Implications of coral reef degradation for fisheries

Thesis submitted by

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Thesis abstract

Tropical coral reef habitats are vulnerable to numerous environmental stressors, affecting the ecosystem services they provide. Coral reef fisheries provide livelihoods and a vital source of nutritious seafood for hundreds of millions of people in coastal communities, yet little is known about how reef degradation may impact these fisheries, which this thesis addresses using a multidisciplinary approach. Fish biomass and nutrient production rates were estimated on reefs impacted by coral bleaching. In Seychelles, biomass production increased on reefs recovering to coral-dominated states following coral mortality and eventually exceeded pre-bleaching levels, driven predominantly by herbivorous fishes, while on reefs that became overgrown with macroalgae, elevated production rates relative to standing biomass maintained fisheries productivity. Across four Indo-Pacific locations, reef structural complexity positively impacted fish biomass and nutrient production rates, particularly in the unfished Chagos Archipelago. Collectively, these results suggest that while coral-dominated reefs with little human impact may support more productive fish assemblages, reefs with moderate levels of habitat degradation and fishing pressure can continue to provide crucial provisioning services to people. Interviews with trap fishers in Seychelles revealed that reef degradation could have notable impacts on catches, especially when caused by coral bleaching, however other factors such as increased fishing effort were perceived as the main drivers of declining catches and subsequent changes in fishing behaviour. Reef fish biomass and nutrient availability were highest when coral cover was low in French Polynesia, and people's consumption of reef and pelagic fish was influenced by their social background. Fish consumption habits varied between islands, with those who had more traditional Polynesian diets rich in fish benefitting from higher nutrient intakes. This thesis demonstrates how the condition of coral reef ecosystems can impact production, extraction, and consumption of fish, and that small-scale fisheries on degraded reefs can remain important sources of nutritious seafood.

Thesis word count: 38,959

“Fish feed people and they need habitats.”

- a Seychellois trap fisher

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= worsened). Every fisher (*n* = 34) is represented in each type of fishing response on the left (number of traps (white), gear usage (lighter purple), and distance travelled (darker purple)), therefore the number of data points used to generate flows on the left side of the plot is three times higher compared to the right, however both sides are proportionally comparable. Gear usage refers to changes in gear type and/or deployment of gear.

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Chapter 1

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Chapter 3

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Chapter 4

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Author's Declaration

I declare that this thesis is my own work and has not been submitted in substantially the same form for the award of a higher degree elsewhere. Each data chapter is written in the style of a journal article and all chapters are the result of collaborations with co-authors. I am the lead author in all sections in this thesis and was responsible for the conceptual design, analyses, data visualisation, interpretation, and writing of all data chapters. I was also responsible for the sampling design and data collection for **Chapter 3**. Existing datasets were used for **Chapters 1**, **2**, and **4**. The contributions of other authors to each chapter are as follows:

Chapter 1: Ecological reef data were collected by Nick Graham and Shaun Wilson. James Robinson, Casey Benkwitt, Nick Graham, and Aaron MacNeil provided advice on data analysis. All authors suggested edits to manuscript drafts prior to submission for publication.

Chapter 2: Nick Graham collected ecological reef data. James Robinson and Nick Graham provided advice on data cleaning and manipulation. Eva Maire assisted with obtaining human gravity and sea surface temperature estimates. Aaron MacNeil provided advice on statistical analysis. All authors suggested edits to manuscript drafts.

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Contributions during my PhD

Peer-reviewed publications

Chapter 1: Hamilton, M., Robinson, J.P.W., Benkwitt, C.E., Wilson, S.K., MacNeil, M.A., Ebrahim, A., Graham, N.A.J., 2022. Climate impacts alter fisheries productivity and turnover on coral reefs. *Coral Reefs* 41, 921–935. https://doi.org/10.1007/s00338-022-02265-4

Chapter 4: Hamilton, M., Maire, E., Monteil, C., Vane, V., Graham, N.A.J., Brun, V., Robinson, J.P.W., Claudet, J., Parravicini, V., Hicks, C.C., 2024. Drivers of nutrient intakes from fisheries in French Polynesia. *Ecosystems and People* 20 (1), 2351385. https://doi.org/10.1080/26395916.2024.2351385

Robinson, J.P.W., Darling, E.S., Maire, E., Hamilton, M., Hicks, C.C., Jupiter, S.D., MacNeil, M.A., Mangubhai, S., McClanahan, T., Nand, Y., Graham, N.A.J., 2023. Trophic distribution of nutrient production in coral reef fisheries. *Proc. R. Soc. B.* 290, 20231601. https://doi.org/10.1098/rspb.2023.1601

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Chapter 2: Hamilton, M., Robinson, J.P.W., Maire, E., MacNeil, M.A., Graham, N.A.J. Coral reef habitat complexity promotes fisheries nutrient productivity.

Chapter 3: Hamilton, M., Souffre, A., Woodcock, R., Chang-Time, N., Marday, M., Pascal, A., Govinden, R., Martin, S.M., Graham, N.A.J., Hicks, C.C. Impacts of reef habitat disturbance on the Seychelles artisanal trap fishery.

Ford, A.K., Hamilton, M., Nand, Y., Puotinen, M., Jupiter, S.D., Dulunaqio, S., Naisilisili, W., Mangubhai, S. Comparing impacts and recovery of locally managed reefs after exposure from a category 5 cyclone.

General introduction

The loss and degradation of tropical coral reef habitat is an issue at the forefront of conservation and can be caused by numerous stressors. The climate crisis is a major cause of coral reef degradation, causing marine heatwaves and inducing coral bleaching that often results in the widespread mortality of reef-building corals (Helgoe et al., 2024). A warmer climate also increases the frequency of the highest-intensity tropical cyclones (Walsh et al., 2016) which can result in a high degree of physical damage on coral reefs (Puotinen et al., 2016). Other causes of reef degradation include outbreaks of coral-eating crown-of-thorns sea stars (*Acanthaster planci*) (Deaker and Byrne, 2022), water quality (including eutrophication) (Duprey et al., 2016; MacNeil et al., 2019), and destructive fishing practices (e.g. using explosives; Wells, 2009), amongst others. Coral reefs support a vast proportion of total global marine biodiversity despite constituting a very small fraction of marine habitat area (Knowlton et al., 2010), however the global average hard coral cover declined by an estimated 14% from the period 2005-09 to 2015-19, with a 26% increase in global average algal cover on reefs over the same period (Souter et al., 2021). Although the causes and extent of coral loss may vary, the loss of reef-building corals and physical structure is widespread across tropical coral reefs, which is likely to lead to a loss of biodiversity and ecosystem services (Perry and Alvarez-Filip, 2019).

A key ecosystem service provided by coral reefs is the provisioning of food through fisheries. Coral reef fisheries provide food security to hundreds of millions of people worldwide (Cruz-Trinidad et al., 2014; Cisneros-Montemayor et al., 2016; Bell et al., 2018), as well as fisheries livelihoods and economic contributions in many tropical nations (Bartelet et al., 2024). Coral reefs are often part of complex social-ecological systems, with people dependent on and affected by the ecology of reefs, and reef ecosystems impacted by humans through resource extraction and management (Barnes et al., 2019; Dacks et al., 2020). Reef degradation will have direct effects on coastal communities with intrinsic links to local reef environments, requiring adaptation and mitigation efforts as coral reefs continue to change throughout the Anthropocene (Cinner et al., 2016). As such, an improved understanding of how degraded reef habitats will impact the production, extraction, and consumption of reef fish that people rely on is needed.

Loss of hard corals and fisheries productivity

Changes in the benthic state of coral reef habitats have notable effects on reef fish communities, therefore reef degradation has the potential to impact important food fish species targeted by fisheries. The biomass of many species across multiple trophic groups has been found to be positively associated with live hard coral cover, which can be particularly apparent when fish biomass decreases following sudden reductions in coral cover, for example after coral bleaching or severe storms (Russ et al., 2021). As is the case in many ecosystems, there are winners and losers when habitat changes occur on coral reefs (Fulton, 2011). Reef fishes that directly depend on coral, such as specialised coral-feeding species, experience severe population declines when coral cover is reduced (Cole et al., 2008), however these species are generally not important targets for food fisheries. Hempson et al. (2017) found that reductions in planktivorous prey populations following coral loss led to predatory reef fish switching to less-abundant benthic-feeding prey species, resulting in a decline in commercially important predatory grouper populations over time, highlighting how the degradation of coral habitats can alter the trophic structure of reef fish food webs. Other fish species with more generalist habitat requirements may be able to avoid population declines, or even increase in numbers on degraded reefs and sustain reef fisheries yields, however the diversity of species targeted and in catches is likely to be reduced (Pratchett et al., 2014).

Benthic-feeding fishes in lower trophic levels, such as herbivores, often benefit from increases in algal and microbial food sources following mortality of hard corals. Species such as parrotfish (Scarinae) are well adapted to feeding on algal detritus and microbes (e.g. cyanobacteria; Clements and Choat, 2018) that dominate benthic communities following coral mortality (Diaz-Pulido and McCook, 2002). Therefore, the biomass of herbivorous fishes can increase on reefs following severe coral bleaching (Graham et al., 2020) and cyclones (Ceccarelli et al., 2016). Dead coral habitats can also support diverse invertebrate communities across various phyla, which can be several orders of magnitude more abundant and productive compared to live coral habitats and provide a food source for fishes that feed on invertebrates (Fraser et al., 2021). As a result, the abundance and biomass of invertebrate-feeders (invertivores) may also increase on reefs following coral mortality (Ceccarelli et al., 2016; Fraser et al., 2021).

In instances where hard corals do not recover and reefs shift to an alternative benthic state, reef fish communities are altered further. For example, the abundance and diversity of species found on reefs dominated by macroalgae tends to be lower than coral-dominated reefs (Feary et al., 2007; Chong-Seng et al., 2012). Fleshy macroalgae are not palatable to most herbivorous fish species (Puk et al., 2016) and macroalgal overgrowth can hinder the feeding activities of parrotfish (Fox, 2018). Therefore, species that have the necessary adaptations to feed on and inhabit macroalgae reefs (such as some rabbitfish (Siganidae) and unicornfish (Acanthuridae); Puk et al., 2016) can be more abundant in these habitats, as well as juveniles of many coral reef-associated fishes that utilise macroalgae reefs as nursery grounds (Fulton et al., 2020). Low trophic level reef fishes are commonly targeted in inshore reef fisheries (McClanahan et al., 2008; Hicks and McClanahan, 2012; Houk et al., 2012) with catches from tropical macroalgal habitats constituting significant portions of fisheries yields in recent years (Wilson et al., 2022). It is likely that altered fish assemblages on reefs dominated by algae (Robinson et al., 2019a) have influenced fisheries catch compositions over time, however historical baselines of typical macroalgae cover on reefs and associated herbivore populations are unclear (Bruno et al., 2014). Due to the positive associations of species in low trophic levels with post-disturbance reef habitats, they are likely to become increasingly important components of fisheries yields on contemporary degraded reefs (Rogers et al., 2018a).

Reef fisheries management measures have typically been based on the standing biomass of fish assemblages (MacNeil et al., 2015; McClanahan et al., 2015). However, more recently there has been an increasing focus on reef fish productivity (the rate that biomass is produced over time) which can better reflect resource production and extraction processes that are relevant to the dynamic nature of fisheries (Morais and Bellwood, 2020; Seguin et al., 2023). Like biomass and abundance trends, short-term increases in fisheries productivity on dead coral habitats following reef disturbance have been described by theoretical (Rogers et al., 2018a) and empirical (Morais et al., 2020a) studies, driven mainly by fishes in lower trophic groups. However, it should not be assumed that biomass trends will match productivity trends; parrotfish biomass has been found to decrease with rising human population (a proxy for fishing pressure) while productivity remained stable, suggesting productivity can safeguard against biomass losses as fishing pressure increases, at least to moderate levels (Morais et al., 2020b).

