground</td>
<td>27</td>
<td>1272.6</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Ordinal model</td>
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<td></td>
<td></td>
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<tr>
<td>Gear</td>
<td>2</td>
<td>393.8</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Fishing ground</td>
<td>3</td>
<td>2178.6</td>
<td>&lt;0.001</td>
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</table>
Table III-2. Manly-Chesson selectivity values for functional groups.

<table>
<thead>
<tr>
<th>Functional group</th>
<th>Line selectivity</th>
<th>Net selectivity</th>
<th>Spear selectivity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Browser</td>
<td>0.000</td>
<td>0.458</td>
<td>0.213</td>
</tr>
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<td>Corallivore</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
</tr>
<tr>
<td>Detritivore</td>
<td>0.001</td>
<td>0.007</td>
<td>0.003</td>
</tr>
<tr>
<td>Excavator/scraper</td>
<td>0.026</td>
<td>0.062</td>
<td>0.082</td>
</tr>
<tr>
<td>Grazer</td>
<td>0.013</td>
<td>0.158</td>
<td>0.182</td>
</tr>
<tr>
<td>Macro-invertivore</td>
<td>0.011</td>
<td>0.095</td>
<td>0.048</td>
</tr>
<tr>
<td>Micro-invertivore</td>
<td>0.008</td>
<td>0.030</td>
<td>0.008</td>
</tr>
<tr>
<td>Pisci-invertivore</td>
<td>0.103</td>
<td>0.060</td>
<td>0.061</td>
</tr>
<tr>
<td>Piscivore</td>
<td>0.839</td>
<td>0.115</td>
<td>0.375</td>
</tr>
<tr>
<td>Planktivore</td>
<td>0.004</td>
<td>0.006</td>
<td>0.003</td>
</tr>
<tr>
<td>Spongivore</td>
<td>0.000</td>
<td>0.008</td>
<td>0.023</td>
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</tbody>
</table>
Table III-3. Manly-Chesson selectivity values for size classes (10 cm bins).

<table>
<thead>
<tr>
<th>Size class (cm)</th>
<th>Line selectivity</th>
<th>Net selectivity</th>
<th>Spear selectivity</th>
</tr>
</thead>
<tbody>
<tr>
<td>11-20</td>
<td>0.032</td>
<td>0.228</td>
<td>0.101</td>
</tr>
<tr>
<td>21-30</td>
<td>0.150</td>
<td>0.342</td>
<td>0.366</td>
</tr>
<tr>
<td>31-40</td>
<td>0.135</td>
<td>0.125</td>
<td>0.127</td>
</tr>
<tr>
<td>41-50</td>
<td>0.216</td>
<td>0.253</td>
<td>0.407</td>
</tr>
<tr>
<td>51-60</td>
<td>0.467</td>
<td>0.051</td>
<td>0.000</td>
</tr>
<tr>
<td>&gt; 60</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
</tr>
</tbody>
</table>
Table III-4. Adaptive gear-based management guidelines based on fishing gear selectivity.

<table>
<thead>
<tr>
<th>Fisheries-independent survey results</th>
<th>Management action</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low predator abundance or biomass</td>
<td>Reduce or eliminate hook-and-line and/or spear fishing</td>
</tr>
<tr>
<td>Low herbivore abundance or biomass, or high macroalgal cover</td>
<td>Reduce or eliminate spear fishing</td>
</tr>
<tr>
<td>Low diversity of fishes or low coral cover</td>
<td>Reduce or eliminate net fishing</td>
</tr>
</tbody>
</table>
Figure III-1. Map of Wakatobi National Park. Wakatobi is located in Southeast Sulawesi, Eastern Indonesia (country map of Indonesia in the top-right corner). Landings data were collected in Mola Village (triangle), and underwater visual census (UVC) was conducted at \( n = 19 \) sites (circles). Light gray shaded areas represent distinct fishing grounds reported in landings data.
Figure III-2. Overall catch composition. Percentage of total landings for species that make up the top 95% of catch. Colors indicate functional groupings.
Figure III-3. Landings of functional groups and size classes by gear type. Proportion of landings for each gear type (i.e., hook-and-line, net, and spear) by functional group (a) and size class (cm; b).
Figure III-4. Correspondence analyses for functional groups and size classes.

Correspondence analyses representing the relationships between fishing gears and functional groups (a) and size class (cm; b).
Figure III-5. Multinomial logistic regression for functional groups. Probability of capturing functional groups in relation to fishing gear and location. Probabilities were calculated using multinomial logistic regression, and the analysis was limited to fishing locations where all gear types were used. Marker colors indicate fishing ground and bars represent 95% confidence intervals.
Figure III-6. Ordinal logistic regression for size classes. Probability of catching different size classes (cm) in relation to fishing gear used and location. Probabilities were calculated using ordinal logistic regression, and the analysis was limited to locations where all fishing gears were used. Maker colors indicate fishing gear and bars represent 95% confidence intervals.
Supplementary Information

