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DRIVERS AND DYNAMICS OF COMMERCIAL CORAL-REEF FISHERIES FOOTPRINT EXPANSIONS AND IMPLICATIONS FOR STOCKS, ECOSYSTEMS, AND SOCIETIES

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Cuetos Bueno, Javier

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DRIVERS AND DYNAMICS OF COMMERCIAL CORAL-REEF FISHERIES FOOTPRINT EXPANSIONS AND IMPLICATIONS FOR STOCKS, ECOSYSTEMS, AND SOCIETIES

by

JAVIER CUETOS BUENO

A thesis submitted to the University of Plymouth

in partial fulfilment for the degree of

DOCTOR OF PHILOSOPHY

School of Biological and Marine Sciences

May 2021

Dedication

Para Fini y Tiri

Author's declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award.

Work submitted for this research degree at the Plymouth University has not formed part of any other degree either at Plymouth University or at another establishment.

The works submitted for this thesis study were financed by grants provided by Margaret A. Cargill Foundation small grants program administered by the Micronesia Conservation Trust, and by U.S. National Oceanic and Atmospheric Administration. Some datasets used in the study were also funded by U.S. Sports Fish Restoration Program, the Guam Division of Aquatic and Wildlife Resources, U.S. Department of Agriculture's Food and Nutrition Services, Commonwealth of the Northern Mariana Islands Nutrition Assistance Program, and Federated States of Micronesia National Food Safety Program.

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Abstract

Drivers and dynamics of commercial coral-reef fisheries footprint expansions and implications for stocks, ecosystems, and societies

Javier Cuetos Bueno

Coral-reef fisheries have provided food security and recreation for societies across the tropics for countless generations, and are also estimated to provide nearly $6 billion USD in net benefits to the world annually while supporting the livelihood of over 6 million fishers and their families. Yet, unsustainable fisheries regimes with ensuing impacts to coral-reefs and societies that depend on them have been reported over the last decades across most tropical regions. Alongside, management frameworks continue to struggle to ensure sustainable fishing regimes in the face of limited evidence-based guidance and the prevalent context of limited capacity and resources. This thesis aimed to advance on the field of small-scale multi-species fisheries by enhancing our understanding of exploitation and stock dynamics, the drivers behind those dynamics, and potential novel management paths towards sustainable fishing regimes. Within, it focuses on poorly understood coral-reef fisheries and on the drivers and progressive dynamics associated to increased commercialization of those fisheries, ensuing localized depletions and fisheries expansions, and inevitable impacts to stocks and societies.

We used three islands in Micronesia (western tropical Pacific) with extensive multi-species coral-reef fisheries that are dominated by nighttime spearfishing as case studies to test our hypothesis. The islands presented useful gradient of levels of fishing pressure and reef-fish trade networks within and across. Our studies targeted multispecies fisheries that generally included over 100 species at any given island, but specific analyses focused on the most dominant species that had more data available. Those were mostly members of parrotfish, surgeonfish, grouper, emperor, snapper, and rabbitfish families. Previously unexplored records of 13 years of reef-fish exports from Chuuk (Federated States of Micronesia) to Guam (USA) were compiled and analyzed to explore how environmental and socioeconomic factors combined, and evolved, to drive export patterns over time (Chapter 2). Extensive commercial landings records and coupled fisher interviews that were collected over one year and an existing limited subsistence landings datasets from Chuuk served to assess impacts on stocks of the export-driven commercial fisheries expansions (Chapter 3). Lastly existing unique historical and snapshot landings datasets from Guam (USA) and the Commonwealth of the Northern Mariana Islands (USA) were used to assess i) potential development of landings variability dynamics and masking effects associated to fisheries expansions (Chapter 4), and ii) variability of species responses to fishing pressure and potential implications for restructuring of fisheries (Chapter 5). Analysis of export records highlighted how coral-reef fisheries are increasingly becoming subject to complex exogenous market drivers that may easily be hidden and out of the control of local fisheries managers and stakeholders, in this case changes on wellfare programs in Guam coupled with global rises on crude prices that drove a boom-and-bust cycle for exports between Chuuk and Guam. Chuuk extensive landings datasets provide evidences regarding disproportionate impacts on stocks and ecosystems of commercial fisheries (which are fueled by growing trade networks) as compared with subsistence counterparts, as highlighted by compromised status of species disproportionally targeted by commercially fishers that were generally more vulnerable, and evidence of growing depletions on areas more accessible to markets. Analysis of CNMI datasets highlighted how expansions of fisheries footprints following localized depletions at more accessible stocks provided for maintained supply to markets over 11 years (albeit with increasing variability and changes in catch composition), which could mask ongoing localized depletions and disproportionally impact subsistence fishers that cannot

access less exploited remote areas. Finally, combined CNMI and Guam datasets revealed how regardless of fisheries expansions, fisheries are bound to be impacted as evidenced by signs of fishing ‘down’ and ‘across’ food webs and species replacements as more resilient species that often showed size-truncated landings increasingly substituted others with slower growth-rates and weaker density-dependent responses that diminished or even disappeared from landings.

Cumulatively, ongoing complex commercial coral-reef fisheries footprint expansion dynamics across multiple geographical scales can have profound and long-lasting implications for targeted stocks, the fisheries sector that depends on them, the ecosystems they sustain, and ultimately the societies that rely on them for food security and other ecosystem services, suggesting that deep re-evaluations of coral-reef fisheries commercialization tradeoffs are warranted.

Further research areas and considerations for future evaluations of coral-reef fisheries management paradigms such as reconsideration of approaches for defining spatial and taxonomic management units, and re-evaluation of underlaying assumption regarding compensatory density dependence responses to fishing and associated stock assessment frameworks and size-based management policy approaches may improve management of such complex multi-species fisheries.

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1. Introduction

Coral-reef fisheries have provided food security and recreation for societies across the tropics for countless generations (Moberg and Folke, 1999; Cesar, Burke and Pet-soede, 2003), generally under sustainable harvesting regimes (Johannes, 1978; McClenachan and Kittinger, 2013; Birkeland, 2017). Over recent decades, coral-reef fisheries have also increasingly provided for economic prosperity, especially for many developing nations that have limited opportunities for alternative livelihoods beyond reef-related fishing (Donner and Potere, 2007). Currently, coral-reef fisheries are estimated to provide nearly $6 billion USD in net benefits to the world annually, while supporting the livelihood of over 6 million fishers and their families (Cesar, Burke and Pet-soede, 2003; Teh, Teh and Sumaila, 2013). Yet, unsustainable fisheries regimes with ensuing impacts to coral-reef and socioeconomic resilience have been reported over the last decades across most tropical regions (Newton *et al.*, 2007; Mcclanahan and Hicks, 2011; Pauly and Zeller, 2014; Birkeland, 2017). Multi-species, data-poor, small-scale coral-reef fisheries are highly complex and dynamic, and modern management frameworks continue to struggle to ensure sustainable management regimes in the face of limited evidence-based guidance and a prevalent context of limited capacity and resources (Johannes, 1978; McManus, 1996; Pauly and Zeller, 2014). Therefore, improving our understanding of coral-reef stock and fisheries dynamics is fundamental to ensure the sustainability of those critical fisheries, and the ecosystems and societies they sustain.

Key dynamics of coral-reef fisheries that are desired for further research were explored during this thesis and are introduced in more detail below with specific focus on: i) growing commercialization of coral-reef fisheries (1.1); ii) fisheries expansions and associated potential masking affects (1.3); iv) increased variability on landings alongside growing fishing pressure (1.5); and v) stock and ecosystem impacts of coral-reef fisheries (1.6).

1.1. Growing commercial fisheries

Subsistence coral-reef fisheries on island nations were historically managed through small-scale reef tenure systems that intertwined many principles of fisheries management into tradition and culture, generally providing for sustainable harvesting regimes (Johannes, 1978; McClenachan and Kittinger, 2013; Birkeland, 2017). In contrast, the development of commercial coral-reef fisheries and fisheries technology over the second half of the twentieth century removed key links between management and societies, often resulting in unsuitable fisheries and inevitable depletions (Johannes, 1981; Cuetos-Bueno and Houk, 2014; Pauly and Zeller, 2014). Fisheries status has generally been linked to human population density (Mora, 2008; Cinner *et al.*, 2016; McClanahan *et al.*, 2020). While commercial fisheries remain typically less than 50% of subsistence fisheries for most island nations (Gillett, 2016), they may have disproportional impacts on stocks and the ecosystem. Disproportionate impacts from commercial fisheries can arise because profit-driven harvesting often focuses on the largest species that have slow growth rates and high ecological functionality (Lokrantz *et al.*, 2008; Houk *et al.* incl. Cuetos-Bueno, 2012; Taylor *et al.*, 2014). This progressive shift from subsistence to commercial fishing in recent decades and potential associated ecological impacts have prompted a growing debate regarding the tradeoffs for coral-reef fisheries (Brewer *et al.*, 2009; McClenachan and Kittinger, 2013; Birkeland, 2017).

1.2. Fisheries expansions and masking effects

Alongside growing commercialization, expanding footprints of coral reef fisheries have appeared. Globally, fisheries depletions have been widely reported for decades but many commercial coral-reef fisheries have maintained consistent, demand-driven landings (Zeller, Booth and Pauly, 2005; Cuetos-Bueno and Houk, 2014). For example, despite overall declines of coral-reef fish landings in the islands of Guam (~80%) and Saipan (~50%) from 1950s to 2000s as resources became increasingly compromised, commercial landings have been maintained for the latest decades (Zeller, Booth and Pauly, 2005; Van Beukering *et al.*, 2006, 2007; Cuetos-Bueno and Houk, 2014). For coral reefs, evidence generally supports initial localized depletions due to unsustainable fishing pressure on reefs nearby high demand centers, followed by expansions of commercial fishing effort to remote areas that remain within the range of commercial markets because investments in fishing infrastructure are engaged (Sadovy *et al.*, 2003; Birkeland, 2004; Aswani and Sabetian, 2010; Cinner *et al.*, 2016). The impacts of fisheries expansions are increasingly becoming evident, with distance from commercial markets predicting significant amounts of variation in reef fish biomass at local and global scales (Brewer *et al.*, 2009; Cinner *et al.*, 2012; Maire *et al.*, 2016). Yet consistent supply to markets through fisheries expansions may dilute or mask some of these impacts (Crona *et al.*, 2016).

Consistent revenues and landings despite localized depletions are dangerous because they can provide a false sense of sustainability to managers and consumers that purchase fish in local and international markets. This phenomenon where local ecosystem signals of depletion are diluted or masked by seafood markets has been described for other fisheries such as UK North Sea Cod and Indo-Pacific live reef fish trade (Sadovy *et al.*, 2003; Crona *et al.*, 2016). Several factors can contribute to the perception of sustainable fisheries in the face of depletion, including local expansion of fishing activities to further and deeper grounds (Lindfield *et al.*, 2015), and trade from other locales following local economic extinctions (Dulvy, Sadovy and Reynolds, 2003; Sadovy *et al.*, 2003). Combined, these factors can temporally maintain or even increase the supply of fish being provided to markets while masking the effects of localized depletions, further endorsing this false sense of sustainability. While fisheries expansion may delay impacts to commercial landings, understanding if fisheries expansions on coral reefs are producing such masking effects is of critical importance if undesired depletions at more accessible fishing grounds that subsistence fishers rely on for food security are to be avoided, and fundamental services provided by coral-reef ecosystems near population centers are to be maintained.

