INVESTIGATING HISTORICAL, SOCIAL, AND ECOLOGICAL DIMENSIONS OF CORAL REEF RESILIENCE

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DEDICATION

I dedicate this dissertation to my parents, Ajit and Soumya, who gave me the freedom to play, swim, write, dive, travel, and pursue my interests, even when it wasn't entirely clear where I was headed.

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ABSTRACT

Coral reefs are complex social-ecological systems that shape, and have been shaped by, a range of historical, environmental, and social processes. Global declines in reef health highlight the need to understand the factors that support reef resilience and those that further decline. This dissertation uses multiple methodologies and approaches to explore different aspects of resilience, integrating marine historical ecology, biocultural approachces, and large-area imaging to assess benthic habitats. I investigate the historical ecology of the 1000-year-old pole-and-line tuna fishery in the Maldives archipelago and examine the reasons for its persistence over time. Written accounts of traders and travelers, ethnographies, and archaeological data indicate that a centuries-long trade in money cowries served as a condition for the establishment of the tuna fishery, which in turn drove cultural and market dynamics towards the consumption of pelagic fish. This preference for tuna has kept reef fishing historically light, but new markets for reef fish are changing local consumption patterns. I conducted interviews with residents and fishers across one of the central atolls in the Maldives to better understand the ways in which different species of fish are valued today. Results indicate that reef fish have been an overlooked part of local diets, with preferences that vary strongly with gender and age. Seasonal spikes in the local catch and consumption of reef fishes and an informal network of sharing point to previously undocumented local practices that should be considered while developing management plans. Finally, these social and cultural shifts are taking place as coral reefs alter in function in response to increasingly frequent climate change related marine heatwaves. During one such thermal stress event in Kāne‘ohe Bay, O‘ahu in 2019, I used structure-from-motion photogrammetry to quantify the fine-scale spatial, temporal, and taxonomic differences in coral bleaching and mortality. Spatial differences in bleaching were strongly linked to habitat complexity and coral composition, with reefs that were dominated by *Pocillopora* experiencing most severe bleaching. Mortality was also influenced by species composition and fine-scale differences in thermal stress, with heat-susceptible species seeing significant declines in cover in this period. Together my results highlight the importance of integrating human dimensions into our understanding of reef resilience, and the role that emerging technologies can play in quantifying the environmental and ecological processes that underpin reef response to climate change.

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CHAPTER 1

INTRODUCTION

Climate change is the defining issue of our time. Every natural and human system on this planet currently experiences its effects. These changes in the environment have largely been driven by human activity. Atmospheric concentrations of carbon dioxide, methane, and nitrous oxide are at their highest now than they have been in the last 800,000 years (IPCC 2014). More than half of the observed increase in global average surface temperature from 1951 to 2010 has been caused by increases in greenhouse gas concentrations (IPCC 2014). The scientific community today recognizes the Anthropocene as a geological reality, an epoch in which human behavior is having planetary effects (Crutzen, 2002). The burning of fossil fuels has had impacts on the permafrost, causing reductions in sea ice and glacial area. It has increased thermal stratification in oceans and caused changes in precipitation, wind, and ocean circulation. These physical changes have had cascading effects on associated biological systems, pushing large numbers of species closer to extinction, and threatening the resilience of a range of linked human-natural ecosystems. In short, it is impossible today to understand natural systems and environmental processes as operating outside of the complex and overlapping perturbations caused by climate change.

Perhaps nowhere are these effects more pronounced than in the world's coral reefs and the islands that they fringe. While coral reefs have altered in form and function many times over the course of their multi-million-year history, increasing sea surface temperatures due to climate change have resulted in sharp declines in their health and diversity in the past few decades (Pandolfi et al., 2003). Coral bleaching, has, in particular, caused significant losses in coral cover worldwide. Bleaching occurs most frequently when increased sea surface temperatures result in the expulsion of symbiotic zooxanthellae from the coral animal (Hoegh-Guldberg, 1999). In the past five decades, back-to-back bleaching events have reduced coral cover on tropical reefs by nearly 50% (Eddy et al., 2021) with projections indicating that almost all coral reefs will degrade into the future, even if global warming remains below 2°C (Bindoff et al., 2019). Extensive coral mortality has resulted in large-scale changes to reef environments, leading, in the worst cases, to collapses in three-dimensional complexity and reef architecture (Alvarez-Filip et al., 2009), phase shifts into algal-dominated states (Hughes, 2022), and declines in the abundance and diversity of reef fishes with fewer species and reduced trophic linkages. Not only have these changes altered how these ecosystems function, they have had significant impacts on coastal and islander communities. Sea level rise, extreme weather events, and reduced wave attenuation from degraded coral reefs have resulted in losses to life and property, causing the displacement of some islander communities and creating the world's first 'environmental refugees' (Connell, 2013). In parallel with these climatic stressors are the mixed effects of an increasingly capitalist, globalized economy. On the one hand, this has led to the diversification of island economies, notably through investment in the tourism sector (Coulthard et al., 2017). Islands have rapidly developed in response to this, generating local income, infrastructure, and creating new opportunities for people (Kerr, 2005). On the flipside, islands today sustain not only their own population – a large proportion of which are still reliant on fishing and agriculture – but also a visiting tourist population, that shares in the consumption of these products, and in the use of these ecosystems. These shifts in demography and economy have fundamentally altered the way people today interact with the marine environment. However, if it might appear as if we have moved away from our reliance on natural ecosystems to "other sectors", it is only because these links have become less visible and more intertwined. If anything, we rely more on, and are tied more closely to, natural ecosystems and their fluctuations than we have ever been before.

1.1 THE EMERGENCE OF SOCIAL-ECOLOGICAL SYSTEMS RESEARCH

Human societies have altered and been changed by ocean spaces and marine resources for millennia, but it was only in the 1970s that Western ecological studies began to pay more attention to the linked nature of social and ecological systems. This was largely driven by the emergence of the resilience concept in ecology that challenged the dominant view that ecosystems existed in a single stable state, as was previously thought. Holling (1973) proposed that systems can have "multiple basins of attraction" and exist in several regimes. This shifted the portrayal of systems as deterministic and predictable to ones that were more organic, constantly developing, and also interacting with their adjoining social systems (Folke, 2006). While there had been much work on the social dimensions of resource and environmental management, and in parallel, on the ecological drivers of sustainability, Berkes and Folke (1998) emphasized the integrated concept of linked social-ecological systems (SES) for conservation science. This was based on the recognition that ecological and social systems are coupled and influence each other, and that any division between them was artificial and arbitrary (Aswani et al., 2018; Liu et al., 2007). Fundamental to this perspective is that neither organizational nor ecological processes can be understood in isolation (Sterling et al., 2017). SESs are defined by their complexity, dynamism, unpredictability, and heterogeneity at multiple spatial and temporal scales (Liu et al., 2007; Ostrom, 2009). The resilience of an SES is its capacity to adapt to change to maintain its same basic structure, functions, and feedbacks (Folke, 2006). All this makes these systems challenging to describe and understand, but SES research has helped bridge the social and natural sciences, offering solutions to complex problems using interdisciplinary approaches.

Eleanor Ostrom was the first to use SESs as a framework and a common vocabulary to better manage natural resources (Ostrom, 2009). Her work emerged as a critique of Garrett Hardin's "tragedy of the commons" theory (Hardin, 1968), which proposed that multiple users of an open-access resource will ultimately overexploit it until the resource collapses, even if this has socially disastrous consequences. At the heart of this framing is a conflict between individual interests and the interests of the group, with Hardin postulating that individuals will act in their self-interest in the absence of coercive institutions, privatization, or top-level management. Ostrom (1990) challenged this view, demonstrating with case studies from around the world that communities are often able to overcome the free-rider problem through cooperation, trust, and strong local and collective governance. Importantly, many common pool resources – like the atmosphere, for example – are not separable or divisible, and privatization is not an option. Users are intertwined with the commons and may use it in variable and numerous ways (Berkes, 2021). Recognizing these interdependencies, and of the linked nature of social and ecological systems, can help design adaptive management plans that take their feedbacks into account, and remain sustainable over time.

1.2 MARINE SOCIAL SCIENCES AND FISHERIES

Since it first emerged, the field of social-ecological research has spurred the growth of a diversity of related inter-disciplinary approaches and new frameworks for engaging with conservation problems. For example, studies in historical ecology have emphasized the role of history in mediating present day human-environment interactions (Kittinger et al., 2012). Biocultural approaches have helped connect biodiversity with cultural and traditional practices, explicitly starting with and building on place-based perspectives that encompass people's values, needs, and knowledge and how these affect ecological relationships and human wellbeing (Sterling et al., 2017). In the oceanic realm, this broad range of approaches and multi-disciplinary methods that have centered the human dimension have collectively come to be known as the marine social sciences (McKinley et al., 2020). The overarching goal of the marine social sciences is to use multiple disciplinary lenses to better understand human values around the marine world, and to be able to provide solutions for conservation challenges that are equitable, inclusive, and effective.

Two of the biggest challenges in marine conservation today are a) the sustainable management of marine resources, in particular, fisheries and b) understanding what the effects of climate change will be on the structure and continued functioning of marine ecosystems. Globally over 500 million people depend on fish and fisheries for their lives and livelihoods (FAO, 2018). Fish are an important source of protein in many small island developing states (SIDS). Over 4.5 billion people obtain more than 15% of their protein intake from seafood (Bene et al. 2015) and it sometimes makes up 50-90% of dietary protein in Pacific Island countries, 50% in west Africa, and 37% in southeast Asia (Eddy et al. 2021). However, most global fisheries are considered to be either fully or over-exploited. One analysis found that over 55% of coral reef fisheries in 49 countries were not sustainable, according either to their ecological footprint or exploitation status (Newton et al., 2007). Fisheries have become one of the focal areas for SES and historical research because of the range of social, cultural, and environmental processes that have intersected historically to influence its status and management. Not only are they a commodity, but they are also a natural and cultural heritage for many island nations (Pauwels & Fache, 2016). In the recent decades, the industrialization and globalization of fishing has dramatically increased harvest. International markets now play a much bigger role in determining the catch and monetary value of fisheries products. Simultaneously, local markets on many islands are much more influenced by tourist desire and demand, which can influence diets and fishing practices (Wabnitz et al., 2018). Still, fisheries remain traditionally and culturally important and define many islanders' identities, values, and ways of life (Johannes 1981).

In addition, marine ecosystems – and coral reefs in particular – face increasingly severe and frequent threats from heatwaves. Coral reefs are extremely heterogenous systems, with a high degree of spatial and temporal variability in the processes and mechanisms that make them resilient or vulnerable to stress. A range of biotic (coral life history traits, morphology, *Symbiodineacea* species, thermal tolerance) and abiotic (temperature, nutrients, salinity, exposure) processes can interact to influence reef response to disturbance. Effectively managing these systems requires acknowledging that reef resilience is not static, and coral resistance or recovery can change over time in response to changing conditions. Long-term monitoring studies, including fine-scale tracking of reef response to stress, will be essential for the creation of nuanced management strategies.

1.3 EMERGING TOOLS AND TECHNOLOGY IN MARINE SCIENCE

Accompanying the rise in inter-disciplinary work to better address marine conservation problems has been a growth in the variety of tools and technologies now available to better quantify changes in the ecological processes that govern the functioning of marine systems. One of these is structure-from-motion photogrammetry (hereby, SfM), the process of estimating the 3-dimensional structure of a scene from 2-dimensional images. The use of digital imagery in benthic monitoring has been on a slow and steady rise since the 1980s, but the evolution of GPU technology, the reduced cost and quality of compact and digital single lens reflex cameras (DSLRs) and the development of advanced computer software to analyze these data in the early to mid-2000s accelerated the use of these tools for monitoring in the marine realm (Burns et al. 2015). In short, SfM uses matching features in a series of overlapping images to reconstruct a “sparse” 3D point cloud model of the photographed scene. This 3D model can then be refined for further analysis. The ability to create large-area images of habitats can be extremely informative to assess a range of processes, from small-scale changes in individual growth or competition to larger spatial patterns in community composition or structural change.

In the coral reef context, SfM has quickly begun to replace traditional monitoring tools for a few reasons. One, it allows for the creation of strong, visual baselines in systems that are rapidly changing, allowing for accurate and unbiased monitoring of the same reef patches over time. Two, it is a relatively cheap, fast, and repeatable method to employ in the field, enabling large areas to be surveyed in short amounts of time. Third, and perhaps most importantly, the 3D reconstruction it enables has opened up new opportunities for exploring the physical structure of reefs with a precision that traditional monitoring tools have not been able to provide.

The increasing frequency of coral bleaching events worldwide has raised serious questions about how rapidly corals will be able to adapt to future ocean conditions and the consequences of degraded reefs on reef function, fisheries, and the integrity of associated habitats. Understanding how corals recover, grow, or decline post-disturbance and identifying the conditions on reefs that enable them to do so can aid managers and conservationists. While the future of coral reefs ultimately depends on actions taken to reduce global warming, management interventions to ameliorate the impacts of local stressors can go a long way in aiding reef recovery. Apart from its value to coral reef scientists, SfM and the 3D products it creates can also be powerful communication tools, by helping people experience underwater habitats they might not have had the opportunity to experience firsthand, and thereby removing some of the abstraction of managing complex systems that are often out of sight for many.

1.4 STUDY SYSTEMS

Islands exemplify many of the social-ecological challenges that we face at a global scale. They are biodiversity hotspots, hosting half the world's marine biodiversity (UNEDP 2014b). They are also home to a diversity of cultures and identities, with biodiversity-based tourism and fisheries accounting for over half of the GDP of small island developing states (SIDS) (Coulthard et al. 2017). At the same time, they face the brunt of climate change-related impacts, with sea level rise, ocean acidification and extreme weather posing increasingly severe threats to life and property. While their smallness and insularity combined with their high endemism makes them especially vulnerable to these and other perturbances, there is simultaneously a recognition that island systems have been historically resilient in large part because of their community structures and the linked nature of societies and ecosystems here. This is well illustrated in Epeli Hauʻofa's seminal work, where he reconceptualizes Oceania as a "sea of islands", challenging the colonial view of Pacific islands as fragmented bodies of land in a vast sea (Hauʻofa 1994). Islands are important places of study because the sustainability challenges we face as a society are often exacerbated here, but they also hold the key to solutions that are grounded in an understanding of mutually dependent social and ecological systems. I conducted my dissertation research in two unique island systems: the Maldives archipelago and Oʻahu, Hawaiʻi. In the Maldives, I primarily focused on understanding the link between fisheries – historical and contemporary – and coral reef health. In Oʻahu, in the wake of a coral bleaching event, I tracked coral response to thermal stress in Kane‘ohe Bay, using SfM to tease apart fine-scale patterns in bleaching and mortality. Below I provide a brief introduction to these two systems to help contextualize the research that was conducted there.

1.4 A The Maldives archipelago

The Maldives archipelago is a double chain of atolls situated 700 km southwest of Sri Lanka and about 475 km south of India, extending 7° N to half a degree south of the equator (Fig.1). Geologically, it occupies the central portion of the Chagos-Laccadive submarine ridge, which was formed by the volcanism of the Réunion mantle hotspot about 65 million years ago (Kench, 2012). Only 1.5 m above sea level, it is the lowest country in the world, but its territorial waters are vast (67,000 sq. km) and contain 3% of the world's coral reefs (Stevens and Froman, 2018). Its 26 atolls of roughly 1900 islands are grouped into seven administrative provinces: the Upper North, North, North Central, Central, South Central, Upper South, and South province. Each of these are comprised of between 2-4 atolls. Every province has a capital island.

The current population of the Maldives – 540, 520 – is wholly Islamic. A Buddhist tradition was present prior to the introduction of Islam in 1153, but much of the artefacts that remain from this period have been damaged or destroyed. Ninety-three sultans have governed the Maldives from 1153 to 1968. In 1968, a constitution making the Maldives a presidential republic was approved (Maloney 2013). Tourism began to be developed on the archipelago soon after. A total of 194 of the ~1900 islands in the Maldives are locally inhabited. Resorts are found on 152 islands, and as of 2020, 118 other islands had resorts planned or in progress. Today, tourism accounts for 30% of the country's annual GDP (Stevens and Froman, 2018).

Coral reefs cover 4500 sq. km of the area of the Maldives, making this the 8th largest reef system in the world. They have experienced multiple El Niño-related bleaching events as a result of increased sea surface temperatures due to climate change. Episodes of coral bleaching have been reported from 1977, 1983, 1987, 1991, 1997, 1998, 2020, and 2016 (Ibrahim et al. 2016). The bleaching event of 2016 caused approximately 75% bleaching across the archipelago, and most reefs are in different stages of recovery or decline following this.

In parallel with these ecological changes, there have been rapid developments to the commercial fisheries of the Maldives. While the traditional fishery for pelagic tuna continues to be an important part of the country's GDP, luxury tourism is now the number one driver of its economy. This has had mixed effects on the environment – on the one hand, it has led to the recognition that there is a need for policies aimed at sustainably managing marine resources in the long-term, but on the other, the development, pollution, and expense of managing resorts and catering to a predominantly Western elite has been highly destructive to the environment (Cowburn et al., 2018). One of the dynamics tourism has shifted in the Maldives is its fisheries practices. In particular, tourism has created a demand for fresh reef fish that did not exist before. Unmanaged reef fishing can have serious repercussions for reef health, especially in systems that are already threatened with bleaching disturbances. I was interested in investigating these shifting pressures on reefs in the Maldives, with a focus on the human dimension, since this was a prominent gap in our understanding of these coral reef systems.

1.4 B Kāneʻohe Bay, Oʻahu

Kāneʻohe Bay, on the windward coast of O'ahu, is the largest sheltered body of water on the main Hawaiian Islands. Geologically, it is a part of the former caldera formed by the Koʻolau volcano. It is bounded by a barrier reef on its oceanic side with a shoreline ringed by fringing reefs. Patch reefs, often between 1-3 m deep, run along the entire length of the Bay on its lagoonal side. Shallow coral and sandy reefs make up the offshore portions of the Bay.

Kāneʻohe Bay has a long history of human use, beginning with Polynesian settlement in 1250 CE. Agriculture quickly developed with the cultivation of a range of "canoe plants" like taro, yam, and breadfruit. Fishing was extensive, and fishponds were built along the entire length of the coastline, thereby ensuring the food security of this region. After the arrival of the first Europeans, the entire landscape of Hawaiʻi was modified by plantation agriculture and the introduction of several non-native and invasive species, and finally, rapid urbanization (Bahr et al., 2015). It was only in the 1930s, however, that reefs in Kāneʻohe began to experience the direct effects of development in the form of dredging, sedimentation, and sewage discharge. This began with the construction of the Naval Air Station (today, the Marine Corps Base) on Mōkapu peninsula, for which the southern sections of the Bay were extensively dredged. Coastal development led to the destruction or disappearance of all but three of the thirty fishponds that fringed the coastline. Finally, land run off and sedimentation due to urbanization has been a constant and pervasive influence on these reefs. Multiple sewage outfalls discharged untreated sewage into different sections of the Bay until the late 1970s, leading to the proliferation of *Dictyospheria cavernosa* (bubble algae) which thrived in these highly turbid and nutrient rich waters.

In addition to these anthropogenic stressors, the reefs here have been subject to multiple freshwater kills in 1965, 1988, and 2014 and coral bleaching events in 1996, 2014, 2015, and most recently in 2019. However, coral cover today still stands at ~60%, some of the highest for Oʻahu. This history of stress and recovery makes Kāneʻohe Bay an ideal system to investigate questions about the mechanisms that support reef resilience, and how they change over time. In an era of climate change, it will be crucial to understand the processes that influence recovery, especially in systems that might already be experiencing conditions that are suboptimal for many corals.

1.5 OBJECTIVES OF THE DISSERTATION

This dissertation investigates how historical fisheries practices and contemporary fishing intersect in the Maldives archipelago. In parallel, and in the wake of a coral bleaching event in the Hawaiian Islands, I tracked reef response to thermal stress using SfM photogrammetry. Specifically, my questions are:

i. What is the historical ecology of the pelagic tuna fishery in the Maldives, and what have been its repercussions for the resilience of coral reef habitats in this archipelago?
ii. How do social and cultural factors influence contemporary reef fishing practices here? How do consumption preferences and changing diets relate to marine resource use?
iii. What are the spatial, temporal, and taxonomic patterns in bleaching in Kāneʻohe Bay? What were the environmental and ecological processes that drove these patterns?

This dissertation uses multiple methodologies and approaches to address these questions, integrating marine historical ecology with structured surveys, interviews, and large-area imaging through structure-from-motion (SfM) photogrammetry to assess benthic habitats.

1.6 HOW THIS DISSERTATION IS ORGANIZED

This dissertation sequentially presents each chapter, their methodologies, findings, and implications. This introductory chapter (Chapter 1) outlines the major challenges facing coral reef habitats today, the inter-relationships between social and ecological systems, emerging tools in marine science, and a brief introduction to the study systems where this research was conducted. A concluding chapter (Chapter 5) synthesizes these results and attempts to contextualize this work for global conservation and management issues.

Chapter 2 presents a historical ecology of the offshore tuna fishery of the Maldives and its implications for coral reef health in these islands. Archival research, combined with reviews of more recent archaeological and scientific work allows for an assessment of the historical drivers of tuna fishing in the Maldives, the reasons for its growth, and its present-day role in maintaining the resilience of coral reef habitats. In particular, this chapter explores the role of trade and exchange in the Indian Ocean region from the 12th century onwards and the social and cultural factors that enabled a pelagic fishery to thrive even in the presence of more easily accessible nearshore coral reefs. The implications of these historical dynamics are discussed in relation to reef health and resilience.

Chapter 3 presents a detailed case study on fish preference and consumption patterns in Dhaalu atoll, one of the central atolls in the Maldives. This chapter focuses on how tuna and reef fish are valued and consumed today and the implications this has for marine resource use. In contrast to Chapter 2 that examines the historical influence of tuna in the Maldives, this chapter addresses the rising role of reef fish in people's diets in the backdrop of luxury tourism and the rise of international markets. It uses both qualitative and quantitative analyses to examine changing pressures on reef ecosystems via changes in fish consumption. It also provides management recommendations for an emerging reef fishery through the examination of seasonality, religion, and sharing networks in influencing the catch and consumption of reef fish species.

Chapter 4 provides an analysis of how climate change related marine heatwaves – in particular, the coral bleaching event of 2019 – impacts coral reef resilience. While this represents a departure from the earlier two chapters in that it focuses more specifically on ecological change, it is relevant because it examines the mechanisms that aid reef resistance and recovery, which has implications for reef fish communities and subsistence fisheries. This chapter uses structure-from-motion photogrammetry as its primary tool in tracking changes in coral reef state during a thermal stress event in 2019. The principal findings are discussed with respect to how environmental and ecological processes can help determine bleaching severity and mortality following a disturbance event.