**Supplementary Figure S1.** Number of species recorded for each fishing gear type (i.e., hook-and-line, net, and spear) in relation to cumulative individuals sampled in landings data.
Supplementary Figure S2. Percentage of total landings for species that make up the top 95% of catch for hook-and-line fishing. Colors indicate functional groupings.
Supplementary Figure S3. Density distribution for sizes of fish caught (cm) by fishing gear (colors). The vertical dashed lines represent mean size for each gear type.
Supplementary Figure S4. Percentage of total landings for species that make up the top 95% of catch for spear fishing. Colors indicate functional groupings.
Supplementary Figure S5. Percentage of total landings for species that make up the top 95% of catch for net fishing. Colors indicate functional groupings.
Supplementary Figure S6. Length-frequency for *Lethrinus ornatus*. Data were pooled for all fishing gear types (i.e., hook-and-line, net, and spear). The red dashed line indicates estimated length at maturity obtained from FishBase (22 cm).
Supplementary Figure S7. Length-frequency for *Siganus spp*. Data were pooled for all fishing gear types (i.e., hook-and-line, net, and spear). The red dashed line indicates the biomass-weighted mean length at maturity using FishBase for species in genus *Siganus* (*S. vulpinus, S. dolius, S. puellus, S. punctatissimus, S. guttatus, S. corallinus, and S. argenteus*) recorded in underwater visual census (19.4 cm).
Supplementary Figure S8. Length-frequency for *Parupeneus* spp. Data were pooled for all fishing gear types (i.e., hook-and-line, net, and spear). The red dashed line indicates the biomass-weighted mean length at maturity using FishBase for species in genus *Parupeneus* (*P. barberinus, P. cyclostomus, P. trifasciatus, P. multifasciatus, and P. crassilabris*) recorded in underwater visual census (22 cm).
Supplementary Figure S9. Length-frequency for *Scarus* spp. Data were pooled for all fishing gear types (i.e., hook-and-line, net, and spear). The red dashed line indicates the biomass-weighted mean length at maturity using FishBase for species in genus *Scarus* (*S. ghobban, S. niger, S. flavipectoralis, S. dimidiatus, S. schlegeli, S. psittacus, S. forsteni, S. quoyi, S. spinus, S. prasiognathos, and S. oviceps*) recorded in underwater visual census (22.8 cm).
Supplementary Figure S10. Length-frequency for *Chlorurus* spp. Data were pooled for all fishing gear types (i.e., hook-and-line, net, and spear). The red dashed line indicates the biomass-weighted mean length at maturity using FishBase for species in genus *Chlorurus* (*C. sordidus, C. bleekeri,* and *C. microrhinos*) recorded in underwater visual census (21 cm).
CHAPTER IV: Fishing Gear Restrictions Can Provide Conservation Benefits for Coral Reef Fisheries

By

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In review in *Fish and Fisheries*

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**Keywords:** Ecosystem-based management, Fisheries ecology, Fisheries management, Gear-based management, Population dynamics
Abstract

Gear-based management for coral reef fisheries is often overlooked in the scientific literature. Some empirical studies have demonstrated the conservation benefits of gear-restricted areas (i.e., prohibiting certain fishing gears), which can support greater biomass than unrestricted areas and protect species that play key functional roles on reefs. However, the basic population dynamics of reef fishes under specific gear-restriction regimes remains uncertain. Here, we constructed a multi-species, length-based fisheries population model to observe relative biomass, catch, and change in size distributions of reef fishes with gear-restriction management. We used fishery-dependent and -independent data to determine the catchability of functional groups and size classes for hook-and-line, net, and spear fishing, which are widely used on reefs globally. We found that spear fishing (i.e., prohibiting hook-and-line and net fishing) maintained the highest overall biomass, while a ban on spear fishing (i.e., permitting hook-and-line and net fishing) maintained the lowest biomass. However, allowing only hook-and-line fishing generated the highest overall catch and maintained higher biomass of most functional groups. Our results demonstrate that gear restrictions can achieve conservation and fisheries objectives simultaneously and were primarily driven by the catchability for the most abundant functional group - planktivores (high catchability for hook-and-line and low catchability for spear fishing). Thus, gear restrictions can be a critical management tool for maintaining biomass levels that promote coral reef health and resilience.
Introduction

Coral reefs are under immense pressure to support the livelihoods of millions of people in an increasingly globalized world (Hughes et al., 2017). The lifestyles and identities of many tropical, coastal communities are tightly connected to reef fisheries, and there are often few alternative sources for income and nutrition (Cinner, 2014). Fishing is, however, one of the primary drivers of marine ecosystem structure and function and has had profound negative effects, both direct and indirect, on coral reefs (Pandolfi et al., 2003). For example, fishing directly impacts reefs by reducing fish abundance and biomass and indirectly through compromising ecosystem functions (DeMartini & Smith, 2015). Thus, scientists and managers are tasked with developing ecosystem-based management policies that can support fisheries production and livelihoods while also preserving ecological functions that are vital for coral reef health and resilience (Cinner et al., 2020).

Research and management efforts for tropical marine fisheries have focused primarily on the use of no-take marine protected areas (MPAs), which prohibits all fishing activities within a designated area indefinitely, thus curbing the adverse effects of overfishing (Edgar et al., 2014). Well-enforced no-take MPAs can increase biomass, biodiversity, and protect key ecological functions on coral reefs (Lester et al., 2009). In addition, the accumulation of abundance and biomass of fishes within no-take MPA boundaries potentially spills over to adjacent fishing areas and enhances yields (Abesamis & Russ, 2005; Halpern, Lester, & Kellner, 2009). However, no-take MPAs remain controversial for many fisheries and a lack of support from fishing communities often results in low compliance and, thus, many MPAs generate minimal to no benefits (Gill et al., 2017; McCook et al., 2010). This is especially true for developing countries with
limited resources for implementing and enforcing no-take MPAs (Donner & Potere, 2007). There is, therefore, a need to explore alternative management options that may be better aligned with socio-cultural contexts and capacities of communities with reef fisheries (McClanahan & Abunge, 2016).

Fishers on coral reefs have expressed more support for gear-based management over no-take MPAs (McClanahan et al. 2005), but this strategy has received scant attention in the scientific literature. The motivation for investigating gear-based management is that fishers on coral reefs use multiple gear types (e.g., hook-and-line, nets, and spears), and each gear exhibits selectivity for certain species, functional groups, size classes, or combinations of these attributes (Mbaru, Graham, McClanahan, & Cinner, 2020; McClanahan & Mangi, 2004). For example, hook-and-line fishing targets piscivorous fishes with baited hooks (Humphries et al., 2019). Nets, spears, and traps generally target more species than hook-and-line fishing, and small traps and nets with small mesh sizes can have high catch rates for small and immature fishes (Cinner, McClanahan, Graham, et al., 2009; Hicks & McClanahan, 2012). Gear-based management seeks to limit or prohibit the use of fishing gears that target key functional groups and juvenile fishes, and avoid gears that directly destroy reef habitat.

Some fishers support gear-based management because these regulations can be easy to circumvent (Cinner, McClanahan, Graham, et al., 2009), but empirical studies have provided evidence that gear-restrictions can increase biomass of reef fishes and protect species that play key functional roles in reef ecosystems (Campbell et al., 2020). For instance, coral reefs that allow only hook-and-line fishing can support greater fish biomass than multi-gear or unrestricted fishing areas (Campbell, Edgar, Stuart-Smith, Soler, 

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Bates, 2018). Importantly, gear-restrictions can increase the biomass of herbivores, which promote reef health and resilience by consuming macroalgae and exposing reef substrate for coral recruitment (Bozec, O’Farrell, Bruggemann, Luckhurst, & Mumby, 2016; Steneck et al., 2009). While empirical studies show that gear-restricted areas can support greater biomass than unrestricted areas, and gear selectivity studies provide a framework for gear-based management, the population dynamics of fishes under various gear-restriction regimes remains uncertain.