1.3. Trade networks and exogenous drivers

Fisheries footprint expansions that initially occurred locally have increasingly grown to remote areas previously non-targeted for commercial purposes as worldwide demand for fresh fish has coupled with improvements to refrigeration and transportation (Birkeland, 2004; Swartz *et al.*, 2010). Expanding trade networks and footprints provide for additional complexity to local fisheries though the introduction of additional fishing pressure and exogenous drivers (Crona *et al.*, 2015). Examples of such complex exogenous drivers that have resulted on important changes to local fisheries dynamics include demand trends linked to religious holidays or rules changes (Bell, 1968; Cuetos-Bueno and Houk, 2014), shifts on end-consumer size-preference (Reddy *et al.*, 2013), introduction of mobile connectivity (Abraham, 2006), and road development projects (Schmitt and Kramer, 2010). While growing tourism industries have also been linked to increased demand for local seafood and additional fishing pressure, their direct impact on local coral-reef fisheries has generally not been formally characterized. However, recent studies from the popular tourism destination of Palau suggest that contrary to general perceptions, tourism direct pressure may actually remain disproportionally small as compare with local levels of consumption and fishing (Dacks et al. 2020). As international trade networks for coral-reef fisheries grow, studies of such trade networks have been to date limited to high-valued commodities such as those targeted by the live reef fish, sea cucumber, and aquarium trades (Sadovy *et al.*, 2003; Anderson *et al.*, 2011; Rhyne *et al.*, 2012). Alternatively, little research has been carried out on increasingly prevalent international trade networks of multi-species coral-reef fin-fisheries that are the backbone of food and economic security for many coastal nations across the tropics (Johannes, 1981; Grafeld *et al.*, 2017). Given the inherent complexity of understanding and managing small-scale coral-reef fisheries, a better appreciation of how international trade networks and associated exogenous drivers interact with local demand and ecological/environmental drivers to drive fisheries dynamics would be required to address their potential added impacts on local fisheries, societies and ecosystems (Berkes *et al.*, 2006; Cinner, Daw and McClanahan, 2009; Sadovy and Yin, 2015).

1.4. Landings variability

While fisheries expansions may provide for maintained commercial landings, growing evidence suggest that increasing variability can also be expected associated to those expansion. Fishing variability has previously been identified as a potential indicator of fisheries status. Yet, studies to date have focused mostly on how truncated age structures can drive increased variability because of the growing reliance placed upon annual recruitment that becomes more dependent on variation in annual environmental cycles (Hsieh *et al.*, 2006; Anderson *et al.*, 2008). In coral reefs, anecdotal evidence suggests that increased variability in reef-fish landings in accordance with growing human populations could be instead linked to accessibility to less exploited resources. Results from several studies suggest that differences on stock status between more and less accessible reefs can be expected to grow with fishing pressure, which in turn would drive catch success and landings to increasingly becoming dependent on favorable conditions that provided better access to those less exploited stocks (Houk *et al.* incl. Cuetos-Bueno, 2012, 2017; Taylor *et al.*, 2014; Hernandez-Ortiz, 2020). Eventually, growing variability could be expected to amplify seasonal peaks in landings towards “race-to-fish” dynamics such as improved catch success and landings becoming concentrated at the start of a favorable timeframe or season, but rapidly declining to reference levels afterwards (Huang *et al.*, 2014; Birkenbach, Kaczan and Smith, 2017; Rosenberg, 2017). While overall landings may be temporarily maintained as such dynamics develop, growing variability is a cause of concern for fishers and managers alike, as seafood prices, fishers’ income and seafood supply increasingly become more variable and follows interannual high-and-low cycles. Unfortunately, limited availability of coral-reef fisheries timeseries datasets have hampered further exploration of those hypotheses.

1.5. Fisheries impacts and species responses

While fisheries expansion can temporarily provide for maintained landings, impacts on fisheries and ecosystems should be expected eventually. Compensatory density dependence mechanisms allow populations to increase their numbers at greater rates than as required for replacement when densities decline, therefore potentially offsetting increased mortality from fishing. Density-dependent responses are fundamental principles of population ecology and fisheries management, and provide the basis of surplus production models and sustainable fisheries (Rose *et al.*, 2001). Compensatory responses following increased mortality (i.e. fishing) can result in increased reproductive output from the remaining adult individuals, leading to populations becoming dominated by smaller individuals, which could translate to shifts in sizes of fish landed (Jennings *et al.*, 1999; Shin *et al.*, 2005). Alongside compensatory density dependence responses, species replacements can also occur, as fishing moves 'down' the food webs as species from upper-trophic-level are sequentially replaced by species from lower trophic-level species as the former are depleted (Pauly *et al.*, 1998). Additionally, species replacements also occur as less resilient species within the same trophic levels with slower growth-rates and weaker density-dependent responses are sequentially replaced by more resilient counterparts (Clua and Legendre, 2008; Houk, Cuetos-Bueno, Tibbatts, et al., 2018). I refer to the later phenomenon from here on as fishing 'across' food webs. This situation where species replacements may occur can cause shifting baselines that are not new to fisheries or coral reefs (Knowlton and Jackson, 2008; McClenachan, 2009); nor are the difficulties of predicting the outcomes of complex trophic interactions when species replacements occur (Polovina, 1984; Houk, Cuetos-Bueno, Kerr, *et al.*, 2018).

In commercial coral-reef fisheries, compensatory responses and fishing 'down' and 'across' the food webs and associated species replacement dynamics can be extremely complex due to the presence of hundreds of species. Further, capturing where coral-reef fisheries reside along exploitation gradients remains difficult because long-term datasets that can quantify harvesting patterns and potential depletions are rare (Claro *et al.*, 2009; Pauly and Zeller, 2014). Consequently, fisheries-management frameworks often fail to address potential fisheries-driven population shifts and species replacements, instead focusing on species with higher yields that have become dominant components of modern landings over time. This is a concern for coral reefs because ecological functions, economic values, and social benefits suffer as larger species with slow growth rates and/or weak density-dependent responses disappear and biomass turnover rates increase within the system (Houk, Cuetos-Bueno, Kerr, *et al.* 2018, Figure 1). A deeper understanding of how different species within complex multi-species fisheries respond to fishing pressure could support the development of tailored fisheries management policies that move beyond traditional approaches that may inadvertently commit systems to species replacements and associated undesired impacts (Friedlander and Demartini, 2002).

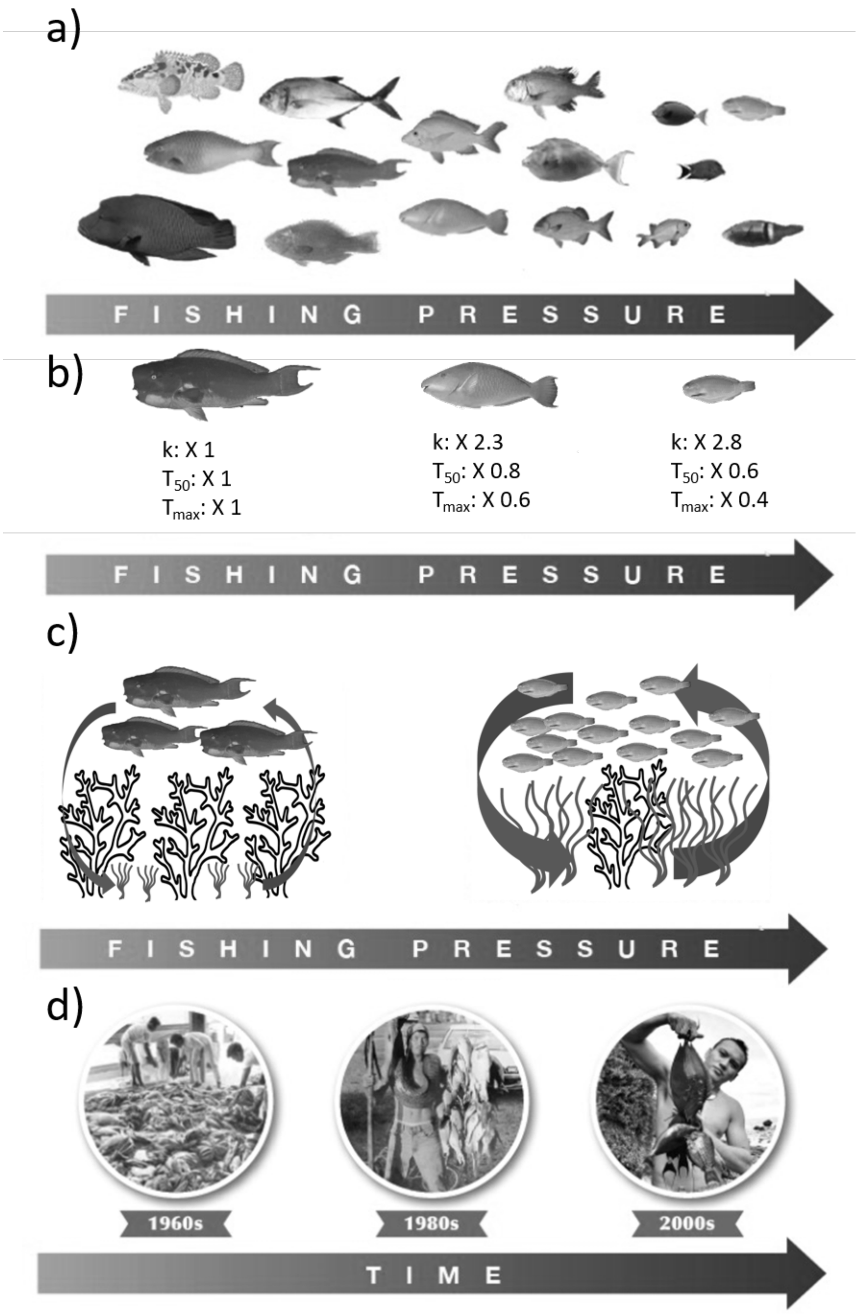

Figure 1. Depiction of evolution of coral-reef fisheries through fishing pressure gradients (or time), including (a) species replacements as less resilient species are increasingly replaced by more resilient counterparts with (b) higher fish turnover rates (associated to relative growth-k, mean age of maturity-T_{50}, and maximum age-T_{max}), (c) increased carbon turnover rates and secondary effects to ecosystems (i.e. phase shifts from coral-dominated to algae-dominated states), and (d) issuing impacts to societies as fisheries and ecosystem services are impacted.

1.6. Micronesia: A case study

Coral-reef ecosystems across Micronesia host a wealth of biological biodiversity, ecological complexity, and fisheries potential (Hasurmai *et al.*, 2005; Allen and Bartram, 2008; Gillett, 2016). These rich and extensive marine resources have played a central role in Micronesian societies for generations, while being sustainably exploited for subsistence purposes under customary ways (Johannes, 1978; Sudo, 1984). While subsistence fishing remains dominant regarding overall landings, over the past few decades, growing local and international fish markets have increased fishing pressure around population centers, leading to decreasing fishing success and profitability (Zeller *et al.*, 2007; Rhodes *et al.* incl. Cuetos-Bueno, 2011; Cuetos-Bueno and Houk, 2014). These trends are generally attributable to the growing influence of a western monetary society coupled with a lack of alternative income sources. Given limited job opportunities and a high dependence upon fishing for food and income, declining fishing success is now a priority concern for Micronesian societies. Further, declining coral-reef condition has recently been linked with fishing pressure (Houk and Musburger, 2013; Houk *et al.* incl. Cuetos-Bueno, 2015; McLean *et al.* incl. Cuetos-Bueno, 2016). Declining reef health across Micronesia has uncertain consequences for fundamental ecosystem services provided by healthy reefs. Currently, fishing communities and resource managers are struggling to address these challenges, as modern fisheries paradigms are not coupled with adequate forms of management.

Micronesia subsistence and commercial fisheries, while similar on the fishing methods used (i.e. disproportionally dominated by nighttime spearfishing), vary greatly regarding fishing effort. Subsistence fisheries targets preferably nearshore areas during short fishing times to reduce effort associated to capturing usually just enough landings for daily meals, while commercial fisheries target any fishing area within reach that would maximize their daily landings and profitability (Rhodes *et al.* incl. Cuetos-Bueno, 2011). Similar to many regions across the tropical Pacific, Micronesian coral-reef fisheries are generally data-poor. Yet, important differences occur across jurisdictions associated to capacity and resources of relevant management agencies. Building upon this situation, standardized fisheries monitoring protocols and tools were initiated by Cuetos-Bueno in close collaboration with members of the University of Guam Marine Laboratory and other regional stakeholders, resulting in a standardized regional fisheries monitoring framework. The present thesis and associated studies are founded on ongoing efforts under this framework. For our studies, new fisheries-dependent datasets in Chuuk (Federated States of Micronesia) were collected. Those were complemented by existing fisheries-dependent datasets from Guam (United States of America) and Commonwealth of the Northern Mariana Islands (CNMI hereafter; United States of America, Figure 2).