Finally, the concluding Chapter 5 discusses the major findings of this research and its contributions to our understanding of historical and social processes contributing to reef resilience the Maldives. Simultaneously, assessments of coral reef habitat in Kāneʻohe Bay provide a view of the ways in which reefs are likely to alter in response to future climate change. The chapter ends with a discussion on future opportunities for research.

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CHAPTER 2

THE HISTORICAL ECOLOGY OF THE PELAGIC TUNA FISHERY IN THE MALDIVES

2.1 ABSTRACT

The traditional offshore pole-and-line tuna fishery of the Maldives has historically promoted low levels of reef fishing in this archipelago. While the tuna fishery is old and extensive – some evidence suggests it has been in place for over a thousand years – the reasons for its development have not been closely examined. Why did an offshore fishery develop in such small and isolated islands with abundant and easily accessible nearshore reefs? Why is tuna considered the "king of fish" in the Maldives, in contrast to many other islands across the globe where reef fish are prized for a wide variety of cultural and social reasons, often deeply rooted in community histories? In this chapter, we use a historical approach to uncover some of the drivers of this fishery, and the long-term consequences it has had for the resilience of this island chain. We trace the written accounts of travelers, voyagers, and traders, in addition to more recent research to gain an understanding of how early Indian Ocean trade networks may have shaped the development of this fishery over time. We propose that the early growth of the tuna fishery was likely tied to the trade in money cowries (*Monetaria moneta)*, of which the Maldives was a major global supplier. A regional demand and market for dried tuna from the fourteenth century onwards contributed to the income of Maldivians and promoted and supported reef health by encouraging relatively low levels of reef fishing. However, the emergence and substantial growth of the Maldivian tourist industry in the past few decades is resulting in a shift in local consumption preferences and increased exploitation of reef fisheries. Exploring this history is important, not only to help contextualize the modern governance of the offshore tuna fishery, but also for a more nuanced understanding of the social, cultural, and ecological dynamics that have shaped Maldivian coral reefs in the past with implications for those that will do so in the future.

Keywords: marine historical ecology, coral reef resilience, trade, tourism, fisheries

2.2 INTRODUCTION

Humans have fished for millennia. But in the past six decades, rapid industrialization and overfishing has made achieving sustainable fisheries one of the most challenging global management problems (MacNeil et al. 2010). This governance and management challenge has been complicated by the effects of climate change, especially on coral reefs, where multiple coral bleaching events have degraded and changed these habitats, causing large-scale reductions in diversity, habitat extent, and system functionality (Perry and Morgan 2017; Pratchett et al. 2018; Stuart-Smith et al. 2018). It is now predicted that the greatest fisheries losses will occur among reef-based fisheries (MacNeil et al. 2010). In this context, pelagic fisheries have gained attention as a way in which some of the pressures of reef and coastal fishing may be shifted to the open ocean, targeting fish species that are faster growing and better able to sustain the nutritional demands and health of a region's population (Bell et al. 2015; Birkeland, 2017; Wabnitz et al. 2017). Pelagic fishing is, however, not a recent phenomenon – drivers for and practices of offshore fishing extend into deep antiquity. Evidence for systematic pelagic fishing extends back to 42,000 years before the present from East Timor, when the humans who colonized Wallacea are thought to have developed complex maritime technology to fish in the deep sea for species like tuna (O'Connor et al. 2011). The diverse and expert knowledge and skill of traditional fishers across the globe attests to the variability, age, and importance of reef and pelagic fishing practices (Johannes, 1981). Engaging with the historical ecology of these practices and traditions – why a particular method of fishing began and what local, regional, or global forces sustained it – can help contextualize modern resource management, and provide a framework to better understand the drivers of human influence on the environment. As Braje et al. (2017) point out, if conservation is to be successful over the *longue durée*, then deep historical perspectives integrating archaeology, ecology, and anthropology will be essential for a holistic understanding of human-ecosystem change through time. This is especially relevant for fisheries research, where the problem of "shifting baselines" (Pauly, 1995) has exposed how neglecting the past can have disastrous consequences for how we understand and govern marine habitats today. Using a marine historical approach to better understand past change can help provide a basis for management today that is more complete in its assessment of resources, and when used in conjunction with a social-ecological systems (SES) framework, has the potential to attend to conservation problems today at the scale and complexity they require.

In the Indian Ocean, the Maldives present an interesting case study on how the historical development of an offshore tuna fishery has enabled reef fishing pressure to stay at subsistence levels for centuries. Rooted in an archipelago of 26 atolls and 1900 islands in the central Indian Ocean (Fig.1), a traditional offshore pole-and-line fishery targeting skipjack tuna has been practiced for over a thousand years. Skipjack tuna (*Katsuwonus pelamis*) and yellowfin tuna remain the most important export commodities from the country (FAO, 2012). Of the 0.43 million people who live in the Maldives, the fishery sector employs about 20% of the workforce (MEE, 2016b) and contributes to 3% of the country's GDP (Ahusan et al., 2015). As of 2014, skipkjack tuna comprised 37.45% of total fish catch, and all fisheries products accounted for over 80% of total exports, bringing in over USD 120 million (FAO, 2012; Simoes and Hidalgo 2011). The cultural value of tuna in these islands, past and present, has contributed greatly to the continued success and sustainability of the tuna fishery over time. Much Maldivian cuisine is centered on tuna in fresh, dried, or pickled form. From the Maldives, the pole-and-line fishing practice was successfully introduced into the Lakshadweep (the northernmost islands on the Chagos-Laccadive ridge, politically part of India) in the 1960s by local fisheries departments (Arthur, 2008; Jaini et al., 2018). Today, dried skipjack tuna caught using this method forms the main export commodity from the Lakshadweep (Jaini et al., 2018). Importantly, by driving a low level of reef fishing, offshore tuna fishing has helped bolster the resilience of these reef systems to climate change events, ensuring that the abundance of critical, functionally important guilds of reef fish remains high on these reefs (Sluka and Miller, 2001). In a study assessing reef fish biomass in these islands, Chang et al. (2020) found that the Maldives supports an average fish biomass of ~293 g/sq. m, high compared to other islands around the world. Healthy populations of herbivores like parrotfishes are known to be especially critical for coral reef recovery, often preventing the proliferation of macroalgae in disturbed reef environments (Mumby et al. 2006).

However, the history of the pole-and-line fishery — when it began to develop, the reasons it grew over time, and its contemporary relationship with coral reefs in the Maldives — has not been very well documented. In particular, we were interested in examining the factors that might have propelled the early development of this fishery and the reasons why fishing for tuna offshore might have promoted a relatively low-level of reef fishing in more easily accessible nearshore waters. We focus on the early history of this island nation and the impact of trade on the growth of its tuna fishery, examining the written accounts of travelers and traders for references to tuna or dried fish through time, and the places where tuna might have been exchanged. We also explore early methods of processing tuna and the factors that contributed to its success as a commodity, both locally and for export. While this study is at times inductive, we use a number of historical sources as well as more recent archaeological and historical research to demonstrate that the growth of this fishery was closely associated with a trade in money cowries, of which the Maldives was a major global supplier. A key insight emerges in this history in the way that social and cultural practices linked to one natural resource (money cowries) serve as a condition of possibility for the emergence of and, then, a driver for, the exploitation of another natural resource (tuna), with significant linkages to the ecological wellbeing of a third natural resource (nearshore reefs and their companion species). Finally, we conclude by drawing on this long historical perspective to call back into view links between the tuna fishery and coral reef resilience in the Maldives archipelago in the contemporary context of the growing impact of tourism on this relationship.

2.3 HISTORICAL DRIVERS OF TUNA FISHING IN THE MALDIVES

2.3.A Setting the context: Maldives in the Indian Ocean world

The early history of the Maldives is infamously obscure, complicated by its isolation and lack of written historical records (Maloney, 2013; Mohamed, 2005b). The islands were likely settled around the first to third centuries CE from Sri Lanka and southern India (Litster, 2016; p 14). Several Buddhist relics, monuments, and other artefacts of material culture recovered from this period attest to Buddhism being the dominant religion at that time (Mohamed, 2005a; Litster, 2016). In 1153, the population was converted to Islam by a visiting saint. The state chronicle *Dhivehi Tarikh* credits conversion to Sheikh Yusuf Shams al-Din al-Tabrizi, who, by reciting the Qur'an, was said to have freed the islanders of a sea demon. Over the following eight centuries, the Maldives was ruled by a succession of 93 sultans, until it became a republic in 1965 (Yang, 2019; p 22).

The veil of information that shrouds the early history of these islands has nevertheless been lifted a few times in the past thousand years, by a few key accounts (Bell, 1882; p 30). The Moroccan traveler Ibn Battuta spent 4 years in the Maldives in the 14th century and his famous *Rehla of Ibn Battuta* provides some of the earliest details of post-Islamic Maldives

(Gibb, 1953, pp 241-253). Francois Pyrard de Laval, a French explorer, was shipwrecked in the Maldives in the early 17th century and left an account that is considered to be one of the earliest ethnographies of the islands (Maloney, 2013). Two British navy lieutenants Young and Christopher visited in the 19th century and detailed life on the islands in their memoir, creating some of the first maritime charts of the Maldives (Bell, 1882; p 12). In the 18th and 19th centuries, two British officials from Sri Lanka – H.C.P. Bell (1882) and T.W. Hockley (1935) - wrote more comprehensive articles on Maldivian culture and the social history of these islands, which formed the basis for much of the sociological work that came after this period. Between the 14th-18th centuries, a few Chinese and European accounts provided glimpses of life in the Maldives, around the time that it was becoming an important trading center (Yang, 2019; p 29). Much of what is explored in this paper relies on these records for early historical details. An obvious limitation of the present work is its reliance on texts and ethnographic materials that were written primarily by visitors – there is a lack of accessible local writing from this period. Still, this demonstrates both the challenges and opportunities for marine historical ecology to engage with and glean from scant historical evidence (Kittinger et al., 2011; McClenachan et al., 2012; Kittinger et al., 2015).

By the first millennium CE, trade and movement was widespread in the Indian Ocean, so the Maldives already had some contact with the larger region during their phase of settlement — the famous navigational log *Periplus of the Erythrean Sea* documents the export of tortoise shell from the Maldives in the first century CE (Casson, 1989), and the islands' abundance of coconuts and freshwater was noted as far as Rome in the third to fifth centuries (Litster, 2016, pp 72). But it was only in the ninth century that references to the Maldives began to appear more regularly in passages and notices from Arab visitors and traders. In particular, the islands were gaining attention for their abundance in cowries. It is this shelled mollusk that would establish the Maldives as a critical point of exchange for trade and travel in the early Indian Ocean world.

2.3.B The pull of cowries

The oldest written reference noting the importance of cowries to Maldivians dates to 851 CE, when a Persian merchant Sulaiman wrote that "the wealth of the people [in the Maldives] is constituted by cowries" (Litster, 2016; p 6). Cowries (*Monetaria moneta)* were the standard currency of Indian Ocean trade for almost a thousand years from the ninth to nineteenth century. While the cultural and ritual functions of cowries extend back millennia (Hogendorn, 1981), their primary function by the 9th century CE was as currency. Maldivian cowries were especially sought after because they were small, cheap, and abundant, and large quantities could be transported easily (Hogendorn and Johnson, 1986). They were also not easy to counterfeit and retained their luster for a long duration (Hogendorn and Johnson, 1986; Litster, 2016).

It has been suggested that it was the presence of money cowries that might have provided the impetus for human settlement in the Maldives (Mikkelsen, 2000; Litster, 2016). Whether or not this is true, Maldivian cowries were unquestionably a highly sought-after product that drew traders from the western Indian ocean. In the tenth century, Al-Idrisi, an Arab traveler, was one of the first to note that "commerce [in the Maldives] is carried on by means of (cowry) shells" preserved in the King's treasury (Gray and Bell, 2010; p 432). Several methods of cowrie collection appear to have been employed in the Maldives. Wood floats and coconut branches were placed in the water to provide structure for the animals to attach to, or shells were collected by wading, whereby women, "twice a month, when the tides suit" stood in waist-deep water and detached cowries directly from the undersides of stones (Bell, 1882; p 87). Shells were processed locally on islands (by sun-drying and burial in the sand) and then shipped to Male', for storage and export (Hogendorn, 1981).

There is evidence to suggest that trade in cowries, while it grew rapidly, is likely to have first started regionally, with places like Bengal in India, where "kings and great lords [have] houses built expressly to store these shells and treat them as part of their treasure" (Gray and Bell, 2010; p 239). Ibn Battuta also recorded this trade with Bengal in 1327 and wrote that cowries "are sold to the inhabitants of Bengal for rice, because the cowries are also current in Bengal, and also to the inhabitants of Yemen who use these instead of sand as ballast in their ships." (Gibb, 1953; p 243). The shells were also shipped via the Red Sea and across the Sahara to West Africa's savanna region (Hogendorn, 1981). While Hogendorn (1981) notes that cowries were used as currency within the Maldives, Yang (2011) refers to accounts of Huang Xingceng from the 1520s that suggest that silver rather than cowries served as local money in the Maldives, while the latter were only sold or exported to bring wealth. Nevertheless, by the 15th century, the reach of Maldivian cowries had expanded to parts of Arabia and West Africa, and cowries would eventually make their way into European markets, functioning "as a lubricant for the European colonial machine" (Yang, 2011) and fueling the transatlantic slave trade (Hogendorn and Johnson, 1986). Portuguese, Dutch, and British traders were involved in the cowrie trade by this time, either purchasing shells directly from the Maldives, or from ports in Bengal (Hogendorn, 1981). Historically speaking, cowrie money was the first "global money", existing across an extensive geographical range and used by a variety of people at various periods (Yang, 2019; p 249). It linked the Maldives to markets in East and Central Asia, Southeast Asia, South Asia, coastal Africa, and the Middle East, and eventually Europe.

The early trade in cowries, however, was most likely driven by Arabs and Persians, who were the dominant traders in the Indian Ocean in the 9th century (Pearson, 2003). It is these early Arabic connections that resulted in Islam arriving to the Maldives in 1153. In the Indian Ocean of the 12th century— already increasingly fused by Islamic connections — the conversion of the Maldives to Islam would have further enhanced its position as part of the growing network of trade routes and emporia in existence at the time (Pearson, 2003).

In addition to the cowrie trade, or perhaps because of it, the Maldives' strategic location between port cities in the Western Indian Ocean and Southeast Asia made these islands a convenient stopover point for travelers and traders in the region. Duarte Barbosa, a Portuguese official who passed through the Maldives in the 1500s, wrote that "many ships of the Moors which pass from China, Maluco [Indonesia], Peegu [Burma], Malaca [Malaysia], Çamatra [Sumatra], Benguela [Bengal] and Ceilam [Sri Lanka] towards the Red Sea touch at these islands to water and take in supplies and other things needful for their voyages" (Dames, 1921; p 108). The Indian Ocean region was connected by a monsoon-driven trade, and the "predictability of a homeward wind made the Indian ocean the most benign environment in the world for long-range voyaging" (Pearson, 2003; p 19). The southwest monsoon (May to September) and northeast monsoon (November to March) separated the year into two halves, and ships would sail between the Red Sea, Persian Gulf, India, and parts of East Africa when the winds were known to be stable. The geographical location of the Maldives, therefore, was advantageous in other ways to seafarers, who also began to use these islands as stop-over points for victualling and replenishing supplies on their voyages.

To summarize, constrained by what could be grown on land, Maldivians benefitted from regular and sustained exchange in several commodities with passing groups of traders, merchants, and voyagers across the long arc of their history. Significantly, the Maldives' abundance in cowries put the islands on the map of Indian Ocean traders, and the establishment of Islam in 1153 further connected them with larger Muslim networks of trade active at the time. While coconuts, coir (the fibrous husk of coconuts), fish, ambergris, and tortoise-shells were exchanged in smaller quantities (Bell, 1882), cowries were almost certainly the most valuable and well-recorded item of export from the Maldives for the better part of a millennium. The presence of cowries in the Maldives supported and may have been a critical driver for the start of a regional, and later, global trade network centered around these islands (Table 1). Certainly, by the 14th century, the islands were important waypoints for sailors going both east to Southeast Asia, India and Sri Lanka and west, to Madagascar and parts of the African east coast. This regional-global trade context also served as a condition of possibility for the emergence of another significant trade with striking implications for the long-term dynamics of human engagements with nearshore reefs in the Maldives.

2.3.C Dried tuna and the trade growth for "Maldive fish"

The lack of abundant freshwater and arable land, and the size and geography of the low-lying, sandy islands of the Maldives essentially prevented the development of large-scale agriculture in the archipelago (Litster, 2016). Nevertheless, taro, yams, millet and fruits were cultivated to some extent, especially in the northern islands (Gray and Bell, 2010; Munch-Peterson, 1982). Coconut palms were cultivated throughout and were critically important, with the net worth of islands designated on the basis of their coconut trees that locals used for several different purposes (Maloney, 2013). But rice and wheat had to be regularly imported from Sri Lanka, India and Burma (Gray and Bell, 2010), and there was frequent exchange between islands for produce. "God had willed that these people should visit each other" and "what is plentiful in one island is rare in another", wrote de Laval (Gray and Bell, 2010; p 114.). Interestingly, he noted that islands were separated by their craft, with jewelers, potters, toddy-drawers, mat-weavers, blacksmiths, and carpenters all located on different islands and travelling to each other regularly on boats "covered with a little deck, working and dealing in their goods, and it is sometimes more than a year ere they return to the island of their home" (Gray and Bell, 2010; p 115.). While these island-specific differences are less pronounced today, it not uncommon to hear Maldivians speak of islands that have been historically renowned for certain activities. In the island of Rinbudhoo in Dhaalu atoll, for instance, a vibrant community of silversmiths continues to work to this day following traditional practices and techniques, actively exporting their goods to nearby islands.

However, like for many other island chains, the principal food in the Maldives was fish. “I believe there is no place throughout India, nor elsewhere, where the fishery is richer and more plentiful” de Laval wrote in 1619 (Gray and Bell, 2010; p 194). Faunal archaeological data indicates a historical reliance on fishing (Munch-Petersen, 1982; Maloney, 203). Most notably, scombrid (tuna) remains were the major fish taxon recovered during these archaeological studies, both from Buddhist (pre-1153) as well as Islamic times (Litster, 2016). This potentially dates tuna fishing to the ninth century CE. However, the earliest written record is only from Ibn Battuta’s account in 1327. He was the first to note in some detail the local diet, which he said consisted of “a fish like the lyroûn, which they call koulb al mâs. Its flesh is red; it has no grease, but its smell resembles that of mutton. When caught at the fishery, each fish is cut up into four pieces, and then slightly cooked. It is then placed in baskets of coco leaves and suspended in the smoke. It is eaten when perfectly dry.” (Gibb, 2010; p 242). Further, he mentions that this fish was “exported to India, China, and Yaman [Yemen]”, making this the first direct reference to the fact that dried tuna was an item for export by the 1300s. de Laval, in the 1600s, was next to document this fishery noting that “they [cobolly maas] are cooked in sea water, and then dried in the sun upon trays, and so when dry they keep for a long while… there is great traffic in them, not only in the country, but throughout the rest of India, where they are in great request.”(Gray and Bell, 2010; p 191) In both these passages, Ibn Battuta and de Laval refer to a fish called *kalu-bili-mâs* or *cobolly maas*, which is the local name for skipjack tuna (*Katsuwonus pelamis*; today referred to in Dhivehi as *kalhubilamas)* (Abdulla and O’Shea, 2005).

While these provide early references to how tuna was being fished, Bell’s account of these islands from the late 1800s detailed the nuances of tuna cutting and curing. Elaborating on the process that Ibn Battuta first recorded in 1327, Bell (1882) again noted that once caught, each fish was either sliced longitudinally at the center in half, making four pieces in all (called *gadu*) or sectioned into several strips, thus creating pieces of different names and values (*gadu mas* or pieces along the back and belly; *medu mas* or pieces along the side; and *kira mas*, or pieces between the head and ends). In this case, *gadu mas* would fetch the highest price, followed by *medu mas* and *kira mas*. He documented, again, how these fish were “thrown into a cauldron of boiling salt water… and placed on a wattle loft or shelf above the fire... till well blacked and dried." (Bell, 1882; p 94). This process, of smoking and drying the fish, would have allowed it to be preserved in the absence of refrigeration. For the rest of the catch, the largest fish was given to the "king's kitchen" and the remainder to "the clergy, the poor, and to their friends… however small the catch, this division must always be made" (Gray and Bell, 2010; p 191). Pyrard's is the only account to suggest that the king required people to pay taxes in local products. The king "imposes on his subjects an ordinary tax… consisting of coco-cordage, of shells called *boly* (cowries) and of dried fish", he wrote (Gray and Bell, 2010; p 228). These were likely sold to traders in Male', illustrating again the value of dried tuna as an export commodity at the time.

It is also striking that the method of fishing, drying, and processing tuna remained more or less unchanged from when it was first noted in the fourteenth century by Ibn Battuta until the nineteenth century in Bell's report. In fact, it was only the mechanization of the tuna fishing fleet in the 1970s, and the development of larger-scale industry that modernized methods of fishing and processing skipjack tuna (Adam et al. 2003).

Bell also noted that there were several other species being fished by islanders including "sawfish, swordfish, searfish and sharks" but that their "soft, oily nature, unadapted for curing… [meant they were] never salted for the foreign market." (Bell, 1882; p 93). On the other hand, tuna, once dried, had the "appearance and consistency of blocks of wood", which would have made it easy to package and ship. The fact that tuna lent itself to this method of smoking and drying *en masse* unlike other reef fish or pelagic species was critical to its durability, transportability, and marketability. Further, the fact that different cuts of tuna were valued differently, and that there was a well-defined method in place for processing, even in the fourteenth century, suggests that it was more than just a local fishery by this time. "The fishery is of great yield and is the chief employment of the islanders" Pyrard wrote in 1619, "… they are daily dispatching ships with cargoes of this [fish] to Achen, in Sumatra, and elsewhere". Duarte Barbosa also remarked in the 1500s that the islands have "a great store of dried fish" that were carried with cowries to the Kingdom of Cambaia (present-day Gujarat) and Bengal (Dames, 1921; p 105). Ma Huan, a Chinese official who visited the Maldives in 1425 on Zheng He's treasure fleet from China, noted that dried tuna was used by travelers on ships during their voyages (Yang, 2019). In reconstructing Safi bin Wali Qazwini's account of life on Indian ships in 1669-70, Qaisar makes a passing reference to "smoked fish from the Maldive Islands" being part of the dietary staple on board (Pearson and Gupta, 1999). Dried tuna, apart from being exported, might have played a vital role in fulfilling the protein requirements of sailors and travelers in the Indian Ocean who spent long periods of time at sea.