In this study, we constructed a fisheries model and used fishery-dependent and independent data to determine the catchability of functional group-size class combinations of reef fishes for each gear type. We modeled hook-and-line, net, and spear fishing, which are widely used gear types in coral reef fisheries around the world. The aims of our model were to observe changes in biomass, catch, and size distributions of fishes in relation to fishing effort and under various gear-restriction scenarios. Our baseline model scenario allowed all fishing gears with equal fishing pressure, and subsequent scenarios included a full factorial design of prohibiting gear types. Modeling fishing gear restrictions allowed us to observe the basic dynamics of a reef fishery when fishing effort shifts between gear types, rather than overall effort decreasing when gears are prohibited.

**Methods**

**Model summary**

We developed a length-based, multispecies population model to simulate gear-restriction scenarios for coral reef fisheries. Our model focused on representative reef species from nine functional groups (Table S1): browsers (*Naso lituratus*), detritivores
(Ctenochaetus striatus), excavators/scrapers (Scarus niger), grazers (Siganus punctatus), macro-invertivores (Parupeneus multifasciatus), micro-invertivores (Scolopsis bilineata), pisci-invertivores (Cephalopholis argus), piscivores (Aethaloperca rogaa), and planktivores (Caesio teres). Functional groups were designated based on primary literature from global datasets (Cinner, Graham, Huchery, & MacNeil, 2013; Froese & Pauly, 2020; MacNeil et al., 2015). We utilized gear-specific catchability parameters (specific to functional group and size class) to model hook-and-line, net, and spear fishing. These parameters were derived from fishery-dependent and -independent data collected from coral reefs in Wakatobi National Park in Southeast Sulawesi, Indonesia (Carvalho et al., 2020). Hook-and-line fishing trips included one to three fishers using small, baited hooks and monofilament line. Spear fishers used 1-meter long wooden spearguns propelled by a single rubber tube. Spear fishing trips ranged from one to six fishers. Nets used were 75 × 3 m gillnets with a small mesh size, and sometimes multiple nets were tied together. Net fishing trips can include as many as 14 people. Initial population sizes for each functional group were based on fishery-independent surveys, and recruitment was modeled using a Beverton-Holt stock-recruitment relationship. The purpose of this model was to simulate relative biomass and catch in response to gear-restrictions. Therefore, we have prioritized generality and realism rather than providing specific quantitative estimates for biomass or catch targets in a particular coral reef systems (Levins, 1966). By using catchability values for the most commonly used fishing gear types on coral reefs, this model was strategically designed to understand the basic emergent properties of fish communities in response to gear-restriction management. All simulations followed the same model sequence: (i) introduce recruits, (ii) impose natural and fishing mortality, and (iii) allow fish to grow.
Recruitment

We used the Beverton-Holt equation to model stock-recruitment relationships:

\[ R = \frac{B}{\alpha + \beta B} \]

where \( R \) was recruitment, \( B \) was spawning stock biomass, \( 1/\alpha \) was the maximum per capita production of recruits, and as \( B \) increases \( R \) approaches \( 1/\beta \). The spawning stock biomass \( (B) \) was the biomass of fish greater than or equal to length-at-maturity \( (L_{50}) \). We assumed that fish were evenly distributed within each size class when estimating \( B \) for functional groups that had an \( L_{50} \) within a size class. We parameterized the function using the dimensionless parameter for steepness \( (h) \), which was the proportion of recruits in the absence of fishing \( (R_0) \) and when spawning stock biomass was at 20\% of the unfished level \( (Mace & Doonan, 1988) \). Thus, \( \alpha \) and \( \beta \) can be related to steepness with the following equations:

\[ \alpha = \frac{B_0}{R_0} \frac{1 - h}{4h} \]
\[ \beta = \frac{5h - 1}{4hR_0} \]

\( (Mangel, Brodziak, & DiNardo, 2010) \). Steepness \( (h) \) was estimated as the ratio of length-at-maturity and asymptotic length: \( h = L_{50}/L_\infty \) \( (Wiff, Flores, Neira, & Caneco, 2018; Table S1) \). Recruitment in the absence of fishing \( (R_0) \) was estimated through an optimization function such that biomass reached a level that resembles fish populations on remote or pristine coral reefs \( (Campbell et al., 2020; MacNeil et al., 2015) \). The spawning stock biomass at equilibrium from the optimization function was used as the estimate for \( B_0 \).

Natural mortality
Natural mortality \((M)\) was a function of the midpoint of each size class \((L_{i,j})\), asymptotic length \((L_{\infty,i})\), and instantaneous growth rate \((k_i; Gislason et al., 2010)\):

\[
\ln(M_{i,j}) = 0.55 - 1.61[\ln(L_{i,j})] + 1.44[\ln(L_{i,\infty})] + \ln(k_i).
\]

We assumed that \(M\) was an allometric function of body length and constant across time (Figure S1; Gislason et al., 2010). Thus, early stages of life experienced the greatest mortality for each functional group, but mortality rapidly decreased as size increased (Figure S1).

**Fishing mortality**

Fishing mortality was modeled with the equation:

\[
F_{i,j,g} = q_{i,g}s_{j,g}E_g,
\]

where \(F\) was the fishing mortality for functional group \((i)\) and size class \((j)\) by gear type \((g)\), \(q\) was catchability for each functional group, \(s\) was selectivity of size classes, and \(E\) was fishing effort. Selectivity for size classes \((s)\) was modeled with a normal function \((\mu, \sigma)\) for hook-and-line fishing and with a logistic function \((\kappa, L_{50})\) for net and spear fishing. To estimate \(q\) and parameters for \(s\), we used optimization to minimize the sum of squared error for the function:

\[
\frac{y_{i,j}}{n_{i,j}} = q_iS_j,
\]

where \(y\) was the ratio of catch per fishing trip and \(n\) was the number observed by fisheries-independent surveys (Table S2; Figures S2-4). Data for \(y\) and \(n\) were taken from Carvalho et al. (2020). In addition, the products of \(q_{i,g}s_{j,g}\) were scaled such that values for all functional group-size class combinations summed to one for each gear type. This step ensured that fishing mortality was modulated by differential catchability and selectivity rather than differences in effort among gear types. Total catch \((C)\) was calculated using the
Baranov catch equation:

\[ C = \frac{F}{F + M} \left( 1 - \exp^{-(F+M)} \right) N \]

where \( F \) was total fishing mortality (for all gear types), \( M \) was natural mortality, and \( N \) was the fishable stock.