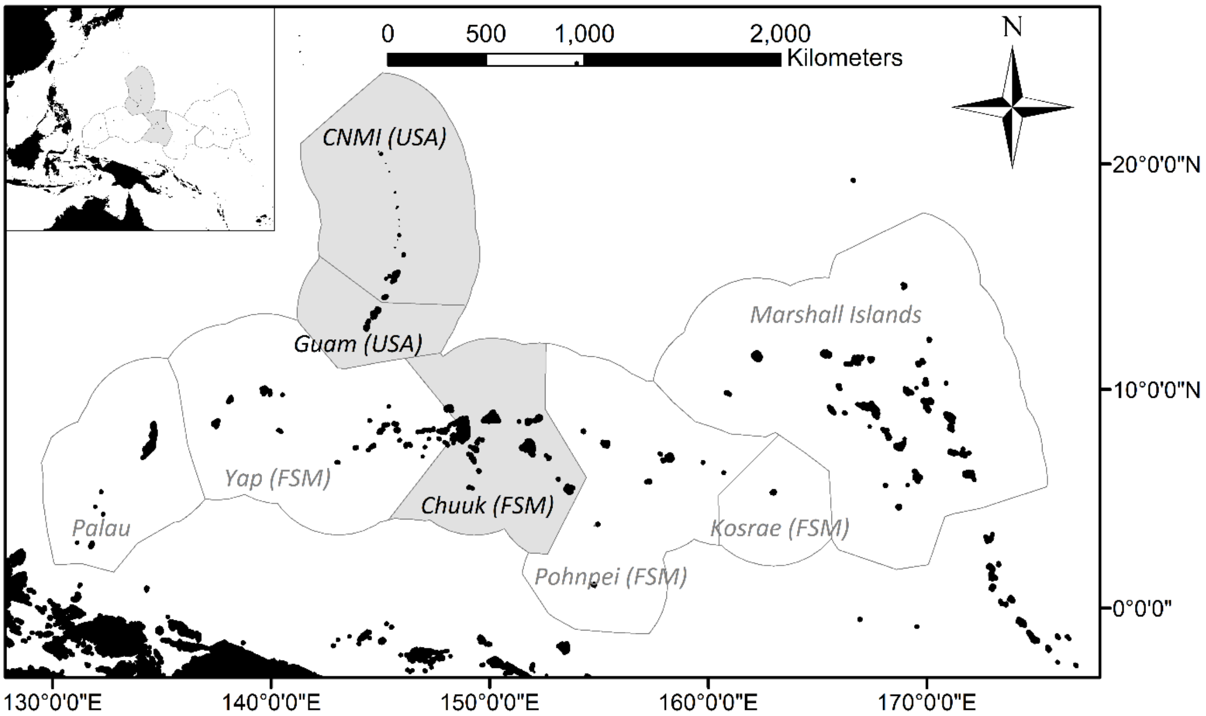

Figure 2. Map of Micronesia, highlighting the jurisdictions of Guam (USA), Commonwealth of the Northern Mariana Islands (USA), and Chuuk (Federated States of Micronesia), where research was carried out for this thesis.

1.7. Research aims and structure

This synthesis presents a summary of research upon which the PhD in Marine Sciences will be based. It presents a critical overview and synthesis of the submitted research outputs previously published in scientific peer review journals, and how they contribute to the related research discipline.

The aim of this thesis is to advance on the field of small-scale multi-species fisheries by enhancing our understanding of exploitation and stock dynamics, the drivers behind those dynamics, and potential novel management paths towards sustainable fishing regimes. Within, it focuses on poorly understood coral-reef fisheries that are fundamental to many societies across the tropics, and on the drivers and progressive dynamics associated to increased commercialization of those fisheries, ensuing localized depletions and fisheries expansions, and inevitable impacts to stocks and societies.

The combined studies draw from novel fisheries-dependent datasets recently collected in Chuuk (Federated States of Micronesia), and unique historical datasets from Guam and the Commonwealth of the Northern Mariana Islands (USA) in order to: i) explore dynamics and underlying drivers of demand-driven expansions of coral-reef fisheries within and across jurisdictions (Chapter 2; Cuetos-Bueno and Houk, 2018); ii) assess impacts of commercial fisheries and fisheries expansions (Chapter 3; Cuetos-Bueno *et al.*, 2018); iii) evaluate potential variability dynamics and masking effects of fisheries expansions (Chapter 4; Cuetos-Bueno, Hernandez-Ortiz and Houk, 2019); and iv) identify variability of species responses to fishing pressure and potential implications for restructuring of fisheries (Chapter 5; Cuetos-Bueno, Hernandez-Ortiz and Houk, 2019; Houk, Cuetos-Bueno, Tibbatts, et al., 2018). Finally, the novelty and contribution of this thesis to existing research body was evaluated, modern fisheries management approaches were examined in light on new findings, and relevant implications and opportunities for future research and revision of foundational management principles and approaches that may provide for improved management of such fundamental, yet complex, multi-species fisheries were draw (Chapter 6).

2. *Expanding footprints and complex fisheries driving forces*

Chapter based on Cuetos-Bueno, J. and Houk, P. (2018) 'Disentangling economic, social, and environmental drivers of coral-reef fish trade in Micronesia', Fisheries Research, 199.

Improvements on refrigeration and transportation have resulted on expanding trade networks and footprints that provide for additional complexity to local coral-reef fisheries that are already inherently complex and difficult to manage though the introduction of additional fishing pressure and exogenous drivers (Crona et al., 2015). Given the compromised status of many coral-reef fisheries and the need to understand the complexity that associated exogenous drivers add to local fisheries, the extensive coral-reef fish trade between Chuuk and Guam was used as a case study to assess how even remote small-scale coral-reef fisheries can be driven by complex exogenous forces facilitated by trade networks, and what potential social and ecological impacts can occur as a result of those forces

Coral-reef fisheries have historically played a key nutritional and cultural role in the main Micronesian urban center of Guam while balancing sustainable harvesting with subsistence needs, but evidence suggests that Guam's reef-fisheries production has been insufficient to fulfill growing demand, resulting in a growing reliance upon imports since the 1960s (Johannes, 1981; Myers, Callaghan and Fitzgerald, 1983; Amesbury and Hunter-Anderson, 2003; Houk, Cuetos-Bueno, Tibbatts, *et al.*, 2018). In contrast with Guam, Chuuk reef-fish assemblages are some of the healthiest in Micronesia (Houk *et al.* incl. Cuetos-Bueno, 2016), and its fishery has provided growing reef-fish to Guam through regular flights for the past four decades. We used trade between Chuuk and Guam to the potential impacts of complex exogenous forces that facilitated by trade networks on a remote small-scale coral-reef fishery. Multi-year trade trends, seasonal dynamics, and social and ecological impacts of the commercial reef-fish trade were examined. First, a novel export record that highlights the economic value and temporal trends in reef-fish trade over 13 years was uncovered. Then, how environmental and socioeconomic factors combined, and evolved, to drive export patterns over time was showed. Finally, the rapid expansion and decline of reef-fish exports from Chuuk to Guam was placed within the context of consumer demand and economic profitability. The findings serve to assess and forecast ecological and socioeconomic consequences for both Chuuk and Guam, offering an improved appreciation for the complexity of local coral-reef fisheries alongside increasingly globalized markets (Cuetos-Bueno and Houk, 2018).

2.1. Methods

In the absence of any formal historical monitoring programs or datasets of Chuuk fisheries, hard-copies of bills-of-shipping associated with commercial flights between Chuuk and Guam collected and stored by the Chuuk Office of Food Safety were used for this study. Records from 2003 to 2014 were available at the time of this study, yielding 1554 reports of overall daily reef-fish exports over the twelve-year period that were digitized into an electronic database. Exported reef-fish was caught the night before been exported to Guam, disproportionally using night-time spearfishing. Limited data from 2015 (January-July) were available at the time of this study, but was used for preliminary estimates of 2015 exports. For analysis other than estimation of overall exports, daily exports were standardized within each individual month as the percentage difference between daily exports and the monthly mean, while mean daily exports for each month were standardized within each individual year as the percentage difference between each monthly mean and the corresponding yearly mean. Environmental datasets were collected from readings taken locally by Chuuk airport weather station (windspeed; http:/ncdc.noaa.gov/cdo-web/) and available global datasets from United States Naval Observatory (moon calendars; http:/aa.usno.navy.mil). Guam retail imported reef-fish prices were extrapolated from known local Guam prices, while prices at origin in Chuuk were estimated based on personal communications with market owners. Air-freight costs were extracted from available bills-of-shipping records. Last, annual disbursements from the US Department of Agriculture Supplemental Nutrition Program (hereafter SNAP) that provides nutritional assistance to low-income individuals and families in Guam (nearly 1/3rd of the population) through monthly disbursements that can be used at local retail stores for food or other essential commodities were directly extracted from SNAP Annual State Activity Reports. Total annual exports were estimated by multiplying mean daily exports by the estimated number of exporting days within each year. To examine inter-annual seasonal trends and examine whether seasons or individual months consistently had higher or lower exports within annual cycles, standardized monthly export averages were contrasted against the mean for all years. To examine the influence of environmental (windspeed and moon calendar) and socioeconomic (monthly SNAP disbursement day) drivers that have monthly cycles on standardized daily export volumes least-squared regression models were used across the entire dataset. Windspeed and moon phases/illumination are well known to influence coral reef fishing success and landings as lower windspeed provide for enhanced access to less accessible fishing grounds that tend to hold healthier stocks, while new moon phases provide for improved nighttime spearfishing success due to effects on fish behavior (Bos and Gumanao 2012; Rhodes et al. 2008). Because fish was always exported on the same day as it was caught, not lag-time analyses was needed. Further, multiple regressions models were also constructed for each year to appreciate the relative influence of each factor during each year using a step-wise process to develop the best-fit and least complex interactive model. Finally, gross profitability (net sales – costs of goods) of the trade sector was estimated by comparing available datasets of net sales in Guam and estimated costs of acquiring and transporting goods from Chuuk.

2.2. Results

Analysis of available timeseries of reef-fish trade records between Chuuk and the urban center of Guam provided valuable insights into how exogenous forces are increasingly driving local coral-reef fisheries, and how footprints are expanding even to remote locales such as Chuuk, as trade networks grow. During the study period (2003-2015) reef-fish imports to Guam amounted to over 1,900 mt, with a gross value of US$19.3 million. Within that timeframe, a close relationship was found between issuances from SNAP and annual exports until 2010 (Figure 3a). Stable exports between 2004 and 2007 were followed by a mean annual increase of 25 mt year^{-1} until 2010 that amounted to an overall increase of 55% (or 74 mt). Then a disconnection between SNAP issuance and annual exports followed the 2010 peak, and stark declines characterized by annual decreases amounting to 48% (or 98 mt) between 2010 and 2014 regardless of maintained growth on SNAP issuances (12% increase), that were linked to growing profitability losses due to increasing fish purchase and shipping costs (Figure 3.a). Economic indicators suggested that exports profitability decreased between 47% and 79% over the 14-year period due to a combination of fairly stable fish prices in Guam (12% increase) and growing transportation (158% increase) and Chuuk fish acquisition (80% increase) costs. Interannual seasonal trends were dominated by consistently higher exports during February, March, and especially April, coinciding with known high demand in Guam associated to Catholic lent period (Figure 3b). Daily landings were strongly driven by demand from Guam; SNAP disbursement days were found to increasingly be a predominant driver of daily exports (Figure 3a and 4) rather than environmental factors known to affect fishing success and commercialization, such as windspeed and moon phase (Figure 4).

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Figure 3. (a) Annual exports were well predicted by Guam Supplemental Nutrition Assistance Program (SNAP) disbursement from 2004 to 2010 (black dots), followed by a strong decoupling since 2011 probably resulting from export costs (gray dots). (b) Mean standardized daily exports (% difference with annual mean, gray bars) and Chuuk mean windspeed (black line) for each month of the 2003–2014 study period. Cuetos-Bueno and Houk, 2018.

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Figure 4. Environmental and socioeconomic drivers of mean standardized daily exports: (a) windspeed grouped into 1 km h^{-1} bins, (b) lunar days, and (c) proximity to monthly SNAP-disbursement day. Black lines indicate 95% confidence intervals associated with significant regression models. Cuetos-Bueno and Houk, 2018.