Considering the impacts of altered reef states following severe coral bleaching events on fish assemblages, such as reductions in coral cover or regime shifts, it is necessary to better understand how fisheries productivity may be impacted by climate-induced disturbances. Although previous studies have documented changes in biomass across trophic groups of reef fish on post-bleaching reefs, such as increases in herbivore biomass (Graham et al., 2020; Robinson et al., 2019a), the selective removal of large-bodied herbivores by fisheries can disproportionately affect biomass (Edwards et al., 2014). The impacts of coral bleaching may also affect the biomass of various size classes of fish differently, for example smaller fish can be more negatively affected which could influence recruitment to fisheries in subsequent years (Graham et al., 2007). Therefore, rate-based biomass productivity estimates over multiple years are required to inform fisheries management and promote sustainable harvests from post-bleaching reef habitats.

Reef structure and fish nutrient productivity

In addition to the quantity of live hard coral on reefs, the physical structure of the benthos is also an important factor affecting fisheries productivity (Rogers et al., 2018a; Morais et al., 2023). The erosion of reef structure, also known as reef flattening, often occurs following bleaching-induced coral mortality when coral skeleton formations break down, which can reduce reef complexity in less than six months (Bauman et al., 2009) and have negative effects on reef fish communities and ecosystem services, including fisheries (Alvarez-Filip et al., 2009; Kochan et al., 2023). The structural complexity of coral reefs can be correlated with hard coral cover (i.e. reef-building corals; Graham and Nash, 2013), however structure is also provided by other topographical features across reef zones including the dead reef matrix (Duvall et al., 2019). There are several methods of estimating structural complexity on coral reefs, for example SCUBA diver estimates of linear rugosity and vertical relief, and using remote sensing to estimate fractal dimension; however, due to the variety of structures present on most reefs at varying scales, it is unlikely that any one metric can represent structural complexity in ecological studies (Lazarus and Belmaker, 2021).

Although fisheries productivity and yields are often viewed purely in biomass terms, reef fisheries also supply nutrients that are essential for human health to coastal communities and have the potential to address inadequate nutrient intakes in nations where nutrient deficiencies are prevalent (Hicks et al., 2019; Mellin et al., 2022; Viana et al., 2023). Tropical fish have a high concentration of nutrients that are bioavailable to humans, with particularly high concentrations of calcium, vitamin A, and omega-3 fatty acids compared to some other animal-source foods (Golden et al., 2021; Hicks et al., 2021). Calcium is necessary for healthy bone growth (Singh and Prasad, 2023), vitamin A is necessary for vision, reproduction, and the immune system (Oruch and Pryme, 2012), and the omega-3 fatty acids found in fish (docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA)) contribute to anti-inflammatory responses and promote cardiovascular health (Bäck and Hansson, 2019). Other nutrients concentrated in tropical reef-associated fish that perform essential functions within the human body include iron (Abbaspour et al., 2014), zinc (Chasapis et al., 2020), and selenium (Roman et al., 2014).

By combining estimates of biomass productivity (Morais and Bellwood, 2020) with nutrient concentration estimates of fish (MacNeil, 2023), the nutrient productivity of reef fisheries can be investigated (Robinson et al., 2023). The nutrient content of reef fish varies across species, especially between trophic groups, and is also influenced by reef habitat nutrient pathways through which fishes acquire energy (i.e. individuals of the same species can have differing nutrient concentrations based on their association with particular habitats; Robinson et al., 2022a). Due to the importance of reef habitat complexity in shaping the structure of fish assemblages (Darling et al., 2017), the nutrient productivity of fish assemblages is likely to be influenced by the structural complexity of reefs, with implications for fisheries nutrient yields.

Due to increases in abundance on reefs with reduced coral cover, herbivorous fishes make large contributions to nutrient productivity on reefs in many tropical regions (Robinson et al., 2023) and will be important for supplying nutrients to fisheries on degraded reefs. However, the foraging rates of key herbivorous fisheries targets, such as parrotfish, are reduced on reefs without sufficient physical structure (Bozec et al., 2013), and may not support populations that can sustain fisheries yields. Both abundance and biomass of herbivores have been found to be highest at intermediate levels of reef habitat complexity (McClure et al., 2021), aligning with theoretical simulations of herbivore productivity (Rogers et al., 2018a; Rogers et al., 2018b), which suggests that fisheries nutrient productivity may also be maintained by herbivores following moderate degradation of reef structure. Herbivorous reef fishes typically have low concentrations of some nutrients, such as omega-3 fatty acids, compared to fishes in other trophic groups (Robinson et al., 2023), therefore although herbivores may dominate total nutrient yields on degraded reefs, fish from other sources (such as pelagic fisheries) may be required for optimal human nutrition (Robinson et al., 2022a).

Predatory reef fishes, such as groupers, are also important fishery species in many parts of the world (Jennings and Polunin, 1997; Fitzpatrick et al., 2015; Lindfield et al., 2016) and rely on an ample abundance of prey species to sustain their populations (Stewart and Jones, 2001). Small prey species are reliant on the branching structure provided by some hard corals and therefore lose access to refuges from predation when such fine-scale structure degrades (Wilson et al., 2006). Due to a lack of refuges, prey can become more accessible, enhancing the hunting efficiency and productivity of predatory fishes, at least temporarily. However, as reef structure becomes more degraded, prey populations are diminished and reefs support fewer predators, lowering their productivity (Rogers et al., 2018a). Fisheries targets in higher trophic levels have different nutrient concentration profiles from herbivorous fishes, for example piscivores have high vitamin A concentrations (Robinson et al., 2023), therefore the impact of changes in reef habitat complexity on the productivity of different trophic groups of reef fish will affect the supply of various nutrients to fisheries.

Recent work has investigated the links between reef structural complexity and biomass productivity (Morais et al., 2023), and reef benthos and nutrient productivity (Robinson et al., 2023), however the links between structural complexity and fisheries nutrient productivity remain unclear. As reef structural complexity has the potential to influence the size and trophic structure of reef fish communities, which in turn influences fisheries nutrient productivity, it is necessary to gain a better understanding of how human nutrition may be impacted by the structural degradation of coral reefs.

Fishing activity on degraded coral reefs

The harvest of reef fish by fishers is a key link between coral reef habitats and human societies. The effects of climate change are expected to negatively impact fisheries catch potential and employment opportunities in many tropical nations (Cheung et al., 2021). As small-scale coral reef fisheries are vital to the food security of fishing communities (Cruz-Trinidad et al., 2014), changes in fishing activity and fish landings will have consequences for the supply of fish to consumers and their nutrition.

The responses of fishers to habitat change consist of individual actions, decisions, and attitudes (Daw et al., 2009), which can collectively shape how a fishery adapts to climate change (Ilosvay et al., 2022). Fishers must constantly respond to many environmental factors that influence fishing, for example the ecology of target species, seasonal changes, and sea conditions (Rasekhi et al., 2023), yet climate-induced changes in habitat and species distributions will likely cause fishers to make additional adaptations to their fishing practices (or not, depending on the individual; Daw et al., 2009; Ojea et al., 2020). The extent of fisher responses to climate change impacts varies, from short-term, practical adaptations in fishing activity based on fishers' local knowledge of fishing grounds (coping mechanisms), to larger changes over the long term, such as changing target species, modification of fishing gears and technologies, or diversification of livelihoods (adaptive strategies; Galappaththi et al., 2022). The adaptations made by fishers to maintain catches may lead to profound changes to the supply of fish landed to markets.

Given the range of potential fisher responses to reef degradation, further exploration of how individual actions may alter reef fisheries is needed. Fisheries management can be improved by incorporating ecological information regarding habitat changes (Brown et al., 2019) which can be informed by fishers' local ecological knowledge (LEK) of their fishing grounds. As reef fisheries are social-ecological systems involving interdependencies between fishing communities and reef ecosystems, fishing adaptations can potentially result in feedbacks that further impact reef habitats, for example increasing fishing pressure on highly abundant herbivorous fishes following coral bleaching may sustain catches but reduce algal grazing rates and therefore the potential for reef recovery (Cinner et al., 2013). Some shifts in fishing behaviour may improve the sustainability of fisheries on post-bleaching reef habitats. As an increasing proportion of catches are derived from macroalgal habitats (such as those that may arise following a regime shift from coral dominance; Graham et al., 2015), the species caught tend to be less vulnerable to fishing (Wilson et al., 2022), suggesting these habitats may be able to withstand an increase in fishing effort as fishers adapt their fishing grounds. In response to hypothetical scenarios of declining catches on coral reefs, variation between fishers was found in terms of whether they would increase, decrease, or maintain their fishing intensity (Cinner et al., 2011), which could provide useful information to managers in similar real scenarios regarding fishing pressure on particular stocks or habitats.

Due to ecological shifts in targeted fish species on different degraded reef habitats, as well as variation in fishers' responses to such changes, understanding how a fishery will adapt to disturbances can be challenging. Consulting fishers directly about what changes they have witnessed on their fishing grounds and how they have responded provides a relatively fast method for gathering LEK and adaptation trends within a fishery (Daw et al, 2011), which could inform fisheries management in areas impacted by reef degradation.

Food and nutrient provisioning from degraded reefs

Nutrients that can be highly concentrated in small-scale fisheries yields, such as calcium, iron, and vitamin A, also have a high prevalence of inadequate intakes in many tropical nations (Beal et al., 2017), therefore reef fisheries are a crucial source of food and nutrient security (Belton and Thilsted, 2014). As the catch potential of marine fisheries is expected to decline in the coming decades as a result of climate change and habitat degradation (Golden et al., 2016), and ecological changes associated with reef habitat degradation have the potential to alter the food and nutrient provisioning services of coral reefs (Woodhead et al., 2019), it is important to understand how these changes may impact the supply of seafood to people and the subsequent nutritional health implications.

In Pacific regions, larger declines in productivity are expected for coral reef fisheries compared to pelagic fisheries for the remainder of the 21st century, with an increase in the biomass of some pelagic species projected in some areas (Bell et al., 2013). Although pelagic fish may become more readily available, eating a diversity of species from reef and pelagic fisheries is required to maximise nutrient intakes from small-scale fisheries due to the differing nutrient concentrations of fish species (Robinson et al., 2022a). For example, reef fish generally contain higher concentrations of calcium and zinc (Robinson et al., 2022a), therefore a reduction in the availability of reef fish could impact people's intakes of these nutrients. As changes occur in the supply of fish from fisheries, people's preferences, needs, and socioeconomic circumstances will influence the substitutions made between fish species (Woodhead et al., 2019), and may lead to a reduction in fish consumption if fish is substituted for terrestrial-sourced foods.

In regions where food systems have been transformed by globalisation, dietary transitions have occurred where traditional foods such as fish and local plant produce have been substituted with imported foods that tend to be less nutritious and have a higher fat and sugar content (Hawley and McGarvey, 2015; Brewer et al., 2023). At the same time, increasing urbanisation has led to more sedentary lifestyles, for example in many Pacific Island nations, which has also contributed to an increase in the prevalence of overweight, obesity, and diabetes (Hawley and McGarvey, 2015). These shifts in island societies have resulted in fewer people employed in traditional livelihoods such as small-scale fisheries, which reduces the nutritional benefits that fishing families and communities receive from these fisheries (Kawarazuka and Béné, 2010). As small island nations become more reliant on imported foods (Brewer et al., 2023), the increased availability of different types of foods does not necessarily equate to an increase in the availability of nutrients (Atzori et al., 2024). Therefore, reef fisheries are a means of local food production that can improve people's nutritional health, which could contribute to traditional diets that may be complimented by healthier imported foods (Thow et al., 2011).