While it is difficult to ascertain exactly how this trade was organized, by the fifteenth century it had diversified to include Mappila merchants from the Malabar coast (modern Kerala) who carried items from the Indian west coast to Sri Lanka, Maldives, Laccadives and Malacca (Subrahmanayam, 1995). By the nineteenth century, Bohra merchants monopolized the fish trade from the Maldives to Sri Lanka using a fleet of *buggalows* and schooners that sailed between the islands (Bell, 1882). The Bohras also carried out a profitable trade in fresh coconut, copra, and tortoiseshell. Even though written references to tuna are not ubiquitous, they appear frequently enough to suggest that by the mid-fifteenth century, trade in "dried fish", most likely skipjack, was well-established and growing rapidly around the subcontinent. Dried tuna from the Maldives became such a popular commodity in Sri Lanka that by the eighteenth century it had its own local name: "Maldive fish" (Hockley, 1935). It remains an important ingredient in Sri Lankan cooking today. According to T.W Hockley (1935), the annual worth of "Maldive fish" to Sri Lanka at this time was "well above £200, 000" – over USD 16 million in today's currency (Officer and Williamson, 2019).

While it appears that dried tuna began as a commodity piggybacking on more valuable cowries, over time, the export of tuna and other fish products appears to have become profitable in itself. By the 19th century, the cowrie trade had collapsed, for reasons related both to changing global economies, as well as the introduction of a competitor – the ring cowrie *Monetara annulus,* that resulted in hyperinflation (Litster, 2016; Yang, 2019). Tuna quickly and naturally replaced it as the primary commodity of export from the Maldives.

2.3.D Why fish for tuna: the advantages of a pelagic fishery

It is not surprising that fishing has been an important part of the Maldives' sociocultural and economic history, as it has for islands around the world. What is striking is the emergence of an early offshore fishery that was so strongly linked to a regional trade. This offshore fishery acted as a driver for local subsistence practices, thereby exerting a negative pressure on the exploitation of nearshore reefs. But offshore fishing requires more time, resources, effort, and risk than fishing in nearshore waters, on reefs or in lagoons. We propose a few reasons why investing in a pelagic fishery might have benefitted Maldivians more than reef fishing.

Firstly, Indian Ocean islands experience a heavy southeast monsoon from June to November, when storms and rough weather prevent reef and offshore fishing for several months in the year. Skipjack tuna, fished in abundance during the dry season, would have been ideal to smoke, dry, and preserve during the monsoon months. In the Maldives, dried tuna maintained its edibility for long periods, allowing it to be stored in bulk without refrigeration. This parallels the ways in which cod was dried as stockfish in Norway, because of its ability to store well for several years once cured (Nedkvitne, 2016). Smoking and drying would have allowed it to be supplied year-round, as and when outside demand for it arose. Rihakuru, a traditional dish of salty fish paste made by slow-boiling tuna is an example of how fish were and continue to be preserved in the Maldives today. Like colatura from the Mediterranean or prahok from Cambodia, rihakuru can sit on the shelf for long periods of time – over a year if prepared well (Naila et al., 2011). In contrast, reef fish were and are not considered suitable for drying and preservation in this manner. They were likely fished in smaller quantities in nearshore reefs and lagoons for direct consumption, especially during the rainy season when travelling offshore might have been more challenging. Importantly, however, locals seemed to have developed strong cultural values around tuna and a preference for its consumption over time. Tuna appears in several folk tales from the Maldives as the “king of fish”, superior to other fish because of its taste, texture, and firmness of flesh (Romero-Frias, 2012). Today, the majority of all fish-based traditional cuisine is still centered around tuna in some form or another (e.g., recipes in Sattar, 2017).

Secondly, skipjack tuna, while pelagic, are often found fairly close to islands in the Maldives (“six or seven leagues out” (Gray and Bell 2010; p 189); or about 40 to 60 kilometers offshore). This is because clear oceanic waters — prime habitat for tuna — surround the outer atolls. In the Maldives, the geomorphology of the islands enabled easy access to deeper waters, and live bait to chum the water for tuna could have been caught easily on reefs on the way out. Fishing for tuna, while it still required more effort and coordination than fishing in the lagoon or on nearby reefs, might not necessarily have required fishermen to plan multi-day fishing trips; instead, a single day offshore would have yielded substantial catches. The tuna fishery continues to result in high yields – the reconstructed total catch of tuna from

1950-2010 was approximately 3.7 million t, 80% of which was skipjack tuna caught using the traditional pole-and-line fishing method (Hemmings et al. 2014).

Lastly, Maldivians were seasoned seafarers and had developed specialized craft for tuna fishing. They were known to make "sewn boats", a design found throughout the Indian Ocean and one that would have made navigating these reefs easy because of the elasticity of the materials used (Maniku, 1998). Boats were constructed from coconut timber held together by coir and caulked with whale oil, with rigging and sails made of coir. Even today the term used for boat building in the Maldives – *dhoani banun* ("boat tying") is reflective of the process used in the past. Before the fleet was mechanized, *masdhoanis* (tuna fishing vessels) were traditionally sail and oar driven (Anderson, 1997a). *Masdhoanis* were between nine and fourteen meters long, with a platform at the stern (*fenfilaa*) where fishermen could stand and fish with poles. In fact, Maldivian boat building appears to have been well known and unique as it integrated the features of boats from many parts of the Indian Ocean region (Mohamed, 2005a). The earliest schools established in the Maldives are thought to have been navigation oriented (Mohamed, 2005a) and *veshi* or oral poems created 'oral maps' that communicated nautical directions of coral reef passages and dangerous currents (Romeros-Frias, 2012). All this suggests that Maldivians were not limited in their navigational and seafaring abilities and that boats for tuna fishing were only one among many designed for different types of sea travel. In sum, fishing for tuna might not have been as logistically or technically challenging as one might imagine an offshore fishery to have been at the time.

From an ecological point of view, perhaps without consciously intending to, Maldivian fishing practices developed to take the best path towards sustainable nearshore fisheries. Skipjack tuna, with its short life span, early age at sexual maturity, and rapid population turnover is a much more reliable resource than many reef fish species for harvest today (Birkeland, 2017). Skipjack grows almost ten times as fast as large coral reef fishes like groupers and snappers, that often live for several decades and are easily over-exploited (Birkeland, 2017).

2.3.E Contemporary tuna fishing in the Maldives

Today, skipjack tuna is still caught in the Maldives using the pole-and-line fishing method. This occurs in multiple stages. Live bait is first caught in nearshore waters using a net (today made of nylon, earlier of cotton). The reef fish caught — usually planktivores like fusiliers (*Caesio sp*.) and triggerfish (*Odonus sp.)* — or sprats (*Spratelloides gracilis*) are kept in holding tanks on the boat. Once offshore, the water near a potential fishing ground is chummed with baitfish, attracting tuna to the surface. Barbless hooks, attached to a long pole (today made of fiberglass, earlier of bamboo), are then used to pull fish out of the water (Adam and Anderson, 1998; Adam, 1999). Earlier, sea birds guided fishermen to locate schools of skipjack. In particular, the brown noddy (*Anous stolidus*) was an important indicator of where schools of skipjack might be located. Today, fish aggregation devices aid in detecting schools of tuna. Because the pole-and-line method results in little to no bycatch or discards (Miller et al. 2017), the Maldivian pole-and-line fishery was the first in the Indian Ocean to be accredited by the Marine Stewardship Council as a sustainable fishery (Stevens and Froman, 2018). While there has been some concern about the sustainability of the baitfish fishery that the tuna fishing industry relies on, the live bait fishery management plan launched by the Marine Research Centre and the Ministry of Fisheries and Agriculture aims to improve post-harvest mortality rates and monitor catch records in the coming years (Gillett et al., 2013). One of the questions this paper raises is what the effects of historic bait fishing have been on these reefs. Quantifying potential differences in the communities of reef fish species in reefs that have experienced sustained bait fishing and those that have not may help shed some light on whether the long-term removal of species like fusiliers, cardinalfish, and damselfish has impacted reef fish community structure in these coral reef systems.

The processes that govern the modern tuna fishery were first introduced in the mid-1970s, when the Maldivian government mechanized the offshore tuna fishing fleet. Tuna catches (both skipjack and yellowfin) rose rapidly thereafter, from 35942 t in 1970 to 76374 t by 1990, peaking at 186000 t in 2005 (MEE, 2015a; p 35). As of 2014, 20945 t of skipjack tuna and 14537 t of yellowfin were landed in the Maldives (Hemmings et al. 2014). The earnings on exports from tuna and other fisheries (bêche-de-mer, lobster, etc.) has continued to rise since, even as tourism has become the main driver of the country's economy today, accounting for about 30% of its direct annual GDP (Stevens and Froman, 2018). However, while the tourist sector employs many non-Maldivians, the fisheries sector continues to employ about 20% of the local population (MEE, 2016b). Frozen tuna is exported to foreign markets in Germany, the United Kingdom, Japan, France and the United States – the fresh tuna supplied from the Maldives, in fact, accounts for over 15% of the fresh tuna imported into the European Union (MEE, 2015a; pp 32). Yellowfin tuna is an important component of this, representing over 28% of total marine exports from the Maldives (Adam and Jauharee, 2009). Dried “Maldive fish” (usually skipjack) is still exported to Sri Lanka by smaller cottage industries. Skipjack stocks are generally thought to be high in the Maldives, and while yellowfin tuna catches have fluctuated in the past decade, they seem to have stabilized since 2010 (Hemmings et al. 2014).

However, even as the tuna fishery maintains its economic and cultural importance in these islands, the rapid rise in tourism since the 1970s as well as growing foreign demand for reef fishes for consumption or display have led to the emergence of a reef fishery in recent years (Adam, 2004). The total estimated annual catch of reef fish in 2014 was 10780 t (Hemmings et al. 2014; Pauly and Zeller, 2015). An export-based grouper fishery (primarily supplying Thailand, Taiwan, and Hong Kong) also took off in 1994. In 2010 over 600 t of grouper species were exported from the country both in fresh/chilled form and live, mainly via air freight in containers or in bins developed for the shipment of live organisms (Sattar et al., 2011). A management plan for this fishery recommended size limits for some species and protected areas to safeguard spawning aggregations (Sattar et al., 2011), programs that are currently being implemented. An export-driven aquarium trade has also expanded in these islands, and as of 2008, about 140 species of fish and 5 species of invertebrates were being exported from the Maldives, regulated by species-specific quotas (Saleem and Islam, 2008). While these two industries supply external demand and have been subject to some state regulation, reef fishes also have a growing and important local market. Much of this demand comes from resorts, where catches are either landed directly (Sattar et al., 2014) or supplied by local buyers and traders who purchase directly from fishermen (*pers.comm*, M Shimal). Jacks (Carangidae), snappers (Lutjanidae), and emperors (Lethrinidae) form the bulk of the catch bought by resorts, with quantity determined primarily by the bed capacity of the resort (Sattar et al., 2014). Hemmings et al. (2014) estimate that reef fishes constitute 83% of tourist consumption.

Within local communities too, reef fishes appear to be becoming more common in diets, with many households consuming between one and five reef fish per week (Sattar et al., 2014). While this is still a low number, guest houses are developing rapidly on islands previously only inhabited by local communities (428 as of 2017), bringing tourists to islands that they might not earlier have visited. This is also driving an increased demand for reef fish (MEE, 2017). Recent studies suggest that there are efforts being made to address this problem and to create management strategies that will help regulate catches of reef species more effectively (MEE, 2017). However, there is still more research needed to understand what is driving the demand for reef fish locally – whether these are more the results of tourist preferences, changing local tastes, or the unavailability or inaccessibility of tuna today to people outside big market centers in the Maldives. Examining how seafood trade today interacts with production (Crona et al. 2016), and the place of reef fish and tuna in both international and local markets in the Maldives, will help to better understand the current drivers of these respective fisheries.

2.4 CONCLUSIONS

In many ways, the Maldives is confronted by problems and challenges very similar to those faced by other small island states, chief among them being the threat of sea level rise, coastal erosion, and rapid development fueled by an ever-growing tourist industry (UNEP, 1994; Zubair et al., 2010). At the same time the linked ecological, social, and cultural history of the tuna fishery also provides a glimpse into the factors that sustained a biologically robust fishery for centuries, and the implications this has had for long-term social-ecological resilience of these islands' reef system. Over the past 1000 years, the pelagic tuna fishery has kept reef fishing light in the Maldives, promoting the functional resilience of these reefs and buffering them from climate change-related disturbances, like mass coral bleaching events. However, while it was the earlier form of regional trade in money cowries that led to the development of a pelagic fishery that indirectly supported coral reef resilience, it is now ironic that a more recent globalization, in the form of tourism, has the potential to endanger this same system. Just as the centuries-long cowrie trade served as a condition for the emergence and establishment of the tuna fishery with various cultural and ecological outcomes, the health of nearshore reefs is again linked to transnational and regional dynamics driven by market and cultural phenomena in other domains. One and a half million tourists visited the country in 2017, three times its local population (MMT, 2017; Stevens and Froman, 2018). While the efforts made by many resorts to make their practices more sustainable and conservation-oriented must be applauded and encouraged, tourism still exerts a huge ecological strain on the Maldives, and in island societies in general. In coral reefs around the world, demand for top predators like groupers, and herbivores like parrotfish has transformed reef trophic dynamics and, in some cases, pushed benthic communities to less-desirable alternate states (Mumby et al. 2007; McCauley et al. 2010). While there are notable exceptions to this narrative, especially where local management and protection have reversed these trends (Friedlander et al., 2002; Johannes, 2002; Kikiloi et al., 2017), one of the biggest challenges in coral reef management today remains centered around operationalizing concepts of ecological resilience to sustainably manage reef fisheries (Anthony et al., 2015). In the Maldives, the resilience of these reefs is intimately tied to the tuna fishery. Our work suggests that it is going to be increasingly important to not only understand and respond to the drivers and dynamics of ecological wellbeing in the Maldives today, but to also reflect on deep time perspectives for governing and managing reef resilience and seafood sustainability. Complex historical ecologies such as those exemplified in the Maldives in centuries-long linkages between money cowries, pelagic tuna, nearshore reefs, and local communities can be drawn upon to better inform present and future marine resource management, and to better understand how tourist and local consumption as well as international markets are shaping the demand for fisheries products today. For instance, encouraging the consumption of skipjack tuna over reef fish species in resorts may go a long way towards reversing current trends in tourist demand for reef fish. Simultaneously, while tuna still remains an essential component of local diets, there needs to be more effort directed towards examining just how much is being consumed in households, and in tracking the (monetary, social) value of tuna to locals today.

Meanwhile, as the possibility of increased exploitation of pelagic fisheries to meet consumer needs gains attention from conservationists and reef managers in other island ecosystems (Bell et al., 2009, 2015; Birkeland, 2017; Wabnitz et al., 2017), the Maldives provides an interesting case study of an archipelago that has historically sustained this model for centuries. It is true that successful adaptation to increased environmental stress, in many cases, will depend on societies abilities to invest in alternate fisheries or activities (Brander, 2008). However, both the external and intrinsically cultural factors that have contributed to the persistence of the tuna fishery in the Maldives are unique to this island chain – and dietary preferences, in particular, have played a large role in ensuring the success of tuna here, in the same way that preference for reef fish species has shaped fisheries history in many Pacific island contexts (Johannes, 1981). This will have to be taken into consideration when offshore fisheries are promoted in places that do not necessarily share the same social and cultural values for pelagic fish. Finally, integrating historical perspectives into contemporary conservation will be crucial to uncover and better understand the dynamic forces that have shaped and continue to shape island ecologies. As habitats change rapidly in the Anthropocene, long-term historical data will be needed to frame current management practices and create sustainable, practical, and equitable plans for the future.

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2.6 TABLES

Table 2.1: Summary of important sources and accounts documenting the growth of the tuna fishery in the Maldives from the ninth to the twenty-first century.

Time period	Source	Details recorded	References
First to ninth century (pre-Islamic)	Faunal archaeological collections	Scombrid (tuna) remains major fish taxon recovered from this period; more diverse reef fish assemblages recovered post-9th century	Maloney, 2013; Litster, 2016 and references therein
Fourteenth century	Ibn Battuta	First (?) written record in post-Islamic Maldives documenting the processing of and trade in skipjack tuna; export to Bengal, Gujarat (India) and Yemen recorded	Gibb, 1953
Sixteenth century	Francois Pyrard de Laval	Second detailed record of skipjack tuna processing in the Maldives and trade expansion	Gray and Bell, 2010
Nineteenth century	Harry Charles Purvis Bell, Thomas William Hockley	First ethnographic accounts of the Maldives; details of cutting and curing skipjack tuna; places	Bell, 1882; Hockley, 1935

		of export and uses of tuna	
Fifteenth to nineteenth centuries	Merchant records and notes by traders and visitors (Dutch, Chinese, Arabs, Mappillas, Bohras)	Places of trade and uses of skipjack tuna; growth of “Maldive fish” in Sri Lanka	Dames, 1921; Bell, 1882; Hockley, 1935; Qaisar, 1987; Mohamed, 2005a, Yang 2019
Twenty-first century (post-mechanization)	Fish catch records and reconstructions	Tonnage of skipjack tuna and other species fished, management of modern tuna and reef fishery	Adam and Anderson 1997; Adam, 1998; Sattar et al. 2011, 2014; Hemmings et al. 2014

2.7 FIGURES

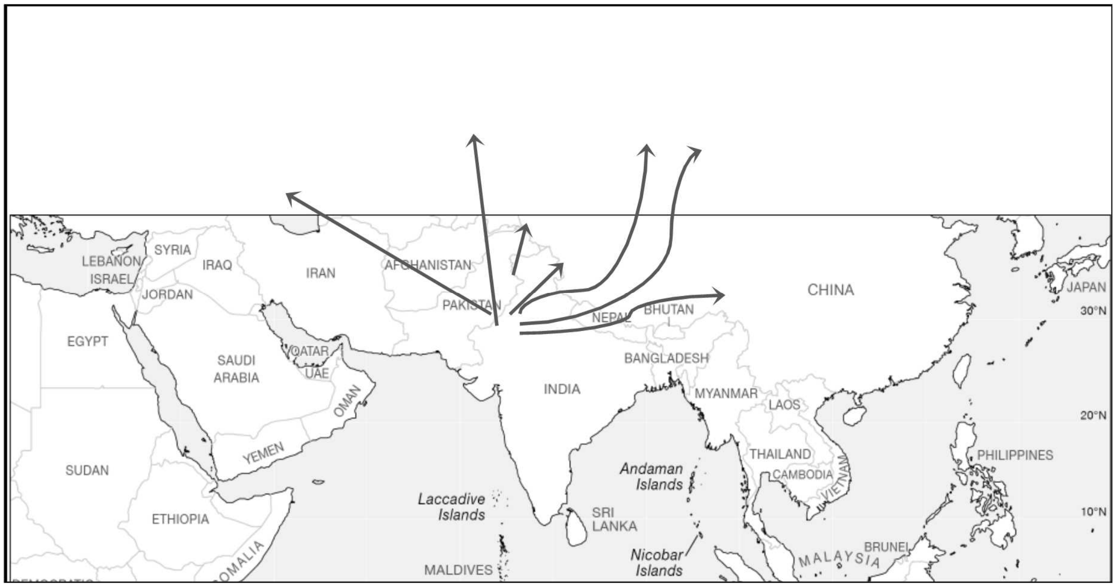

Figure 2.1: Map of the Maldives in the Indian Ocean, with arrows indicating places where dried tuna and other fish products were being traded between the 14th to 19th centuries. While it is likely that tuna had a wider reach, especially to parts of east Africa and Southeast Asia, the places marked are only those that had a direct written reference to tuna being shipped here. Map credit: CartoGIS Services, ANU College of Asia and the Pacific, The Australian National University.

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CHAPTER 3

EXPLORING FISH PREFERENCES, CONSUMPTION PATTERNS, AND REEF FISHING DYNAMICS IN DHAALU ATOLL, MALDIVES

3.1 ABSTRACT

People's preferences and choices around food directly influence their resource use and the resilience of dynamically linked natural and human systems. In this chapter we examine fish preference and consumption patterns in Dhaalu atoll, Maldives, where fisheries have experienced rapid change in response to tourism and development. We find that reef fishes are now a significant part of local diets, with 58% of interview respondents preferring to eat reef fish over the historically more popular and sustainable tuna. Our findings suggest that preferences, which vary with gender and age, are an important yet underutilized indicator of changing pressures on reefs. While demand from nearby resorts currently drives the majority of reef fishing in these islands, we document seasonal spikes in the local catch and consumption of reef fishes and record an informal network of sharing that should be considered while developing management plans. Reef fishers identified the impacts of coral bleaching and development on reef fishing, and in particular, the negative effects of changing gear and bait fishing practices on their catch. Rising levels of reef fish consumption could have significant environmental impacts in the Maldives with implications for island food security and community wellbeing.

Keywords: preferences, human dimensions, reef fisheries, coral reef resilience

3.2 INTRODUCTION

How people assign value to places and species ultimately impacts how they are used and managed (Jackson et al. 2008; Jones et al. 2016). Management in turn affects community health and wellbeing in part by shaping how critical resources like land and water are utilized (McKinnon et al. 2016; Coulthard et al. 2017). On islands with little agricultural land, fish are frequently the primary source of protein, contributing in some small island states to over half of the animal protein intake (Bennett et al. 2018). Fisheries management in these contexts has direct consequences for people's nutrition and for the ecological resilience of coral reef habitats (Bell et al. 2018).

However, fisheries are complex systems involving multiple stakeholders (Brewer and Moon 2015; Hoque Mozumder et al. 2018). Often, conflicts arise when governance fails to consider the plurality of values - including not only economic and ecological but also social and cultural - that a resource such as fish might possess (Lam et al. 2019). For example, Chinese values around luxury seafood and a preference for "plate-sized" red coral groupers pushes fishers in the Philippines to target sub-adults of this species that have not yet spawned, impacting the resilience of these fish stocks and the long-term livelihoods of fishers (Fabinyi et al. 2018). In the Andaman Islands, commoditization of the leopard coral grouper (*Plectropomus leopardus*) since the 1990s has transformed the socioeconomic value of this fish, with certain communities that catch and export it now referring to this species simply as "dollar" (Advani, 2019).