**Growth**

Individual fish grew according to the von Bertalanffy Growth Function (VBGF):

\[ L_{i,t} = L_{i,\infty} \left( 1 - e^{-k_i(t-t_{i,0})} \right). \]

Estimates of asymptotic lengths \((L_{i,\infty})\) and instantaneous growth rates \((k_i)\) were obtained from FishBase (Froese & Pauly, 2020; Table S1). To accommodate the binned size structure of fish populations in our model, we calculated the time for fish to grow from the lower to upper limit of each size class (Hilborn & Walters, 1992):

\[ t_{i,j} = \frac{1}{k_i} \log \left( \frac{L_{i,\infty} - L_{i,\text{lower}}}{L_{i,\infty} - L_{i,\text{upper}}} \right). \]

Here we assumed that fish were distributed evenly within each size class and the proportion that grew into the next size class at each time step was \( \phi_{i,j} = 1/t_{i,j} \) (Hall et al., 2006). Representative species of each functional group grow at different rates and, thus, timesteps were rescaled such that \( \phi_{i,j} = t_{\text{min}}/t_{i,j} \). This step prevented fish from skipping multiple size classes in a single timestep, and all fish from the fastest growing functional group-size class combination reached size class \( j + 1 \) in a single timestep (Hall et al., 2006). Thus, the number of fish from functional group \( i \) and size class \( j \) that grew to the next size class was \( N_{i,j+1} = N_{i,j} \phi_{i,j} \).

**Gear-restriction scenarios**

Our baseline management scenario included all fishing gears (i.e., hook-and-line,
net, and spear) with total effort equally divided among gears. Subsequent management scenarios included a full factorial of gear combinations. For each management scenario, we tested a range total fishing effort, which was divided equally among each gear type permitted in a particular management scenario. We ran each model to equilibrium and compared the total biomass and catch for each management scenario and total effort level. Also, we compared biomass and catch of each functional group across management scenarios and range of effort. To determine the impact of gear-restrictions on the size distribution of fishes, we calculated the proportion (based on kg) of fish in the smallest two size classes, 5 – 15 cm (i.e., recruits and smallest size available for capture), for biomass and catch and compared these values across management scenarios.

Results

Gear restrictions had a considerable impact on fish biomass and catch for coral reef fishes. Spear fishing (i.e., hook-and-line and net fishing prohibited) maintained higher total biomass compared with alternative gear-restriction scenarios across the full gradient of fishing effort (Figure 1A). Thus, a higher level of effort was required to reach half of the pristine biomass (0.5B₀) when spear fishing was used exclusively, E_{spear} = 0.58 (Figure 1A). Prohibiting spear fishing (i.e., allowing hook-and-line and net fishing) resulted in the lowest total biomass and required the least fishing effort to reach 0.5B₀, E_{line,net} = 0.32 (Figure 1A). However, hook-and-line fishing (i.e., net and spear fishing prohibited) maintained the same level of biomass as a spear ban when biomass was higher than 0.5B₀. However, hook-and-line fishing and a ban on spear fishing produced the highest catch-per-unit-effort (CPUE) (Figure 1B). At high fishing effort (E > 0.9), CPUE converges for
alternative gear-restriction scenarios (i.e., ban on net fishing and allowing all fishing gears). Spear fishing generated the lowest CPUE for almost the full range of fishing effort, but converged with net fishing and a ban on hook-and-line fishing at high fishing effort ($E > 0.9$) (Figure 1B). At 0.5B$_0$, hook-and-line fishing produced the highest catch ($C = 0.87$) and had the highest CPUE (Figure 1B). Net fishing produced the least catch at 0.5B$_0$ ($C = 0.72$), followed by prohibiting hook-and-line fishing and allowing only spear fishing (Figure 1B).

The size distribution of overall biomass was most affected by hook-and-line fishing such that a higher proportion of biomass was concentrated in the smallest two size classes, 5 – 15 cm, compared with alternative management scenarios (Figure 2A). However, hook-and-line fishing had the lowest proportion of small fishes in the catch across the full range of fishing effort (Figure 2B). Net fishing caught the highest proportion of small fishes, but this did not result in a greater proportion of small fishes in the biomass (Figure 2). Spear fishing had the least impact on the size distribution of biomass compared with other management scenarios.

Hook-and-line fishing maintained the highest biomass for browsers, detritivores, excavator/scrapers, grazers, and micro-invertivores, and caught the lowest proportion of small fishes for these functional groups (Figure 3 and S5). However, hook-and-line fishing maintained the lowest biomass of planktivores (and resulted in the highest proportions of small planktivores compared with other management scenarios; Figure S6) and depleted pisci-invertivores and piscivore at low fishing effort ($E < 0.3$) (Figure 3). Spear fishing maintained the highest biomass for micro-invertivores and planktivores, but depleted browsers at moderate fishing effort ($E = 0.6$). The magnitude of change in biomass in response to fishing varied among functional groups. Total biomass was heavily affected by
planktivore biomass, as this was the most abundant functional group. Thus, at $0.5B_0$ of the total biomass, planktivore biomass was just above, or just below for hook-and-line fishing, $0.5B_{0,\text{planktivores}}$ and biomass of many functional groups was below $0.5B_{0,i}$ (Figure 3). However, detritivores were the least vulnerable to fishing and biomass remained well above $0.5B_{0,\text{detritivores}}$, across the full range of fishing effort (Figure 3B). Micro- and macro-invertivores also were exceptions in that biomass of these functional groups was above $0.5B_{0,i}$ for most management scenarios, particularly scenarios that prohibited net fishing (in this case, $i$ being micro- or macro-invertivores) (Figure 3E and 3F).