As social-ecological systems, coral reef fisheries and the provisioning services they provide to people will likely be altered by changing reef habitats (Woodhead et al., 2019), which has the potential to affect consumption habits within the food environments of tropical coastal communities. Given the range of factors related to reef environments and food cultures that have the potential to affect nutrient intakes, research into the implications for human health is needed.

Thesis aims and research questions

This thesis takes a multidisciplinary approach to investigate how tropical coral reef degradation affects various aspects of small-scale fisheries. Research topics include ecological responses of fish productivity to reef habitat condition and societal responses of fishers and coastal communities to changing fisheries resources. The four research questions I address in this thesis are:

1) How are fish biomass productivity and turnover impacted on post-bleaching reef habitats?
2) How is the nutrient productivity potential of fish influenced by reef structural complexity?
3) What are the perceptions and responses of reef fishers to reef habitat degradation?
4) To what extent are people's nutrient intakes in coastal communities influenced by coral reef condition?

In **Chapter 1**, I estimate fisheries productivity and turnover before a severe coral bleaching event and on two post-bleaching reef habitats using a time series from Seychelles spanning over two decades. Very few studies include long-term patterns of reef fish productivity (for example, Yan and Bellwood, 2023), and my first chapter is the only study to date that estimates fisheries productivity on multiple post-bleaching reef states across fishing grounds and marine protected areas. In **Chapter 2**, I explore biomass and nutrient productivity across four locations in the Indo-Pacific (the Chagos Archipelago, the Great Barrier Reef in Australia, Maldives, and Seychelles) with a focus on the importance of reef structural complexity. The nutrient productivity of reef fish is a recent concept (Robinson et al., 2023) which, so far, has not been investigated in terms of reef structural complexity. I focus on the perceptions and responses of fishers to reef degradation in **Chapter 3** from interviews with Seychelles trap fishers. Few studies have documented the practicalities of changes in fishing behaviour and effort in response to degraded reefs and how this may impact the future of reef fisheries. In **Chapter 4**, I investigate the influences of reef habitat condition and societal factors on people's nutrient intakes from reef and pelagic fisheries in French Polynesia. I combine ecological and socioeconomic data to assess which factors contribute to fisheries-derived nutrient intakes and discuss the potential implications for human health.

Positionality statement

I would like to acknowledge my positionality and the principle that science is affected by the personal biases that all researchers hold. I am from southwest Scotland, where I attended a state school before completing undergraduate and postgraduate degrees at a Scottish university. I worked in fisheries science and management in the Shetland Islands prior to this PhD. My academic and employment background put me in a relatively privileged position in terms of being selected for this project, which was only available to applicants from the UK, therefore my positionality has influenced my access to this PhD.

My study sites for this thesis include Seychelles (three chapters), the Chagos Archipelago, Maldives, Australia, and French Polynesia (all one chapter). Due to the COVID-19 pandemic, Seychelles was the only study site I visited during this research, where I interviewed local fishers during a three-month internship with the Seychelles Fisheries Authority in 2022 and took part in the long-term coral reef monitoring survey. I have previously interviewed small-scale fishers as part of my university studies in Cambodia and Philippines, and have worked closely with shellfishers in Shetland. My natural science background and previous interactions with fishers have shaped my understanding of fisheries and have influenced my approach to this research, including the research questions I have pursued, my interpretation of results, and my writing of this thesis. For example, my understanding of the Seychelles trap fishery will be influenced by my experience of the Shetland creel fishery, and my interactions with fishers in Seychelles was determined through my involvement with the Seychelles Fisheries Authority research section. I was not present when the interview data I used from French Polynesia were collected (nor have I ever been to French Polynesia), therefore my understanding of the data and quantitative approach to analyses likely differs from the researchers who originally collected the data.

Chapter 1

Climate impacts alter fisheries productivity and turnover on coral reefs

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Abstract

Alteration of benthic reef habitat after coral bleaching and mortality induces changes in fish assemblages, with implications for fisheries. Our understanding of climate impacts to coral reef fisheries is largely based on fish abundance and biomass. The rates at which biomass is produced and replenished (productivity and turnover) are also important to sustaining fisheries, yet the responses of these metrics following bleaching are largely unknown. This study examined changes in fish productivity and turnover after mass coral bleaching events in Seychelles, on reefs that were recovering to coral-dominated habitats and those that shifted to macroalgae-dominated regimes. Productivity of fish assemblages increased on all recovering reefs, particularly on fished reefs resulting in levels similar to protected reefs 19 years after bleaching. Herbivore/detritivores, such as scraping and excavating parrotfish, appeared to drive biomass production through increased abundance on recovering reefs. Productivity on regime-shifted reefs remained stable at 1994 levels in fished areas, with increases observed on protected reefs. Large increases in browser productivity (particularly on protected reefs), combined with increases for invertivores, maintained post-bleaching productivity on macroalgal reefs. For all trophic groups of reef fish, net turnover was generally higher on fished regime-shifted reefs than on recovering reefs, suggesting fish biomass is more readily replenished on macroalgal reefs. Reef structural complexity was a positive predictor of productivity for all diet groups. These findings indicate that post-bleaching reef fish productivity is strongly influenced by benthic recovery trajectories and demonstrates the importance of species in lower trophic levels for sustaining small-scale inshore fisheries following climatic disturbances.

Introduction

Mass coral bleaching events often cause extensive coral mortality and reef degradation (Hughes et al., 2018) that can influence reef fish populations and associated fisheries (Cinner et al., 2012; Pratchett et al., 2014). Approximately six million fishers are employed in reef fisheries (Teh et al., 2013) that supply hundreds of millions of people in tropical nations with livelihoods and nutrition (Johnson et al., 2013). Yet, ongoing climate-induced habitat degradation and overfishing threaten the food provisioning services provided by coral reefs worldwide (Allison et al., 2009; MacNeil et al., 2015).

A key factor that determines the response of reef fish assemblages to coral bleaching is the recovery trajectory of corals following climate disturbances. Reefs where live corals recover tend to be associated with higher fish biodiversity, whereas those that shift to a macroalgal state are likely to have lower overall abundance and species richness of reef fishes (Roth et al., 2018; Fulton et al., 2019; Graham et al., 2020). Both recovery trajectories can induce long-term changes in fish species composition and abundance across multiple trophic groups (Bellwood et al., 2012; Robinson et al., 2019a), and some fish species may benefit from altered reef states (Pratchett et al., 2014). For example, the hunting efficiency of predators can increase in the short term as prey become more exposed on degraded reefs (Rogers et al., 2018a), while increases in algal growth as coral cover declines can benefit herbivorous fishes (Wilson et al., 2006) and may favour the juvenile recruitment of some taxa (Fulton et al., 2020). These changes in fish assemblages on post-bleaching reef habitats impact species biomass and the resources available to fisheries (Graham et al., 2007; Karr et al., 2015).

Standing biomass is a useful indicator in reef fisheries management (MacNeil et al., 2015; McClanahan et al., 2015), but does not necessarily reflect how productive fish stocks are or how well they may sustain fishery yields (Morais et al., 2020a). Predatory fish may grow large and have high biomass on reefs with high coral cover and structural complexity, yet growth rates, which underpin productivity, may be relatively low due to reduced hunting efficiency (Rogers et al., 2018a; Rogers and Mumby, 2019). Conversely, species with low biomass may still be able to sustain fisheries on reefs with reduced coral cover if increased food resources result in enhanced productivity of individuals (McClanahan, 2018). For example, herbivore growth can be enhanced by improved food quality or quantity following coral mortality (Taylor et al., 2019). However, the enhanced productivity that some species initially experience can weaken over time, particularly if reef structure becomes severely degraded (Rogers et al., 2018b). Changes in fisheries productivity following coral bleaching will therefore be determined by shifts in species abundances and growth rates that are linked to the availability and quality of resources (Brandl et al., 2016; Taylor et al., 2019), and long-term shifts in species composition will dictate assemblage-level productivity. However, the long-term productivity responses of fish assemblages, trophic groups, and individual species on post-bleaching reef habitats are poorly understood.

Productivity has been a major focus in the management of exploited fish stocks (Conn et al., 2010) but, due to data deficiency and complexity of reef systems, has been understudied in mixed-species coral reef fisheries. Fish biomass has been found to accumulate on some post-bleaching coral reefs (Graham et al., 2020), leading to increases in fisheries yields (Robinson et al., 2019b). However, the rates at which biomass is produced and stored as standing biomass (i.e. biomass turnover) are unknown, thus limiting our understanding of the long-term stability of fisheries yields (Morais et al., 2020a). Recent studies suggest that high fish biomass and productivity coincides with low turnover and may indicate low recruitment rates within fish populations (Brandl et al., 2019; Morais et al., 2020b). Fast-growing and short-lived species with higher turnover rates, such as siganids (Grandcourt, 2003), may be more adaptable to changing reef environments than long-lived species with longer generation times (Bellwood et al., 2012), making them important fishery targets on post-bleaching reefs (Robinson et al., 2019b). As the frequency of coral bleaching events increases (Hughes et al., 2018), it is important to understand bleaching impacts on the productivity of fish species and subsequent implications for reef fisheries.

This study aims to determine how the productivity and turnover of fish assemblages have responded to post-bleaching habitat degradation on coral reefs in Seychelles. Following a severe bleaching event in 1998 that caused >90% mortality of hard corals on inner Seychelles reefs (Graham et al., 2006), benthic habitats reorganised into two novel reef states: recovering reefs dominated by branching corals and reefs that regime-shifted to macroalgae-dominated states (Graham et al., 2015). The long-term productivity and turnover responses of fish on these post-bleaching reef states are investigated, as well as short-term effects from a second bleaching event in 2016 that caused 70% coral mortality on recovering reefs (Wilson et al., 2019), with a focus on the implications for small-scale reef fisheries. The specific research questions are: 1) How are productivity and turnover of fish assemblages affected on post-bleaching reefs? 2) Which trophic groups of fish and key fisheries target species are responsible for driving these trends? 3) Can productivity trends be explained by benthic reef variables?

Methods

Reef survey data

Surveys of fish communities and benthic composition were carried out at 21 inshore sites on shallow fringing reefs in the Seychelles (Graham et al., 2015), stratified across carbonate and granitic reef habitats (Fig. S1.1). Nine sites were within four marine reserves (established in the 1970s) where no fishing took place, although poaching was a known issue according to expert knowledge at Seychelles Fisheries Authority (SFA). Twelve sites were regularly fished by artisanal fisheries (Fig. S1.1).

Artisanal fisheries are of high importance in Seychelles as they provide food to the local population and tourism sector, as well as exports of high-value fish that generate earnings to support local fishers and their livelihoods (Robinson and Shroff, 2004). Seychellois fishers deploy traps and handlines from both motorised and unmotorised vessels (Christ et al., 2020), to target fish such as siganids, scarids, lethrinids, lutjanids and mullids within inshore reef habitats (Robinson et al., 2019b; SFA, 2023). These gears and fishing approaches are common in coral reef fisheries throughout the tropics.