Value differences can be especially pronounced in islands where tourism, urbanization, and development are transforming local economies (Wabnitz et al. 2018; Rubio-Cisneros et al. 2019). Numerous studies have documented the complex and diverse ways in which people understand and relate to fish (Johannes et al. 2000; Grant and Berkes 2007; Todd 2014), how fish and fisheries help to maintain or build sharing networks within communities (Dacks et al. 2020), their traditional and spiritual value (Johannes 1981; Mohamed et al. 2019), and their importance to community identities (Santos 2015; Torrente et al. 2018). However, despite general consensus among scientists and policymakers that resource management is "people management" (Berkes and Folke 1998), and an understanding that there are severe consequences to social-ecological resilience when the human dimensions of these systems are ignored (Drew 2005; Cinner 2011; Aswani et al. 2020), prioritizing and integrating cultural and social values into marine management has remained a challenge (Apgar et al. 2015). In particular, values around certain kinds of fish and how they might drive people's preferences and consumption patterns remain an under-addressed part of planning (Fabinyi et al. 2014). This is partly because values have been understood and conceptualized in a variety of ways over time (Kenter et al. 2019) and have only recently begun to be operationalized for conservation science (Bennet et al. 2017).

In this study, we attempted to gain an initial understanding of the ways in which communities in the Maldives might value different species of fish (in particular, reef fish and tuna) by assessing their preferences and consumption patterns. We were also interested in understanding how the dynamics that currently shape reef fishing feed back into seasonal patterns of consumption, and are influenced by social, developmental, and environmental changes occurring on islands. We would like to note that while preferences and choices help structure people's actions, they are only one part of the larger landscape of value relations. Few people make choices based purely on their preferences and desires, but the latter can nevertheless be a useful and effective indicator of how people think about, use, and value resources in places that are rapidly globalizing. In this way, they may be revealing of how future policies could impact different sections of society and their wellbeing.

In the Maldives, with its extensive coral reef ecosystems, an economy once dependent on fishing now relies on tourism. Tourism directly and indirectly accounts for two thirds of the country's GDP (World Bank, 2015). In 2019, a record number of 1.7 million tourists visited the Maldives. The resulting pressures on the country's resources have been significant (Stevens and Froman 2018). Dredging, channel blasting, coastal development, island reclamation, and the construction of resorts on previously uninhabited islands have had severe implications for water quality, waste management, and local wildlife (Stevens and Froman, 2018). Notably, the tourist industry has created new markets for fisheries products by creating a steadily growing demand for reef fish (Sattar et al. 2014). Reef fishes make up 83% of the fish consumed by tourists (Hemmings et al. 2014) and resorts can demand 500 kg of reef fish per day (Supplementary Information). However, it has been unclear to what extent reef fish are being eaten outside of resorts and whether local preferences for fish are changing.

Historically, tuna has been at the center of traditional cuisine in the Maldives. While there is an unfortunate paucity of historical information on reef fish consumption, archeological work across the archipelago has found that scombrid (tuna) remains dominate in both the Buddhist (pre-1153 CE) and the Islamic (1153-present) periods of settlement. As Litster (2016, pp. 244) writes, "the dominance of tuna in all periods, despite the availability of inshore reef fish highlights a deliberate and continued practice perhaps linked to the… cultural preference for tuna". While reef fish do appear in the archeological record, they are found in significantly smaller quantities, suggesting that they were fished to a much lesser degree. This points to a relatively underutilized reef fishery, despite the availability of reef fish, and stands in contrast to other islands in the tropics where reef fishing has played a more prominent role in society and been practiced for millennia. In some cases, this long-term demand for nearshore and reef species has become unsustainable and contributed to its overfishing (Newton et al. 2007; Van Houtan et al. 2013). In Palau, there are efforts now underway to shift consumer demand towards more pelagic species like tuna to help offset pressures on the reef (Wabnitz et al. 2018; Dacks et al. 2020). While knowledge of reef fish behavior and reef fishing methods are extensive in islands with a long history of reef fishing, in the Maldives, it is references to tuna – as an item of trade, a dietary staple in the islands, and the methods used to fish it – that abound in ethnographic and other writing. The pole-and-line fishery for pelagic tuna dates back to the 14th century (Yadav et al. 2019) and current records indicate that more than half the tuna caught is consumed locally rather than exported (Miller et al. 2017). Tuna fishers constitute a powerful political force, often becoming island leaders and representing the interests of this sector at the national level. To a large extent, it's this historical reliance on and connection to tuna that has enabled reef fish populations here to remain healthy even in the face of major climate change-related disturbances (Perry and Morgan 2017; Cowburn et al. 2019). However, shifting preferences and consumption patterns could intensify pressures on coral reefs (Lewis et al. 2020). While there are some informal rules that govern the fishing of some lagoon fish on particular islands (Mohamed 2012), apart from the grouper fishery, reef fisheries in the Maldives currently do not have a national management plan (Sattar et al. 2014).

We aimed to gain insight into the ways in which people value tuna and reef fish today by documenting individual preferences and consumption patterns of fish across four islands in Dhaalu atoll, Maldives. Until recently, the market for reef fish had been primarily centered around resorts but there have been reports of increases in the consumption of reef fishes on local community islands in the past few years. However, we expected strong preferences for tuna and a higher consumption of tuna over other fish given the age of this fishery and the ubiquity of tuna in traditional cuisine. We collected social and demographic data on age, gender, and profession, among other variables to help understand what influenced individual preference. Additionally, we also gathered information regarding seasonality in reef fishing, catch composition, reef fish markets, and fishing practices from fishers to better understand the dynamics that governed reef fishing. Since these fisheries are local and small-scale, we paid particular attention to how fishing practices may be linked to fish consumption patterns, cultural events, and community networks, and how these may be changing over time.

3.3 METHODS

The Maldives is a double chain of 26 atolls and over 1190 islands in the central Indian Ocean, extending from 0.5°S to 7°N of the equator. 539, 834 people live across its 190 inhabited islands, although close to 40% of the total population is concentrated in the capital city of Malé. This study was conducted on 4 islands in Dhaalu atoll, in the central province of the Maldives. Dhaalu is an atoll ringed by 59 islands, of which 6 are inhabited by local communities. Historically, the chief employment on these islands has been tuna fishing, but a significant proportion of residents today also work in government jobs, in local schools and offices, in small businesses and shops, and in resorts. Currently, there are six resorts in Dhaalu located on separate resort islands that lack an indigenous population. Three more have been approved for this atoll, as of 2019. Guest houses are a more recent phenomenon but are relatively common on most community islands today. In contrast to resorts, these have become more affordable options for tourists as well as local visitors.

We selected Dhaalu atoll for this study for two primary reasons. One, unlike some of the better-studied northern atolls, there is little information on the current state of Dhaalu atoll's fisheries, even though it is commonly regarded as an important contributor to the national tuna fishery (pers. comm). Central atolls like Dhaalu and Faafu also appear to be gaining importance for reef fishing – both for the fishing and export of groupers, as well as for supplying reef fish markets within the country (Sattar et al. 2014).

Second, we were interested in visiting islands along a gradient of population, relative development, and access/proximity to resorts to better evaluate the demographic and social variability in individual fish preference and consumption. The four islands we selected represented some of these differences, while still sharing a common geography, culture, and identity as part of Dhaalu atoll. Kudahuvadhoo, the capital of the atoll, was the largest and most populated island, and the only one with an ice plant and an airport. In contrast, Rinbudhoo had the smallest population, no direct ferries to Malé, and the least number of commercial fishers. Meedhoo and Hulhudheli lay in the middle – their harbors had recently been expanded, and on Meedhoo, a large part of the island had recently been reclaimed for a housing development project. Due to the small size of these islands, people do not live in separate towns or villages, but in one continuous settlement. In most islands a main road runs through the length of the island with smaller streets radiating out from it. Even though they differ in some regards, the islands in this atoll are all well-connected to each other, with frequent movement of people and goods occurring between them.

We used structured surveys with a combination of fixed responses and open-ended questions to collect data on individual preferences and assess the household consumption of reef fish and tuna (see Supplementary Information for survey instrument). Surveys were conducted in English or Dhivehi (the local language), based on the respondent's preference. We used a mixed approach to identify respondents, with both snowball and convenience sampling. To begin, island council members directed us to long-time residents or fishers to invite to be surveyed, who directed us to other potential respondents. We also recruited participants in public spaces, e.g., around harbor areas, in cafes, or during daily community gatherings outdoors, and interviewed them if they consented to participate in the study. Two of the people who were invited to participate in the study declined to do so.

Of the 100 respondents we surveyed, 56 were fishers (full-time, part-time, subsistence, or recreational), 78 were male and 22 were female (see Table S1 for island-level differences). The ethnic (Maldivian) and religious (Muslim) background of respondents was homogenous; these characteristics of our sample are similar to the population of this atoll, and to the archipelago in general. The mean age of men interviewed was 43.5 (+/- 14.3 SD) and of women was 42 (+/-14.2 SD) (Fig. S1). Since our surveys were not a random sample of the population, they may not adequately represent the entire population of these islands. However, our study was aimed at gathering baseline information and identifying potential social and cultural factors which may influence preferences, consumption, and fishing for future investigation.

We used a two-way ANOVA to test for differences in household consumption of reef fishes and tuna (consumption (kg) ~ fish_type + island). Consumption was generally reported as a weight (kg) of fish consumed per household per week. In a few instances, it was reported for the individual – in these cases, we extrapolated the value for the number of household members to get an estimate for the entire household. We used a log (x+1) transformation on the data to improve normality of residuals while avoiding zero values.

We used a generalized linear mixed model (GLMM) with a binomial link function to determine the best predictors of fish preference among the population interviewed. We coded preference for reef fish as 0 and tuna as 1 and tested for the effects of a) gender (m/f), b) age (19-80), c) profession (tuna fisher, reef fisher, other), d) historical preference (i.e., dominant fish one grew up eating) and e) island (random effect) on an individual's current preference for tuna or reef fish (grouped into these two categories based on more detailed species-specific responses, see Supplementary Information). We included profession in our model to assess if one's role as a fisher influenced their preferences for certain species of fish. In our interviews, reef fishers often mentioned they took home a small proportion of their catch to consume with family; tuna fishers said the same. We thought that identifying as a tuna or reef fisher might therefore influence what is preferred by an individual. We defined historical preference as the past preference for a particular species of fish that an individual had when they were younger. All respondents gave us the relative percentage of different reef fish and tuna species in their diets in the past versus today. Our global model was: preference ~ gender + age + profession + historical preference + island (random). We sequentially dropped variables using the *drop1* function to select our best model (preference ~ gender + age + island). All analyses were run in R (R Core Team 2021).

Finally, we interviewed reef fishers to understand the dynamics related to reef fishing (e.g., seasonality, gear, markets), which we then coded inductively and condensed into six broad themes given in Table 2 below. While these conversations generated a rich amount of information, we limited our discussion in this manuscript to addressing the main factors that fishers identified as influencing reef fish catch and consumption and the changes they have observed over time.

3.4 RESULTS

We expected tuna to be consumed at a higher quantity than reef fish in households. Strikingly, we found no significant differences in the reported average weekly household consumption of fresh tuna and reef fish in the islands surveyed (Fig 1; Table S2, $p>0.05$).

Meanwhile, 58% of all interview respondents said they preferred to eat reef fish over tuna today. Our model indicated that gender and age were key determinants of people's preferences for certain species of fish (Fig 2; Table 1). Men preferred to eat reef fishes (in particular, snappers, emperors, groupers, and chubs), while women reported a preference for tuna (skipjack, frigate, or yellowfin tuna). After gender, age was a significant determinant of individual fish preference, with preference for reef fish increasing in people around the age of 40-45. Profession and historical preference were dropped from the final model because they did not have a significant effect on the variance explained.

When it came to the dynamics that influenced reef fishing, fishers noted several factors – from seasonality and market demand to coral bleaching and changing gear – that could influence current and future consumption patterns (Table 2). In general, they perceived changes in the abundance and composition of their catch in response to coral bleaching (specifically, a post-bleaching decline in *Chromis* spp.used for bait) and developmental changes on the island (e.g., reclamation, harbor construction), as well as modifications in fishing practices and gear over time. Some noted that fish abundance had decreased during land reclamation and after, and also during the dredging of the channel and harbor areas. Others did not observe a change in reef fish species due to development on land.

Notably, almost all fishers spoke of a decrease in bait species and linked it to the extensive use of more exploitative methods of bait fishing recently, including the use of lights and SCUBA. They also identified a clear seasonality in the catch and consumption of reef fishes, with a spike in reef fish consumption occurring during the period of Ramadan and Eid when community barbeques and gatherings were more frequent. Reef fish were seen as the more appropriate fish for frying during these times, with the demand for reef fish and their price increasing during this period. In general, a wide variety of reef fish species were targeted by fishers in Dhaalu atoll. The most popular species fished were snappers (in particular, *Lutjanus gibbous*), groupers (*Epinephelus tauvina, E.microdon, E.caerulopunctatus*, *Cephalopholis argus*, *Variola laoti*), emperors (*Lethrinus* spp.), jacks (*Caranx* spp.), sea chubs (*Kyphosus* spp.), soldierfish (*Sargocentron spillifera*), and rainbow runners (*Elegatis* *bipinnulata*). While reef fishers used several kinds of gear on reefs, handlines were the most commonly used. They were used with or without a weight, and with or without bait (live or dead).

In parallel to buying and selling fish, there appeared to be an active informal system of sharing fish with friends, family, and neighbors. 14% of respondents said the reef fish they obtained was procured exclusively through sharing, while 58% obtained it through a combination of sharing and/or direct fishing. Only 17% exclusively bought their reef fish.

3.5 DISCUSSION

While the tuna fishery – and tuna – retains a place of prominence in Maldivian culture, our results indicate that reef fishes have so far been an overlooked part of local diets. Notably, reef fishes were preferred by a small but significant majority of our respondents, indicating that reef fish consumption may increase in the future. These dynamics need be carefully examined in order to better support local communities' social adaptive capacities to urban development and accelerating tourism, and in managing their resilience to sea level rise, coral bleaching, and other threats due to contemporary global climate change (Marshall et al. 2010; Wongbusarakum et al. 2021)

Preferences were influenced by people's gender and age. Our interviews suggest that the preference for tuna amongst women might be partly rooted in the popularity of traditional cuisine and the diversity of culturally important dishes that are cooked with tuna (e.g., *rihakuru*, *garudiya*, *maashuni*). In contrast, reef fish were associated with a "bad smell," and women found the process of cleaning and gutting reef fish unappealing. Five of the women interviewed said they would never eat reef fish because they disliked it so much. Women's involvement in small-scale fisheries in the Maldives has not been the focus of any formal research before, even if women's roles, while less visible, might include a range of activities related to fishing like cleaning, cooking, selling, etc. (Lama, 2018) In the past, women used to be responsible for sewing nets and cleaning the catch of fish once it was landed. "Now the nets are imported and catch [of tuna] is sold to collector vessels or taken directly to Malé", an older respondent mentioned. However, another said that she had been fishing "daily from the shore since the age of 20… since I had children". She explained that she began fishing to provide her children with fresh fish since her husband was a tuna fisher and was frequently away. This suggests that women's involvement in small-scale fisheries, while not necessarily direct, might still be important to consider especially from the point of view of island food systems and the processes that contribute to the nutritional health of communities. The gender-based differences in preference we record in this study could also point to a deeper split in values relating to marine resources, and more broadly to the way in which the ocean is seen and used by men and women in the Maldives. This underscores the need to advance methodological and analytical approaches to gender for a comprehensive understanding of human-ecological interactions in coastal fisheries (Kleiber et al. 2105; McLeod et al. 2018).

Fish preference also varied by age, which reflects generational changes in diet (Fig. 2). Reef fishes were commonly perceived to be the healthier fish amongst older people (>40 years), with multiple respondents stating that their doctors had advised them to eat less tuna and more reef fish. However, 70% of people over the age of 40 still cited tuna-based preparations as their favorite dishes, suggesting that while there is a preference for reef fish as an everyday food, it does not replace traditional preparations made with tuna. The nutritional implications of these differences in diet with age could be significant, especially for younger people whose food choices today are more influenced by global trends. These patterns in preference were largely consistent across the 4 islands, but respondents on Rinbudhoo showed a slightly stronger preference for frigate tuna (*Auxis thazard*) over all other fish. This was likely related to their observance of community fishing days for frigate tuna which enter the island lagoon during particular lunar periods, prompting fishers to pool resources and organize fishing days during this time. During the course of our survey, 20+ fishers were involved in landing a catch of over 1500 frigate tuna in one evening. This catch was shared between all community members and was distributed to several households on the island (Box 1). This observation points to the underexamined cultural and social role that reef fish might play in community wellbeing, for instance by maintaining or enhancing social networks (Dacks et al. 2020). These networks seemed prevalent in the islands we surveyed, with 58% of all respondents obtaining their reef fish via an informal system of sharing with friends and family, or by direct fishing. Understanding these networks is important for developing bottom-up management that is sensitive to the impacts certain policies might have on social relationships and the role those relationships might play in supporting communities' responses to current or future challenges.

Box 1: Fish for an Island

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Nadia walked briskly up to me, her hands full of food containers. “You wanted short-eats, no?” she asked as she led me to the group of women who were waiting close by. Earlier in the day while interviewing her, I had asked her about recipes for Maldivian short-eats, fried tuna-filled snacks that often accompany their morning or evening coffee. The women had just returned from a meeting at the school with plenty of leftovers, so we made our way to one of their homes. Inside, Nadia arranged a plate of gulha, samosa, and boakiba in front of me, and poured me a glass of juice. Three other women—all part of the Women's Development Committee on this island of Rinbudhoo—stood around the table, giggling at my obvious pleasure. These were all snacks Nadia had prepared at home, which she often shipped to Malé or sold to tourists. Her boakiba—fish cake—was fantastic, spicy and dense, but not heavy.

A few minutes later, we heard that the boat that had gone out that afternoon was just pulling into the lagoon. The previous day, my collaborator Fisam and I had been told that we should try to make it out to see the catch of frigate tuna when it was landed the next evening. “You have to go fast!” Nadia said, motioning for me to finish eating quickly. Fisam and I made our way to the beach on the island’s north-eastern edge, the sand a muted pink and orange in the late light of the setting sun.

Rinbudhoo is one of six inhabited islands in Dhaalu atoll in central Maldives. The 26 atolls of the Maldives are made up of individual islands, “uncut emeralds in a sea of sapphire” as T W Hockley, a visiting British official, wrote in 1935. Its waters are vast, home to 3% of the world’s coral reefs. Fishing and fisheries are central to the culture and economy here. I was there for my doctoral research, trying to understand how the ecology of these coral reef systems is changing in response to major climatic disturbances like coral bleaching events. But in the past few years, I have been drawn to the dynamics playing out on land, and to exploring the ties between people and their reefs. Fisam and I were here to conduct a pilot study on the values—both monetary and cultural—that people had for different species of fish, and whether those were changing. Some studies in ecology happen far from humans, but on islands like these, things are necessarily more intertwined. I was coming to appreciate that.

We walked up to the beach where the dhoani had just pulled up onto the sand. Dusk was setting in as the catch began to be offloaded. Handfuls of tuna were thrown from the bowels of the boat onto the beach, forming a grey-black heap where they landed. Someone then sorted them into a different pile, tallying the count with one fish thrown to the side for every hundred counted. The fish just keep coming: 300, 500, and then 1,000 fish glittered under the singular lamp illuminating the scene. A small crowd had gathered by this time and, as the counting neared its end, wheelbarrows were brought out to further separate the catch. The call for evening prayer came and went. People sat at the water’s edge, gutting and cleaning the tuna. Entrails and viscera were buried in the sand, and the fish were rinsed in seawater. An eagle ray, smelling the blood, hovered close to the boat. A total of 1,565 fish were caught that day, and the catch was distributed to everyone on the island. Much of it would be boiled in homes to make rihakuru, a fish paste that is often eaten with rice. Some of it would be dried or smoked. This way, the fish would keep for long, and could be used for months after. Pieces of this smoked fish are what had made Nadia's boakiba so delicious.

A community fishing day like this is not a rare event, but it is certainly not common practice on the islands anymore. For a few days around the time of the full moon, frigate tuna enter the lagoons of some islands in large numbers, likely a seasonal response to the availability of prey fish in these waters. For a large catch to be landed, a collective effort is required. Someone brings the boat, and a handful of fishers bring their nets. In Rinbudhoo, on this particular day, around 20 fishers had gone out together. The fish were not for selling—all of it was shared. Done every month, or every other month for a part of the year, fishing days like this fed everyone on the island.

But how much longer would a practice like this last? Most islands in the Maldives now have a harbour, continuously being developed and expanded so that larger boats can dock there. The dredging that results from this, along with other coastal development projects, has had an impact on the abundance of fish inside lagoons. The offshore tuna fishery for skipjack and yellowfin tuna also requires live bait that are fished in lagoons or on reefs near islands. Some fishers on other islands told us how they thought that unsustainable levels of bait fishing, combined with the effects of dredging, was why they didn't see frigate tuna near their islands anymore. "If there are no fish for the frigate tuna to eat, why would they come here?" one of them asked.

An elderly reef fisher we spoke to told us how, in the past, people never fished out juvenile bait fish inside the lagoon. It was important to leave them in the water to ensure their population remained healthy. Now, he said, people fished for bait throughout the year, and more intensively than before. While there is some national monitoring of the live bait fishery, fishers told us repeatedly how a greater effort was required to catch bait fish today. This has led to people diving for bait or using bright lights to attract schools to the surface at night—practices that can have serious repercussions in the long run if they're not managed.

What would change if community-wide fishing days were no longer practiced, though? If a bigger harbour brought more boats, more tourists, more revenue, were fishing days a small price to pay? To whom did it matter, anyway, and what purpose did it serve? I couldn't help but think of a colleague's research in the Nicobar Islands, where hasty government aid and rehabilitation programs after the tsunami of 2004 had radically altered previously isolated Nicobarese societies, affecting the structure of their households, fisheries management, and resource use. In particular, post-tsunami policies had overlooked Nicobarese traditions of sharing and collective ownership and eroded customary practices by not being cognizant of the role they played in those communities.

Often, the value of a certain practice is difficult to quantify and understand until it is no longer performed, and every other practice or process it's linked to suddenly becomes more vulnerable. In our surveys across these islands, Fisam and I noticed just how much things had changed both on land and in the water as islands were reclaimed and expanded. Would Nadia still make and sell her boakiba if she had to buy her tuna? Would people simply switch to fishing for another species, if frigate tuna no longer entered these waters? Perhaps some of these changes were inevitable. But tonight, at least, the air was thick with the smell of rihakuru, and we would all eat well tomorrow.

Cultural values and preferences have implications for social-ecological resilience by influencing what is fished, when, and how intensively. Fishing practices in turn affect people's choices when it comes to seafood consumption, especially in smaller, localized fisheries. Our interviews with fishers highlighted several important dynamics related to reef fishing (Table 2). One of most significant concerns fishers had, and one that was mentioned often, was around the use of baitfish species. Multiple respondents noted a reduction in damselfish (*Chromis* spp.) in response to coral bleaching events in the past decade. While damselfish are not consumed, they are frequently used as live bait for the tuna fishery. Along with reductions due to coral bleaching, our interviews revealed a sense among fishers that baitfish populations (*Spratelloides* spp., *Caesionid* spp.) were declining due to the increased use of lights and SCUBA to catch bait, and that other less preferable species such as triggerfish (Balistidae), damselfish (Pomacentridae) and cardinalfish (Apogonidae) were being targeted as a result of this. Mohamed (2019) previously found that many elderly fishers talked about current fishing practices resulting in the unavailability of baitfish, and that "all fishermen agreed that the lack of bait was due to the methods they used." While there is some natural seasonal fluctuation in baitfish numbers that fishers recognize, our study highlights the urgent need for a thorough understanding of the impacts of these new practices on baitfish populations.