The maximum sustainable yield (MSY) for pisci-invertivores and piscivores was lower than all functional groups, and at $0.5B_0$, piscivore catch was almost zero and pisci-invertivore catch was $< 0.5 \text{ MSY}_{\text{pisci-invertivore}}$ (Figure 4). The MSY for browsers also occurred at low fishing effort ($0.15 < E < 0.3$) and was depleted for net fishing, ban on hook-and-line fishing, and spear fishing (Figure 4). At $0.5B_0$, excavators/scrapers and grazers were near MSY, except below MSY for hook-and-line fishing (Figure 4). The catch of detritivores, macro- and micro-invertivores, and planktivores was below MSY for all management scenarios at $0.5B_0$ (Figure 4).

**Discussion**

In this study we used fishery-dependent and -independent data to develop gear-specific catchability and selectivity for functional group-size class combinations of coral reef fishes and integrated these data with a fisheries model to investigate the impacts of gear-restrictions on population dynamics and yields. We show that total biomass and functional group-specific biomass at a given level of fishing effort differs considerably
between gear restriction scenarios. This finding is supported by a country-wide assessment of coral reefs in Indonesia that found greater total biomass of reef fishes at gear-restricted sites compared with open access areas (Campbell et al., 2020). Thus, gear restrictions can provide conservation benefits by maintaining higher biomass than unrestricted fishing.

Out of all gear restriction scenarios modeled, spear fishing (i.e., hook-and-line and net fishing prohibited) maintained the highest total biomass and caught relatively low proportions of small fishes. This result was due to the low catchability of planktivores, which were the most abundant functional group, by spear fishing (Campbell et al., 2020). Our findings are corroborated by empirical studies that have found higher biomass in gear-restricted areas compared with open access areas (Campbell et al., 2018; Campbell et al., 2020). Thus, our model extends the implications of empirical research by demonstrating that permitting only spear fishing can maintain greater biomass than unrestricted fishing, even when displaced effort from banned gears is transferred to spear fishing.

The change in biomass for each functional group in response to fishing effort shows that fewer ecological functions are impacted by hook-and-line fishing, or less impacted, compared with net and spear fishing (Humphries et al., 2019; Mbaru et al., 2020). For example, herbivore (i.e., browsers, excavators/scrapers, grazers) and macro-invertivore biomass was greater for hook-and-line fishing (i.e., net and spear fishing prohibited) than other gear restriction scenarios. This finding is consistent with coral reef fisheries in Bonaire, where parrotfish populations were conserved by permitting only hook-and-line fishing (Steneck et al., 2009). However, hook-and-line fishing may lead to cascading effects on fish communities that were omitted from our model (Dulvy, Freckleton, & Polunin, 2004; Jennings & Polunin, 1996b). For example, the removal of piscivorous fishes
can ease top-down control on prey species – also known as prey release (Carr & Hixon, 1995). If we considered prey release in our model, natural mortality curves of non-piscivorous fishes would shift lower as the abundance of piscivorous fish decreases. However, piscivorous fishes were depleted at low levels of effort for all management scenarios and, thus, we expect our qualitative results to be robust to the effects of prey-release.

Our results demonstrated that a ban on spear fishing (i.e., hook-and-line and net fishing permitted) resulted in the lowest total biomass among gear restriction scenarios, and scenarios that permitted any spear fishing had higher total biomass than scenarios that prohibited spears (i.e., hook-and-line fishing, net fishing, and ban on spear fishing). The wide catchability for many functional groups by net fishing and relatively high catchability for small individuals is partly driving this pattern and allows nets to overexploit fishery resources (Friedlander, 2015; McClanahan & Mangi, 2004). Net fishing resulted in the lowest biomass for browsers, detritivores, excavator/scrapers, grazers, and macro- and micro-invertivores. Similar patterns of reef fish depletion have been observed empirically. For example, net fishing was associated with low biomass and the loss of key functional groups on coral reefs in Kenya (McClanahan, Hicks, & Darling, 2008). Importantly, herbivore biomass was lowest for net fishing. Herbivores play key functional roles on coral reefs, such as opening space on reefs for coral recruits to settle and controlling macro-algal growth (Hughes et al., 2007; Mumby, Hastings, & Edwards, 2007). Net fishing also inflicts direct physical damage to reef structure via entanglement, which many reef fishes rely on for refuge from predators (Mangi & Roberts, 2006; Rogers, Blanchard, & Mumby, 2014). In addition, the high catchability for small fishes by nets can lead to growth overfishing for
most functional groups, where fishes are caught below sizes that achieve optimal yield (McManus, 1997). Net fishing is, therefore, quite capable of diminishing the resilience of coral reef ecosystems and inhibiting recovery after disturbances, such as coral bleaching events (Cinner, McClanahan, Graham, et al., 2009).

Total catch for all gear restriction scenarios increased non-linearly with fishing effort, and relatively high yields were maintained at low biomass in our model. This result was due to the high resilience of certain functional groups to fishing. For example, catch for excavator/scrapers, grazers, macro- and micro-invertivores, and planktivores was near MSY at high fishing effort. The relationship we observed in our model between biomass, catch, and effort has been observed empirically in coral reef fisheries. For example, high yields were maintained at high levels of fishing effort in Fijian coral reef fisheries (Jennings & Polunin, 1996a). In addition, a study on Kenyan coral reef and seagrass fisheries demonstrated that high yields can be maintained at biomass levels lower than 20% of the pristine biomass (McClanahan et al., 2008). High yields at low biomass and high effort can also result from augmented recruitment from source populations outside of the fishery. Thus, future research can expand this model by considering self-recruitment and larval connectivity as data become available. Although total yield might increase with effort and the use of destructive fishing methods for some coral reef fisheries (i.e., Malthusian overfishing), the shifts in community structure and low biomass at high fishing effort compromise ecosystem functioning and resilience (Hughes et al., 2007).

Allowing only spear fishing may provide some conservation benefits by maintaining higher total biomass than other gear restriction scenarios; however, we observed a tradeoff between total biomass maintained and biomass of particular functional
groups. Hook-and-line fishing (i.e., prohibiting net and spear fishing) maintained a low total biomass, but generated the highest catch, caught the lowest proportion of small individuals, and maintained the highest biomass for browsers, detritivores, excavator/scrapers, grazers, and macro-invertivores. Thus, the tradeoff dissolves in favor of hook-and-line fishing, which can provide conservation and fisheries benefits.