2.3. Discussion

The Chuuk-Guam coral-reef fish trade was facilitated by several biological and socieconomic factors, including high demand for fresh reef-fish in Guam, healthier stocks and cheaper production in Chuuk, and enhanced trade networks. The trade has been the main motor of commercial fishing in Chuuk for the since the early 2000s, while providing for food security to Guam's residents, especially for vulnerable social groups like those supported by the SNAP program that have fewer alternatives for affordable sources of high-quality protein (Cuetos-Bueno pers. obs.). Increasing annual exports between 2003 and 2010 were mainly driven by increases in Guam food stamp (SNAP) allowances that doubled across the study period. Following this boom in exports,, sharp declines followed the 2010 peak. This decline waslinked to reduced profitability, as important increases in fish acquisition and air-freight costs alongside stagnant fish prices in Guam reduced profits beyond sustainable thresholds. Daily exports within each month were constrained by both environmental and socioeconomic variables, but with increasing reliance upon Guam's demand and purchasing power. Analyses also revealed a clear, if damped, negative effect of both lunar phase and windspeed on daily exports, with increasing exports as expected positively related to lower windspeeds and proximity to new moon phases. But ultimately, proximity to SNAP disbursement days was the dominant predictor of modern daily exports, and larger proportions of Chuuk fish were increasingly exported to Guam around these high-demand days.

This study highlighted the growing instability in Guam's fresh reef-fish trade industry, and an uncertain future for Chuuk fishers, Guam retailers, and a society dependent on healthy protein (Cuetos-Bueno and Houk, 2018). The expectations for the Chuuk-Guam reef-fish trade have profound socioeconomic and ecological implications for both jurisdictions. While decreasing exports that in 2014 made 41% of comercial fish demand would have an important economic impact in rural communities in Chuuk where most commercial fishers reside and few income alternatives exist, reduced fishing pressure may in contrast benefit fish stocks and their functional roles in the ecosystem, offering improved opportunities for the limited but growing tourism sector and longevity of sustainable fisheries. Contrasting impacts are expected for Guam, including growing fishing pressure on Guam's already compromised fish stocks, increased fishing violations, and high levels of conflict among fishers, as several of Guam's markets that previously imported reef-fish from Chuuk have established fishing operations in Guam to compensate for the unprofitable trade industry that once flourished. Alongside, as dwindling Chuuk imports and local supply remains insuficient to meet local reef-fish demand, Guam retailers are moving towards alternative sources of imported protein (mainly meat and poultry from USA) and global suppliers of reef-fish, expanding their footprint well beyond the Micronesia region (Huges 2003; Figure 5). Evidence of similar footprint expansions are becoming increasingly noticeable across the tropics, highlighting growing concerns for small-scale fisheries even in remote locales that have traditionally avoided external fishing pressure (Sadovy and Yin, 2015). Overall, this study provides novel insights into exogenous fisheries drivers that may easily be hidden from local fisheries managers and stakeholders, but which could increasingly impact small-scale fisheries worldwide as trade networks continue to expand.

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Figure 5. Map of sequential expansion of the Guam reef-fishing footprint (imports to Guam) across Micronesia (Palau, and Chuuk) and beyond (Philippines, Vietnam, and Indonesia), highly resembling other reported fisheries expansions such as the Hong Kong-based live reef food fish trade. Cuetos-Bueno and Houk, 2018.

3. Impacts of commercial demand and expanding footprints

Chapter based on Cuetos-Bueno, J. *et al.* (2018) 'Human and environmental gradients predict catch, effort, and species composition in a large Micronesian coral-reef fishery', *PLoS ONE*, 13(5).

In contrast with traditional subsistence fisheries that were managed sustainably for generations, the development of commercial coral-reef fisheries over the second half of the twentieth century removed key links between management and societies, often resulting in unsuitable fisheries and inevitable depletions (McClenachan and Kittinger, 2013; Johannes, 1981; Pauly and Zeller, 2014). This progressive shifts from subsistence to commercial fishing in recent decades and potential associated ecological impacts have prompted a growing debate regarding the tradeoffs of commercial coral-reef fisheries (Brewer et al., 2009; Birkeland, 2017).The previous analysis of exports datasets suggested lower fishing footprint existed in Chuuk when compared to other Pacific coral-reef fisheries, as socioeconomic factors associated with demand were the main driver of exports (Cuetos-Bueno and Houk, 2018). Yet, growing anecdotal evidence suggests growing fisheries impacts on stocks in Chuuk over the last decades associated to growing commercialization and trade (Rhodes *et al.* incl. Cuetos-Bueno, 2011; Houk *et al.* incl. Cuetos-Bueno, 2016).

This situation offered a unique opportunity to: (1) assess the ecological impacts on local stocks of expanding fisheries footprints associated to growing commercial trade, using the extensive coral-reef fisheries in Chuuk as a case study and (2) provide a deeper examination into species-based catch records for one of the largest coral-reef fisheries in Micronesia (Cuetos-Bueno *et al.*, 2018). Detailed commercial catch records and coupled fisher interviews were collected over one year to (i) investigate drivers of catch-and-effort statistics, and (ii) assess populations of target species that comprised 75% of landings. Catch and effort were first examined across geographic sectors and seasonal environmental gradients because both are related to fishing access and commercial demand. The magnitude of these relationships provided an initial indication of fishery status that was tested with subsequent species-based evaluations. For example, fishing success was expected to increase with favorable weather conditions that dictate fishing access. If this is true, then understanding which species were most sensitive to environmental gradients becomes desirable from a management perspective. Family and species-based examinations were conducted to depict stock status. These included comparing fish sizes to their proportional contribution to landings within each dominant fish family. The premise was that smaller species within each family and more productive species lower in trophic position, may be taking the place of larger vulnerable species, especially predators (Friedlander and Demartini, 2002; Richards *et al.*, 2012; Houk *et al.* incl. Cuetos-Bueno, 2017). Next, target species from all trophic levels comprising 75% of total landings were further examined to determine if catch success was dependent on favorable environmental regimes, and whether skewed size-frequency distributions existed. Both are potential indicators of impacted stocks and are linked with differing management strategies (Nadon *et al.*, 2015; Houk *et al.* incl. Cuetos-Bueno, 2017). Finally, data were integrated from a previous study (Cuetos-Bueno, 2012) to compare distinctive commercial versus subsistence fishery landings and contrast the roles of subsistence versus commercial exploitation.

3.1. Methods

Comprehensive fisheries-dependent datasets were collected through a combination of commercial fisher interviews and catch monitoring between November 2013 and October 2014. Daily visits to the thirteen Chuuk prominent fish markets were conducted to collect fisher interviews (n = 839 interviews). Interviews gathered information regarding fishing location, gear, expenses, and other relevant fishing and socioeconomic factors. Three of the largest markets were selected to generate data on catch composition using a photographic monitoring system. During each visit, all fish being sold in the market were photographed on top of a measuring board (n = 79,097 individual fish). Individual photographs were entered into a dedicated database where fish were identified, and length was measured to the nearest cm fork length. Fish lengths were then converted to biomass using local length-weight parameters when possible (Cuetos-Bueno and Hernandez-Ortiz, 2017), or regional parameters from other monitoring programs in Micronesia when not available for Chuuk (Houk, Cuetos-Bueno, Kerr, *et al.*, 2018). To compliment the photographic surveys, visual estimates of catch composition were opportunistically collected in other markets. During these surveys, individual fish from landings were identified to the highest taxonomic resolution possible, and sizes were visually estimated to the nearest cm fork length (n = 37,894 individual fish). Lastly, the total daily landings of reef fish purchased by each market were recorded directly from fish market purchase records.

The relationship between the proportional contribution to family landings and species-based maximum lengths (L_{max}) within each dominant family for any evidence of fishing 'down' and 'across' the food webs (Pauly *et al.*, 1998) was first assessed. Regression models were used to examine biomass versus body-size relationships; the null hypothesis was that a linear relationship existed based upon foundational theory and empirical data from remote systems (Houk and Musburger, 2013). A series of species-based analyses were then performed to assess potential indicators of fishery status with respect to spearfishing, the most dominant form of commercial fishing (86% of overall landings). Proportional contributions to landings were contrasted across differing moon phases and seasons using Kolmogorov-Smirnov tests for the top 20 species that made up 75% of landings. Next, fish size distributions were examined. The skewness of fish size distributions was calculated for all species, and these values were binned into three categories based upon natural breaks that represented species dominated by smaller fish (skewness>0.5), (ii) dominated by larger fish (negative skewness), and (iii) neither (skewness 0 - 0.5) (Jenks and Coulson, 1963). Together, species-based tests provided guidance for discussion on potential management and policy. Finally, catch composition estimates from the present study were compared against those from a subsistence fishing study conducted in Chuuk lagoon in 2012 that documented landings from 21 subsistence fishing trips that were comparable in terms of fishing methods used (960 individual fish; Cuetos-Bueno, 2012). Vulnerability indices for each species were extracted from Fishbase (Cheung *et al.*, 2005; Froese and Pauly, 2016), and vulnerability-frequency distributions were compared across subsistence and commercial landings using Kolmogorov-Smirnov tests. Further, species were binned into functional groups for a more general comparison between subsistence and commercial landings. Functional groups were defined by family and body size (i.e., large-bodied parrotfishes), with size groupings determined by Jenks breaks of asymptotic lengths defined in (Houk, Cuetos-Bueno, Kerr, *et al.*, 2018). Species vulnerability indices were averaged across each functional group, and a linear regression model examined if vulnerability could predict proportional contributions to commercial and subsistence fishing. Functional groups that contributed >2% of commercial landings were used for these comparisons, representing 91% and 88% of overall commercial and subsistence landings, respectively.

3.2. Results

Exports to Guam were a primary driver for the local commercial coral-reef fishery, as they accounted for 41% of overall (265 mt) annual landings in 2014. Furthermore, the impact of the export sector was even stronger in driving distribution of fishing effort and landings, as on average, nearly 75% of overall weekly catches were landed during the three days when flight connections to Guam existed (Figure 6a). Regardless of extensive coral-reef fish exports over the last couple of decades, Chuuk landings still (compared to other main Micronesian islands) maintain a high contribution from large-bodied predators and secondary consumers (Figure 6b). Yet, there was a general trend of decreasing proportional contributions from large-bodied species when moving from low to high trophic levels, as biomass within lower trophic-level families (i.e. parrotfishes) was dominated by large-bodied species, meanwhile landings from higher trophic-level families such as groupers and snappers were dominated instead by medium-sized species (*Plectropomus areolatus* and *Lutjanus gibbus*). Additionally, many of the dominant commercial fishes had positively skewed size distributions and/or were disproportionally caught during favorable moon phases and seasons. In total, species with skewed distributions or environmentally-constrained catch success made up 57% of the overall landings (Table 1). Most of those represented larger species within their respective families, and mid-to-high trophic level piscivores and invertivores (large-bodied groupers, emperors, and snappers). In contrast, fishes without catch success being dependent on environmental conditions and without skewed size distributions were mainly a mixture of large- and small-bodied herbivores.

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Figure 6. Mean (dark gray bars) and overall (light gray bars) weekly reef-fish landings for different days of the week with respect to Chuuk-Guam flights (airplane icon, Tuesday, Thursday, and Saturday; left). Proportional contributions to overall commercial reef fish landings of top twenty species making 75% of landings, caught by spearfishing (dark gray), bottom fishing (black), and net fishing (light gray, right). Cuetos-Bueno et al., 2018.

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Figure 7. Positive relationship between mean species vulnerability index and difference in proportional contribution to commercial vs subsistence landings for all dominant fish groups (gray solid line), and for all groups but rabbitfishes (gray dashed line, a), and vulnerability frequency distributions within commercial (dark gray line) and subsistence (light gray line) landings, revealed increasing vulnerability among commercial landings (b). Cuetos-Bueno et al., 2018.

Availability of subsistence landings data from a previous Chuuk study (21 fishing trips in 2012; Cuetos-Bueno, 2012) that were also dominated by nighttime spearfishing allowed for comparisons with commercial landings datasets. Subsistence landings during the 2012 study were dominated by small-bodied herbivores, mainly parrotfishes and surgeonfishes (Figure 7a). Alternatively, commercial landings reported here were dominated by large-bodied predators, rudderfishes, unicornfishes, and rabbitfishes, many of them groups with low local demand but highly sought-after in Guam markets. Contrasts of catch composition revealed that vulnerability indices were significantly higher for commercial landings than subsistence counterparts (Figure 7b. Further, with the exception of rabbitfishes, a positive relationship existed between vulnerability indices and proportional contribution to commercial vs subsistence landings.

Table 1. Twenty species that represented 75% of Chuuk commercial reef-fish landings, their functional group, individual contribution to landings, skewness of size-frequency distribution, and significant dependence of fishing success upon environmental conditions (season and moon phase). Species whose fishing success was found to be dependent upon environmental conditions and with skewed distribution are highlighted by dark gray background. Species whose fishing success was found to be dependent upon environmental conditions (moon phase and seasonality) or with skew distribution highlighted by light gray background. Cuetos-Bueno et al., 2018.