Surveys were first completed in 1994 prior to a major coral bleaching event in 1998 and then every three years from 2005 to 2017. A second bleaching event occurred in 2016, which caused declines in hard corals (particularly branching) that had been recovering from the 1998 event (Fig. 1.1; Wilson et al., 2019). Surveys took place between March and April at all 21 sites, with the exception of 2017 when three sites within a protected area (Cousin, Fig S1.1) were not surveyed. Replicate sites were classified as “recovering coral” (*n* = 12) or “regime-shifted” (*n* = 9) based on their benthic trajectory to either a coral-dominated or macroalgae-dominated state, respectively, following the 1998 bleaching event (Graham et al., 2015). Recovering sites were defined as those where hard coral cover was greater than that of macroalgae following bleaching in 1998 and remained higher than macroalgae for the remainder of the time series (Fig. 1.1 a). Regime-shifted sites were defined as those where macroalgae cover increased after 1998 and remained higher than coral cover (Fig. 1.1 b). Although coral cover on recovering reefs declined notably in 2017 following bleaching in 2016, coral cover was still higher than on regime-shifted reefs (Fig. 1.1 a).

Eight replicate point counts of non-cryptic reef fishes (≥ 8 cm in length) were carried out at each site by underwater visual surveys along the base of the reef slope. Abundance and the lengths (nearest cm) of all species were estimated within a 7 m radius (154 m^2) point count area (Polunin and Roberts, 1993). One diver (Simon Jennings) conducted fish point counts in 1994 and a second diver (Nicholas Graham) conducted all other counts from 2005 to 2017. Fish length estimation was validated by divers estimating the lengths of randomly selected plastic pipes prior to the first point count at each site (as described by Graham et al., 2007), with no evidence that bias among divers influenced fish counts. Replicates at each site were at least 15 m apart and divers swam for approximately one minute between point counts (Graham et al., 2006).

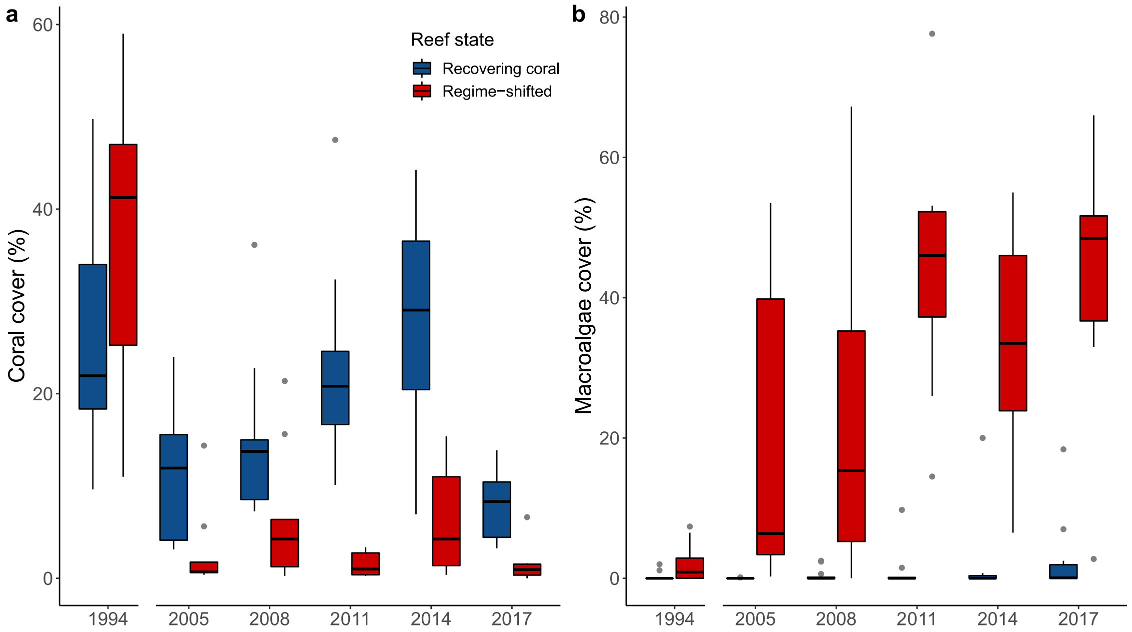

Figure 1.1: Comparisons of hard coral (a) and macroalgae (b) cover on each reef state (recovering coral in blue, regime-shifted in red) before and after a major coral bleaching event in 1998. Thick horizontal lines display medians and coloured sections of each box represents the interquartile range. Reef sites considered to be outliers are shown as points. Breaks in the x-axes represent an eleven-year gap between surveys, during which the 1998 coral bleaching event occurred. A second bleaching event occurred in 2016.

Visual estimates and transects of reef structural complexity and benthic composition were also carried out within each point count area after fish counts were completed. The overall structural complexity of each point count area was scored from 0 (sand or rubble with no vertical relief) to 5 (exceptionally complex) (Polunin and Roberts, 1993). Coral and macroalgae cover were estimated using the plan view technique, where a diver hovered 1 to 2 m above the reef to estimate the percentage cover within each point count area. An appraisal of both techniques found they were correlated with other methods of measuring reef cover and complexity (Wilson et al., 2007).

Productivity calculations

A trait-based approach was used to calculate productivity, as described by Morais and Bellwood (2020), using details of diet, position on the reef, and maximum total length for each species. Species were grouped by diet (Table S1.1) and reef position (benthic, pelagic, or benthopelagic, as well as reef-associated or reef-dwelling), according to Morais and Bellwood (2018), using information from published sources (Morais and Bellwood, 2018, 2019; Benkwitt et al., 2020; FishBase (and references therein; Froese and Pauly, 2020); Jennings et al., 1995). Maximum total lengths for each species were obtained from FishBase (Froese and Pauly, 2020) and Morais and Bellwood (2018). Any individual fish with an estimated length greater than or equal to the maximum length for the species (0.8 and 0.9 % of observations, respectively) had its length reduced to 0.1 cm below the maximum, with the assumption it was overestimated in the field; this avoided numerical issues in productivity calculations.

The productivity of every individual fish was calculated using the *rfishprod* package (Morais and Bellwood, 2020) in R (version 4.0.3; R Core Team, 2021). First, the growth coefficient at the maximum theoretical size for each species, K_{max} (described by Morais and Bellwood, 2018), was calculated at the population level using species traits (diet, reef position, maximum length) and the mean sea surface temperature over the study period (28°C for Seychelles; Liu et al., 2014). Traditionally, the growth coefficient of a population (K) as it approaches the population asymptotic size (L_∞) is used in models of fish growth, however K_{max} combines K and L_∞ for a species population into a single parameter, standardised to the maximum reported size for the species, L_{max}, by assuming $L_\infty = L_{max}$ (Morais and Bellwood, 2018). Consequently, K_{max}, but not K, allows comparisons between growth rates of fish from different geographies and habitats by constraining estimates to each species' L_{max} (Morais and Bellwood, 2018). As such, it was assumed that all individuals of the same species belonged to the same population with identical species-specific K_{max} estimates after bootstrapping over 1,000 iterations, regardless of individual lengths.

The estimated daily growth in length was calculated per fish over one year by incorporating age estimates into the Von Bertalanffy Growth Function:

$$L_{t+1} = L_{max}\left(1 - exp(-K_{max} \times t)\right) \qquad [1]$$

where L = total length (cm) and t is the estimated age in days (simulated as being derived from otolith rings using *rfishprod*; Morais and Bellwood, 2020). Length-weight relationships were used to convert the daily growth in length into daily accumulation of somatic mass, using the formula:

$$W = a\,L^b \qquad [2]$$

where W = mass (grams), L = total length (cm) and a and b are species-specific length-weight parameters (Froese, 2006). Daily productivity estimates for each individual were simulated over 365 days, accounting for the growth of individuals as the year progressed. That is, growth on any day resulted in a small change in length that affected the productivity estimate of the following day.

Natural mortality was estimated using the *rfishprod* package (Morais and Bellwood, 2020), to simulate fish being removed from the system (e.g. through predation). The instantaneous rate of mortality (M) was calculated per fish based on its observed length estimate, species maximum size and K_{max} value, giving the probability of survival to the next day. Individual survival was then simulated over one year by calculating the cumulative survival rate over 365 days from the date surveyed and multiplying the survival probability at time t by survival at $t - 1$ (i.e. the previous day), resulting in the survival probability gradually decreasing as the year simulation progressed. Once a fish was removed, it did not contribute to productivity for the remaining days in the year, therefore productivity represented the growth (mass produced) of individuals present on the reef each day (Morais and Bellwood, 2020). This probabilistic stochastic removal of individuals was iterated 100 times. After each iteration, the estimated mass produced per day per individual was summed over the year to obtain annual estimates of net productivity. Mean annual net productivity estimates across all iterations were used in all analyses.

Fish below 8 cm in length were not surveyed and therefore productivity estimates within the size range of juvenile recruits to reefs and their subsequent growth over a year could not be estimated. However, contributions of juvenile fish to the production of biomass are assumed to be negligible (Morais et al., 2020a). It should be noted that the productivity of each individual fish was dependent on the traits and parameters stated above. The productivity of predatory fish was not adjusted in relation to the length-based removal of smaller individuals through natural mortality or variation in prey availability. Similarly, the productivity of herbivores was not adjusted based on variation in macroalgae or live coral cover between reef sites. This trait-based approach standardised by species is consistent with previous studies into the productivity of reef fishes (Morais et al., 2020a, 2020b; Benkwitt et al., 2020).

Simulating fishing selectivity

Next, fishing mortality on target species was simulated to account for the effects of trap fisheries on fish productivity. Although fish landings from handlines have historically dominated the Seychelles artisanal fishery (67% by weight in 2017, compared to 13% for traps; SFA, 2018), fish traps were the dominant fishing gear used in the inshore reef areas surveyed and were therefore chosen as the basis for estimating fishing selectivity. Target species were defined as primary, important and occasional targets, according to Grandcourt (1999) and expert knowledge at SFA (Table S1.1). The average size at first capture across all target species from inshore fish trap catches (mean = median = 18 cm) was used to represent the approximate size at which individuals were recruited to the trap fishery, using catch data from Seychelles (Graham et al., 2007). A fishing probability distribution developed by Morais et al. (2020b) was used to simulate size-selective fishing susceptibility of individuals at each cm length (Fig. S1.2). This involved applying a power-Gompertz sigmoidal curve that sharply increased probability of capture at lengths above the target length of 18 cm before plateauing as it approached a set maximum length (100 cm).

For each cm length class, instantaneous fishing mortality (*F*) values were obtained by multiplying the susceptibility to fisheries capture (between 0 and 1) by a fishery capture rate representing fishing intensity. A capture rate of 0.2 was chosen to account for fishing pressure on all fished reefs (found to result in biomass depletion; Morais et al., 2020b) and sensitivity tests examined the effect of varying capture rates on whole fish assemblages for each reef state (Fig. S1.3). The length-specific *F* values were used to proportionally reduce the annual net productivity estimates of individuals considered a fisheries target. Productivity estimates of non-target species, individuals below the target size, and all individuals on protected reefs were unaffected. Although the size of the artisanal fishing fleet around the two study islands of Mahé and Praslin increased from 1994 to 2017 (from approximately 350 to 500 vessels; Christ et al., 2020), long-term estimates of fishing mortality were not available. Therefore, fish productivity was calculated assuming fishing pressure remained constant from 1994 to 2017.

Data analyses

All data analyses and visualisation were conducted in R (version 4.0.3; R Core Team, 2021). Fish biomass and productivity estimates were summed for every point count each year, for different taxonomic groupings (whole assemblage, diet groups and individual species), and then averaged across point counts to give site-level means. Net turnover (%) was also calculated at each site, by dividing net productivity (kg ha^{-1} yr^{-1}) by the standing biomass (kg ha^{-1}) and multiplying by 100. Site-level values were further aggregated to give means (and the standard error of means) for each reef state and management type.

Of the seven primary target species in the inshore Seychelles trap fishery (Graham et al, 2007), the two most productive species per reef state over the post-1998 bleaching time series were chosen to represent species that are of importance to the fishery (Fig S1.4). These were *Chlorurus sordidus* and *Scarus rubroviolaceus* on recovering coral reefs and *Siganus sutor* and *C. sordidus* on regime-shifted reefs.