Other factors influence fisheries objectives such as profitability of different gear types. For example, hook-and-line and spear fishers frequently catch higher proportions of piscivorous fishes than net fishers, which often have higher market values than other coral reef species (Cinner, McClanahan, Graham, et al., 2009). In addition, hook-and-line fishers typically own their fishing gear while net fishers often split profits between individual fishers and net owners, which results in complex social dynamics that influence the use of fishing gears (Mangi, Roberts, & Rodwell, 2007). Gear-based management must be tailored to the local socio-cultural context and balance competing social-ecological objectives in the decision-making process (Matsuda & Abrams, 2006).

The gear-restriction scenarios we modeled are not an exhaustive exploration of potential gear-based management actions, and additional management measures used in tandem with gear-restrictions may help alleviate some trade-offs between fisheries and conservation objectives. For example, gear modification is another strategy that can promote sustainable fishing practices on coral reefs. Studies have shown that increasing the mesh size of nets can prevent growth overfishing and reduce the number of immature fishes caught (Hicks & McClanahan, 2012). Also, trap fishing is another gear type commonly used in coral reef fisheries, and studies have demonstrated that eliminating traps and implementing size restrictions on parrotfishes can increase biomass and catch per unit
effort (Bozec et al., 2016). An increase in the biomass of parrotfishes subsequently leads to higher grazing rates and less coral cover lost per unit of fishing effort (Bozec et al., 2016). Thus, gear-restrictions should be viewed as a tool that can be used within a wider ecosystem-based management framework rather than standalone regulations (Metcalfé et al., 2015).

Coral reef fish populations are affected by a myriad of biotic (e.g., primary productivity) and abiotic (e.g., ocean currents) factors that are absent from our model. However, fishing pressure has been shown to be the dominant top-down process affecting reef fish populations and can mask bottom-up processes in some areas (Nash, Bijoux, Robinson, Wilson, & Graham, 2016). By integrating gear-specific catchability for fishing gears that are widely used on coral reefs, we believe our model can help understand basic fish dynamics under various gear-restriction scenarios. We present a length-based, multi-species, multi-gear model for coral reef fisheries and show that gear-based management can provide conservation and fisheries benefits by allowing only hook-and-line fishing. An interesting next step for this research would be to examine a spatially-explicit fisheries model for coral reef species to compare population dynamics under gear-restriction management with additional spatial management regulations, such as no-take MPAs (Metcalfé et al., 2015). Overall, our study suggests that gear-restrictions can provide a critical management tool in locations at intermediate socio-economic development for avoiding the valley of reef fish depletion – a social-ecological trap whereby the depletion of key functional roles in coral reef ecosystems is deteriorated to an extent where reefs shift to a less productive, alternative stable state (Cinner, McClanahan, Daw, et al., 2009; Steneck, 2009).
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**Figure IV-1. Biomass and catch in relation to effort.** Total biomass (relative to unfished biomass) and catch (relative to maximum catch) including all functional groups in relation to fishing effort. Colors indicate management scenarios. The gray dashed line (A) indicates half of unfished biomass, and horizontal and vertical dashed lines (B) indicate catch and effort at half of unfished biomass.
Figure IV-2. Size distribution of biomass and catch in relation to effort. Overall proportion of biomass (A) and catch (B) composed of small fishes (i.e., kg of fish in the recruitment size class and smallest size class exposed to fishing pressure). Colors represent gear restriction scenarios.
**Figure IV-3. Relative biomass in relation to effort for each functional group.** Relative biomass across a gradient of fishing effort for browsers (A), detritivores (B), excavators/scrapers (C), grazers (D), macro- (E) and micro-invertivores (F), pisci-invertivores (G), piscivores (H), planktivores (I) Colors represent gear-restriction scenarios. The gray dashed lines indicate half of the pristine biomass for each functional group, and circles indicate effort and functional group biomass when the total biomass (i.e., including all functional groups) is half of the pristine biomass.
Figure IV-4. Relative catch in relation to effort for each functional group. Relative catch across a gradient of fishing effort for browsers (A), detritivores (B), excavators/scrapers (C), grazers (D), macro- (E) and micro-invertivores (F), pisci-invertivores (G), piscivores (H), planktivores (I) Colors represent gear-restriction scenarios. The circles indicate catch and effort at which total biomass (i.e., biomass of all functional groups) was half of the pristine biomass.
Supplementary Information

Supplementary Table S1. Life-history parameters for representative species of each functional group.

<table>
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<th>Functional group</th>
<th>Species</th>
<th>$k$</th>
<th>$L_{co}$</th>
<th>$L_{M50}$</th>
<th>$L_{max}$</th>
<th>$h$</th>
<th>$a$</th>
<th>$b$</th>
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<tbody>
<tr>
<td>Browser</td>
<td><em>Naso lituratus</em></td>
<td>0.341</td>
<td>32</td>
<td>15</td>
<td>36</td>
<td>0.47</td>
<td>0.0497</td>
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<td>Detritivore</td>
<td><em>Ctenochaetus striatus</em></td>
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<td>17</td>
<td>15</td>
<td>20</td>
<td>0.88</td>
<td>0.0254</td>
<td>3.027</td>
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<td>Excavator/scaper</td>
<td><em>Scarus niger</em></td>
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<td>25</td>
<td>16</td>
<td>28</td>
<td>0.64</td>
<td>0.0142</td>
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<td>Grazer</td>
<td><em>Siganus punctatus</em></td>
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<td>36</td>
<td>21</td>
<td>40</td>
<td>0.58</td>
<td>0.0206</td>
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<td>Macro-invertivore</td>
<td><em>Parupeneus multifasciatus</em></td>
<td>0.750</td>
<td>30</td>
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<td>35</td>
<td>0.50</td>
<td>0.0315</td>
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<td>Micro-invertivore</td>
<td><em>Scolopsis bilineata</em></td>
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<td>22</td>
<td>12</td>
<td>25</td>
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<td>Pisci-invertivore</td>
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<td>60</td>
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<td>0.0130</td>
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<td>Piscivore</td>
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<td>60</td>
<td>0.57</td>
<td>0.0299</td>
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<td>Planktivore</td>
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<td>40</td>
<td>0.38</td>
<td>0.0169</td>
<td>3.232</td>
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**Supplementary Table S2.** Estimated catchability \( (q) \) parameters for each functional group by hook-and-line, net, and spear fishing.