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3.3. Discussion

Overall, several indicators suggested that a lower human fishing footprint existed in Chuuk when compared to other Pacific coral-reef fisheries as: i) no clear shifts in the spatial distribution of fishing effort or landings existed with seasonal trade wind patterns (Cuetos-Bueno, Hernandez-Ortiz and Houk, 2019; Hernandez-Ortiz, 2020); ii) socioeconomic factors associated with demand were the main drivers of daily landings (i.e. air-freight connections to Guam, Cuetos-Bueno and Houk 2018); and iii) high proportional contributions from larger predators and secondary consumers existed (Jennings and Polunin, 1997; Kaunda-Arara *et al.*, 2003; Dulvy, Freckleton and Polunin, 2004). While these attributes suggested diminished human fishing footprints in comparison to other fisheries, it may also suggest that trade-driven expansion of Chuuk's fisheries to the remote barrier reef provides the highest and most consistent fishing success despite higher travel costs. In addition, skewed size structures and environmentally-constrained catch success were revealed for most target species. Therefore, the cumulative findings of this and previous work reconciled that steady supplies of Chuuk reef-fish to both local and export markets over the past decades may have masked potential growing fishing footprints and shifting populations of target stocks, thereby providing a false sense of sustainability.

The growing dominance of mid-sized species in landings while moving up in trophic position raises potential concerns for fishing 'down' and ''across' the food webs (Pauly *et al.*, 1998 06). While impacts of catchability in Chuuk remain unknown, high market demand for large-bodied species for prevalent export markets exist. It might therefore be reasonable to hypothesize that the replacement of large-bodied species with smaller-bodied counterparts in accordance with trophic position is more a consequence of fishing pressure than natural factors (e.g. habitat availability). In addition, many prevalent species showed catch success dependence upon favorable environmental conditions and skewed size frequencies. While certain environmental cycles are known to increase fishing success and landings (e.g. moon phases), the degree of dependence on favorable environmental regimes can grow as stocks become depleted (Hsieh *et al.*, 2006; Bos and Gumanao, 2012; Lindfield *et al.*, 2015). Identifying if fishing success has increasingly become more dependent upon favorable fishing conditions will be possible as time series datasets become available. Regardless, targeting species when they are most vulnerable can provide short-term fisheries gains, but obviously threatens the sustainability of these populations and is of concern (Rouyer *et al.*, 2012). Skewed size frequencies reflective of diminished size-structures are of concern and could be potentially indicative of compensatory density dependence and high fishing mortality compared to natural mortality (Prince *et al.*, 2015; Houk *et al.* incl. Cuetos-Bueno, 2017). If detected truncated size-frequencies in landings are reflective of compensatory density dependence reponses, this classic population response could help maintain overall catch biomass in the short term, but eventually lead to population instability because the fishery would become more dependent on the success or failure of each recruiting cohort and track environmental variability (Anderson *et al.*, 2008; Rouyer *et al.*, 2012; Kuparinen *et al.*, 2016; Houk, Cuetos-Bueno, Kerr, *et al.*, 2018). Cumulatively, the current observations may reflect a growing 'fishing footprint' in Chuuk.

While the scale of subsistence landings data examined was limited as compared with that of commercial landings, our findings align with previous anecdotal evidence that suggests disproportional impacts of commercial fisheries due to the demand-driven fisheries expansions taking place and the fact that larger, long-lived species with lower intrinsic vulnerability to fishing were disproportionally targeted by commercial fishers and trade (Rhodes et al. incl. Cuetos-Bueno 2011). The parsimonious explanation for this trend is that larger fish provide a greater profit for less effort, coupled with high consumer demand for large-bodied species in commercial and export markets. Preferences of subsistence fishers for more resilient species matches anecdotal evidence regarding local nutritional preferences, which may have evolved from historical localized depletions of less resilient species in nearshore habitats that subsistence fishers target almost exclusively (Smith, 1947; Craig, Green and Tuilagi, 2008; Albert *et al.*, 2015; Houk *et al.* incl. Cuetos-Bueno, 2016), leading to evolving nutritional preferences for smaller, faster growing species (Birch, 1999; Savage, Fisher and

Birch, 2007). Overall, our finding provide novel insights into potential disproportional ecological impacts of demand-driven coral-reef fishing and growing fishing footprints fuelled by increased trade.

4. Fisheries expansions, masking effects, and fishing variability

Chapter based on Cuetos-Bueno, J., Hernandez-Ortiz, D. and Houk, P. (2019) 'Co-evolution of "race-to-fish" dynamics and declining size structures in an expanding commercial coral-reef fishery', Reviews in Fish Biology and Fisheries, 29(1).

Despite anecdotal evidence of depletions many commercial coral-reef fisheries have maintained consistent, demand-driven landings thanks to expansions of fishing effort to remote areas that remain within the range of commercial markets (Birkeland, 2004; Cinner et al., 2016; Zeller, Booth and Pauly, 2005; Cuetos-Bueno and Houk, 2014). While fisheries expansions may provide for maintained commercial landings, recent studies suggest that increasing interannual variability may also be expected associated to those expansion (Houk *et al.* incl. Cuetos-Bueno, 2012, 2017; Taylor *et al.*, 2014; Hernandez-Ortiz, 2020). Consistent annual landings despite localized depletions could mask ongoing localized depletions, potentially providing a false sense of sustainability to managers and consumers. Alongside, catch success and landings could increasingly becoming dependent on favorable conditions that provided better access to those less exploited stocks (e.g. calm season), eventually leading towards "race-to-fish" dynamics such as improved catch success and landings becoming concentrated at the start of a favorable timeframe or season, but rapidly declining to reference levels afterwards (Hernandez-Ortiz, 2020; Birkenbach, Kaczan and Smith, 2017; Rosenberg, 2017).

Landings and export datasets from Chuuk highlighted how sustained landings over time were maintained through expansions of commercial fishing pressure to the remote barrier reefs where fishing success and profitability were highest despite higher travel costs (see Chapter 2 & 3). Alongside, assessments suggested ongoing unsustainable commercial fishing regimes. Together, those findings support anecdotal evidence of localized depletions at reefs near population centers across Micronesia, and suggest strong geographical gradients on stocks status and fisheries expansions as a result (Houk *et al.* incl. Cuetos-Bueno, 2012, 2015, 2016; Cuetos-Bueno and Houk, 2018; Cuetos-Bueno *et al.*, 2018).

A rare landings time series from the Commonwealth of the Northern Mariana Islands (CNMI) offered a unique opportunity to assess the expansion of a commercial coral-reef fisheries from a main urban center (Saipan), and explore how such expansion may provide for sustained landings and a false sense of sustainability because they can mask ongoing localized depletions. Using 11-years of detailed catch records of monthly landings collected by Saipan Nutritional Assistance Program, the evolution of catch variability and ''race-to-fish'' dynamics at different taxonomic levels across the study period for a fishery exposed to high fishing pressure was examined (Cuetos-Bueno, Hernandez-Ortiz and Houk, 2019).

4.1. Methods

This study focused on monthly landings datasets collected by CNMI Nutrition Assistance program (hereafter NAP; Cuetos-Bueno and Houk, 2014). NAP mandatory monthly reports of purchases from all fish markets in Saipan describe purchases of fish at varying taxonomic levels, ranging from species level for some iconic fish (i.e. *Naso unicornis*), to generic groups (i.e. reef-fish). Data from January 2006 to December 2016 were manually entered into an electronic database and data from main fish markets (n = 13) that contributed to at least 1% of overall landings were used for analyses. Data from 2015 were excluded due to curtailed fishing activities due to generalized infrastructure damage as a result of Typhoon Soudelor that lasted several months (August 2015).

NAP datasets were used to explore historical trends in landings with respect to windspeed and seasons. The premise for these analyses was that catch variability was expected to rise alongside growing fishing pressure through time (Anderson *et al.*, 2008; Houk *et al.* incl. Cuetos-Bueno, 2012). Wind represents a significant environmental factor predicting fish landings in CNMI and across Micronesia because prevalent trade high winds and waves limit fishing access (Houk *et al.* incl. Cuetos-Bueno, 2012, 2017; Taylor *et al.*, 2014; Cuetos-Bueno *et al.*, 2018). Beyond monthly estimates, seasons - defined by natural breaks in the wind data - were also compared (Jenks and Coulson, 1963). This process allowed contrast of: calm (May to October) versus windy (November to April) seasons. The influence of moon phases on landings could not be assessed due to NAP data being aggregated by month. First, whether landings became more dependent upon favorable seasons was examined using regression models describing how the ratio of landings between the calm:windy seasons shifted through time. Given a growing reliance upon the calm season through time, ‘‘race-to-fish’’ dynamics such as improved catch success and landings becoming concentrated at the start of a favorable timeframe or season, but rapidly declining to reference levels afterwards (Birkenbach, Kaczan and Smith, 2017) were also assessed by regressing monthly landings versus windspeed across the calm season for each year. While potential threshold effects of windspeed on fishing may exist, mean monthly windspeeds during calm months used for analysis were all bellow such know thresholds, resulting instead on linear relationships (Cuetos-Bueno *et al.* 2018). In both instances, the slopes of annual regression models through time were compared to test if annual relationship were changing. Due to varying taxonomic resolution within NAP datasets, historical trends for one species (*Naso unicornis*; 13% of landings), two functional groups (parrotfishes and rabbitfishes; 40% and 5% of landings respectively), and all reef-fish combined were examined (Houk *et al.* incl. Cuetos-Bueno, 2012).

4.2. Results

Data derived from NAP office monthly reports depicted that reef-fish landings were maintained between 2006 and 2016, with an estimated mean of 42.0 mt year^{-1} (± 1.2 SE), and a mean inter-annual variation of 12.3% (± 2.9). Yet, NAP data also revealed a significant increase in the ratio of annual landings between calm and windy seasons for both reef-fish (Figure 8a,c) and parrotfish (Figure 8b, d), reflecting a growing dependence upon favorable calm seasons for maintaining stable annual landings through time. Ratios of reef-fish and parrotfish landings between calm and windy season changed from 1:1 to 1.2:1 (or a 20% increase over 11 years), and from 0.7:1 to 1.7:1 (143% increase), respectively. Annual regression slopes between monthly windspeeds and reef-fish landings revealed a similarly growing dependency on calm months across the study period (Figure 9a,c). Alternatively, parrotfish landings didn’t show a clear relationship with monthly mean windspeed, but instead had a strong and growing relationship with the start of the calm season, when wave-exposed reefs first become accessible to fishers, supporting the hypothesis of ‘‘race-to-fish’’ dynamics at the start of the calm season (Figure 9b,d). In contrast with total reef-fish and parrotfish landings, no clear patterns of increasing dependence upon favorable fishing conditions or ‘‘race-to-fish’’ dynamics were found for landings of rabbitfishes or *Naso unicornis*.

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Figure 8. Proportion of overall annual reef-fish (a) and parrotfish (b) landings caught during calm (dark gray bars) and winter (light gray bars) seasons. The annual differences between calm-versus-windy landings were also examined across the study period for reef-fish (c) and parrotfish (d). Cuetos-Bueno, Hernandez-Ortiz and Houk, 2019.

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Figure 9. Annual relationship between proportional monthly contribution to overall seasonal (calm) reef-fish landings and mean monthly windspeed (a), and between proportional contribution to overall seasonal parrotfish landings and months away from start of clam season (b). The growing significant of these annual relationships were examined across the study period for reef-fish (c) and parrotfish (d). Data points represent annual regression slopes. Cuetos-Bueno, Hernandez-Ortiz and Houk, 2019.