Generalised linear models (GLM) were used to assess differences in fish biomass, net productivity, and net turnover between fished and protected reefs in 1994. *Management* was a categorical covariate (“fished” or “protected”). Models were constructed as shown in Equation 3, where *Y* represents fish biomass, productivity, or turnover (all log-transformed).

$$Y \sim \alpha + \ Management_i \tag{3}$$

The effects of reef and management characteristics on the net productivity of each diet group following the 1998 bleaching event were quantified with generalised linear mixed models (GLMM) using the *lme4* package (Bates et al., 2015) in R. Observations from protected regime-shifted reefs in 2017 were not included in analyses, as only one of four survey sites were sampled that year. To model net productivity as a function of the covariates, a GLMM (Equation 4) was used for each of four focal trophic groups important to fisheries: macroalgal browsers, herbivore/detritivores, mobile invertivores and piscivores. Site-level data were analysed for all diet groups to reduce the effect of zero values in the response from individual point counts. As observations were made at the same reef sites over multiple years, *Site* was included as a random intercept to account for temporal correlations within each site. *Year* was also included as a random intercept to account for correlations within each survey year.

$$NetP_i \sim \alpha + \beta_1 \times StructuralComplexity_i + \beta_2 \times Depth_i + \beta_3 \times LiveCoralCover_i + \beta_4 \times DeadCoralCover_i + \beta_5 \times MacroalgaeCover_i + Management_i + Habitat_i + Site_j + Year_k$$

$$Site_j \sim N(0, \sigma^2_{Site})$$

$$Year_k \sim N(0, \sigma^2_{Year}) \tag{4}$$

NetP was log-transformed net productivity (kg ha^{-1} yr^{-1}) and *i* represented a given reef site in a given survey year. *Management* (“fished”, “protected”), *Habitat* (“carbonate”, “granitic”), *Year* (*n* = 5) and *Site* (*n* = 21) were all categorical. Continuous covariates (structural complexity, depth, live coral cover, dead coral cover, and macroalgae cover) were scaled with mean = 0 and standard deviation = 1 ((*x* - mean(*x*)) / sd(*x*)). Standardised covariates allowed the relative effect sizes of explanatory variables to be examined, with higher *t* values of predictors indicative of having a greater influence on net productivity (Cade, 2015). Model assumptions of all GLM and GLMM were checked using the protocol described by Zuur and Ieno (2016), by plotting residuals against fitted values, each covariate in the model, and covariates not in the model. Residuals were checked to confirm there were no temporal or spatial dependencies.

Results

Whole assemblage biomass, productivity, and turnover

Pre-1998 bleaching (1994) estimates on protected reefs were higher than fished reefs for fish biomass (protected: 555.1 ±101.7 kg ha^{-1}, fished: 307.9 ±31.5 kg ha^{-1}; GLM: effect size = 0.55, *t* = 7.7) and productivity (protected: 153.3 ±10.9 kg ha^{-1} yr^{-1}, fished: 98.6 ±9.3 kg ha^{-1} yr^{-1}; GLM: effect size = 0.44, *t* = 6.0) (Fig. 1.2 a – d; Table S1.2). Conversely, net turnover in 1994 was slightly lower on protected reefs (28.0 ±1.7 %) than fished reefs (32.2 ±1.7 %; GLM: effect size = -0.03, *t* = -2.9) (Fig. 1.2 e, f; Table S1.2).

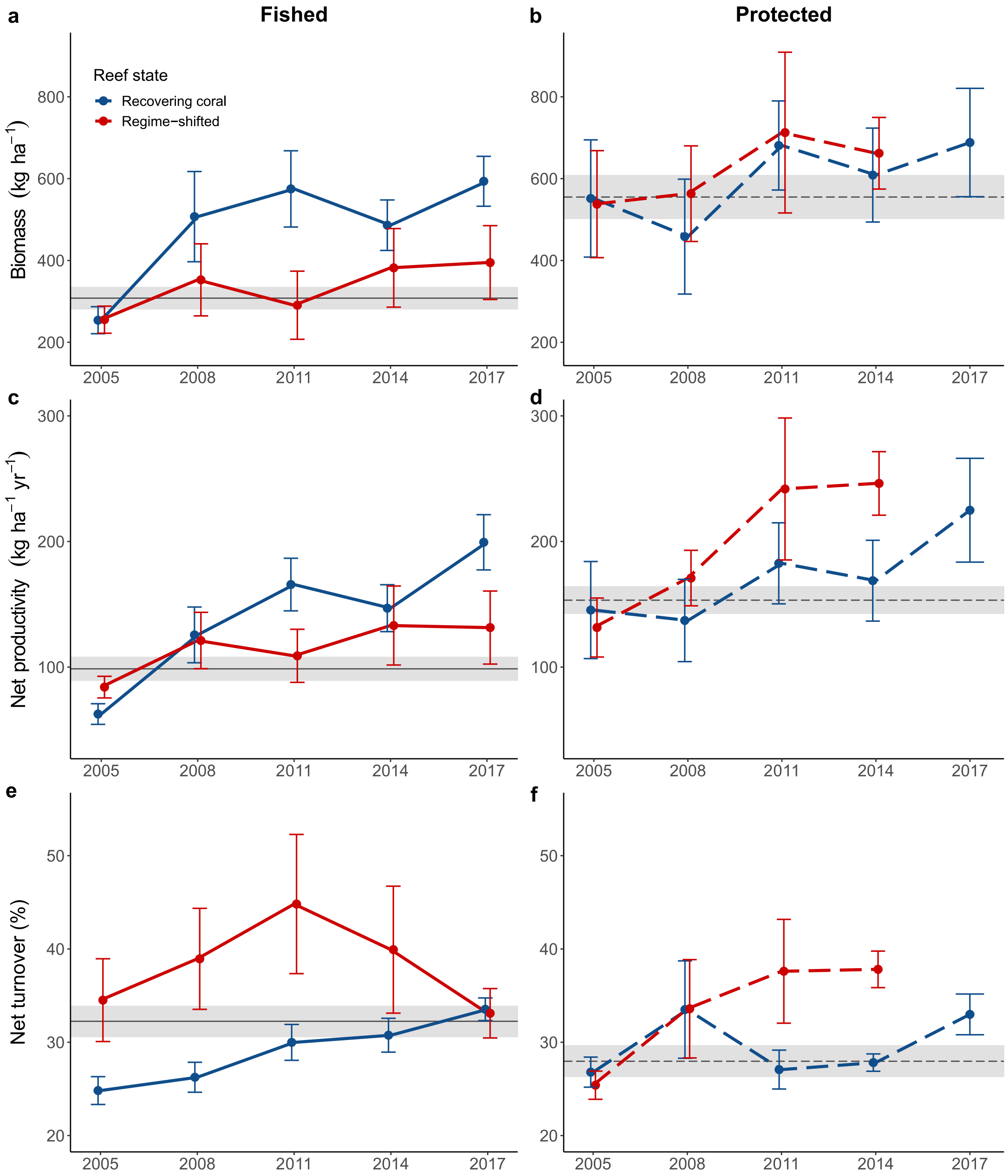

Figure 1.2: Mean biomass (**a**, **b**), net productivity (**c**, **d**), and net turnover (**e**, **f**) of fish assemblages on reefs following recovering (blue) and regime-shifted (red) trajectories after a major coral bleaching event in 1998, on fished (left) and protected (right) reefs. A second bleaching event occurred in 2016. Error bars represent the standard error of the mean across all reef locations surveyed each year. Pre-bleaching estimates from 1994 are shown as grey horizontal lines (with shading for ±1 standard error of the mean). Protected regime-shifted reefs are not presented for 2017 as three of four reef locations were not sampled.

Seven years after the 1998 coral bleaching event, biomass and productivity on fished recovering coral reefs were slightly lower than 1994 values, then increased above 1994 levels and reached values seen on protected reefs by 2017 (biomass: 593.6 ±61.0 kg ha^{-1}, productivity: 199.4 ±61.0 kg ha^{-1} yr^{-1}) (Fig. 1.2 c, d). Turnover on fished reefs in 2005 was lower than 1994 (24.8 ±1.5 %) and steadily increased until 2017, returning close to 1994 levels by 2011 (30.0 ±1.9 %). Biomass, productivity, and turnover on protected recovering reefs remained similar to 1994 until 2017, when productivity and turnover slightly exceeded 1994 levels (productivity: 224.9 ±41.3 kg ha^{-1} yr^{-1}, turnover: 33.0 ±2.2 %) (Fig. 1.2 b, d, f). Assemblage biomass, productivity, and turnover were at their highest levels in 2017 on all recovering reefs, shortly after the 2016 bleaching event.

On reefs that regime-shifted to a macroalgal state, smaller increases in biomass and productivity compared to recovering reefs were observed on fished sites. Estimates exceeded 1994 values by 2017 but with higher variability (biomass: 394.8 ±90.3 kg ha^{-1}, productivity: 131.5 ±29.1 kg ha^{-1} yr^{-1}) (Fig. 1.2 a, c). Turnover on fished regime-shifted reefs in 2005 was similar to 1994, then increased to the highest levels observed on any reefs by 2011 (44.8 ±7.5 %), before decreasing back to 1994 levels in 2017, with high variability in all years. On protected reefs, clear productivity and turnover increases were observed, from slightly below 1994 levels in 2005 to exceeding 1994 levels by 2014 (productivity: 246.2 ±25.3 kg ha^{-1} yr^{-1}, turnover: 37.8 ±2.0 %) (Fig. 1.2 d, f).

Productivity and turnover trends by trophic group

Recovering coral reefs

Similar to the whole assemblage trend on recovering coral reefs, net productivity of all trophic groups on fished reefs increased over post-bleaching years and exceeded 1994 levels, particularly herbivore/detritivores which reached approximately 235% of pre-bleaching productivity by 2017 (112.2 ±12.9 kg ha^{-1} yr^{-1}) (Fig. 1.3 a – d). Net turnover of all trophic groups remained below or at 1994 levels in most years on fished reefs but increased for invertivores in 2014 and 2017, and for piscivores in 2005 (Fig. 1.3 e – h). Herbivore/detritivore turnover was around half the 1994 value by 2005 and increased to almost pre-bleaching levels by 2017 (31.6 ±1.4 %) (Fig. 1.3 f). The highest productivity estimates on recovering reefs generally occurred when turnover was low, particularly for herbivore/detritivores and piscivores (Fig. S1.5).

Productivity was also enhanced on protected reefs, with the exception of piscivores which fluctuated generally below 1994 levels (Fig. S1.6). Post-bleaching turnover was at or above 1994 levels for all trophic groups on protected reefs, except herbivore/detritivore turnover which was at or below 1994 levels (Fig. S1.6).