Resorts have been known to exert a substantial influence on reef fishing (Sattar et al. 2014), and our interviews with fishers confirm that these were the main markets for full-time reef fishers, with fishers generally selling their catch to the resort closest to their home island. Fish were sold by weight and fishers did not indicate any difference in the prices for different species. However, the networks that are involved in the selling of reef fish are complex and are likely to vary by island, depending on the number of buyers and middlemen that transport catch to Malé before it is further distributed. While resorts drive reef fishing in a significant way (buying at between USD 1.3-3 per kg of reef fish directly from fishers) we found that community demand for reef fish during particular times of the month (e.g., the new and full moon) and year (during Ramadan), also increased local reef fishing effort. 39% of respondents reported an increase in their consumption of reef fish during Ramadan. One respondent mentioned that reef fish were essential during this period as "the morning meal always needs fried reef fish". Apart from fresh reef fish, the consumption of canned and smoked tuna (*valhomas*) also increased during Ramadan. Our study was conducted in the early part of 2020, but it is likely that reef fish consumption varies through the year, spiking during Ramadan. This is indicative of a dynamic landscape of personal preference and choice, which has the potential to impact island food systems, the nutritional health of communities, and the ecology of coral reefs in this archipelago. While contemporary reef fishing methods (outside of the bait fishery) are still fairly inefficient (e.g., handlines), an increased demand among the local population, alongside resort demand, could quickly lead to increased fishing on coral reefs, with more efficient and potentially more destructive gear types. Notably, the reef fishery does not currently have a cohesive national management plan in the Maldives. While there are yearly fisheries regulations that recommend the implementation of rules (e.g., General Fisheries Regulation 2020/R-75) there is a lack of data on how and where these are implemented and monitored (Jaleel 2013). Identifying times of the month and year when the extraction of a resource increases – and the reasons for it – can be useful in implementing management designs that are steeped in local knowledge. Similarly, we suggest that future work should seek to better understand the linkages between a resort's consumption dynamics with respect to the increasing exploitation of the reef fishery and the domestic consumption of reef fish among the broader community.

3.6 CONCLUSIONS

In conclusion, our study finds that reef fish are being actively consumed in local households in Dhaalu atoll, Maldives, and 58% of our respondents reported a preference for reef fish over tuna today. This highlights the need to better account for the preferences and choices around fish consumption and their seasonalities in particular cultures and societies across the globe's island and coastal communities. If reef fishes continue to increase in their popularity, and if governing bodies do not monitor and manage their catch across the Maldives, the feedbacks to coral reef ecosystems could be quick and damaging. Here we suggest that preferences, along with consumption data, may be used as an early indicator of changing diets, but also that their incorporation into fisheries planning can help ensure that different stakeholder values guide and inform future management decisions. Second, we document an increase in the catch and demand for reef fish during particular times of the month and year, information that may help guide the formulation of future management plans. Finally, we emphasize the need to examine women's roles in local reef fisheries in the Maldives, especially in the context of island food and nutritional security.

Sustainably managing fisheries so that their ecological and social functions are maintained remains one of the major challenges for marine conservation. It has become increasingly clear that equitable conservation policies will need to take a trans-disciplinary approach to be successful, integrating perspectives from both the natural and social sciences. People's values guide the choices they make and impact their wellbeing and ability to adapt to change (Hicks et al. 2016b). As the pressures of climate change continue to alter habitats worldwide, engaging with and integrating the human dimensions of social-ecological systems will be necessary to help formulate, guide, and improve on conservation outcomes.

3.7 PUBLISHED ARTICLE CITATION

Yadav S, Fisam A, Dacks R, Madin J, Mawyer A (2021) Shifting fish consumption preferences can impact coral reef resilience in the Maldives. Marine Policy, 134 (2021), DOI: https://doi.org/10.1016/j.marpol.2021.104773

3.8 TABLES

Table 3.1: Results of best model (preference ~ gender + age + (1 | island)) for glmm testing determinants of fish preference

Random effect:	**Variance**	**Std.Dev.**		
Island (intercept)	0.370	0.609		
Fixed effects:	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
Female (intercept)	2.92	1.023	2.856	0.004
Male	-2.094	0.588	-3.559	0
Age	-0.045	0.019	-2.404	0.016

Table 3.2: Themes related to fishing and fisheries that emerged during interviews with full-time fishers. Quotes provided in this table elucidate some of the differing views that fishers held with regards to each line of questioning. Topics are ordered in descending order, from most to least mentions.

Theme	**Number of individuals mentioning theme**	**Impact on fishing**
Changes in reef fish abundance and composition	22	"The size of the fish hasn't changed but the numbers have reduced" "Number of fishers more now, so we get less fish" "No change in fish numbers but the reef is dead"

Resort demand	12	“Resorts drive reef fish catch” “Demand for reef fish has increased since resorts came up… more people engaged in reef fishing today” “Now reef fishers here go reef fishing on a demand basis… if resort requests it, they go”
Impacts of coral bleaching	11	“Less baitfish like Chromis because of coral bleaching” “Bait fishing has reduced because of coral bleaching” “Chromis spp. is difficult to find now after coral bleaching”
Seasonality in reef fishing	10	“During Ramadan people stay on the island and fish on reefs” “Reef fish catch is higher during full and new moon periods” “I target trevallies during the 28^{th} and 29^{th} and red snappers during the 14^{th}-17^{th} days of the lunar month”

Impacts of development	7	"There's been no change or decrease in fish even with reclamation" "During reclamation there weren't that many fish around, but it's getting better again" "The entire coastline has changed because of reclamation and the fish have also changed in response to this"
Impacts of changing bait fishing practices	6	"Number of reef fish has decreased because there's light being used in bait fishing" "Diving to catch baitfish should be banned because we end up catching the full community" "Earlier, people wouldn't go beyond the atoll for bait. Now people are able to go further because of bigger engines"
Impacts of changing gear	3	"New fishing tools have made it easier to catch more fish"

3.9 FIGURES

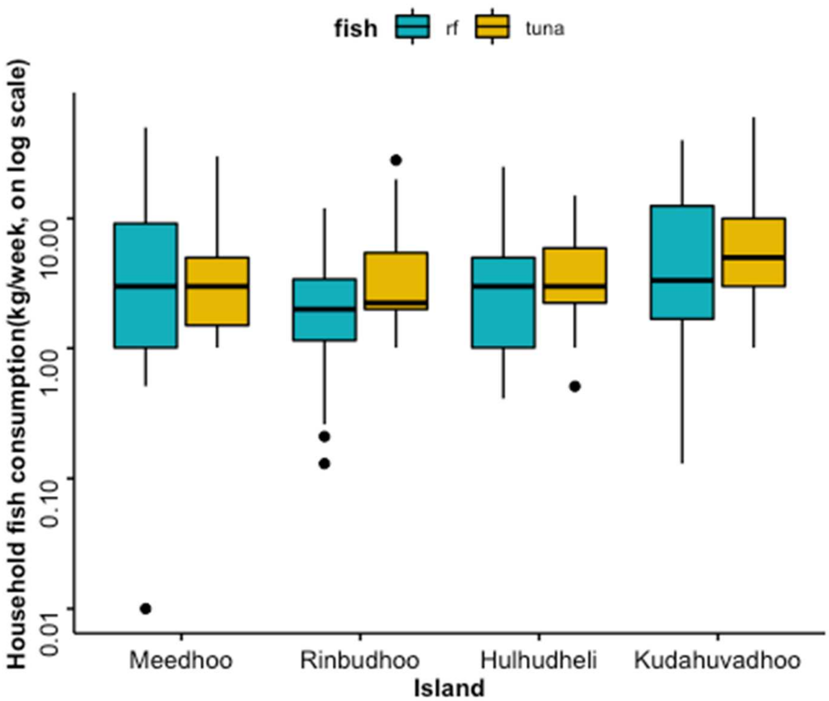

Figure 3.1: Household consumption of reef fish and tuna (kg/week, on log scale) across the four islands surveyed (n=22, 25, 26, 27, for each island respectively). Colors indicate fish consumed (blue=reef fish(rf); yellow=tuna).

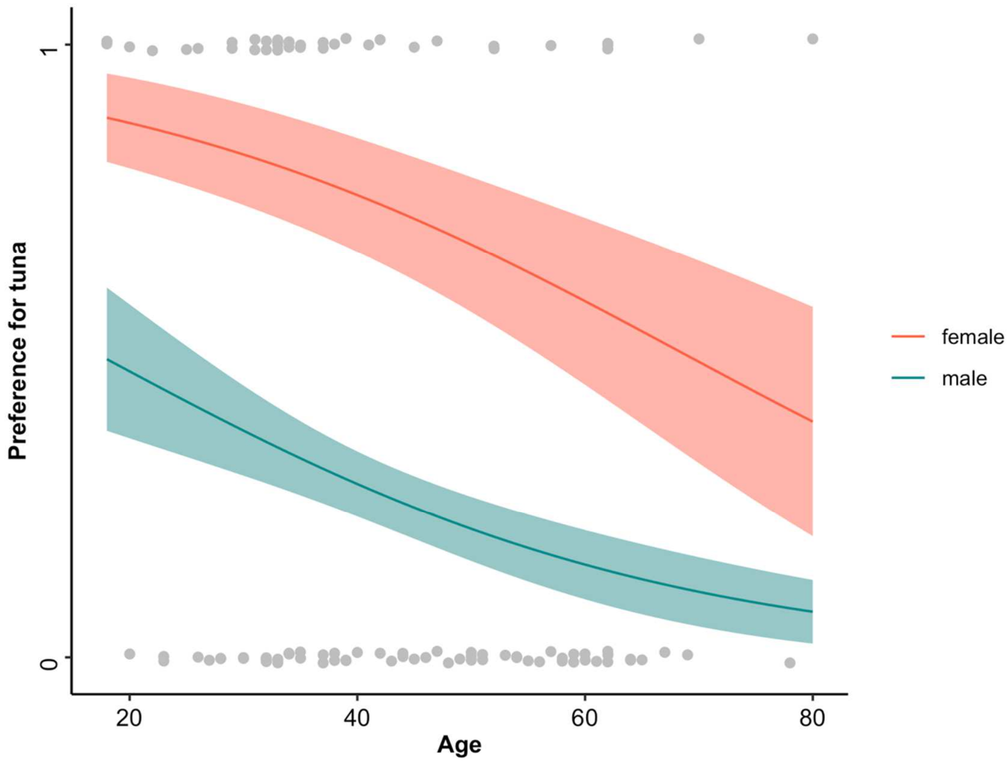

Figure 3.2: Preference for tuna (1) or reef fish (0) as a function of age (x axis) and gender (female=red, male=teal). Grey points are the raw data (n=100). Lines are model predictions with shaded areas showing standard error.

3.10 SUPPLEMENTARY INFORMATION

Survey Methods

All our surveys were carried out on Dhaalu atoll, in the central province of the Maldives (see Table S1 for differences in demographic information between islands). There are currently six luxury resorts in Dhaalu atoll, all located close to community islands (15 minutes to an hour by boat). These form the main markets for reef fish, and all the full-time reef fishers we interviewed either sold their catch directly to resorts or to local buyers on islands, who then sold to resorts or to other buyers in Malé. Depending on the resort and what condition the fish was sold in (whole vs gutted, cleaned, etc.) resorts bought reef fish for anywhere between 20-45 mvr/kg (USD 1.3-3/kg) directly from fishers. Fish were sold by weight, and fishers did not indicate any differences in the prices for different species. Although there are over 40 designated protected areas in the Maldives, and some management of the grouper fishery, we did not encounter any local-level monitoring or management of the reef fishery during our surveys. Geographically, the Maldives presents a significant challenge in this regard. We conducted this study at this relatively small spatial scale because we were interested in assessing the local dynamics that influence marine resource extraction and consumption.

Islands surveyed	**Meedhoo**	**Rinbudhoo**	**Hulhudheli**	**Kudahuvadhoo**
Population (census 2016)	958	278	719	2443
Number of interviews conducted	22	25	26	27
Area	0.45 x 0.27 km	0.95 x 0.32 km	0.95 x 0.30 km	1.15 x 0.87 km
Airport	N	N	N	Y
Ice plant	N	N	N	Y

Minimum distance to nearest resort (km)	0.7956	3.445	6.048	4.223

Table S1: Island-level differences in population, size, relative development, and resort proximity

All interviews were conducted outdoors in public spaces unless we were invited to enter a house. Interviews were conducted in English or Dhivehi (the local language), based on the respondent's preference. Of the total number of interviews, 22 took place on Meedhoo, 25 on Rinbudhoo, 26 on Hulhudheli, and 27 on Kudahuvadhoo. All interviews were conducted in January-February 2020 by SY and AF and ranged from 25 minutes – 1.5 hours. All respondents were above the age of 18. Surveys were approved by the University of Hawaii's Institutional Review Board and local island councils.

We used a mixed methods approach for our study, combining both quantitative and qualitative questions in our surveys. The primary goal of our study was to identify the drivers of individual fish preference and household consumption in Dhaalu atoll. For this section of our interviews, our questions were more structured, aimed at gathering information on variables such as the quantity of different species of fish consumed (kg) in households, the price of fish, individual preference for certain fish (for which we used an identification guide with photographs and drawings of common reef fish), people's professions, the percentage of household income that came from fishing, historical preference (what one grew up eating), etc.

A secondary component of our work was to document fishers' perceptions of change through time. We gathered information on what they fished, where they sold their catch, and seasonality in fishing effort. This part of our interview was more open-ended to encourage discussion and explore topics around reef fishing that might emerge during our conversations. However, our focus was on identifying themes that fishers described as influencing their catch of reef fish. Of the 100 respondents we interviewed, 56 were fishers, and these questions were only directed at them.

Note on researcher positionality

We would like to acknowledge that the goals, personality, and perceptions of a researcher all influence how respondents share their knowledge and participate in a study. In this case, participants were briefed on the objectives of the research as being part of the lead author's PhD, with the primary objective being to better understand local fish preferences and consumption patterns in this atoll. On all islands, we approached local councils before we began our surveys to explain our broader goals and study design and only proceeded when there was clear approval to do so. Care was taken to ensure that our research was culturally respectful. While the lead author (S.Y) has conducted research in these islands for 3 years and the facilitator (A.F) for his entire life, this was our first visit to these particular communities.

Survey Questionnaire

Introduction and consent

Hello, I am a PhD student at the University of Hawaii. I study coral reefs in the Maldives, and I am interested in knowing about the kinds of fish - especially tuna and reef fish - that people are eating today, your favorite dishes, and what you prefer to eat and why. Are you willing to answer some questions about your consumption of fish, and fishing practices (if relevant), sales (if relevant)? Your names will not be used in any part of this study, and all information will be kept confidential. If you feel uncomfortable answering any of these questions, you are free to stop participating at any time.

Name:
Gender:
Age:
Location:
Profession:

Reef fish and tuna consumption

1. Growing up, how much reef fish did you eat (daily, weekly)? Would you say you ate more reef fish or tuna? (% of reef fish, % of tuna)
2. Do you have a preferred species of reef fish or tuna? Do you cook or prepare this in any particular way? (hand out pictures)
3. Roughly how many times a week do you eat reef fish?
4. Do you mostly purchase reef fish or catch it yourself? Do you share your catch with others or do people share their catch with you? What % is bought, caught, or shared?
5. If you buy, how much do you buy per day (or per week)? (__ week, ___ month, ___ year)
6. Do you eat more or less reef fish during certain times of the year (e.g., during the monsoon, Ramadan, Eid)? Do you eat particular species at different times of the year?
7. How often do you eat tuna in your household? Skipjack/yellowfin?
8. Where do you get your tuna from? Is it fresh, canned, or dried?
9. Do you eat more or less tuna during certain times of the year (e.g., during Eid)?
10. Do you have any special preparations of fish during festivals like Eid and Ramadan?
11. What's your favorite fish dish? What are the different ways in which you prepare tuna and reef fish (rihakuru, dried tuna, smoked, curry, short eats, etc)
12. Do you think you eat more reef fish or tuna today? (% reef fish, % tuna)
13. Do you enjoy eating tuna or reef fish more? Why or why not? What kind of tuna/reef fish?

Fishing practice and sales

14. Do you go reef fishing? If so, how long have you been fishing for?
15. How often do you go reef fishing in a week? Does this change during the monsoon?
16. What method of reef fishing do you use, and what gear? (handlines, cast net, spear, etc). Has this changed over time for you, or is it changing?
17. Using these pictures, can you tell me what you generally fish for (a) in the reef and/or (b) in the lagoon?
18. Using these pictures, can you tell me what reef fish you generally fish for, and how?
19. Using these pictures, can you sort the fish that you generally sell vs those you take home to eat?
20. Where or to whom do you generally sell your catch?
21. How much do you get for different reef fish species?

Demographics

22. How many people (adults and children) live in your household?
23. Would you mind sharing the average income of your household?
24. In the last 10-20 years, have you noticed any changes to the number, size, and types of fish being caught on the reef? What do you think is causing these changes?

Analyses

Consumption of reef fish and tuna

Consumption (kg/week) of reef fish and tuna was calculated by respondents answers to Q5. While most respondents answered this question for the household, 8 individuals answered this question at the individual level. In these cases, household consumption values were calculated by extrapolating for the number of people in their household (Q22). We tested for differences in household consumption of reef fish and tuna across the four islands surveyed using a two-way ANOVA (Table S2). There were no significant differences in the consumption of reef fish and tuna across households, while islands differed significantly in their overall consumption of fish. This indicates that there are some local differences between islands that influence what is consumed. For instance, Kudahuvadhoo (the most developed island, with the highest population density) had highest average consumption of reef fish and tuna, while Rinbudhoo (smallest island, with lowest population) had lowest average consumption.

	Df	**Sum. Sq**	**Mean Sq**	**F value**	**Pr (>F)**
fish_identity	1	2.30	2.3027	3.271	0.0724
island	3	5.55	1.8506	2.628	0.0522 *
Residuals	158	111.25	0.7041		

Table S2: ANOVA testing for differences in the household consumption of fish_identity (reef fish and tuna) across islands. Data were log (x+1) transformed to avoid zero values and improve normality of the data.

Preferences for reef fish and tuna

Preferences for reef fish and tuna were assessed from respondents answers to Q2. Species-specific responses to this question were pooled into broad categories of "reef fish" or "tuna". Reef-associated fish species were also considered reef fish. Historical fish preference was assessed by respondents answers to Q1 in comparison with Q12. Summary of data is presented in Table S4. We used a generalized linear mixed model to test for the drivers of preference, with island as a random variable. Preferences for reef fish and tuna were driven by gender and age. Our full model was: preferences ~ gender + age + profession + historical fish preference + island (random) (Table S3) and we sequentially dropped variables to arrive at our best model. Fig. 1 shows the spread of our data (mean and variance of age) with gender among the surveyed population.

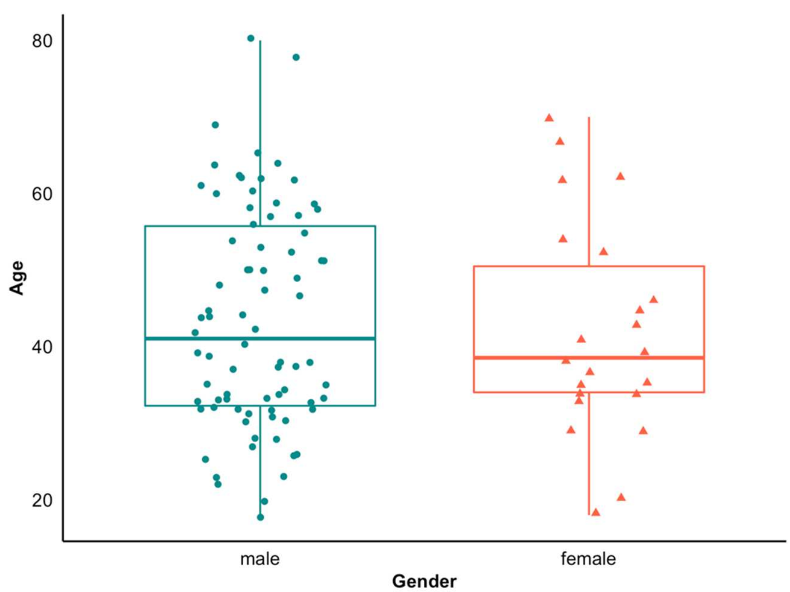

Fig.1: Mean and variance of age with gender among surveyed population

Table S4: Summary of data on gender, profession (i.e., fisher identity, based on full-time reef fishing, tuna fishing, or other) and historical preference of respondents by island.

Respondents who had mixed preference or did not answer (N/A) were not included in the model testing for preference.

Island	**Respondents (n)**		**Tuna fishers**	**Reef fishers**	**Other**	**Historical preferences**			
	Male	Female				Reef fish	Tuna	Mixed	N/A
Kudahuvadhoo	22	5	7	0	20	6	15	5	1
Meedhoo	17	5	8	5	9	3	5	1	13
Hulhudheli	21	5	6	1	19	12	11	2	1
Rinbudhoo	18	7	1	1	23	9	15	1	0

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CHAPTER 4

FINE-SCALE VARIABILITY IN CORAL BLEACHING AND MORTALITY DURING A MARINE HEATWAVE

4.1 ABSTRACT

Coral bleaching and mortality can show significant spatial and taxonomic heterogeneity at local scales, highlighting the need to understand the fine-scale drivers and impacts of thermal stress. In this study, we used structure-from-motion photogrammetry to track coral bleaching, mortality, and changes in community composition during the 2019 marine heatwave in Kāneʻohe Bay, Hawaiʻi. We surveyed 30 shallow reef patches every 3 weeks for the duration of the bleaching event (August-December) and one year after, resulting in a total of 210 large-area, high-resolution photomosaics that enabled us to follow the fate of thousands of coral colonies through time. We also measured environmental variables such as temperature, sedimentation, depth, and wave velocity at each of these sites, and extracted estimates of habitat complexity (rugosity R and fractal dimension D) from digital elevation models to better understand their effects on patterns of bleaching and mortality. We found that up to 80% of corals experienced moderate to severe bleaching in this period, with peak bleaching occurring in October when heat stress (DHW) reached its maximum. Mortality continued to accumulate as bleaching levels dropped, driving large declines in heat-susceptible species (77% loss of *Pocillopora* cover) and moderate declines in heat-tolerant species (19% and 23% for *Porites compressa* and *Montipora capitata*, respectively). Declines in live coral were accompanied by a rapid increase in algal cover. Spatial differences in bleaching were significantly linked to habitat complexity and coral species composition, with reefs that were dominated by *Pocillopora* experiencing the most severe bleaching. Mortality was also influenced by species composition, fractal dimension, and site-level differences in thermal stress. Our results demonstrate that spatial heterogeneity in the impacts of bleaching are driven by a mix of environmental variation and differences in assemblage composition.