4.3. Discussion

The supply of fish to Saipan's commercial markets remained stable between 2006 and 2016, which could suggest sustainable harvesting regimes under maintained fishing effort. Unfortunately, lack of datasets limits our ability to assess how the maintenance of annual landings could have been affected by changes in fishing effort during that timeframe. Regardless, the present study revealed how independently of potential overtime changes on overall fishing effort stable landings were made possible due to a growing reliance on pulsed catch success during the favorable spring and summer calmer seasons. Within the calm months, a ''race-to-fish'' dynamic further evolved for landings of some target species. Parrotfish landings were particularly sensitive to the onset of the calm season as calm-versus-windy landings ratios more than doubled over the study period, and landings also became strongly concentrated towards the start of the calm season in May and June. These findings resonated with localized depletions of parrotfishes reported already in the mid-1990s for the more accessible leeward coast of the inhabited CNMI islands (Graham, 1994; Duenas & Associates, 1997; Trianni, 1998), and more recent reports in the 2010s (Houk *et al.* incl. Cuetos-Bueno, 2012, 2014). The present results also resonated with increased fishing success reported during calm months between 2011 and 2014 (Trianni, Gourley and Ramon, 2018). Elsewhere on Guam, large parrotfish life histories were well predicted by fishing access and greater biomass and landings of large parrotfish were recorded on the windward eastern coast (Taylor *et al.*, 2014; Taylor and Cruz, 2017). In sum, the results suggested that stable commercial landings were an artefact of demand-driven commercial fish sales, but stable landings were associated with increased catch variability attributed to intermittent access to further, remote fishing grounds. While fisheries expansion may take longer to impact commercial landings, subsistence fishers may not be able to cope with increasing costs needed to access remote fishing grounds, and their food security may decline, and a consistent supply of reef-fish to commercial markets may mask localized depletions and fisheries expansions in the CNMI, providing a false sense of sustainability for consumers and managers (Trianni, Gourley and Ramon, 2018).

5. Variable species responses and restructuring of fisheries

Chapter based on Cuetos-Bueno, J., Hernandez-Ortiz, D. and Houk, P. (2019) ‘Co-evolution of “race-to-fish” dynamics and declining size structures in an expanding commercial coral-reef fishery’, *Reviews in Fish Biology and Fisheries*, 29(1); and on Houk, P., Cuetos-Bueno, J., Tibbatts, B., et al. (2018) ‘Variable density dependence and the restructuring of coral-reef fisheries across 25 years of exploitation’, Scientific Reports, 8(1).

While fisheries expansion can temporarily provide for maintained landings, impacts on fisheries and ecosystems should be expected eventually. Compensatory density-dependence responses following increased mortality (i.e. fishing) can result in increased reproductive output from the remaining adult individuals, leading to populations becoming dominated by smaller individuals, which could translate to shifts in sizes of fish landed (Jennings *et al.*, 1999; Shin *et al.*, 2005). Alongside compensatory density dependence responses, species replacements can also occur, as fishing moves ‘down’ and ‘across’ food webs as less resilient species are sequentially replaced by more resilient counterparts from within or lower trophic levels the former are depleted (Pauly *et al.*, 1998; Clua and Legendre, 2008). Limited understanding of such mechanisms and potential associated species replacements on extremely complex coral-reef fisheries are of concern because they can lead to impacts on stocks, ecological functions, and habitats.

As the study of historical reef-fish landings from CNMI highlighted, fisheries expansions following localized depletions can provide for maintained landings, albeit with increasing dependence upon favorable fishing conditions. Yet, changes in the composition and size structure of landings are also expected eventually alongside fisheries expansions because habitat availability, technology, and cost ultimately limit access to new fishing grounds. Rare multi-decadal landings timeseries (Guam) and historical snapshot datasets (CNMI) provided a unique opportunity to explore species responses and restructuring of multi-species coral-reef fisheries subjected to maintained commercial fishing pressure.

A limited set of species records from available CNMI datasets and published reports (1993 and 2009) were used to examine changes in size structure across those 16 years for 19 species that represented 60% of overall landings (Cuetos-Bueno, Hernandez-Ortiz and Houk, 2019). Coupling this, time series from Guam expanding 25 years provided for both investigations at the family level to determine what trophic groups may be most sensitive to fisheries expansions and what groups show truncated size-structures that are of concern and could be reflective of compensatory responses, and to draw relationships with previous findings. Guam dataset allowed to also focus within each major family to examine species replacements through time. Species replacements were examined with respect to size structures and proportional contributions to landings, representing two distinct features of both fisheries-dependent data and commercial sales (Houk, Cuetos-Bueno, Tibbatts, et al., 2018).

5.1. Methods

CNMI historical size-structure datasets included two different snapshot studies conducted in 1993, 2009, and a timeseries from 2011 to 2014. In 1993, 44 fishing trips were monitored, which involved identifying and measuring 5,205 fish from Saipan and nearby Tinian (Graham, 1994). Size-frequency data was manually extracted from histograms contained in reports and digitized for comparison with modern datasets. In 2009, a similar dataset was collected, including 11,506 fish identified and measured (Houk *et al.* incl. Cuetos-Bueno, 2012). Last, a bio-sampling program was begun in 2011 recording fish identification and size data from selected landings three times per week. While these publicly funded datasets were not made available by managing agencies for the present study citing confidentiality concerns, summary tables and size-frequency histograms for 45,912 fish from six target species from the early 2010s were extracted from a technical report (Sundberg *et al.*, 2015). Guam multi-decadal landings datasets have been collected by the local management agency from 1982. Datasets include fish identification and sizes collected during scheduled landings interceptions at ports. The stream of data from this program differs for each fishery, but reporting was highest and most consistent between the late-1980's and mid-2000's.

CNMI size-frequency datasets were used to assess size-structure trends for a subset of 19 target species with sufficient data (N>50) between 1993 and 2009. Those species accounted for 60.7% and 60.5% of landings from Saipan and Tinian during both timeframes, respectively. Shifts in size-structure were hypothesized alongside increasing variability and exploitation, but with differing intensities across species (Houk *et al.* incl. Cuetos-Bueno, 2017; Houk, Cuetos-Bueno, Tibbatts, *et al.*, 2018). Size-differences were also explored for four target species using bio-sampling data from the early 2010s that was extracted from modern reports and studies. Kolmogorov–Smirnov (KS) tests were used to compare species size-structures across different timeframes. Results of species-specific size structure changes with respect to species vulnerability indices and optimal catch sizes were also examined (Beverton, 1992; Cheung *et al.*, 2005; Froese and Pauly, 2016). Weighted regression models were used to assess trends in Guam historical datasets. For spearfishing and hook and line fisheries, several dependent variables sequentially were analyzed, namely: (i) percent contribution of dominant fish families (>10% of landings); (ii) ratios of large-to-small bodied fishes within each dominant family; (iii) mean size for all 'other fishes' not in dominant families; and (iv) percent contribution of large, iconic species grouped together. Last, to better appreciate species-based responses and potential replacements, time series analyses were performed on mean size and proportional contribution for dominant species that made up 70% of landings from their respective fishery.

5.2. Results

Comparisons of size-frequencies for target species across timeframes in CNMI revealed that 15 out of the 19 fishes examined got smaller between 1993 and 2009, with stronger positive skews in their size frequency histograms (Figure 10 a-o). In addition, three of the four species for which additional biosampling data were available from the early 2010s showed further declines. Significant declines in size structure ranged between 3.0% (or 8.3% in terms of biomass, *Acanthurus lineatus*) to 33.5% (or 71.4% in terms of biomass, *Hipposcarus longiceps*). Reduced sizes were coupled with increases of landings below estimates of optimal capture sizes (L_{opt}), including those of three dominant species *Hypposcarus longiceps*, *Siganus argenteus*, and *Naso unicornis*, whose landings below L_{opt} accounted for over 90% of landings by 2009. The one species that showed a significant increase in size structure was the small-bodied soldierfish *Myripristis berndti*, while three other small-bodied species showed no significant changes (Figure 10 p-s). Last, the magnitudes of species-based declines in size structure between 1993 and 2009 were strongly predicted by their vulnerability to fishing indexes for most (Froese and Pauly, 2016) (Figure 11). Yet, two species (*Siganus argenteus*, and *Hypposcarus longiceps*) didn't appear to follow this trend, as observed size declines were much larger than predicted by the overall relationship.

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*Figure 10. Comparison of size frequencies for target species that comprised 60% of commercial landings across three different time periods (1993 light gray, 2009 gray, and 2010–2014 dark gray, * indicates significance between all lines on the plot, P<0.05, Kolmogorov–Smirnov tests). These species all had sample sizes >50 at each timeframe. Cuetos-Bueno, Hernandez-Ortiz and Houk, 2019.*

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Figure 11. Size changes between 1993 and 2009, and negative relationships with species vulnerability indexes. Regression models were examined with (dashed line) and without (full line) Siganus argenteus and Hipposcarus longiceps. Cuetos-Bueno, Hernandez-Ortiz and Houk, 2019.

Significant declines in the proportional contributions of both snappers and groupers to the Guam bottom fishery were found across the 25-year period (30% and 45% net decline, respectively, Figure 12a). In contrast, emperorfish contributions fluctuated non-uniformly, while ‘other fishes’ increased linearly by 75%. The ratio of large-to-small groupers declined strongly during the first ten years, but showed a slight positive response to the fishery expansion in 1995 associate to the opening of a new marina that granted access to new fishing grounds in southern Guam (Figure 12b). Steady decreases in the large-to-small emperor ratios also recovered slightly following the 1995 expansion. The Guam Scuba spearfishing fishery showed similar trends. Parrotfish had the most notable decline in proportional contribution (30% net decline), while no significant trends were found for surgeonfishes and groupers (Figure 12c). In response, the collective group of ‘other fishes’ steadily increased their contribution to landings. The ratio of large-to-small groupers and parrotfishes both declined strongly across the entire study period (over 20-fold decline for both, log-scale used; Figure 12d). Uniquely, the ratio of large-to-small surgeonfishes increased across the entire study period with growing contributions from the iconic *Naso unicornis*, which became the dominant species targeted by SCUBA spear fishers as other large-bodied species (e.g. parrotfishes and groupers) phased out. Last, iconic large fish contributions declined asymptotically by 60%, with a slight increase following the 1995 fisheries expansion. Specific responses to fishing pressure varied across species. Overall, 32% of species had a strongest overtime response to their mean size, while 17% had strongest response to their proportional contribution, and 10% had equal response. No significant response was found for the remaining 46% of species.

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Figure 12. Temporal trends in proportional contributions and large-to-small fish ratios are shown for dominant families of bottom (a,b) and SCUBA spearfishing (c,d) fisheries. Houk, Cuetos-Bueno, Tibbatts, et al., 2018.

5.3. Discussion

Size reductions were observed for 80% and 42% of target species in CNMI and Guam, with greatest impacts to large-bodied species. Size reductions in landings are concerning, but can potentially be reflective of compensatory density-dependent responses that could temporarily provide for maintained stocks (and landings) but would eventually become compromised as (1) fish are increasingly caught before reaching maximum cohort biomass gains or have the chance to breed, and (2) reproductive output is reduced to the point where recruitment success tracks annual environmental cycles and yields greater variability (Anderson *et al.*, 2008; Houk *et al.* incl. Cuetos-Bueno, 2012). Interestingly, overtime shifts on mean sizes were not homogeneous, highlighting growing evidence that size-shifts on landings may greatly vary across species in complex ecosystems characterized by competition among large number of species (Houk *et al.* incl. Cuetos-Bueno, 2017; DeMartini, 2019). Findings from Guam also highlighted how fishing 'down' (Pauly *et al.*, 1998) and 'across' food webs occurred simultaneously, as larger fishes from differing trophic levels were primarily targeted, suggesting that fish size, rather than trophic position, was a primary driver of exploitation. Further, species responses across the study period suggested that smaller species within families may be able to better withstand fishing pressure due to faster growing rates. Yet, exceptions occurred, as large-bodied herbivore species with similar growth rates had very differing responses, as some maintained contribution to landings alongside declining size-structures (e.g. *Hipposcarus longiceps*), while others maintained size-structures but declined in contribution to landings (e.g. *Chlorurus microrhinos*). Impacts of potential habitat changes that may have occurred during the study timeframe and fish populations and fisheries were not explored in this study. Growing local evidence increasingly supports that aside from very localize locales (e.g. highly developed bays), fishing pressure is the main driver of fishing populations across Micronesia (Houk et al., 2015; Houk *et al.* incl. Cuetos-Bueno, 2016). Yet, further explorations of linkages between habitat and fish stocks are desired. Overall, the results from both studies cautioned that unchecked exploitation of multi-species fisheries could quickly remove the suite of 'sensitive' species that declined most in proportional contributions, and allow species with faster-growing rates or potentially stronger compensatory density dependence responses to replace them overtime (Figure 12). While resulting fast-turnover fisheries may provide for maintained landings in the mid-term, compromised populations of less resilient species have ecological and economic consequences, such as declining corals and calcifying substrates within reef ecosystems. For example, fisheries-driven declines in large-bodied herbivores such as large parrotfishes have been identified as the main driver of coral reef health and resilience across Micronesia (Houk *et al.*, 2014; Houk et al., 2015). Because coral reefs provide for key habitat for reef-fish and important ecological and economic services to soceties, eventual impacts to fisheries and the goods and services coral reefs offer to society and tourism industries are to be expected as such fisheries evolve (Van Beukering *et al.*, 2007; Lokrantz *et al.*, 2008).