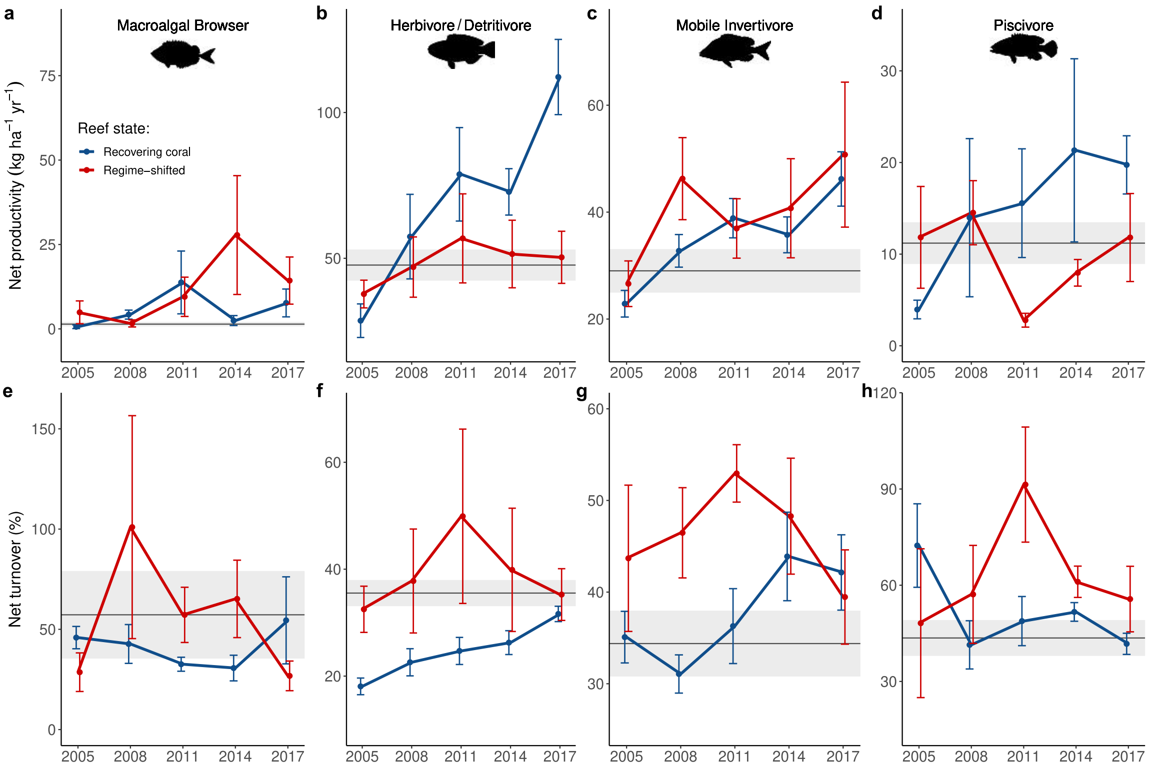

Figure 1.3: Mean net productivity (top) and net turnover (bottom) for selected fish diet groups on fished reefs following recovering (blue) and regime-shifted (red) trajectories after a major coral bleaching event in 1998. A second bleaching event occurred in 2016. Error bars represent ±1 standard error of the mean across all reef locations surveyed each year. Pre-bleaching estimates are shown as grey horizontal lines (with shading for ±1 standard error of the mean). Standard error for macroalgal browser productivity estimates in 1994 is narrow due to low abundance of this group that year (**a**). Note that y-axis scales differ between diet groups. Fish silhouettes are from the *fishualize* R package (Schiettekatte et al., 2019).

Regime-shifted reefs

On fished regime-shifted reefs, productivity was more variable between trophic groups than on recovering reefs (Fig. 1.3 a – d). Browser productivity generally exceeded 1994 levels, particularly from 2011 onwards, peaking in 2014 (27.8 ±17.6 kg ha^{-1} yr^{-1}) (Fig. 1.3 a). Invertivore productivity exceeded 1994 levels by 2008 and peaked in 2017 with high variability (50.8 ±13.6 kg ha^{-1} yr^{-1}) (Fig. 1.3 c). Herbivore/detritivore and piscivore productivity generally stayed similar to 1994 levels although decreased in 2005 for herbivore/detritivores (37.7 ±4.7 kg ha^{-1} yr^{-1}) and in 2011 for piscivores (2.8 ±0.8 kg ha^{-1} yr^{-1}) (Fig. 1.3 b, d). Net turnover tended to be higher and more variable than on recovering reefs for all trophic groups (Fig. 1.3 e – h) and was often higher when productivity was low (Fig. S1.5). Turnover peaked in 2011 for herbivore/detritivores (with high variability; 49.9 ±16.3 %), invertivores (53.0 ±3.1 %), and piscivores (91.4 ±17.9 %) (Fig. 1.3 f – h). Browser turnover peaked in 2008 but had high variability (101.0 ±55.6 %) due to the absence of browsers in most point counts (87.5 %), then decreased below 1994 levels in 2017 (26.8 ±7.4 %) (Fig. 1.3 e).

On protected reefs, both browser and herbivore/detritivore productivity rose sharply over post-bleaching years, exceeding 1994 levels by 2014, with browser productivity distinctly higher and more variable compared to protected recovering reefs (Fig. S1.6). Post-bleaching piscivore productivity on protected reefs was lower than 1994 levels in all years (Fig. S1.6). Differences in turnover between regime-shifted and recovering reefs were less clear on protected compared to fished reefs, however invertivore turnover was consistently higher than 1994 on protected reefs (Fig. S1.6).

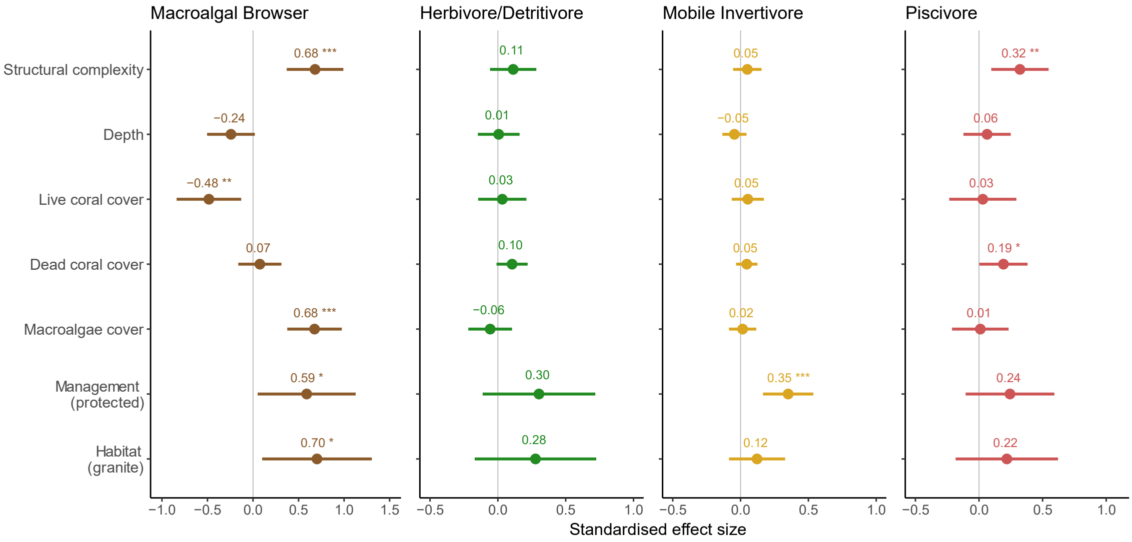

Figure 1.4: GLMM results for select diet groups, showing effect size estimates of predictors on net productivity (the response) in years after the 1998 bleaching event. Effect sizes for each covariate are labelled on each panel, with the level of significance shown (*** = $p \leq 0.001$, ** = $p \leq 0.01$, * = $p \leq 0.05$). Separate models were used for each diet group. Note the x-axis scale for macroalgal browsers differs from other diet groups. Numerical covariates (structural complexity, depth, live coral cover, dead coral cover, macroalgae cover) were scaled from raw values. Factor levels represented by model intercepts (vertical grey lines) were reef state = recovering coral, management = fished, and habitat = carbonate.

Effects of reef characteristics on fish productivity

Reef structural complexity had a significant positive effect on fish productivity for browsers (effect size = 0.68 ±0.16, $t = 4.4$) and piscivores (0.32 ± 0.11, $t = 2.8$) (Fig. 1.4; Table S1.3). Depth had little effect on any group, although browser productivity was marginally lower on deeper reefs (Fig. 1.4). Live coral cover had a negative effect on browser productivity (-0.48 ±0.18, $t = -2.7$) and no effect on any other group, while dead coral cover had a weak but significant positive effect on piscivore productivity (0.19 ±0.10, $t = 2.0$; Fig. 1.4). Macroalgae cover had a strong positive effect on browser productivity (0.68 ±0.15, $t = 4.5$) and no effect on any other group. The productivity of all trophic groups was generally higher on reefs protected from fishing (particularly invertivores; 0.35 ±0.09, $t = 3.8$) and on granitic reefs (particularly browsers; 0.70 ±0.30, $t = 2.3$) (Fig. 1.4; Table S1.3).

Target species

Changes in the net productivity of primary target species on fished reefs were estimated over 2005 – 2017 for the two most productive species on recovering coral (*Chlorurus sordidus* and *Scarus rubroviolaceus*) and regime-shifted (*Siganus sutor* and *C. sordidus*) reefs (Fig. 1.5 a, d). No other primary target species exceeded 10 kg ha^{-1} yr^{-1} at any point in the time series (Fig. S1.4).

Recovering coral reefs

In 1994, *C. sordidus* productivity was higher on recovering reefs (10.2 ±3.4 kg ha^{-1} yr^{-1}) than *S. rubroviolaceus* (1.9 ±0.8 kg ha^{-1} yr^{-1}). Productivity increased for both species after bleaching, reaching their highest values in 2017 (*C. sordidus*: 37.7 ±8.6 kg ha^{-1} yr^{-1}, *S. rubroviolaceus*: 17.16 ±7.3 kg ha^{-1} yr^{-1}) following a decline in hard coral cover (Fig. 1.1). *C. sordidus* abundance followed a similar trend to productivity, initially decreasing from 1994 to 2005 (from 89 to 43 individuals ha^{-1}) before increasing over post-bleaching years to a maximum in 2017 (154 individuals ha^{-1}) (Fig. 1.5 b). A greater number of large *C. sordidus* individuals (30 – 40 cm, close to the length of maximum daily productivity; Fig. 1.6) were observed in post-bleaching years compared to 1994, while the abundance of smaller size classes (10 – 20 cm) also increased after bleaching and exceeded 1994 abundance by 2017. *S. rubroviolaceus* abundance also increased over post-bleaching years to a maximum in 2017 (34 individuals ha^{-1}), particularly for smaller size classes (< 40 cm), but also with greater representation of larger (40 – 60 cm), highly productive individuals (Fig. 1.6). *S. rubroviolaceus* total abundances and abundances per size class were lower than *C. sordidus* in all years (Fig. 1.5 b, c). The net turnover of both *C. sordidus* and *S. rubroviolaceus* was also relatively high on recovering reefs following the 1998 bleaching event (Fig. S1.4).