Keywords: bleaching, SfM photogrammetry, ocean warming, habitat complexity, Hawaiʻi

4.2 INTRODUCTION

Increasingly severe and frequent marine heat waves have caused large-scale losses in coral cover (Heron et al., 2016; Spalding & Brown, 2015). In the past decade alone, consecutive thermal stress events in 2014, 2015, 2016, and 2017 have had global impacts on the structure and functioning of coral reef ecosystems (Arthur et al., 2006; Hughes et al., 2017). Elevated temperatures disrupt the partnership between corals and their algal symbionts (*Symbiodineacea*) causing them to lose their color, and in cases of prolonged stress, die (Hoegh-Guldberg, 1999). Degraded reefs support reduced biodiversity, which has implications for marine food webs, nutrient cycling, and fisheries (Alvarez-Filip et al., 2009; Eddy et al., 2021). Furthermore, they are unable to attenuate wave energy, making coastlines more vulnerable to storms and cyclones (Ferrario et al., 2014). These changes directly affect the social and economic resilience of communities that depend on reef ecosystems for their lives and livelihoods.

Part of the challenge of managing reefs for their resilience is that the effects of elevated temperatures are not homogenous across coral species, habitats, and geographies, with some species and some locations better able to resist and recover from thermal stress than others. Resilience to bleaching involves a range of processes. If corals die, recovery potential is dependent on the replenishment of populations through larval recruitment and growth, which may take decades (Hughes et al., 2000). Yet, corals can also avoid mortality by restoring symbiont populations and regaining colour in months (i.e., individual-level recovery) (Gilmour et al. 2013). Biotic variability in resilience to bleaching is therefore derived from many sources, from regional "supply-side" dynamics to differences in host *Symbiodinium* (Jones et al., 2008) and coral colony size and morphology (Brandt, 2009). Some coral genera like *Acropora* and *Pocillopora* have generally been recorded to be more bleaching susceptible than others but are also often the species that drive recovery after a major disturbance (Burt et al., 2008; Marshall & Baird, 2000). In some cases, corals in deeper reefs have been able to better withstand elevated temperatures than shallower ones (Bridge et al., 2013; Baird et al. 2018) but coral species in some shallow lagoonal environments have also shown a remarkable capacity for resistance to high temperatures through their association with thermally tolerant symbionts and/or via host mediated adaptaion and acclimatization (Craig et al., 2001; Cunning et al., 2016; Drury, 2020; Roach et al., 2020).

Several local environmental factors may also influence spatial differences in bleaching susceptibility. For example, local upwelling may cool warm surface waters, and high water flow resulting from currents and turbulence can result in reduced coral bleaching severity (West & Salm, 2003). Cloud cover (Mumby et al., 2001) and turbid water conditions can help decrease irradiance, but high sediment loads can cause smothering of coral polyps and reduced respiration, a decline in the photosynthetic productivity of zooxanthellae, and have several sublethal effects such as lowered calcification rates, damage to tissue, and reduced growth (Erftemeijer et al., 2012). Colony and reef-scale structural complexity may also work in sometimes opposing ways to influence the degree of thermal stress a reef experiences. Highly rugose environments may be able to create shade within habitats, thereby helping to reduce temperatures in small pockets of the reef. However, colonies that have higher surface complexity and increased light-harvesting ability can also have higher susceptibility to bleaching as a result (Marcelino et al. 2013). On the other hand, colony microcomplexity can modify envrionemntal conditions at small scales (Chamberlain and Graus 1975) thereby altering their response to stress.

In addition to all these factors, the natural history and long-term environmental conditions of a particular reef can also influence how coral taxa respond to disturbance, especially if historical conditions may have favored adaptation or tolerance to stress. Kāneʻohe Bay, where this study was conducted, has experienced a unique history of human impacts (Hunter and Evans, 1995). From the 1940s to the 1970s, extensive dredging, land runoff, and the discharge of raw, untreated sewage in the southern section of the Bay lead to anoxic and turbid conditions and the proliferation of *Dictyosphaeria cavernosa,* which outcompeted corals on many reefs (Hunter and Evans 1995). These reefs were also subject to multiple freshwater kills in 1965, 1969, 1987 (Sukhraj 2014) and more recently, in 2014 (Bahr et al. 2015). After the diversion of the sewage outfall in 1977-78, however, coral cover began to increase, and stands today at nearly 60%. Their recovery is especially striking given that Hawaiian reefs have suffered from coral disease outbreaks in 2011, 2012, and 2015 (Jury & Toonen, 2019) and have been exposed to multiple coral bleaching events in 1996, 2002, 2004, and more recently, in 2014 and 2015 (Bahr et al., 2017). Additionally, the corals in Kāneʻohe are living at temperatures 1-2 °C higher than surrounding waters and under elevated pCO_2 conditions (Bahr et al., 2015), yet these parameters vary extensively across the Bay (Guadayol et al. 2014). This history of living under elevated stress is thought to be one of the main factors contributing to the resilience of these reefs (Jury and Toonen 2019). However, reef response appears to change with every bleaching event because of changes in local environmental condtions. For instance, Bahr et al. (2017) reported that patterns of bleaching and mortality in Kāneʻohe Bay differed after 1996, 2014, and 2015, due to differences in the direction and magnitude of thermal stress and degree of freshwater inflow into the Bay prior to the bleaching event. Reef resilience is not static and understanding how changing conditions interact to affect patterns of coral bleaching and mortality – especially as temperature anomalies become more frequent – is a top conservation priority.

New tools and techniques like structure-from-motion photogrammetry (hereby, SfM) now enable robust and efficient quantification of reef structure and community change in ways that traditional techniques have not been able to accomplish before (Pizarro et al., 2017). Photogrammetry is the process of extracting quantitative information about a scene (in this case, a reef) through the collection of a series of 2-dimensional images (Burns et al. 2015; Pizarro et al., 2017). These overlapping 2D images can then be stitched together to estimate 3-dimensional structure and may be utilized to extract data on a range of metrics, from community demography, to several measures of surface complexity (rugosity, fractal dimension, and height range) and estimates of shelter space and volume (Torres-Pulliza et al., 2020; Million et al., 2021). Because SfM generates high resolution orthophotos and photogrammetric products can be spatially registered, using this technique can be especially useful to track changes in colony health through time.

In this study, we tracked the fine-scale responses of 30 coral reefs throughout Kāneʻohe Bay using SfM during a bleaching event in the summer and autumn months of 2019. Our primarly goal was to quantify the spatial, temporal, and taxonomic variability in bleaching severity and mortality across the Bay. In addition, the spatial and temporal resolution of our data also allowed us to test hypotheses about the environmental and ecological factors that may have influenced these patterns. To assess this, we collected data on temperature, depth, sedimentation, and wave velocity, alongside estimates of habitat complexity. We hypothesized that differences in coral assemblage and reef-level environmental conditions would influence bleaching severity and mortality. In particular, based on previous work in Kāneʻohe Bay, we expected bleaching to be lower in reefs that experienced conditions of lowered irradiance, potentially mediated by depth, the amount of suspended matter in the water column, and wave velocity (Bahr et al. 2017). We also expected bleaching severity and associated mortality to be highest in shallow reefs or those that experienced high temperatures, since the magnitude of thermal stress is a well known driver of the degree of bleaching and mortality (Eakin et al., 2010; Hughes et al., 2017). We predicted that reefs that were dominated by heat-susceptible species would experience more severe stress and elevated mortality (Loya et al., 2001) and expected the three-dimensional complexity of a reef to also influence the degree of bleaching and mortality it experienced.

4.3 METHODS

4.3.A Field methods

Data collection using Structure-from-motion photogrammetry (SfM)

We collected imagery at 30 patch reefs spread across the north-south extent of Kāne‘ohe Bay (Fig.1). These sites have been monitored since 2017 and represent a broad range of exposures and environmental conditions (Caruso et al., 2021). We began our surveys in August 2019 when we began to detect extensive coral paling due to rising temperatures.

Our field methods have been described in detail in Roach et al. (2021). In short, we used a spool and line set-up to image approximately 112 m^2, to create orthomosaics and digital elevation models (later cropped to 64 m^2 for annotation). We used a Canon EOS Rebel SL3 DSLR in a waterproof housing with a wide angle 18-mm lens to ensure high overlap between images since these sites were all relatively shallow (2-5 m). Images were collected via SCUBA or snorkel depending on the depth of the site. The swimmer operating the camera system collected imagery by swimming in an outward spiral with the camera held roughly 1 m above the benthos, starting from the central point of the spool. Another individual held the center pole stationary over a cinder block used to mark the central point of these sites. Once the swimmer reached the outer edge of the spiral, they returned inwards in the same spiral swim pattern to the center, with the camera continuing to take pictures. An average of 3500-4500 images were collected per site; roughly 3 images/second. A site took approximately 20 minutes to map in the field. At each site, we placed 3 calibration markers in the area prior to imaging to help align images during processing. At each of these markers, we noted a) depth and b) compass bearing in relation to the center of the reef area being imaged. These were then used to accurately align and georeference models respectively.

We monitored each of the 30 patch reefs every 3-4 weeks between August 2019 - November 2019, which corresponded to peak bleaching period. Following this, we resurveyed sites in January 2020 and again in September 2020, one year after the bleaching event. This resulted in a total of 210 reef models across all sites and time points. We discarded 30 of these models due to holes in the model or poor-quality imagery.

Quantifying the environmental characteristics of reefs

Data on temperature, sediment, and wave energy were collected as part of a study on coral clonality and we refer the reader to this for further details (see Caruso et al., 2021). In short, temperature data was collected alongside photogrammetry imagery at each site at 10-minute intervals on Hobo Pendent or Water Temp Pro V2 loggers from the center of each site. We summarized hourly temperatures per day to calculate daily means. We used this to estimate Degree Heating Weeks (DHW) as time spent above the maximum monthly mean (MMM+1 degree, or 28° C for Kāneʻohe Bay; Jury & Toonen, 2019). DHW have become a common predictor of coral bleaching, with significant bleaching usually occurring at over 4 DHW, and we use mean DHW in our analyses of bleaching and mortality. We used average temperature values from October 16th -31st for the entire month due to a gap in sampling in the first two weeks of October.

16” capped PVC pipes were used to collect sediment data every 1-2 months for each site between 2017-2019. Given that these sites differ significantly in their water residence times, these sedimentation rates are likely more indicate of the suspended particulate matter in the water column rather than how much new material is being deposited on a reef. Sediment data were not collected during the bleaching period, but we use mean sediment values for every site over the two-year duration of collection in our analyses.

Current meters were deployed at a cement block at a single site in every region in 2019 and used to calculate root mean square (RMS) wave velocity (Caruso et al., 2021). Regions were primarily defined based on water flow conditions, with sites in the north-northwest (region 5) having lowest water residence times (~1 day), those in the central section of the Bay (regions 2, 3, 4) experiencing moderate water residence times of 2-10 days based on their relative exposures, while sites in the southernmost section (region 1) had significantly higher water residence times of 1-2 months (Lowe et al., 2009). These values were extrapolated to all sites within a region. Depth was measured from the center of each site.

4.3.B Data processing and analysis

Processing 3D reef models and measuring bleaching severity

Images for every site were aligned in Agisoft Metashape Pro (Version 1.7.6). Prior to alignment, photographs that were out of focus or in blue water were manually removed. 2D orthophotos and gridded digital elevation models (DEMs) were created for each site following a standard workflow that begins with photo alignment, and leads to the creation of a 3D dense point cloud, from which textured meshes, DEMs, and orthophotos (also referred to as orthophoto mosaics, or orthomosaics) were outputted (Burns et al. 2015). Depth and compass measurements were used to accurately calibrate and georeference individual models. Completed orthomosaics were imported into QGIS 3.16 for further analysis. All models were cropped to an 8 m x 8 m square, so that the area analyzed in every mosaic was 64 m^2. 640 random points (or 10 per m^2) were overlaid on the mosaic shapefile. For each point, we assessed benthic status in 22 categories (e.g., coral, cca, turf, macroalgae, rubble, dead skeleton; see Supplementary Table 1). When the substrate was a coral species, we assessed its bleaching status using the categories 0-3, where 0=healthy, 1=pale, 2=significantly bleached, 3=stark white. When a coral died, its identity changed most commonly to “dead skeleton”, “turf”, or “cca”. While we identified a total of nine coral species in our reef sites, *Porites compressa* and *Montipora capitata* make up the large majority (>90%) of the coral cover on many reefs here. We therefore restricted our analyses to individuals of these species and *Pocillopora*, that were abundant in a number of our survey sites. *Pocillopora* (*P.meandrina* and *P.damicornis*) were grouped by genus due to their diverse colony morphologies in Kāneʻohe Bay and recent taxonomic reclassifications that make them difficult to accurately identify visually (Johnston et al., 2018). We tracked the same 640 points through time for every reef site (Fig.1). From this we summarized data on the community composition at every site and used a multivariate analysis to assess how the relative proportion of different substrates changed through the bleaching event.

DEMs were also exported into *QGIS* and cropped to the same size as orthomosaics (Fig.1). We divided them into 16 contiguous squares (covering an area of 64 m^2) from which surface rugosity (R) and fractal dimension (D) were calculated for 2 x 2 m grids for every DEM, making up a total of 16 values per site, using the same methodology as Torres-Pulliza et al. (2021). R values were log-transformed, and all 16 R and D values from the first survey time were used in models assessing bleaching severity and mortality. Completed annotation shapefiles and habitat complexity metrics were imported into the statistical software R for further analysis (R Core Team, 2021).

Data analysis

We quantified the drivers of bleaching severity using a cumulative link mixed model since our response variable was categorial. The response variable in our model was bleaching severity (i.e., status 0-3). Our fixed effect variables were maximum DHW, depth, mean sediment, wave velocity, coral species, rugosity, and fractal dimension. Site was included as a random effect to account for site-level differences not explained by fixed effects. For model selection we built our full model, an environmental model with only environmental data (DHW, depth, sediment, wave velocity), and an ecological model with only our ecoloical data (rugosity, fractal dimension, species composition). We dropped non-significant fixed-effects terms sequentially, based on log-likelihood ratio tests. We selected our best model based on the lowest Akaike Information Criteria (AIC) values (Supplementary Table 4). Models were fitted using “clmm” in the R package “ordinal” (Christenson 2018).

To identify the strongest predictors of mortality we used a generalized mixed effects model (glmer) with a binomial distribution. Our fixed effects were mean DHW, depth, mean sedimentation, wave velocity, fractal dimension, rugosity, and substrate, while site was a random effect. We used mean DHW as opposed to maximum DHW in this analysis to better capture change in temperature through time, but both mean and max had the same effect in our model. Similar to the clmm, we built our full model, an environmnetal model, and an ecological model seperately. We dropped non-significant variables sequentially to get our best model (Supplementary Table 5).

4.4 RESULTS

4.4. A Coral bleaching and mortality

We recorded extensive coral bleaching during August-December 2019, with 80% of all corals showing some signs of bleaching in this period (Figs.2b,3a). Sea water temperatures in Kāneʻohe Bay peaked in August and September 2019 (Fig.2a), but degree heating weeks (DHW) were highest in October (7° C week). Mean DHW between August-November was 5.3 (° C week). Sites varied from each other in their mean daily temperatures, which ranged from 26-31°C through the bleaching period (Fig.2a). Although many corals began to bleach in August when seawater temperatures were at their highest, peak bleaching coincided with maximum degree heating weeks in October (7 DHW, Fig.3a). Bleaching severity varied markedly with species, with *Pocillopora* the most severely affected, followed by *Porites compressa* and *Montipora capitata* (Fig.2b). *Pocillopora* generally bleached earliest and experienced a second peak in bleaching in some sites in November. *P.compressa* and *M.capitata* experienced similar patterns in bleaching severity, with the majority of surveyed corals in status 1 or pale (Fig. 2b).
All three species we tracked experienced some mortality from bleaching. Mortality was lowest for *Porites compressa* (19%) followed by *Montipora capitata* (23%) and *Pocillopora* (77.5%) (Fig.2c). Due to the methods we used, these rates are more indicative of the death of individual points on coral colonies rather than whole colony mortality. Mortality rates in this study are therefore best interpreted as a decrease in overall coral cover rather than the loss of entire colonies. In general, mortality peaked in October but continued to accumulate throughout the bleaching period (Fig.2c). However, maximum mortality for *M.capitata* occurred in January after temperatures had dropped. Mortality was strongly linked to bleaching stress, with the chance of mortality for all species increasing with bleaching status, peaking at status 3 (stark white).

4.4.B Compositional and environmental drivers

Bleaching severity and mortality were each influenced by species composition and local abiotic conditions, creating variation in the impacts of thermal stress across the study site (Figs.3, 4). Sedimentation rates varied substantially across reefs, ranging nearly 300-fold from 0.01 g/day to 2.93 g/day across sites (see Caruso et al. 2021). RMS (wave velocity) ranged from 0.8 to 12.56 cm/s. Sites in the northern sections of the Bay (Region 5) had higher sediment levels as well as higher RMS than sites in other regions (Fig. 3b). In contrast, sites in Region 1 clustered together based on their rugosity (R). Depth varied between 0.5-3.5 m across all reef sites (with a ~0.4 m daily tidal fluctuation). In addition, sites differed in their relative cover of different substrates with live coral cover highest in Regions 2 and 4 (Fig 3c). Turf, bare coral skeleton, and sand and rubble made up over half of the cover in sites in Regions 1 and 3. Crustose coralline algae (CCA) had highest cover in region 5 (Fig. 3c).

Our analysis showed that habitat complexity (rugosity R, fractal dimension D) and coral species were important predictors of bleaching severity (Table 1). Coral assemblage had the largest effect on bleaching severity, with sites dominated by heat-sensitive *Pocillopora* experiencing more severe bleaching than others ($p < 0.001$). Following this, sites that bleached more severely were associated with higher scores of fractal dimension D ($p < 0.001$, Table 1). In contrast, there was a negative relationship between bleaching severity and rugosity ($p < 0.05$), with more severe bleaching occurring in reefs with lower rugosity scores (Fig.4). Sediment loads had a slight negative effect on bleaching severity, with corals bleaching more severely in reefs with lower levels of sedimentation. We did not find an effect of depth, wave velocity, or DHW on bleaching severity (Supplementary Table 2).

Coral mortality was strongly affected by thermal stress, coral species composition, and fractal dimension. Predictably, heat-susceptible *Pocillopora* suffered maximum mortality during this event and had the largest effect in our model (Table 2). Notably, fractal dimension (D) had the same effect on mortality as it did on bleaching severity, with sites with higher D experiencing more mortality. Variability in average thermal stress across reefs also impacted mortality rates, with mortality increasing in reefs that experienced a higher number of degree heating weeks (Fig. 4).

The 3D mosaics resulting from our imagery allowed us to quantify fine-scale compositional changes across a large area (30 sites, and 19200 points covering 1920 sq m of area). By quantifying proportional change in the cover of key taxonomic groups at each site, we identified a marked shift in the composition of reefs as mortality progressed (Fig.5a,b). Moreover, even though sites varied considerably in their initial compositions, there was a common trend towards an increase in benthic algal cover post-mortality (Fig.5c). A decrease in coral cover was accompanied by an increase in the cover of turf and macroalgae (Fig.5b).

We did not note any significant changes in the three-dimensioanl structural complexity of reefs during this one year period (Supplementary Fig.5).

4.5 DISCUSSION

The results of this study show that corals in Kāneʻohe Bay experienced a moderate to severe bleaching event in 2019, with up to 80% of corals showing some signs of stress during this period. In general, reefs around O'ahu did bleach more extensively (~43%) than other Hawaiian islands during the 2019 event (Winston et al. 2020). Variation in bleahing severity in Kāneʻohe Bay was mediated by sediment levels and species composition, while mortality was driven largely by temperature and the identity of the coral.

4.5.A Severity and extent of bleaching

Peak bleaching stress in all parts of the Bay occurred in the month of October – while temperatures were highest in August and September, October had the highest degree heating weeks (7 DHW). This follows a similar pattern to the bleaching events in 2014 and 2015, when DHW were highest in September and October (Ritson-Williams & Gates, 2020). However, cumulative thermal stress over the bleaching period was lower in 2019 (this study) at 5.3 DHW over the 4-month bleaching period, as opposed to 6 DHW in 2014 and 12 DHW in 2015. Corals generally begin to show significant signs of stress at above 4 DHW; however, in 2019, many corals began to bleach in August when DHW were only 3.3. After rising to 32°C in August, seawater temperatures dropped to 27°C in November, and to 25.5°C by December. In general, Kāneʻohe bay experiences significant fluctuations in SSTs, swinging from 19°C in winter months to 29.3°C during normal summers (Caruso et al., 2021; Ritson-Williams & Gates, 2020). In the past, temperatures have crossed 30°C only in 1996, 2014, and 2015, for a maximum of 17 days in 2015. During this bleaching event, some sites experienced temperatures above 30°C for an entire month.

The overall rates of bleaching we record in this study are higher than those recorded in 2014 (~65%) and 2015 (~50%) (Bahr et al., 2017). However, it is worth however that many corals in Kāneʻohe Bay appear pale through much of the year, and our cumulative bleaching estimates likely reflect that. Previously, surveys have often been conducted following peak temperatures and not at the granularity of the present study, which could have resulted in lower estimates of past bleaching. Notably, though, average mortality for *P.compressa* and *M.capitata* (21%) was slightly lower than cumulative mortality following 2015 (22%). Increased rates of bleaching but lower average mortality suggests some degree of acclimatization to repeated thermal stress in these species. Bleaching in 2019 followed a similar pattern to 2015 with sites in the northern region bleaching most severely followed by those in the central and southern sections of the Bay (Bahr et al., 2017).