6. Research and management implications

The work presented in this thesis provides novel insights into some fundamental dynamics associated to growing coral-reef fisheries commercial expansions and the underlying drivers behind those dynamics. Further, it provides for potential novel management paths towards sustainable fishing regimes. Those two main themes are discussed in more detail bellow.

6.1. Fisheries expansions

Cumulatively, the work conducted under this thesis uncovered complex coral-reef commercial fisheries footprint expansion dynamics across multiple geographical scales that have profound implications for targeted stocks, the fisheries sector that depends on them, and ultimately the societies that rely on them for food security and other ecosystems services. Below, I attempt to put into perspective the different dynamics associated with the coral-reef fisheries expansions identified across this thesis.

6.1.1. Growing trade networks

As global trade networks expand beyond main urban centers to reach remote areas around the world, management of local fisheries that become exposed to those networks is hampered by the associated added complexity (Birkeland, 2004; Swartz *et al.*, 2010; Crona *et al.*, 2016). Important resources and efforts have been focused on understanding those new dynamics in industrial and high value fisheries (Dommen, 2000; Anderson *et al.*, 2011; Rhyne *et al.*, 2012; Guillotreau *et al.*, 2017). Yet, parallel efforts towards small-scale fisheries that have also entered growing trade networks have been limited. In coral-reef fisheries, official records and assessments of trade networks have mostly focused to date on local networks (Thyresson *et al.*, 2013; Rodrigues and Villasante, 2016; Grafeld *et al.*, 2017). Such records and assessments are all but non-existent for international trade networks, with a few exceptions for high value commodities such as sea cucumbers and the live reef fish trade (Sadovy *et al.*, 2003; Anderson *et al.*, 2011). This situation is concerning as not only do small-scale coral-reef fisheries struggle to provide for fundamental food and economic security alongside key ecosystem functions in many coastal nations across the tropics, but they are increasingly been exported through expanding international trade networks (Nichols, 1991; de Andrade Cunha, de Carvalho and de Araujo, 2012). Concerns regarding the impacts of growing international trade on coral-reef fisheries are not new (Johannes, 1981), yet management agencies have generally failed to establish programs to track and assess this trade. Secondary sources of information can provide valuable insights. The 2018 study (Cuetos-Bueno and Houk, 2018) drew from one of such secondary data sources (bills of shipping) to conduct an assessment of reef fish trade between Chuuk and Guam. While datasets contained only aggregated taxonomic information, assessment of aggregated export volumes combined with coupled economic datasets and informal interviews with trade stakeholders provided valuable insights into drivers and trade dynamics that have profound implications for stakeholders and resources managers in both exporting and importing jurisdictions. These findings aligned with those of another similar study that explored coral-reef fisheries trade between Rio Grande do Norte (Brazil) and north America and Europe; also based on secondary sources (export certificates), including important impacts to local fisheries and stocks of exogenous drivers such as variations in currency exchange rates and foreign demand for specific species/families (de Andrade Cunha, de Carvalho and de Araujo, 2012). Both studies also suggest important mean export levels (150-250 mt per year) for relatively small jurisdictions, supporting anecdotal reports of large hidden international flows of reef-fish, and highlighting the need to uncover those flows. As evidence of similar trade networks increasingly become noticeable across the tropics, concerns for small-scale fisheries even in remote locales grow, highlighting the need for better information frameworks. While exploring for secondary sources of data may not be a universal solution or provide the level of information needed for tailored management (e.g. taxonomic resolution), it can provide for valuable local assessments, and facilitate the formal inclusion of those datasets into local fisheries management frameworks (Pauly and Zeller, 2014). Alternatively, less-intense snap-shot approaches such as value chain assessments can also provide for general management guidance (Kaplinsky and Morris, 2000; Purcell *et al.*, 2017). Whatever the framework, enhanced monitoring programs and more studies are needed to understand growing small-scale fisheries trade industries. This will require transcending disciplines and geo-political boundaries as small-scale commercial fisheries footprints continue to expand.

6.1.2. Expanding footprints

While studies of coral-reef fisheries timeseries have highlighted generalized declines of overall landings (commercial plus recreational/subsistence) over the last decades, landings from the commercial sectors within those fisheries have often been maintained or even increased over time (Cuetos-Bueno and Houk, 2014; Pauly and Zeller, 2014). As localized depletions have occurred around urban centers that are the focus of commercial demand (Cinner and McClanahan, 2006; Aswani and Sabetian, 2010), expansion of commercial fishing effort to more remote and less exploited areas have evolved because infrastructure and equipment has developed to keep up with market demand, providing for maintained commercial landings regardless of localized depletions (Winterhalder, 2001; Birkeland, 2004; Aswani and Sabetian, 2010; Cinner *et al.*, 2016). Spatial expansion dynamics such as these have been widely studied in complex social-ecological freshwater fisheries landscapes (Carpenter and Brock, 2004), but have received limited attention with respect to coral-reef fisheries, where the evidence that does exist is indirect and based on fisheries-independent studies that characterize fish biomass and explore linkages to proxies of fishing pressure (Friedlander and Demartini, 2002; Brewer *et al.*, 2012; Damasio, Peninno and Lopes, 2020).

The assessment of the CNMI and Chuuk fisheries summarized here (Cuetos-Bueno *et al.*, 2018; Cuetos-Bueno, Hernandez-Ortiz and Houk, 2019) offered new insights into fisheries expansions within national boundaries. While no actual fishing effort data was available for CNMI, additional fisheries-dependent datasets provided a secondary line of evidence to support the hypothesis of fisheries sequential halo depletions and expansions, which in this case were linked not only to distance to port, but to weather-driven accessibility (Williams *et al.*, 2011; Houk *et al.*, 2014). Alternatively, datasets collected in Chuuk intentionally included geographical information regarding fishing activities. Those datasets enabled determination of how commercial fishing pressure halos have increasingly expanded towards the most remote reefs within Chuuk lagoon, where fish biomass was greater, and increasing fishing success compensated for higher traveling costs as compared to reefs near population centers or markets (Houk et al. incl. Cuetos-Bueno, 2016; Cuetos-Bueno et al., 2018).

Comparison of in-country dynamics and international (cross-border) trade dynamics provided a unique opportunity to assess for the first time the expansion of multi-species coral-reef fisheries through various geographical scales. These combined results suggest a scenario very similar to that documented on freshwater lakes complexes, where localized depletions driven by accessibility are followed by expansions to less accessible areas within each single lake (or island in our case), but that this process will eventually lead to a cycle of further expansions and depletions to other lakes (or islands in our case) following an expanding halo from the main origin of fishing pressure (Carpenter and Brock, 2004; Post *et al.*, 2008; Wilson *et al.*, 2020). Evidence of localized depletions was apparent in Guam, which were subsequently followed first by an expansion to the less accessible Guam southern reefs. Alongside, fishing footprint expansions to other islands such as Chuuk that were not accessible to Guam fisheries but to markets through growing trade networks were also documented. A local expansion process similar to that observed in Guam then appeared to occur in Chuuk, where increasing trade-driven commercial demand led to localized depletions in more accessible reefs, and the expansion of fishing pressure to less accessible reefs within Chuuk lagoon. Interestingly, the international expansion of Guam reef-fish fishing footprint appears to have been conditioned as much by socio-economic factors (i.e. trade networks, profitability, and local policies) as purely biological and geographical factors, as has been the case for similar expansions previously explored for high-value fisheries commodities (Sadovy *et al.*, 2003; Anderson *et al.*, 2011; Januchowski-Hartley *et al.*, 2020). Understanding the complex dynamics of fisheries expansion across heterogeneous socio-ecological systems is a fundamental frontier for the management of such fisheries and additional research.

6.1.3. Masking effects

Fisheries expanding their footprints have been linked to potentially misleading masking effects. The processes of serial localized overfishing and ensuing depletions masked by consistent supplies provided by expanding fisheries footprints is not a new idea, and has been widely studied for large-scale industrial fisheries (Pauly, Watson and Alder, 2005; Bhathal and Pauly, 2008; Crona *et al.*, 2016). The research presented here has provided new insights into how these masking effects may be also occurring in small-scale coral-reef fisheries. For instance, while maintained landings in CNMI over 11 years might at first glance suggest a sustainable fishery and healthy stocks, the stability of landings was found to mask the increasing dependence of fishers on pulse fishing of less accessible (more remote) reefs and declining size-structures of most commercial stocks. Elsewhere in Guam, the apparent recovery of the fishery in the mid-1990s was in fact an artifact of expanding footprints to new fishing grounds facilitated by a new marina built in southern Guam and the increasing targeting of less desirable species, while growing international footprints also provided for maintained supply. These results and the underlying dynamics they unmask are especially concerning for local managers and communities, as they suggest these 'hidden processes' will eventually lead to subsistence fishers and communities being exposed to depletions of the more accessible stocks that their socioeconomic and ecological resilience rely upon.

6.1.4. Fishing variability

Growing fishing variability alongside increasing fishing pressure has previously been identified and linked to truncated age structures and higher reliance upon annual recruitment success (Hsieh *et al.*, 2006; Anderson *et al.*, 2008). Studies from coral-reef fisheries summarized here suggest that increases in fishing variability could be also linked to a combination of i) increasingly differentiated stocks across access gradients (e.g. wave energy), and ii) variable effort applied to less exploited stocks across those gradients associated to pulse access (e.g. favorable weather conditions). Previous research has both predicted and found evidence of clear gradients of fish biomass and fishing success across spatial and temporal gradients of accessibility, including for coral-reef fisheries in Micronesia (Graham, 1994; Post *et al.*, 2008; Williams *et al.*, 2011; Houk *et al.* incl. Cuetos-Bueno, 2012). A unique timeseries dataset of monthly landings from CNMI was used to test and validate the novel hypothesis that landings variability would increase over time in expanding spatially-complex small-scale fisheries due to growing dependence upon environmentally-driven intermittent access to further, healthier fishing grounds. This analysis suggests that “fish-to-race” dynamics may eventually develop when fishing success becomes dependent upon the onset of conditions that allow access (e.g. start of calm season). It also suggested that the development of those dynamics may not be homogeneous across the different components of the fishery, but that they will become more pronounced for less-resilient species whose stocks may be more susceptible to development of fisheries-driven spatial gradients (Friedlander and Demartini, 2002; Richards *et al.*, 2012). Recent access to an equivalent landings dataset from nearby Palau has provided additional insights into this hypothesis (*Cueto-Bueno in prep*). Similarly to Saipan, coral-reef landings variability in Palau was found to increase over time, alongside anecdotal evidence of generalized depletions (*Cueto-Bueno in prep*). But in Palau, where a large lagoon system and less prevalent trade winds provide for easier access year-around to large reef areas, growing variability instead was associated to the traditional favorable spring fishing season, when anecdotal evidence suggest large numbers of targeted species spawn (Johannes, 1981). Despite the underlying dynamics remaining unclarified, growing variability is a cause of concern for fishers and managers alike, as both fishers' income and seafood supply increasingly becomes more variable and follows interannual high-and-low cycles leading to the conclusion that examining even coarse interannual landing records through time with respect to factors that may drive temporal fishing success can provide one indication of localized depletions and are desirable for further research.

6.1.5. Disproportional impacts of commercial fisheries

Loss of traditional resource ownership and management systems, development of new fisheries technologies, increased human populations, and access to markets have all been proposed as key drivers behind generalized world-wide declines of coral-reef fisheries over the past decades. Yet, debate remains regarding the relative importance of each factor (Birkeland, 2004; McClenachan and Kittinger, 2013; Pauly and Zeller, 2014). While human population has been found to be strongly linked to current trends of fish biomass and fisheries status (Cinner *et al.*, 2016; Friedlander *et al.*, 2018; McClanahan *et al.*, 2020), centuries of sustainable levels of harvesting have been also suggested alongside historically high human populations (McClenachan and Kittinger, 2013; Giovas *et al.*, 2016). Alternatively, over temporal in fisheries status have increasing been linked less to human population changes, but more to changes in fisheries management, techniques, and/or supply chains (Johannes, 1981; Cuetos-Bueno and Houk, 2014; Pauly and Zeller, 2014). Combined findings from this thesis provided new insights into this debate, validating the importance of enabling factors such as new fishing techniques and growing trade networks alongside weak management systems on coral-reef fisheries declines. But perhaps more importantly, the unique comparison of commercial and subsistence coral-reef fish landings datasets highlighted how growing commercialization may be the fundamental underlying factor that drives those trends in the presence of the beforementioned enabling factors. Limited studies of coral-reef fisheries development projects further support this hypothesis, linking fisheries declines primarily to the introduction of incentives to increase commercialization (Sadovy, 2007; Gillett, 2010; Barclay and Kinch, 2013). While commercial coral-reef fisheries are important contributors to local economies in many developing nations across the tropics, growing evidence regarding their disproportional contribution to degrading stocks and potentially compromised food security and ecosystems that will ultimately also impact societies demands a deep re-evaluation of their tradeoffs.