<table>
<thead>
<tr>
<th>Functional group</th>
<th>( q_{\text{line}} )</th>
<th>( q_{\text{net}} )</th>
<th>( q_{\text{spear}} )</th>
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<tr>
<td>Browser</td>
<td>0.00</td>
<td>3.55</td>
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<td>Detritivore</td>
<td>23.59</td>
<td>1.28</td>
<td>0.88</td>
</tr>
<tr>
<td>Excavator/scaper</td>
<td>110.97</td>
<td>3.89</td>
<td>6.27</td>
</tr>
<tr>
<td>Grazer</td>
<td>104.91</td>
<td>3.90</td>
<td>10.00</td>
</tr>
<tr>
<td>Macro-invertivore</td>
<td>170.69</td>
<td>2.88</td>
<td>4.65</td>
</tr>
<tr>
<td>Micro-invertivore</td>
<td>109.42</td>
<td>1.76</td>
<td>2.09</td>
</tr>
<tr>
<td>Pisci-invertivore</td>
<td>754.37</td>
<td>3.38</td>
<td>6.60</td>
</tr>
<tr>
<td>Piscivore</td>
<td>484.22</td>
<td>2.95</td>
<td>9.39</td>
</tr>
<tr>
<td>Planktivore</td>
<td>117.89</td>
<td>0.73</td>
<td>1.61</td>
</tr>
</tbody>
</table>
Supplementary Figure S1. Natural mortality ($M$) in relation to size of each functional group. $M$ year$^{-1}$ was calculated using equation 1 (Gislason et al., 2010) and scaled to a single time step in the model.
Supplementary Figure S2. Size selectivity ($s$) by hook-and-line fishing. Selectivity for line fishing was modeled using a normal function ($\mu = 37.37$, $\sigma = 18.40$).
Supplementary Figure S3. Size selectivity ($s$) by net fishing. Selectivity of net fishing was modeled using a logistic function ($\kappa = -0.03$, $L_{50} = 11.89$).
Supplementary Figure S4. Size selectivity (s) by spear fishing. Selectivity of spear fishing was modeled using a logistic function ($\kappa = 0.02, L_{50} = 42.64$).
Supplementary Figure S5. Proportion of catch composed of small fishes (i.e., kg of fish in the recruitment size class and smallest size class exposed to fishing pressure) for browsers (A), detritivores (B), excavators/scrapers (C), grazers (D), macro- (E) and micro-invertivores (F), pisci-invertivores (G), piscivores (H), and invertivores (I). Colors represent gear restriction scenarios.
Supplementary Figure S6. Proportion of biomass composed of small fishes (i.e., kg of fish in the recruitment size class and smallest size class exposed to fishing pressure) for browsers (A), detritivores (B), excavators/scrapers (C), grazers (D), macro- (E) and micro-invertivores (F), pisci-invertivores (G), piscivores (H), and invertivores (I). Colors represent gear restriction scenarios.
CHAPTER V: CONCLUSION

Summary of results

In this dissertation we explored the relative impacts of fishing and habitat condition on coral reef fishes across three regions in Indonesia: Raja Ampat, Wakatobi, and Lombok. In addition, we investigated the selectivity of fishing gears (i.e., hook-and-line, net, and spear) in Wakatobi and constructed a fisheries population model to simulate various gear-restriction scenarios. The main questions addressed in this dissertation were:

1. How does fishing pressure and habitat condition affect size distributions, specifically the abundance size spectra, of coral reef fishes (Chapter 2)?

2. What are the similarities and differences in selectivity of fishing gears for functional groups and size classes of coral reef fishes (Chapter 3)?

3. How do gear restrictions impact biomass, catch, and size distributions of coral reef fishes (Chapter 4)?

In Chapter 2, we found that fishing pressure was the best predictor of size spectra slopes when all reef fishes were aggregated regardless of taxonomic identity. Low values for size spectra slopes indicate relatively few large-bodied and/or many small-bodied fishes. We found a significant, non-linear relationship between size spectra slopes and fishing pressure such that sites with high fishing pressure (i.e., low total biomass) had steep size spectra slopes, and size spectra slopes became shallower as fishing pressure decreased. We also found a significant correlation between fishing pressure and structural complexity such that structural complexity decreased as fishing pressure increased. Our findings are corroborated by studies in Fiji, Hawaii, America Samoa, and Marianas Archipelago which found that spatial differences in fishing pressure or human population gravity were
significant predictors of size spectra for reef fishes (Robinson, Williams, & Edwards, 2017; Wilson et al., 2010). Also, our results suggest that steeper size spectra slopes at sites with high fishing pressure was primarily due to the removal of large-bodied individuals through fishing, and not due to the proliferation of small-bodied fishes through prey-release (Dulvy, Polunin, Mill, & Graham, 2004). Habitat condition, specifically structural complexity, has been shown to affect size distributions of coral reef fishes by providing refuge from predators and, thus, affecting the survival and competition among reef fishes (Rogers, Blanchard, & Mumby, 2014).

Fishing pressure and structural complexity were also significant predictors of carnivore and herbivore size spectra slopes when analyzed separately. The relationship between size spectra slopes of carnivores and fishing pressure was steeper than that of herbivores, which indicates that carnivorous reef species are impacted by fishing more than herbivores. This result was expected as fishers on coral reefs generally prefer large-bodied carnivores, which have relatively high value in domestic and international markets (Sadovy & Yin, 2015).