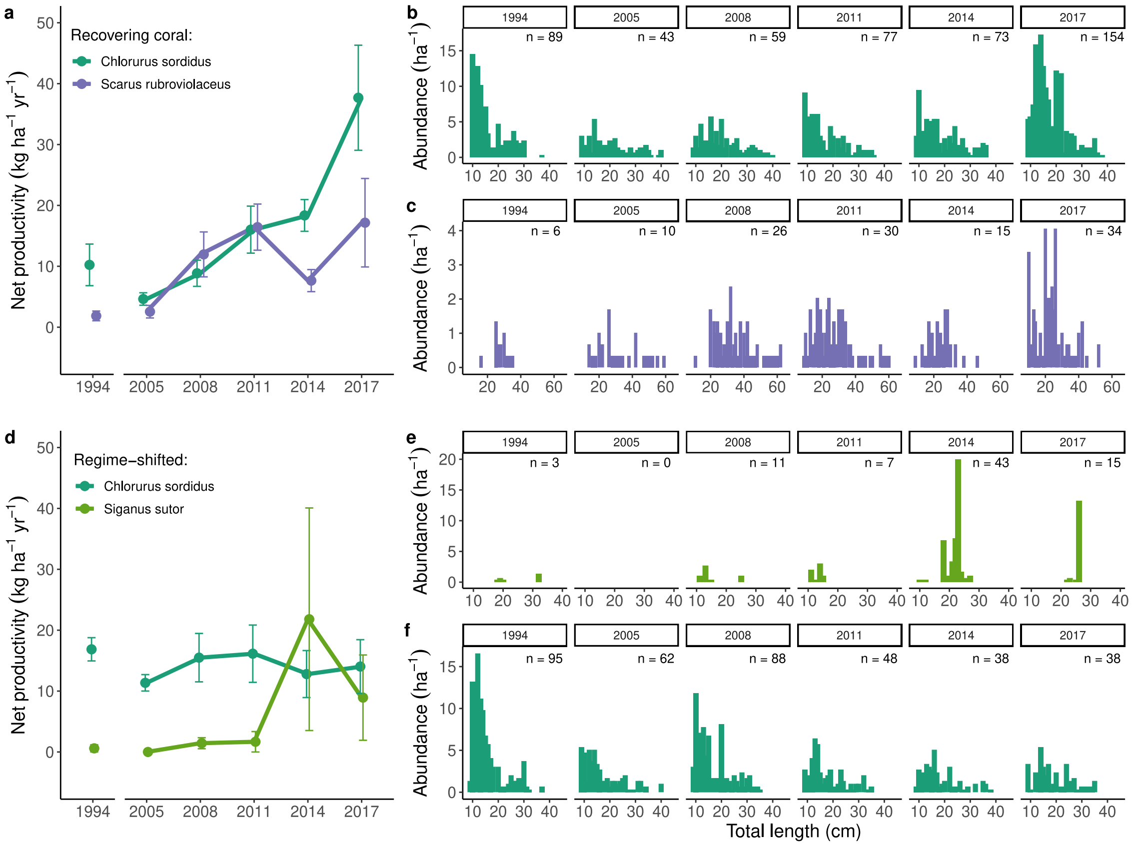

Figure 1.5: Net productivity of the two most productive primary target species in the inshore Seychelles trap fishery on fished recovering coral reefs (*Chlorurus sordidus* and *Scarus rubroviolaceus*; **a**) and regime-shifted macroalgal reefs (*Siganus sutor* and *Chlorurus sordidus*; **d**) over time. Error bars are ± one standard error of the mean. Note the eleven-year gap in the time series between 1994 and 2005, during which the 1998 coral bleaching event occurred. Length-frequency histograms for each species are displayed on the right (**b**, **c**, **e**, **f**), in line with the corresponding productivity plots, using the mean abundance at each length across all fished recovering or regime-shifted reef sites per year. Total abundance across all lengths is displayed for each year.

Regime-shifted reefs

On regime-shifted reefs, *S. sutor* productivity remained at 1994 levels until peaking at 21.8 kg ha^{-1} yr^{-1} in 2014, though this was highly variable (±18.3 kg ha^{-1} yr^{-1}) (Fig. 1.5 d). *S. sutor* productivity decreased in 2017 but remained higher than 1994 levels (8.9 ±7.0 kg ha^{-1} yr^{-1}). Post-bleaching *S. sutor* abundance reflected the productivity trend (though no individuals were observed in 2005) (Fig. 1.5 e). *S. sutor* populations were mostly comprised of small individuals (< 20 cm) between 2005 – 2011, before increasing to 43 individuals ha^{-1} and shifting towards larger fish (> 20 cm) with higher daily productivity in 2014 (Fig. 1.6). *C. sordidus* productivity decreased in 2005 (11.4 ±1.3 kg ha^{-1} yr^{-1}), before returning to 1994 levels from 2008 – 2017 (mean = 14.6 ±4.2 kg ha^{-1} yr^{-1}) (Fig. 1.5 d). *C. sordidus* abundance dropped from 1994 to 2005 (from 95 to 62 individuals ha^{-1}) following bleaching (particularly the smallest sizes) and remained at a similar level for the remainder of the time series (Fig. 1.5 f), similar to the productivity trend. Net turnover of primary fishery target species tended to be dominated by herbivorous species on fished macroalgal reefs (Fig S1.4).

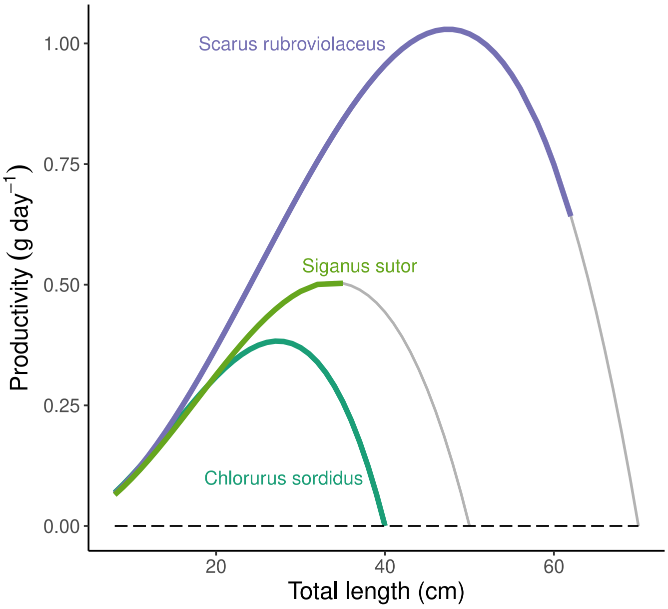

Figure 1.6: The relationship between total body length and individual mass produced per day (in grams) for three highly productive herbivorous fish species on fished reefs (shown in Figure 1.5). Relationships are plotted from 8 cm (minimum total length recorded during surveys) to the maximum total length for each species. Thicker, coloured sections of each line represent the range of fish lengths observed during surveys. The dashed line indicates zero productivity.

Discussion

This study demonstrates that benthic habitat states and fishery restrictions influence the long-term production of fish biomass on coral reefs following mass coral bleaching. Post-bleaching fish productivity at the assemblage level increased on recovering coral reefs in both fished and protected areas, but only on regime-shifted reefs that were protected from fishing. Productivity increases were largely driven by herbivore/detritivores (except on fished regime-shifted reefs), and invertivores and macroalgal browsers on all fished reefs, indicating these species groups will be of high importance for climate-disturbed coral reef fisheries. Net turnover of all diet groups on fished regime-shifted reefs generally exceeded that of recovering reefs, indicating that the replenishment of biomass occurs more readily on macroalgal reefs, and may provide a mechanism for yields to be maintained after climate-driven regime shifts in the Seychelles artisanal fish trap fishery.

Increases in productivity and turnover of fish assemblages on both fished and protected reefs indicate that biomass production does not appear to be hindered by fishing on reefs that are recovering from bleaching. The weak influence of fishing activity on productivity and turnover after bleaching may explain why fish biomass was able to accumulate on recovering reefs (Graham et al., 2020), although calls into question the effectiveness of marine reserves for enhancing biomass production following severe coral bleaching. Productivity and turnover increases on recovering reefs following bleaching suggests enhanced growth rates of individuals coincided with increasing replenishment of standing biomass. Simultaneous increases in assemblage biomass and productivity have previously been documented on reefs following mass coral loss, but in conjunction with lower turnover owing to storage effects in larger individuals (Morais et al., 2020a, 2020b). The return of turnover to pre-bleaching (1994) levels seen on recovering reefs here suggests ample recruitment of smaller individuals, consistent with the length frequencies observed for *C. sordidus*. Recovering coral reefs appeared to provide favourable habitat conditions that enhanced fish productivity regardless of fishing activity, especially after further coral loss following the 2016 bleaching event. This supports evidence from other tropical reefs that shifts in habitat can have a greater impact on fish assemblages than fishing pressure (Russ et al., 2021).

The increased productivity of herbivore/detritivores on recovering reefs suggests low trophic levels are driving the biomass accumulation of whole fish assemblages on these reefs, as has been found elsewhere following climatic disturbances (Adam et al., 2011; Hempson et al., 2018; Morais et al., 2020a; Russ et al., 2021). An increasing abundance of small excavating and scraping parrotfish individuals (*C. sordidus* and *S. rubroviolaceus*, respectively) suggests high recruitment on reefs recovering from bleaching, which will also contribute to increased herbivore/detritivore turnover. Additionally, increasing abundance of large-bodied herbivore/detritivore individuals such as *S. rubroviolaceus* resulted in large *per capita* contributions to fish productivity. The combination of increased abundance, individual growth rates, and turnover of herbivore/detritivores would have contributed substantially to the biomass accumulation on recovering reefs.

Elevated assemblage productivity on regime-shifted reefs protected from fishing suggests the positive reserve effects on biomass production is maintained on post-bleaching macroalgal reefs. Higher fish biomass within marine reserves following disturbances has been documented elsewhere (McClure et al., 2020), however this study indicates this effect can be influenced by benthic state following coral bleaching. Biomass and productivity were maintained at 1994 levels on fished macroalgal reefs, despite an extreme change in benthic habitat that reduced fish species richness (Robinson et al., 2019a), likely sustaining fisheries production. The elevated turnover on fished macroalgal reefs may have initiated a “buffering productivity” effect (Morais et al., 2020b), where fisheries-induced decreases in productivity are less than decreases in biomass, perhaps acting as a compensatory mechanism allowing the production of biomass to be maintained. However, turnover also increased on reefs protected from fishing, therefore changes in fish assemblage composition on macroalgal reefs is likely the main driver of increased turnover, as species more suited to these habitats become more prominent. These results suggest macroalgal reefs can support fish assemblages that sustain fishery catches, albeit without the elevated biomass seen on protected and recovering reefs.

Enhanced productivity and turnover of invertivores on fished macroalgal reefs suggest these species will become increasingly important for fisheries. Higher invertivore biomass on reefs following habitat disturbances is likely driven by increased productivity and availability of invertebrate prey on dead coral substrate (Rogers et al., 2018a; Fraser et al., 2021). In the inner Seychelles, the contribution of invertivores, such as lethrinids (emperors), to artisanal catches has increased in recent years (SFA, 2018) and may form substantial components of catches on regime-shifted reefs. Herbivorous fish are also a major target for fish traps on reef habitat, with browser species such as *S. sutor* sustaining catch rates on Seychelles' macroalgal reefs (Robinson et al., 2019b). The dominance of smaller-bodied, productive species, such as *S. sutor*, is linked to reef topography and regime. Macroalgal reefs act as nursery and foraging habitats for reef fish species, including productive fisheries targets that undertake ontogenetic shifts in their use of reef habitats (Macreadie et al., 2017; Fulton et al., 2020). *S. sutor*, for example, are associated with regime-shifted reefs but also travel between coral reef and seagrass habitats (Ebrahim et al., 2020a). Enhanced fish productivity on protected macroalgal reefs could result in a spillover effect of some species from these reserves to fished reefs and may benefit inshore fisheries in Seychelles.

The substantial contributions of herbivorous species to fish productivity were likely influenced by the quantity, accessibility, and nutritional quality of benthic food resources (Morais et al., 2020a). Enhanced primary productivity following bleaching and reductions in live coral cover benefit large-bodied herbivores, including scraping and excavating parrotfish (Han et al., 2016; Rogers et al., 2018a; Arias-Godínez et al., 2019). This increase in algal and microbial food resources likely underpins the increased parrotfish abundance and productivity on recovering Seychelles reefs by enhancing individual growth rates (Taylor et al., 2019; Nicholson and Clements, 2020), particularly in 2017 when coral cover was severely reduced after the 2016 bleaching event. The high abundance of macroalgae, such as *Sargassum*, on regime-shifted reefs in Seychelles provides a reliable food source for browsers (Ebrahim et al., 2020b), which presumably contributed to the increased abundance and productivity of browsers seen here. Increased nutrient content of macroalgae has been found up to a year after bleaching-induced coral mortality in Seychelles (Vaughan et al., 2021), which could also have enhanced the secondary productivity of browser species. Enhanced primary productivity also likely benefited invertivores feeding on herbivorous and detritivorous invertebrates (Fulton et al., 2019). Reef structural complexity appeared to promote fish productivity, especially for browsers, although availability of benthic feeding resources has been predicted to be a greater determinant of herbivorous fish biomass than structural complexity (Oakley-Cogan et al., 2020). The relationship between fish productivity and reef structural complexity was consistent with other modelling suggesting reduced reef structure lowers fisheries productivity (Rogers et al., 2014). As such, maintaining reef complexity seems to be important for maintaining fisheries productivity and yields.