6.2. Management guidance

Potential limitations and challenges to some traditional concepts and paradigms behind modern fisheries management have increasingly emerged in recent times (Pauly *et al.*, 2002; Longhurst, 2010;

Finley, 2011; DeMartini, 2019; McClanahan and Azali, 2020). Integrative evaluation of findings from this thesis provided further insights into some of those potential limitations. Bellow, I further explore those, and suggest potential pathways towards improving management of complex small-scale multi-species fisheries and beyond, focusing on potential benefits of reconsidering of spatial (6.2.1) and taxonomic (6.2.2) management units, trade-offs of different size-based management approaches (6.2.3), and iii) management implications of potential variable species responses to fishing pressure (6.2.4)

6.2.1. Reconsidering spatial management units

Spatial management units that provide one foundation for fisheries policies usually represent geo-political boundaries (i.e. entire or many islands including wave-exposure gradients; Sabater & Kleiber, 2014). This delineation is the result of assumed genetic connectivity and geopolitical boundaries, without further consideration for population ecology or fisheries dynamics (Blackhart, Stanton and Shimada, 2006; Reiss *et al.*, 2009). While genetic connectivity may exist across locales with different spatial or environmental regimes, this does not equate to ecological connectivity, as panmixia of metapopulations can be maintained even when exchange between populations is infrequent (Horne *et al.*, 2013; Nadon *et al.*, 2015; Hawkins *et al.*, 2016; Williamson *et al.*, 2016). A burgeoning number of studies provide increasing evidence of mismatch and potential negative impacts between fisheries management units defined by geo-political boundaries or genetic connectivity, and actual units defined by ecological and fisheries dynamics (Guan *et al.*, 2013; Hawkins *et al.*, 2016; Taillebois *et al.*, 2017). Those include limitations of both management units that fail to encompass the whole spatial scale of species ecological dynamics, and management units that fail to account for small-scale spatial ecological and fisheries dynamics. In multi-species coral-reef fisheries, a growing number of studies have reported highly divergent populations of target fishes across areas within single spatial fisheries management units that are genetically connected (Friedlander and Demartini, 2002; Williams *et al.*, 2011). My research has found that divergent populations of target fishes managed within single management units across Micronesia suggest complex and growing differential fisheries impacts, including localized depletions at most accessible reefs, that might suggest limited ecological connectivity across small geographical scales (e.g. areas within each island) that does not compensate for non-homogeneous fisheries spatial dynamics, and limited utility of those management units for adequate fisheries management. This would suggest that management should therefore be heterogenous in space, and that spatial management units in coral-reef fisheries might instead be defined by demographic connectivity, aggregating populations from different locations into single management units only if demographic exchange exist at time scales relevant to processes that control population growth and fisheries dynamics (Carpenter and Brock, 2004; Nadon *et al.*, 2015; Hawkins *et al.*, 2016). Because assessing spatial population structures and dynamics can be complex, and probably impractical for most small-scale multi-species fisheries (Cadrin and Secor, 2009; Berger *et al.*, 2017; Taillebois *et al.*, 2017), the potential of basic indicators such as spatial patterns of stock biomass or fishing success as proxies for ecological/fisheries stock structures that could inform proactive management should be explored.

6.2.2. Reconsidering taxonomic management units

In an effort to simplify management approaches to complex multi-species fisheries, multiple species are often pooled into species complexes single management units (Gulland, 1984; DeMartini, 2019). Few temporal family-based studies have identified fishing-down the food web dynamics on coral-reef fisheries, providing support for the family-based species complex pooling that has become a predominant management approach in many coral-reef fisheries (Kaunda-Arara *et al.*, 2003; Crabtree, 2009; Lindfield *et al.*, 2015). While such grouping may simplify management approaches, limitations of pooling species with potentially disparate population traits and ecosystem services in the same family complexes may exist (Jennings *et al.*, 1999; Kleiber and Maunder, 2008; DeMartini, 2019). Unfortunately, the rarity of species-based historical records for coral-reef fisheries hampers further assessment of those limitations (DeMartini, 2019). My research has provided novel evidence of how species managed under family-based species complexes may be unintentionally committing systems to undesirable species-based replacements, as a suite of 'sensitive' species may inevitably be replaced overtime by counterparts with faster-growing rates or stronger compensatory density dependence responses (Tosatto, 2011). Findings show temporal replacements of less resilient species within family management units aligned with similar replacements found across spatial patterns that reflected gradients of fishing pressure in Guam and predicted species vulnerability to exploitation (Taylor *et al.*, 2014). A similar dataset from nearby Palau allowed further validation of these findings and hypothesis (*Cueto-Bueno, in prep*) and shows additional evidence of fisheries evolution towards more-resilient species within taxonomic management complexes for key families with species-specific records (e.g. parrotfishes and groupers). Interestingly, many of the sensitive 'species' that became replaced overtime in Guam and Palau also contribute disproportionately to ecosystem functioning suggesting that compromised populations of these species may also have ecological and economic consequences, such as declining corals and calcifying substrates within coral reef ecosystems due to reduction of critical functions such herbivory that are fundamental for coral reef resilience, which can also impact the goods and services offered to society and tourism industries (Van Beukering *et al.*, 2007; Lokrantz *et al.*, 2008; McLean *et al.* incl. Cuetos-Bueno, 2016; Houk, Cuetos-Bueno, Kerr, *et al.*, 2018). Overall, these findings highlight potential limitations of species-complexes management approaches for coral-reef fisheries, and suggest that they could commit systems to undesirable species-based replacements that would result in long-lasting impacts not only to the fisheries, but also the ecosystems they sustain. Improvements in official fisheries monitoring to record landings at species-specific levels will be paramount to further understand and identify these potential trends, and accordingly develop tailored management measures to enhance fisheries and ecological sustainability.

6.2.3. Variable size-structure changes and density-dependent responses to fishing pressure

Density-dependent processes are a fundamental principle of population ecology and current fisheries management paradigms, yet, the application of this general concept to specific populations remains controversial due to lack of quantified benchmarks for specific populations and evidence of repeated violations to the principle (Myers and Cadigan, 1993; Rose *et al.*, 2001; Walters and Kitchell, 2001; Pauly *et al.*, 2002). This is especially true for coral-reef fisheries, where complex interactions across hundreds of species can potentially alter density dependence responses (Polovina, 1984; Houk, Cuetos-Bueno, Kerr, *et al.*, 2018). This is concerning for fisheries management, as diminishing size-and-age structures associated to density dependence responses form the basis for widely used fisheries management models that derive fishing-versus-natural mortality and spawning potential ratios that have become prevalent in coral-reef fisheries (Nadon *et al.*, 2015; Prince *et al.*, 2015). Our findings provided evidence of heterogeneous size-structure changes on fish landings among species with very similar life histories, which could be linked to variable density-dependence responses to fishing pressure. This highlights the need to consider when assessing stocks and designing management approaches that species-specific density-dependence responses may exist. This has led to the hypothesis that life histories may dictate how a species *can* respond to exploitation, but that other variables (e.g. variation in recruit survival) may represent an underappreciated, secondary driver of how a species *will* respond to exploitation. Better understanding of the linkages between observed declining on size-structures on landings, the potential dynamics of realization of density-dependence responses across species, and their implications for stock assessments and management of multi-species fisheries is urgently needed. Ongoing research that builds upon the findings presented in this thesis suggest that less than half of species that dominate coral-reef fish landings across Micronesia display size-truncations potentially reflective of compensatory density-dependent responses related to fishing pressure, and that the response was predicted by genetic isolation (Houk *et al.* incl. Cuetos-Bueno, 2021). Cumulatively, it is suggested that unchecked exploitation in multi-species fisheries that does not account for those potential dynamics could allow species with potentially strong compensatory density dependence to quickly replace species with weak responses. Finally, it is also hypothesized that species that show truncated size-structures that may be reflective of strong density-dependence responses may be best managed by size limits, as even limited number of mature fish could result on increased replenishment to compensate for increased mortality. Alternatively, we hypothesized that size limits may not provide enough protection for species that may have weak density-dependence response and are competing for resources and habitat with the former.

6.2.4. Size-based management

Size-based policies that ban catches of fish under certain size limit to ensure enough spawning population biomass and recruitment to compensate for fishing mortality are a common management approach in coral-reef fisheries. However, there are discrepancies regarding optimal benchmarks for catch size limits, and limitations exist for most methods due to several factors (Froese, 2004). Mean size at maturity (L_m) has been proposed as a non-conservative benchmark to reduce recruitment overfishing, and fairly reliable snapshot estimates of L_m can be obtained from local life-history studies (Choat and Robertson, 2002). More conservative targets to address recruitment, cohort biomass, and fecundity have been proposed by setting optimal catch sizes (L_{opt}; Rainer Froese et al., 2016). However, L_{opt} estimates are very sensitive to natural mortality rates (M) that are generally estimated with methods that dependent on an inconsistent metric, the oldest fish recorded when sampling (Froese *et al.*, 2008; Hoenig, 2017; Wamukota *et al.*, 2017). This situation is becoming increasingly concerning in coral-reef fisheries, as growing studies suggest extended longevity (and very low natural mortality) may be more prevalent in coral-reef fish than previously thought (Craig and Axe, 1997; Andrews *et al.*, 2016; Taylor *et al.*, 2020). The reliance on a parameter (M) that is so dependent on sampling effort and fishing pressure hampers the utility of L_{opt}. This situation similarly hampers other common fisheries benchmarks based on mortality estimates, such as fishing-versus-natural mortality ratios and spawning potential ratios (Hordyk *et al.*, 2014; Prince *et al.*, 2015). Alternatively, robust growth estimates (K) are perhaps easier to obtain, allowing for accurate estimation of length at maximum growth rate (L_μ). In addition to the lack of uniformity regarding size-management benchmarks, growing evidence suggests that lower than expected recruitment success for coral-reef fishes may occur, as highlighted by fast growth towards maturity and long lives afterwards increasingly been found for many coral reef fishes (Craig and Axe, 1997; Birkeland, 2017; Taylor *et al.*, 2020). It is therefore suggested that when choosing a size-benchmark for species with strong density-dependence compensatory responses, managers should not only consider carefully the potential underlying limitations of different approaches to determine those benchmarks, but should also apply a conservative criteria and consider at the minimum the largest of the available benchmarks (L_{opt}, L_m or L_μ) as starting points for adaptive size-based policies.

7. Conclusions

This thesis explored innovative research approaches to further our understanding of poorly understood data-poor multi-species coral-reef fisheries, and provide novel insights into exploitation and stock dynamics, the drivers behind those dynamics, and potential management paths towards sustainable fisheries. Regardless of playing a central component in the societies and economies of many coastal nations across the tropics, resources managers continue to struggle to implement sustainable coral-reef fishing regimes that ensure societal needs alongside healthy and resilient ecosystems. This research highlights how expanding trade networks can make local small-scale fisheries, even in remote locations, susceptible to complex external market drivers out of their control. The results also draw attention to disproportional impacts of commercial fisheries compared to subsistence counterparts, putting in perspective generalized depletions over the last decades alongside development of commercial fisheries. Importantly, this work both contributes and further confirms the mounting evidence of how growing market demand and localized depletions of reefs more accessible to markets has led to expansions of fisheries footprints that can provide for maintained supply in the mid-term (albeit with increasing variability) while masking localized depletions and disproportionally impacting subsistence fishers. This suggests that regardless of fisheries expansions, fishing 'down' and ''across' food webs and species replacements are bound to occur under maintained commercial fishing pressure. While providing a rather bleak scenario, this research has provided valuable insights for further research areas and considerations for future evaluations of current coral-reef fisheries management paradigms, and I suggest alternative pathways moving forward that may improve management of such complex multi-species fisheries.

8. References

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