Bleaching was variable for species. *Pocillopora* bleached most severely in the Bay, followed by *P.compressa* and *M.capitata. Pocillopora* has been severely affected by past bleaching events, and these patterns continue with our study (Bahr et al., 2017). While a slightly larger proprotion of *P.compressa* bleached than *M.capitata*, the latter had a higher proportion that bleached more severely. However, *M.capitata* that recovered seemed to do so faster than *P.compressa*. This is in contrast to pattens following the bleaching event of 2015, where *P.compressa* visually recovered more rapidly than *M.capitata* (Matsuda et al. 2020). Higher than normal nutrient and zooplankton concentrations associated with elevated levels of sedimentation in Kāne‘ohe Bay could assist heterotrophically plastic corals like *M.capitata* to meet their metabolic demands and survive through periods of elevated sea water temperatures. This could be one of the reasons this species was able to recover pigmentation faster than *P.compressa* after this bleaching event. However, *P.compressa* experienced less mortality than *M.capitata*, even if it showed a slightly longer lag in recovery time. In contrast, while *Pocillopora* showed greatest mortality during this event, colonies that did not die recovered faster than both *P.compressa* or *M.capitata*.

4.5.B Environmental drivers of bleaching

Several studies have confirmed that anomalously high temperatures are the leading cause of coral mortality and habitat loss worldwide (Sheppard, 2003; Donner et al., 2005). However, local reef conditions can work to mediate the effects of elevated temperature, thereby influencing the response of corals to thermal stress. We find that site-level differences in habitat complexity and assemblage type played an important role in determining bleaching severity during 2019, with reefs that were dominated by *Pocillopora* or those that had lower sediment loads experiencing more severe bleaching than others (Fig.4).

The structural complexity of a reef and its importance for biodiversity has been recognized for decades, but how underlying reef structure can reinforce or buffer the effects of bleaching and mortality is less known (Ferrari et al., 2016). Our study finds that higher levels of complexity at the colony-level scale (i.e., rugosity) were associated with reduced bleaching severity. This pattern might be attributed to the prevalence of heat-resistant *Porites compressa* across these sites, which experienced least bleaching during this event. In addition, *P.compressa* grow in large, mounding colonies in the Bay often forming monospecific stands and contributing to much of the larger-scale 3D complexity on these patch reefs (Supp Fig1a). Reef patches with higher rugosities might also have been able to create more shade within the reef, which could have further protected colonies or parts of colonies from thermal stress. In contrast, higher scores of fractal dimension – which are more indicative of complexity at the micro-scale – were related to higher levels of bleaching severity, potentially reflecting the effect of bleaching on heat-susceptible *Pocillopora* spp. *Pocillopora spp* are intricately branched and were associated with higher D scores than *P.compressa* and *M.capitata* (Supp Fig1b). Fractal dimension and rugosity capture different elements of complexity on a reef and might work in asynchronous ways to affect processes like bleaching and mortality (Torres-Pulliza et al., 2020). While coral diversity in Kāneʻohe Bay is low, species exist in a range of morphotypes and contribute differently to overall reef structure (Miller et al., 2021). While we did not detect changes in the 3D complexity of reefs one year post-bleaching, further monitoring will provide insight into how reef-scale R and D change as corals of different species grow, recover, or die.

Sedimentation has long been known to be a major driver of reef health in Kāneʻohe Bay due to its history of extensive dredging, coastal development, and land run off from adjoining coastal areas (Hunter and Evans, 1995). Variation in sediment loads across sites played a moderate role in determining bleaching response. While higher sediment loads have generally been found to be damaging to reef corals (Erftemeijer et al., 2012), studies have also found that the resulting turbidity may act to shield corals from radiation and the effects of increased temperature (Anthony et al., 2007). The tolerance of different coral species to sediment may vary based on their growth forms, with some morphologies - like hemispherical or columnar colonies - more efficient passive shedders than others. On the other hand, some colony shapes may be able to create vortices that help to flush sediment out of colonies in areas of high water flow (Riegl et al., 1996). Following the bleaching event of 1996, areas of Kāneʻohe Bay near stream mouths suffered little or no bleaching, even though corals experienced the same temperatures as in other parts of the Bay (Jokiel et al. 2004). In our study, elevated levels of sediment reduced bleaching stress potentially by reducing damage from UV raditation. Increased sediment loads in the water column could also be indicative of a higher degree of mixing and movement of water, which might have helped reduce temperatures at local reef scales. However, wave velocity did not have a significnt effect on bleaching severity.

4.5.C Mortality: causes and consequences

All three coral species experienced mortality during this bleaching event. Species mortality in this study (77.5% for *Pocillopora*, 19% for *P.compressa*, 23% for *M.capitata*) were on par with the 2015 bleaching event. However, our estimates of mortality also include partial colony mortality, especially for *P.compressa* and *M.capitata* due to the large size of colonies in Kāne'ohe Bay. Nevertheless, *Pocillopora* generally suffered whole-colony mortality. Higher overall rates of mortality indicate that the extent and duration of the 2019 bleaching event was more severe for these species than expected. While mortality did not lead to changes in the three-dimensional complexity of these reefs in the study period, we observed a rapid takeover of dead corals by algae (turf, cca). This trend towards algae was consistent across reefs, even though they differed in their coral community composition.

Species differences and variation in fractal dimension D between reefs largely drove mortality rates, alongside some fine-scale spatial differences in thermal stress (Fig.4). While high SSTs and degree heating weeks are known to be major drivers of bleaching and mortality, it is striking that differences in DHW existed at the spatial scale of this study. Average DHWs ranged from less than 1 to 24 through the bleaching period across sites, with sites in the northern region of the Bay (5) generally experiencing higher DHW (~10) than those in the south and central regions (~5 DHW). Sites that were more inshore such as those in region 3 also experienced higher DHW (~9), potentially as a result of their higher water retention times. Lowest DHW occured in sites that were close to a channel and slightly offshore. Highest mortality rates coincided with sites that experienced greater than 8 DHW (Supp Fig.2). Similar to its effect on bleaching severity, higher fractal dimension was associated with higher mortality. While higher sediment levels and RMS were associated with decreased mortality rates, they did not have a significant effect on the same. In general, temperature, species thermal tolerance and fractal dimension overtook the effect of all other environmental variables in determining patterns of mortality (Supp Fig. 3).

Pocillopora are some of the most susceptible species in the Bay and were among the worst impacted in Kāneʻohe following the bleaching events of 2014-15, when 80-100% of monitored colonies bleached, and 19% had died by 2016 (Ritson-Williams & Gates, 2020). Branching coral taxa like *Acropora* and *Pocillopora* are generally considered to be more bleaching susceptible than massive forms such as *Porites* and tank experiments on *P.acuta* collected in Kāneʻohe Bay have been found them to be susceptible to elevated temperature conditions (Bahr et al., 2020). Declines in *Pocillopora* raise questions about the larger functional consequences of altered coral assemblages in Kāneʻohe Bay in an era of climate change. Early reports from the Bay documented over 20 common coral species here (Maragos 1972); however, only 14 of these species were observed on a resurvey of the same sites in 2009 (Sukhraj 2014, pp.124). While there have been taxonomic reclassifications of some of these species over time, genera such as *Porites* and *Montipora* appear to have been able to better acclimate or adapt to the unique conditions of this Bay and its historic disturbances, while others have likely declined in this period. While *Pocillopora*-like species are generally fast growing, have early maturity (Baird and Maynard 2008), and have been able to adapt to changing conditions in other places (Guest et al., 2016) their abundance, distribution, and rates of recruitment in Kāneʻohe Bay will need further monitoring. Local conditions affect taxa differently, and it is conceivable that *Pocillopora* will see further declines in these habitats in the future or remain restricted to deeper reefs or reef patches where conditions are more favorable.

4.6 CONCLUSIONS

Our study finds significant spatial heterogeneity in patterns of bleaching and mortality, that were driven by differences in environment (temperature, sediment), and ecology (reef complexity, coral assemblage). Our study provides a fine-scale assessment of bleaching and mortality by using methods that allowed us to conduct repeat surveys of the same reefs as they altered through time. The use of SfM in this study has helped create a permanent digital baseline of these patch reefs for future work. Continuing to track reef 3D reef metrics at different scales will provide greater insight into the mechanisms that help maintain structural complexity in the face of future warming. While the majority of bleached corals were able to recover after this event, *Pocillopora* spp. suffered significant mortality. Kāneʻohe Bay has long been considered an ecosystem under stress where some coral species are still able to adapt and thrive, but future work will need to elucidate how heat-susceptible taxa contribute to the functional diversity of corals in the Bay and what the consequences of their decline will be on associated reef fish species and reef function.

4.7 TABLES

Table 4.1: Parameters and coefficient estimates of fixed effects in the final clmm with bleaching status as a categorical response variable. Full model in Supplementary Table 2.

Variable	Estimate	*SE*	z Value	*P* Value
Sediment load	-0.22102	0.11395	-1.940	0.0524 .
Rugosity	-0.58611	0.28187	-2.079	0.0376 *
Fractal dim	1.13326	0.23916	4.738	2.15e-06 ***
Pocillopora spp	3.18983	0.30445	10.477	< 2e-16 ***
Porites compressa	0.01797	0.06249	0.288	0.7737

Table 4.2: Summary statistics of the the best fit glmer predicting the probability of coral mortality. Fixed effects were degree heating weeks (DHW), substrate (Pocillopora spp, Montopora capitata, Porites compressa) and Fractal dimension (fractal dim). Full model in Supplementary Table 3.

Variables	Estimate	*SE*	*z* Value	*P* Value
Intercept	-3.95635	0.81689	-4.843	1.28e-06 ***
DHW	0.74366	0.30362	2.449	0.0143 *
Pocillopora spp	2.03826	0.34506	5.907	3.48e-09 ***
Porites compressa	0.13781	0.07624	1.807	0.0707 .
Fractal dim	1.29318	0.30840	4.193	2.75e-05 ***

4.8 FIGURES

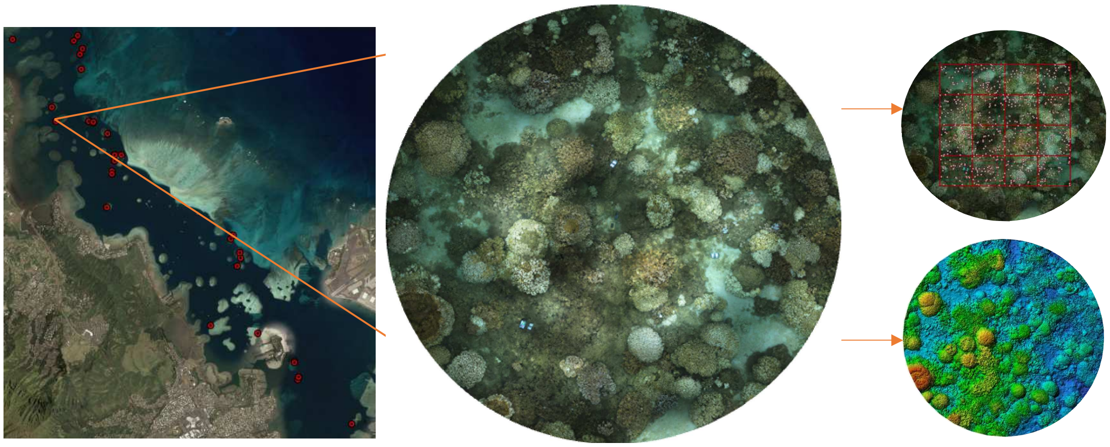

Figure. 4.1: Map of Kaneohe Bay showing 30 study sites and a corresponding orthomosaic for a site. 640 random points within an 8 x 8 m grid were annotated for each site orthomosaic during the study period. Habitat complexity metrics were estimated from DEMs, where colours represent water depth (red/green=shallow, blue=deep).

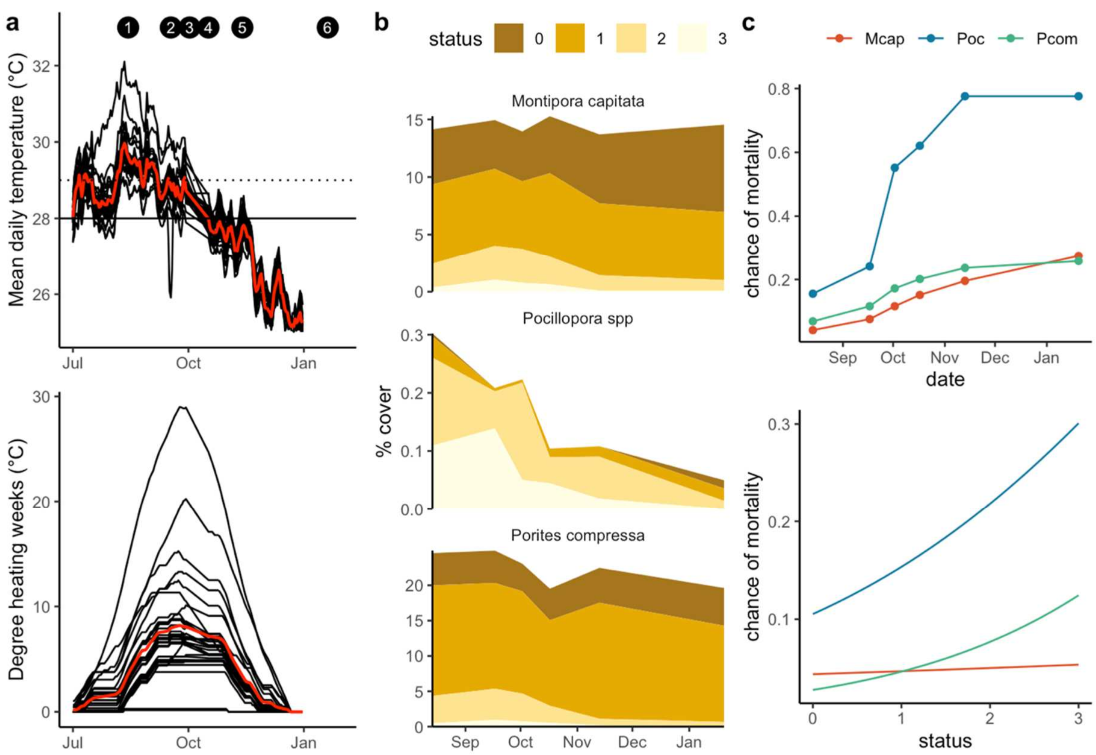

Figure.4.2(a): Temperature profiles and DHW for all 30 sites, July 2019- January 2020. Red line indicates mean temperatures/mean DHW. Solid line corresponds to mean monthly maximum (MMM), dotted line indicates bleaching threshold (MMM+1 deg.C) (b) bleaching severity for 3 species, showing changes in percent cover over time. Status codes correspond to Fig.4.3 and (c) mortality (0=alive, 1=dead) for the three coral species over time and with increasing bleaching status (0=healthy, 3=stark white).

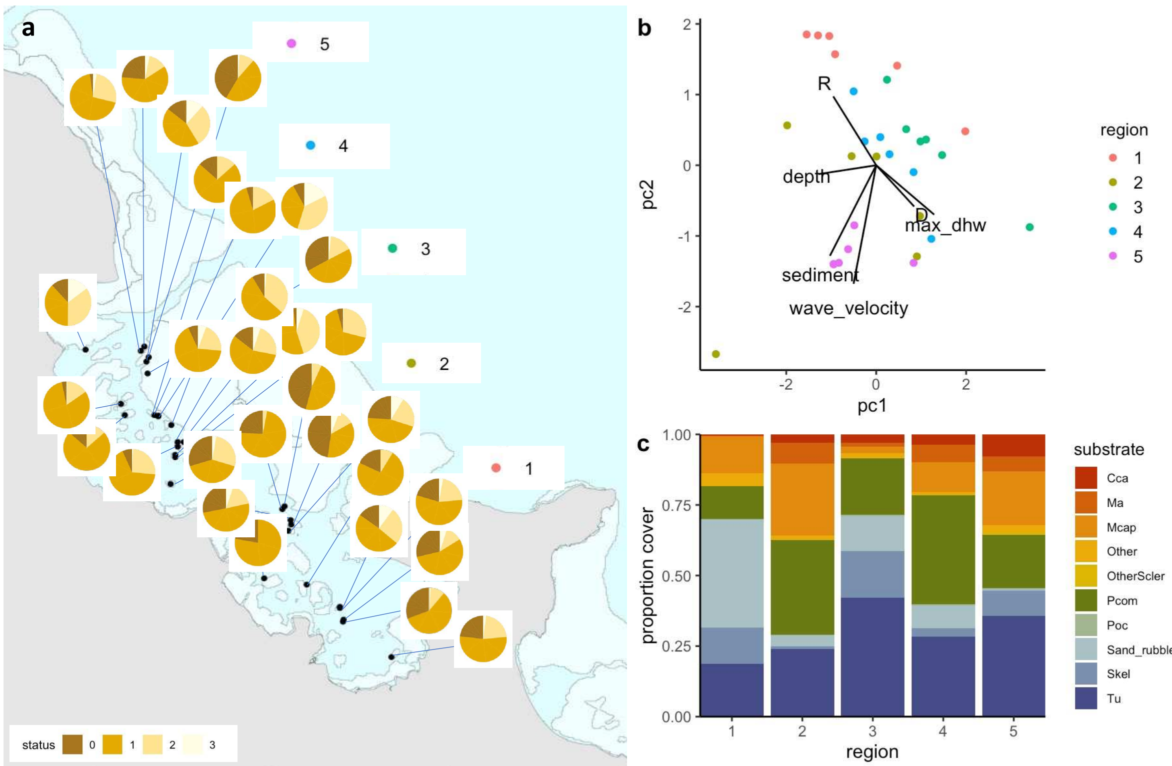

Figure 4.3: (a) pie charts showing proportion bleaching at all sites across 5 regions during peak bleaching (status corresponds to bleaching severity, where 0=healthy, 1=pale, 2=significant loss of pigmentation, 3=stark white), (b) PCA summarizing all environmental and ecological parameters measured, colored by region (R=rugosity, D= fractal dimension, max_dhw=maximum degree heating weeks), and (c) relative proportion of the dominant substrate types across the five regions in the Bay (cca=crustose coralline algae, ma=macroalgae, Mcap=Montipora capitata, Pcom=Porites compressa, Poc=Pocillopora, Skel=skeleton, Tu=turf).

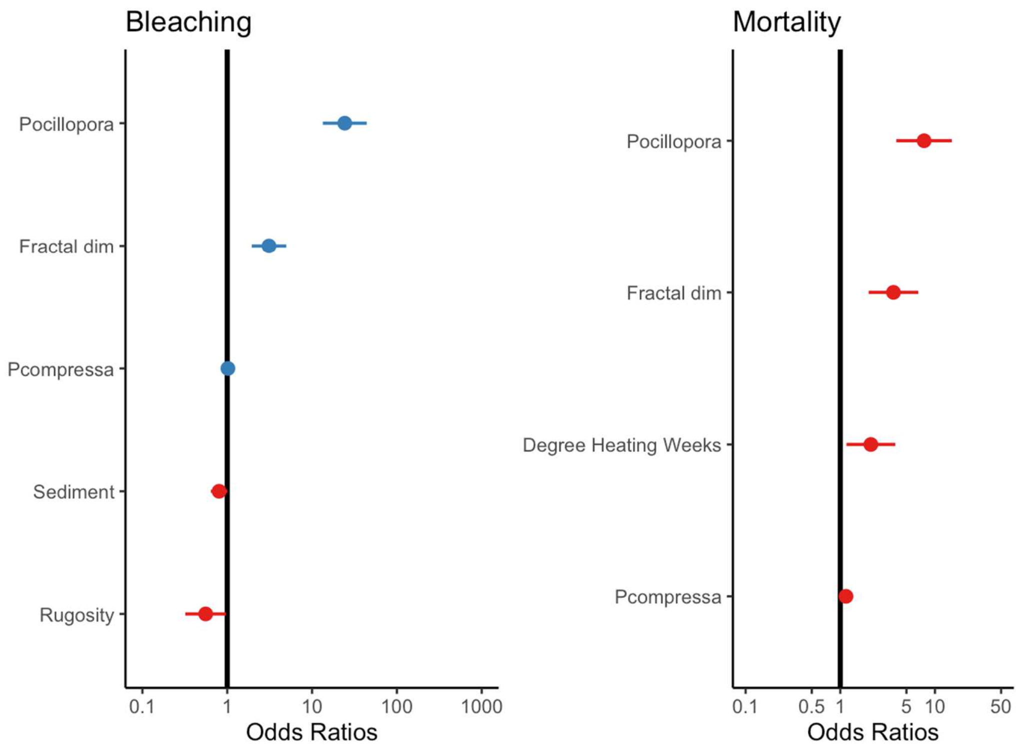

Figure 4.4: The effects of significant environmental and ecological variables on bleaching and mortality. Null line indicates no effect. Lines from individual points indicate confidence intervals. See Supplementary Fig. 4 for full model.

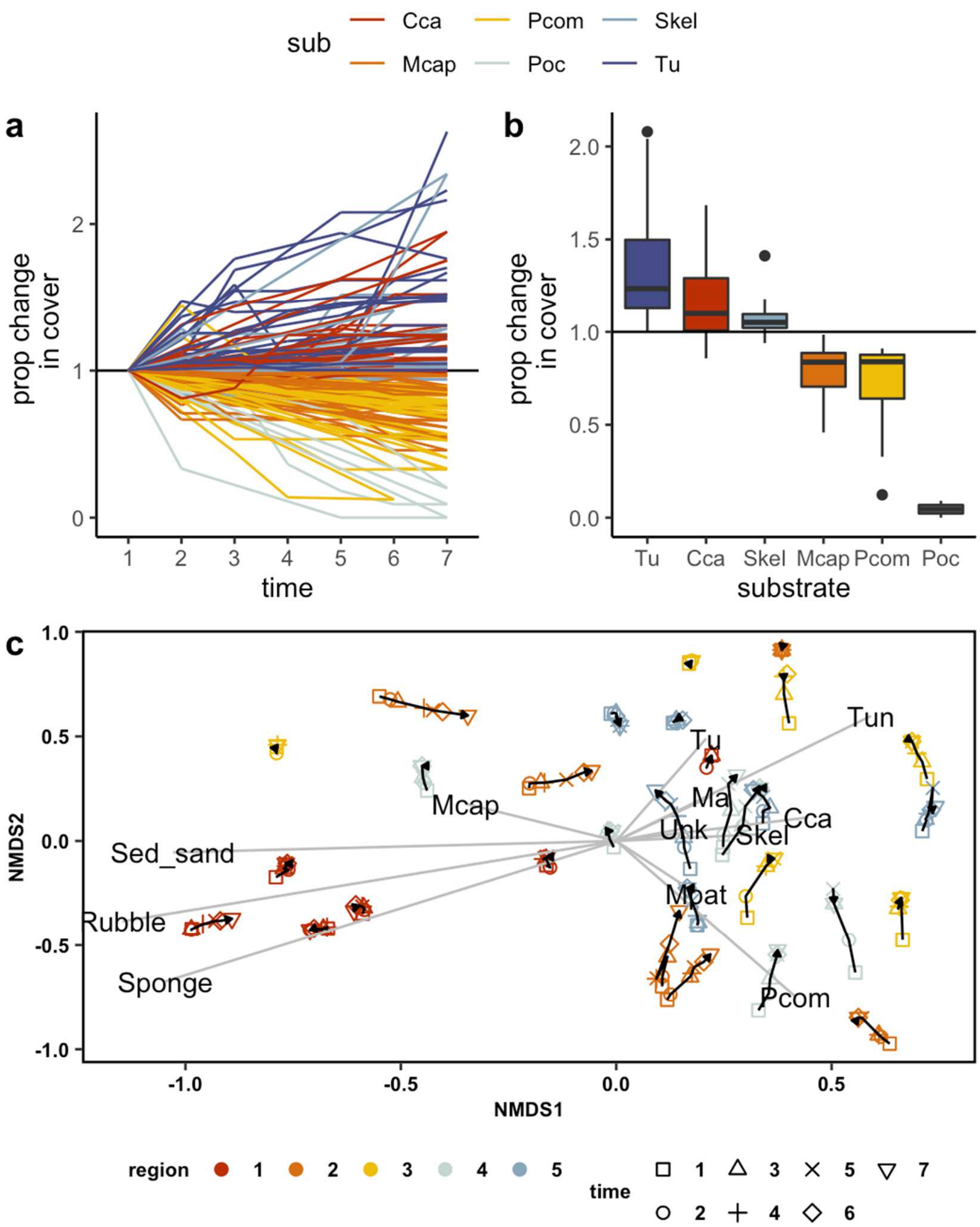

Figure 4.5: Changes in the proportional cover of different substrates over the course of the bleaching event. (a) an increase in turf (Tu) and CCA was associated with a decrease in P.compressa (Pcom) and Pocillopora (Pdam) during October-November (times 3, 4, 5) (b) changes in % cover by substrate type over the bleaching event, (c) NMDS showing a shift towards Tu (turf), Ma (macroalgae), Skel (skeleton), and CCA through survey times across the study regions.