In Chapter 3, we analyzed fisheries-independent and -dependent data from Wakatobi in Southeast Sulawesi, Indonesia. We found that hook-and-line fishing exhibited high selectivity for piscivores and pisci-invertivores, which was to be expected because fishers typically use small, baited hooks that attract these functional groups (Humphries et al., 2019). Hook-and-line fishing had low selectivity for other functional groups, which indicates that hook-and-line fishing affects a narrow range of ecological functions (McClanahan & Cinner, 2008). Also, hook-and-line fishing had higher selectivity for large fishes (50 – 60 cm) relative to small fishes. Net fishing, however, caught the greatest
diversity of functional groups and had high selectivity for small-bodied fishes (11 – 20 cm). Thus, net fishing can compromise a wide range of ecological functions and potentially lead to growth overfishing (Cinner et al., 2009). These results are specific to the nylon nets with small mesh size (6.3 cm) used in Wakatobi, but coral reef fishers around the world use nets with a variety of mesh sizes and specifications. Studies have demonstrated that increasing the mesh size of nets (from 6.3 cm to 8.8 – 9.2 cm) can reduce the chances of growth overfishing and increase yields for coral reef fisheries (Hicks & McClanahan, 2012). Spear fishing exhibited high selectivity for excavator/scrapers, grazers, piscivores, and pisci-invertivores. Also, spears targeted fish between 20 – 30 cm, which was intermediate compared with hook-and-line and net fishing. The selectivity of nets overlaps with spears for herbivores (i.e., excavator/scrapers, grazers, and browsers), but nets likely preempt fishes targeted by spears by removing smaller individuals on average than spear fishers (McClanahan & Cinner, 2008). Spear fishers, however, select for smaller piscivore and pisci-invertivores than hook-and-lines and, thus, can preempt resources targeted by hook-and-line fishers.

We used fishery-dependent and -independent data from Chapter 3 to parameterize a length-based, multi-species, multi-gear model in Chapter 4. Through modeling we were able to investigate population dynamics of reef fishes in response to specific gear-restrictions across a range of fishing intensities. We found that spear fishing (i.e., prohibiting hook-and-line and net fishing) was able to maintain the highest overall biomass across the full range of fishing intensity. However, hook-and-line fishing generated the highest catch and maintained higher biomass of most functional groups compared with other management scenarios. This finding is consistent with empirical studies that have
found greater biomass of certain functional groups at sites that allowed only hook-and-line fishing (Campbell, Edgar, Stuart-Smith, Soler, & Bates, 2018). These results were primarily driven by the catchability of planktivores, which were the most abundant functional group. Spear fishing had the lowest catchability for planktivores, while hook-and-line fishing had a relatively high catchability for planktivores and low catchability for many functional groups. Our model extends the findings of empirical studies by showing that gear-restrictions can achieve greater biomass and catch than unrestricted fishing when effort is transferred to permitted gears rather than reduced overall effort from prohibiting certain gears. Our findings show that gear-restrictions can be an adaptive management strategy, which managers can adjust to fit particular ecological, socio-economic, and cultural contexts.

Limitations

In Chapter 2 we used total fish biomass, which was estimated via underwater visual census (UVC), as a proxy for fishing pressure. We recognized that this is a limitation of our study and that, in some cases, total fish biomass does not necessarily reflect differences or changes in fishing pressure. However, the coral reefs we surveyed have small-scale, dispersed, multi-species, and multi-gear fisheries, which made it infeasible to directly estimate fishing pressure at each site. Faced with these constraints, we validated our assumption by using linear regression of total fish biomass and population gravity values from Cinner et al. (2018), and we believe the significant relationship justified our proxy for fishing pressure in this study.

The UVC methods we used to collect data for Chapters 2 and 3 have inherent biases.
We excluded fishes > 65 cm and < 10 cm because individuals outside this size range are inadequately sampled by UVC (Ackerman & Bellwood, 2000; Kulbicki, 1998). Also, only non-cryptic and diurnally active species are effectively estimated through UVC, so we omitted nocturnal or cryptic species from our analyses in Chapters 2 and 3. Though we were unable to survey the entire fish communities at each site, non-cryptic, diurnal species make up a vast majority of catch from coral reef fisheries.

In Chapter 3, due to time constraints we had to enlist the help of local enumerators in Mola Village on Wangi-wangi Island in Wakatobi. For this reason, we were limited to the level of fish classification in the local Bajau language, which generally identified fish to the genus level and sometimes to the species level. This was not a major obstacle to our research because we were still able to group fishes into appropriate functional groupings for our analyses. In addition, species within the families Carangidae and Lethrinidae (piscivores and pisci-invertivores) are particularly flighty and often underestimated by UVC (Jennings & Polunin, 1995). Therefore, we removed these species from the Manly-Chesson analysis, which consequently inflated the Manly-Chesson selectivity values.

In Chapter 4, we had planned on using the Manly-Chesson selectivity indices from Chapter 3 for parameterizing the fisheries model. However, we found that the most common species caught in Wakatobi, *Lethrinus ornatus*, was a species that is difficult to survey by UVC and was excluded from the Manly-Chesson analysis. We decided that the Manly-Chesson indices were inappropriate for parameterizing the fisheries model. Instead we used an optimization function to determine the catchability for each functional group and selectivity of each size class based on the ratio of each functional group and size class in the catch and ratio observed through underwater visual census.
Future directions

In Chapter 2, we show that total fish biomass (proxy for fishing pressure) can be a good fisheries-independent indicator of size distribution for coral reef fishes in Indonesia. Future studies could expand on this research by quantifying size spectra for reefs globally to develop reference points or thresholds that can be used by fisheries managers as monitoring tools and to guide management decisions. In addition, studies could investigate the relative effects of fishing pressure and habitat condition on carnivores and herbivores in other locations (e.g., Western Indian Ocean and Caribbean) to determine whether our results hold for coral reefs outside of Indonesia.

In Chapters 3 and 4, we investigated the impacts of hook-and-line, net, and spear fishing on functional groups and size classes of coral reef fishes in Wakatobi and modeled fishing gear restrictions. Future studies could expand our model by including other gear types used in coral reef fisheries (e.g., traps) and gear specifications (e.g., different mesh sizes of nets). In addition, our fisheries model could be made spatially explicit to investigate population dynamics when gear-restrictions are implemented with additional management measures, such as no-take MPAs or periodically harvested closures. The effects of reef connectivity and larval dispersal on outcomes from gear-based management can also be explored using a spatially explicit model. Our fisheries model was quite simple due to uncertainties in life history parameters for coral reef fisheries. Thus, research can focus on gathering empirical estimates of life history characteristics for coral reefs fishes to improve modeling capabilities.
References