4.9 SUPPLEMENTARY INFORMATION

Table S1: Description of substrate types assessed during coral annotation. Note that Pdam and Pmea were collapsed into Pocillopora spp. in our analyses.

Code	**Description**
Sed_sand	Sediment and sand
Rubble	Rubble
Plob	Porites lobata
Mcap	Montipora capitata
Pdam	Pocillopora damicornis
Tu	Turf
Ema	Encrusting macroalgae
Brma	Brown macroalgae
Rdma	Red macroalgae
Pav	Pavona spp.
Plut	Porites lutea
Pmea	Pocillopora meandrina
Sp	Sponge
Tun	Tunicate
Bi	Bivalve
Cca	Crustose coralline algae
Mfla	Montipora flabellata
Mpat	Montipora patula
Pcom	Porites compressa
Losc	Lobactis scutaria
Lpur	Leptastrea purpurea
Skel	Dead coral skeleton
Coce	Cyphastrea ocellina
Lpap	Leptoseris papyracea
Unknown	Unknown substrate

Table S2: Full clmm predicting bleaching severity showing all variables tested

		status	
Predictors	*Odds Ratios*	*CI*	*p*

0|1	3.59	0.46 – 27.77	0.221
1|2	85.17	10.97 – 660.99	**<0.001**
2|3	607.15	77.96 – 4728.18	**<0.001**
Max_DHW	0.98	0.93 – 1.03	0.364
Depth	1.02	0.75 – 1.40	0.889
Sediment	0.67	0.48 – 0.92	**0.014**
RMS	1.07	0.98 – 1.17	0.114
sub [Pocillopora spp]	24.23	13.35 – 44.00	**<0.001**
sub [Porites compressa]	1.02	0.90 – 1.15	0.782
R	0.56	0.32 – 0.98	**0.041**
D	3.11	1.95 – 4.98	**<0.001**
Random Effects			
σ^2	3.29		
$\tau_{00\ site}$	0.52		
ICC	0.14		
N_{site}	30		
Observations	7565		
Marginal R^2 / Conditional R^2	0.064 / 0.191		

Table S3: Full glmer predicting mortality showing all variables tested

	mort		
Predictors	*Odds Ratios*	*CI*	*p*
(Intercept)	0.02	0.00 – 0.18	**0.001**
depth	1.22	0.67 – 2.22	0.519
mean dhw	2.25	1.23 – 4.11	**0.009**
Sed Mean [log]	1.07	0.53 – 2.16	0.854
rms	0.66	0.30 – 1.46	0.306
D analysis	3.61	1.95 – 6.67	**<0.001**

R log10 analysis	1.10	0.55 – 2.19	0.791
sub [Pocillopora spp]	7.72	3.92 – 15.18	**<0.001**
sub [Porites compressa]	1.15	0.99 – 1.34	0.067
Random Effects			
σ^2	3.29		
$\tau_{00\ site}$	2.55		
ICC	0.44		
N_{site}	30		
Observations	7565		
Marginal R^2 / Conditional R^2	0.120 / 0.504		

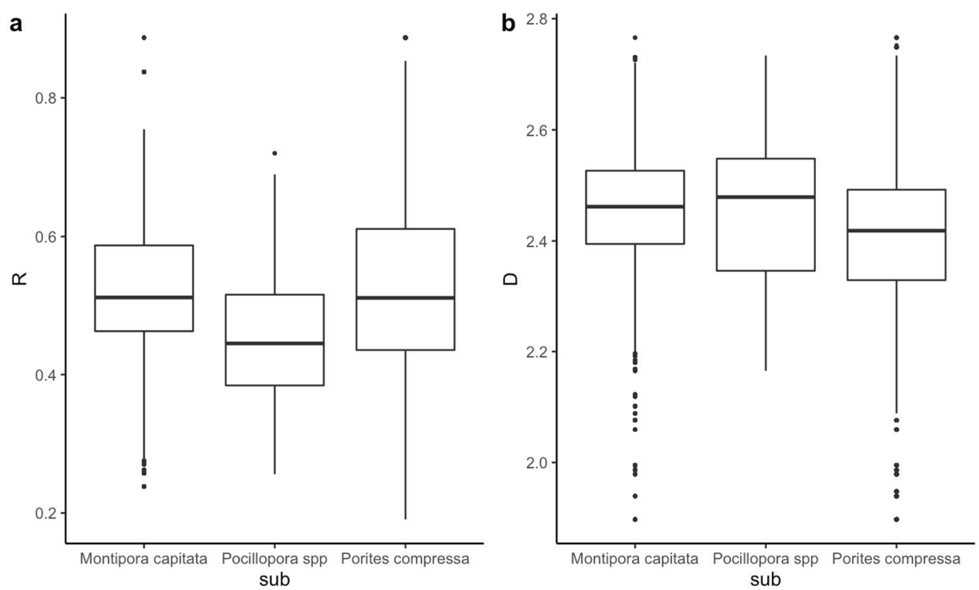

Fig.S1: Relationship between coral taxon and a) rugosity R and b) fractal dimension D

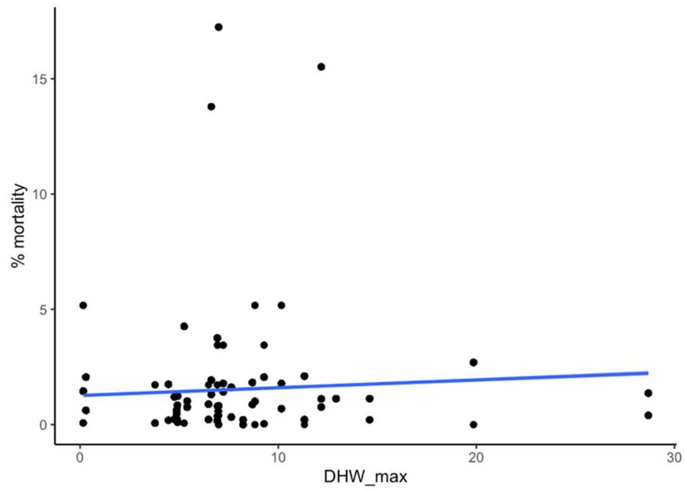

Fig.S2: Max DHW vs % mortality across sites

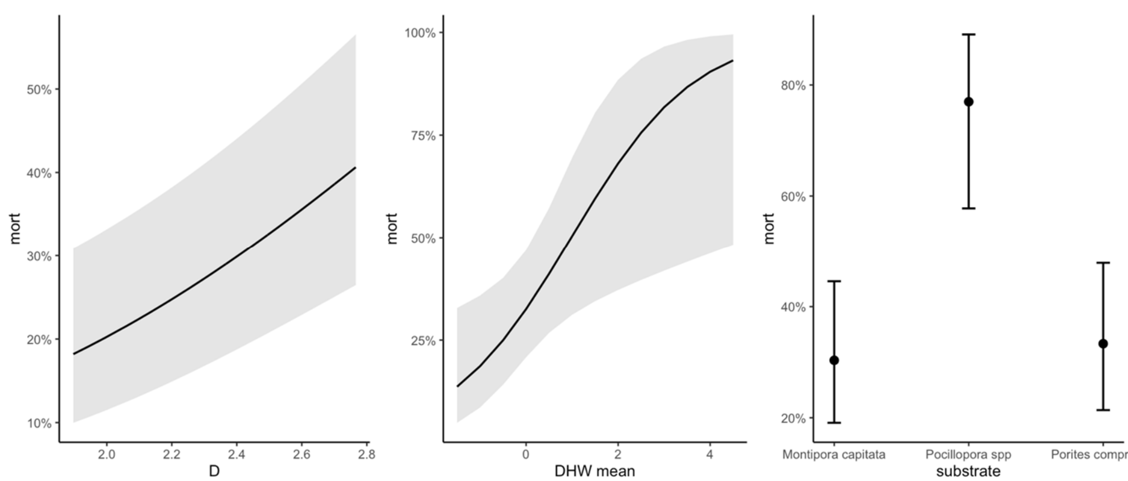

Fig.S3: Modelled relationships between significant explanatory variables and percent mortality, showing predicted values for each model term.

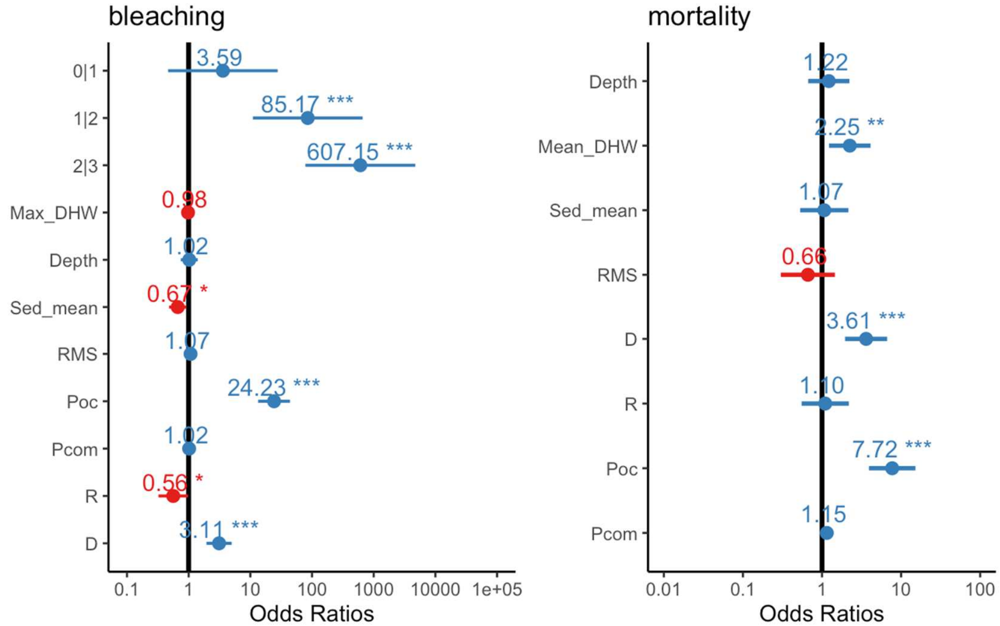

Fig S4: Effects plots for bleaching and mortality, showing the effects of all variables tested

Table S4: AIC scores for models predicting bleaching severity

Models	**AIC**
Environmental model	
Mean dhw + depth + sed + rms	15824
Ecological model:	
Sub + R + D	15675
Best model:	
Sed + R + D + sub	15672

Table 5: AIC scores for models predicting coral mortality

Models	**AIC**
Mean_dhw + depth + sed + rms	7634
Ecological model:	
Sub + R+ D	7583
Best model:	
Mean_dhw + D + sub	7577

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CHAPTER 5

CONCLUSION

5.1 SUMMARY OF FINDINGS

The overarching goal of this dissertation was to explore multiple facets of coral reef resilience to better understand the processes – historical, environmental, and social – that contribute to the recovery, resistance, and persistence of an ecosystem in a healthy state over time.

In Chapter 2, I used a historical approach to examine the factors that sustained a 1000-year-old pelagic tuna fishery in the Maldives, and the implications this has had for the long-term social-ecological resilience of these reef systems. I found, through reviewing ethnographic accounts, travel logs, archaeological data, and more recent research, that the first written accounts documenting trade in dried Maldivian tuna date back to the 14^{th} century, when the Maldives was a key stopover point for many Indian Ocean traders due to its abundance in money cowries. Dried tuna began to piggyback on the trade in cowries, eventually becoming profitable in itself. This trade – along with a few other social and cultural factors that made fishing for tuna easy and profitable – was key in enabling Maldivians to take the best path towards sustainable nearshore fisheries. This in turn has helped their coral reefs remain healthy in the face of multiple climate change related bleaching events, with reef fish biomass in the Maldives some of the highest for the Indian Ocean, and comparable to remote islands in the Pacific like Palmyra atoll. Until now, these links between the tuna fishery, reef fishing, and coral reef resilience had not been explored. This chapter also emphasizes how engaging with historical perspectives can broaden our understanding of the relationships, past and present, with humans and their environment. As Geerat Vermeij writes in the book Marine Historical Ecology and Conservation (p33), "knowledge of the past reminds us that the courses of evolution and the history of ecosystems exhibit predictable properties, all of which indicate the universality of change." Understanding the historical conditions that led to certain changes – and how and why those sustained over time – can help predict what might occur in the future.

While the tuna fishery maintains its economic and cultural importance in the Maldives, the rapid rise in tourism and growing demand for reef fish has led to the emergence of a reef fishery in the recent past. In Chapter 3, I examined the ways in which tuna and reef fish are valued by local communities today by assessing their preferences and consumption patterns. I also explored how current fishing practices shape seasonal patterns of consumption, and are influenced by social, developmental, and environmental changes occuring on islands. This was the first study to look explicitly at changing fish consumption patterns in the Maldives, and I did this through structured surveys and interviews with local community members and fishers in one of the central atolls of the Maldives – Dhaalu atoll. I found that reef fish are now a significant part of local diets, with the majority of people I spoke to preferring to eat reef fish over tuna. Preferences, however, varied with gender and age, with men generally preferring to eat reef fish while women had a strong preference for tuna. In general, preference for reef fish increased in people around and after the age of 40-45. These gender and age based differences potentially point to a deeper split in values relating to marine resources and highlight the need for further research in the realm of gender for a more comprehensive understanding of human-ecological interactions in coastal fisheries. In addition, fishers recorded several factors that could influence fishing and consumption patterns, from seasonality in demand to the effects of recent coral bleaching events on the abudnance of reef fish. Importantly, I recorded a clear seasonality in the demand for reef fish, spiking in the months of Ramadan and Eid, when reef fish became popular to cook and eat communally. I also documented an informal network of buying and sharing fish with friends, family, and neighbors, that will be crucial to consider and incorporate into future management centered on community wellbeing and food security.

Understanding the historical and contemporary use of marine resources as the previous two chapters attempted to do is important because the coral reefs that communties depend on are in rapid decline in many parts of the world due to the impacts of climate change. In Chapter 4, I used SfM to track a coral bleaching event in Kāneʻohe Bay in 2019, and tested the environmental and ecological factors that drove patterns of bleaching and mortality in the Bay. I recorded high spatial patchiness in bleaching severity and mortality, with reefs that experienced higher sediment levels bleaching less severely. Species compositon, along with degree of thermal stress, was an important predictor of moratality. Patterns of bleaching and mortality were similar in 2019 than they were following the bleaching events of 2014 and 2015. Notably, this study recorded a significant decline in the cover of *Pocillopora* species following the event, which raises questions about the future of heat-susceptible species in Kāne‘ohe Bay. This bleaching event was the third one in a decade, and while some coral specoes are able to better resist thermal stress, future warming is likely to impact more vulnerable species. This chapter also explored the use of SfM to track bleaching in one of the first examples of this tool being used for this purpose.

5.2 IMPLICATIONS FOR MANAGEMENT AND FUTURE RESEARCH

Currently, the Maldives does not have a national management plan for its reef fisheries. While there is some management of the grouper fishery, and isolated cases of resort-based management interventions, reef fisheries as a whole do not currently operate under any formal rules. The second and third chapters of this dissertation help contextualize the country’s fisheries by taking a historical and case study approach to investigate some of the dynamics that will need to be considered while designing and planning for local management. Broadly, there will need to be a larger focus on better understanding and developing sociocultural indicators in resource management in these islands.

The links between tuna fishing and coral reef health, while locally understood, were only made explicit with the publication of Chapter 2. By exploring the evolution of the tuna fishery and the long-term effects it has had on coral reef health, I demonstrate the feedbacks that exist between pelagic and nearshore fisheries and reef resilience. While tuna is still fundamental to Maldivian livelihoods and food culture in these islands, it is not as central to the economy as it used to be. This is perhaps inevitable given the rapid growth of tourism and the diversification of livelihoods, but encouraging the consumption of tuna – especially among the tourist population – can go a long way in ensuring that this fishery continues sustainably into the future. I recommend that resorts and guest houses in the Maldives market tuna as a sustainable food choice in these islands, and further explore the fascinating history of its origin to better inform and educate consumers about the benefits of its consumption. This is especially important as the tourist demand for reef fish is driving a rapid increase in reef fishing, as my results from Chapter 3 demonstrate.

In addition, however, the livebait fishery that the sustainable catch of tuna relies on will need attention from managers. While there has been some monitoring of fisher logbooks to understand fluctuations in livebait catch, there is a growing sense among fishers, as I reported in Chapter 3, that many bait species are experiencing local declines due to overharvest (as a result of bigger holds on boats, brighter lights to attract fish, the use of SCUBA in catching bait, as well as declines in fish due to coral bleaching and dredging operations). There will need to be an effort made to review the current state of the livebait fishery (the last one being done in 2015), and to understand how best to sustainably manage these reef-associated species so that they persist into the future. This may involve restriction in gear types, banning the use of SCUBA, imposing catch limits, or area restrictions. However, these management recommendations will need to come out of consultation with tuna and reef fishers, which currently has not taken place. While conducting fieldwork for Chapter 3, I had a striking conversation with an older reef fisher who mentioned how people had never fished for juvenile bait fish inside the island lagoon, as they did today. He said that while they had never fished juveniles earlier on, today live bait are fished throughout the year and more intensively than before. Perspectives like this from elders in the community can help to incorporate traditional and local knowledge into management and identify practices that may be re-established today. It is important that local management come from consultation with fisher communities, past and present, and that the outcomes are centered on improving community wellbeing.

Chapter 3 also identified some sociocultural dynamics related to reef fishing that can help inform its sustainable management. In particular, I identified a clear seasonality in the local catch and consumption of reef fish that was related to the period of Ramadan and Eid. I also recorded an informal network of sharing fish that could be important for food security and social cohesion on these often isolated, small islands. Religion is a central part of people‘s lives in the Maldives, and therefore also feeds into people‘s fishing practices. While my research was only conducted on 4 islands in a single atoll in the Maldives and should not be extrapolated to the entire archipelago, it will be important to better explore how religion, gender, and sharing networks influence local fish consumption patterns in other parts of the country. While this chapter also touched upon the role of resorts in determining reef fish catch, there is a gap in our understanding of how exactly reef fish are exchanged and sold between fishers and resorts, the role of middlemen, and the amount of catch that is landed on private resorts everyday. Quantifying these market dynamics will be a crucial area for future research.

Chapter 4 highlights local environmental and ecological processes that determine coral bleaching severity in Kāneʻohe Bay, Oahu. In line with previous work, our study finds that northern sections of the Bay bleached more severely than those in the central offshore parts of the Bay. While this was predicted to be a moderate bleaching event, we recorded rates of coral mortality that were comparable to those following the bleaching event of 2015. This chapter provides further evidence that the increasing frequency of coral bleaching events is likely to alter coral assemblages in the Bay, with unknown functional consequences. Kāneʻohe Bay is used by recreational and subsistence fishers and communities along this coastline for various activities. Reef degradation could have significant impacts on nearshore fisheries and the health of linked SES.

Avenues for future research include the use of large area imaging to explore clustering in bleaching by coral taxa to further elucidate whether there are predictable patterns in bleaching and mortality at these colony-level scales. The continued monitoring of these habitats using SfM will also provide long-term data on how these reefs respond to future disturbances. Importantly, there is a need to understand how rarer, heat-sensitive taxa are distributed in Kāneʻohe Bay and the mechanisms that enable them to rebound from bleaching events.

5.3 LIMITATIONS

A major limitation of Chapter 2 is that it relies on texts and ethnographic materials written primarily by visitors to the Maldives. There is a lack of accessible local writing from this period, and since I did not conduct any first-hand interviews for this chapter, this review reconstructs a history that lacks local perspective. One of the challenges of historical ecology is gleaning facets of the past from often scant historical evidence, but an opportunity for future work in this area would be to seek out and engage more deeply with local historical writing.

Much of my research for this dissertation was conducted in the central atolls of the Maldives archipelago – specifically, Dhaalu atoll, where I conducted interviews for Chapter 3 and Faafu atoll, where I previously conducted fieldwork and pilot interviews. While community islands share many similarities across the Maldives, my research is not representative of the entire archipelago. Islands in an atoll often have a unique identity, and local demographics, histories, tourism pressure, and reef fishing dynamics are variable across the chain. In addition, this research would have benefitted from a larger sample size, especially of women, and estimates of reef fish biomass from heavily frequented fishing grounds so that ecological data might have been integrated into this research. However, the general themes that emerge from my interviews may serve as useful baselines for further work.

While SfM and large area imaging are powerful tools in marine science today, it is important to be aware of their limitations. The quality of imagery one is able to collect using this method is often very dependent on local weather conditions, and 3D models and photogrammetric products may take several days to process effectively. In Chapter 4, SfM allowed us to track several patch reefs across Kāneʻohe Bay rapidly and effectively as the bleaching event unfolded. As a result, we were able to capture change at a large spatial extent and simultaneously at very fine scales for the entire duration of the event, something that has not been done in this region before. However, model construction, data processing, and data extraction took up to 2 years for 180 models. There are significant tradeoffs in using SfM, which should be discussed prior to the start of a study.