Although enhanced fish productivity appeared to be influenced by the benthic state of reefs, it should be acknowledged that other potential causes were not accounted for. For example, other energy sources that fuel trophic pathways include cryptobenthic fish species that are vital for ecosystem functioning due to their high productivity and turnover rates (Brandl et al., 2019), as well as pelagic inputs that are transferred to reefs through small planktivorous fishes (Morais and Bellwood, 2019). Fish < 8 cm were not surveyed on reefs and so were not accounted for in this study which focused on fish groups targeted by fisheries. Inclusion of smaller fishes may have revealed linkages between low and high trophic levels, for example productive prey species that may sustain piscivore populations that are of relevance to fisheries. Fishery effects on fish productivity also require further research in Seychelles, as accurate estimates of fishing mortality were unavailable. A fishing mortality estimate greater than that included in these analyses may have resulted in larger disparities between fish biomass and productivity due to increased net turnover maintaining higher productivity (Morais et al, 2020b). Connectivity between fished and protected reefs was unaccounted for, and likely contributed to high post-bleaching fisheries productivity (Hopf et al., 2019).

The herbivore and invertivore fish species that sustain Seychelles inshore reef fisheries are likely to remain important on reefs impacted by climate change. Herbivore/detritivores with high productivity, such as parrotfish, will be particularly key to sustaining catch rates on recovering coral reefs. While this group was highly productive regardless of fishing pressure, fisheries management should aim to maintain the biomass required to perform critical herbivory functions (Hughes et al., 2007; MacNeil et al., 2015). The elevated turnover of different trophic groups on macroalgal reefs suggest they may better withstand fishing pressure, as higher turnover rates provide more resilience to exploitation (McClanahan and Hicks, 2011; Russ et al., 2021), although turnover dropped in 2017 following bleaching in 2016. The trophic structure of fish assemblages is skewed towards herbivores on climate-impacted reefs (more so on regime-shifted than recovering reefs; Hempson et al., 2018), such that fisheries management may need to account for greater dependency on fewer species.

Future projections of global fisheries under climate change scenarios indicate stock biomass and yields in tropical fisheries are more likely to be negatively impacted compared to elsewhere (Gaines et al., 2018; Lam et al., 2020). The enhanced productivity and biomass accumulation seen on Seychelles' reefs following coral bleaching suggests reef fish assemblages may be able to maintain fisheries yields several years after climatic disturbance. The particularly high biomass and productivity of herbivores could indicate these reefs may be able to resist future regime-shifts to algal habitats (McClanahan et al., 2011), while also providing benefits to fisheries. However, it remains to be seen what longer term impacts the 2016 bleaching may have on fish assemblages in Seychelles. Increasing intensity and frequency of bleaching events (Hughes et al., 2018) are expected to result in further regime shifts. Transitions from recovering to macroalgal reefs would likely alter fish assemblages and lead to higher fisheries dependence on macroalgal-associated species. Tropical coastal communities that rely on reef fisheries must adapt to species distribution and productivity changes caused by climate change to offset potential negative effects on food security and livelihoods (Cheung et al., 2013; Gaines et al., 2018).

This study documents how fisheries productivity and turnover respond over long timescales in fish assemblages on two differing post-bleaching reef states. The accumulation and maintenance of biomass observed here was driven by highly productive species in low trophic levels that prosper in post-bleaching habitats. These results build on previous work on coral reef fish productivity (Rogers et al, 2018a; Morais et al., 2020a) to reveal the influence of different post-bleaching habitats, providing evidence that fishery production can be sustained on reefs that have experienced severe bleaching. This sustained productivity is promising for tropical coastal fisheries that rely on reefs for food and income security. However, further coral bleaching and macroalgal dominance are likely to increase the contribution of low trophic level fishes to fisheries catches and may increase dependency on those species.

Chapter 2

Coral reef habitat complexity promotes fisheries nutrient productivity

Abstract

Tropical coral reef ecosystems produce highly nutritious catches for fisheries, which provide vital food security to people in coastal communities. The condition of coral reef habitat has a strong influence on reef fish assemblages, affecting species and nutrient compositions of fisheries catches. Currently, little is known about how the physical structure of reefs influences fisheries nutrient yields, providing an opportunity to investigate the production rates of nutrients in reef fish in relation to habitat complexity. This study compared the biomass and nutrient productivity potential of reef fish assemblages at four locations across the Indo-Pacific with varying levels of fishing pressure. Reef structural complexity positively impacted nutrient productivity across locations and trophic groups of fish, except for macroalgal browsers. Biomass and nutrient productivity were highest in the unfished Chagos Archipelago, where structural complexity had a strong positive effect on productivity, especially for piscivores. Productivity was driven mainly by herbivore/detritivores in fished locations, although the effect of structural complexity varied between trophic groups of fish and locations. For example, in Maldives, structural complexity enhanced piscivore productivity to a greater extent than other fished locations. Branching coral cover had little to no influence on nutrient productivity, other than a negative effect for piscivores in the Chagos Archipelago, suggesting that reef complexity provided by structures other than living hard corals are of particular importance to fisheries nutrient yields. The mean length of fish within each trophic assemblage was a positive predictor of productivity, however this was independent of structural complexity. This study highlights the importance of maintaining coral reef structure to support productive fisheries and the negative implications of structural reef degradation for nutrient provisioning services from reef fisheries.

Introduction

Coral reef fisheries make important contributions to the food security of tropical coastal communities by providing protein and bioavailable nutrients vital for dietary health (Hicks et al., 2021). Climate-induced reef degradation and subsequent regime shifts or recovery of reef-building corals can have large impacts on the biomass and structure of reef fish communities (Darling et al., 2017; Russ et al., 2021) which in turn affects catch rates and compositions in reef associated fisheries (Robinson et al., 2019b). As the frequency and intensity of marine heatwaves are expected to increase throughout the tropics and cause widespread coral mortality (Hughes et al., 2018), overall reef fish biodiversity is expected to decrease on coral reefs following these disturbances, with more generalist species potentially maintaining fisheries productivity and catches (Pratchett et al., 2014) and continuing to supply nutrients to fisheries (Mellin et al., 2022). Nonetheless, the number of species available to tropical reef fisheries is likely to be reduced (Robinson et al., 2019b), which could impact the nutrient yields of reef fisheries as catches with a higher species richness (as opposed to higher absolute yield) tend to be more nutrient-dense (Maire et al., 2021). Therefore, changes in reef fish community composition on climate-disturbed reef habitats are expected to alter nutrient supplies to fisheries, with implications for people's nutrition throughout the tropics.

Fish abundance and biomass are strongly linked to the physical structure of coral reefs (Graham and Nash, 2013; McClure et al., 2021), with abundance more positively associated with reef complexity than live coral cover (Kochan et al., 2023). The size structure of reef fish assemblages is also influenced by reef complexity, with smaller fishes particularly impacted by a loss of refuges from predation, however large-bodied species can also be negatively impacted at juvenile life stages (Alvarez-Filip et al., 2011). The relationship between reef structure and the abundance of small-bodied prey has implications for predators, which may have low abundances on reefs with reduced complexity due to fewer refuges that support prey populations (Rogers et al., 2014; Kochan et al., 2023). However, on highly complex reefs with many prey refuges, biomass production rates (productivity) of predators can be relatively low as hunting efficiency decreases suggesting a non-linear relationship between reef complexity and fish productivity (Rogers et al., 2018b). Although some fishes can become more abundant and productive on reefs following mass coral mortality due to increases in food sources, such as herbivores (Morais et al., 2020a) and invertebrate-feeders (Fraser et al., 2021), severe reductions in reef structure are expected to decrease the fisheries productivity of multiple trophic groups (Rogers et al., 2018a).

Recently developed methods that estimate the nutrient contents (MacNeil, 2023) and the productivity (Morais and Bellwood, 2020) of reef fish now allow fisheries productivity to be investigated from a nutrient perspective. The nutrient productivity of reef fish varies between trophic groups, for example herbivores are often major contributors towards total nutrient productivity and contain high concentrations of zinc and iron, while predatory piscivores have high concentrations of vitamin A and omega-3 fatty acids (Robinson et al., 2023). When standing biomass is depleted, productivity may continue to sustain fisheries on reefs with greater structural complexity (Morais et al., 2023), as well as when reef structure becomes degraded (Rogers et al., 2018a), however information on the nutrient productivity of different trophic groups across reefs of varying complexity is limited. Recent work has investigated the nutrient productivity of reef fish in relation to reef benthos (Robinson et al., 2023), yet the effect of structural complexity on fisheries nutrient productivity is unknown. Developing an understanding of how climate-induced reef degradation alters nutrient productivity, through fish communities, will help to reveal climate impacts on the provision of essential nutrients for people, through fisheries.

This study investigates how the physical structure of coral reefs affects the productivity of six nutrients (calcium, iron, selenium, zinc, vitamin A, and omega-3 fatty acids) from coral reef fisheries, that are vital in people's diets (Hicks et al., 2019). For example, iron and zinc deficiencies are associated with impaired immune responses, calcium is required for healthy bone growth and health (Singh and Prasad, 2023), and the anti-inflammatory properties of omega-3 fatty acids promote cardiovascular health (Bäck and Hansson, 2019). By estimating nutrient productivity across four locations in the Indo-Pacific (Seychelles, Maldives, the Chagos Archipelago, and the Great Barrier Reef), this study aims to bridge the gap between climate-impacted coral reef ecosystems and the essential nutrients reef fisheries can provide to people. Specifically, this study investigates: 1) variation in nutrient productivity between locations and fish trophic groups, and 2) the influence of structural complexity and reef benthos on fish nutrient productivity.

Methods

Data collection

Coral reef survey data from a similar time period (2010-2013) were used to allow comparisons between four study locations: the Chagos Archipelago (18 sites in 2010, 7 sites in 2012), the Great Barrier Reef (GBR), Australia (30 sites in 2010-2011), Maldives (11 sites in 2013), and Seychelles (21 sites in 2011) (Fig. S2.1). Reefs in all locations experienced mass mortality of hard corals caused by coral bleaching in 1998 (Berkelmans et al., 2004; Pisapia et al., 2016; Sheppard et al., 2017; Wilson et al., 2019). Additionally, bleaching-induced coral mortality occurred on the GBR in 2002 (Berkelmans et al., 2004) and in Maldives in 2010 (Pisapia et al., 2016). In Seychelles, hard corals at nine sites did not recover after coral bleaching in 1998; these reefs became dominated by fleshy macroalgae following regime shifts (Graham et al., 2015). The northern Chagos Archipelago was a non-fished wilderness area, while there was some recreational fishing at the United States Navy base on Diego Garcia atoll (Graham et al., 2013). All sites in Maldives were fished, with Maldivian reef fisheries typically employing handlines and droplines to target mainly carangids as well as demersal fishes such as snapper (Lutjanidae), emperor (Lethrinidae), and grouper (Epinephelidae) (Sattar et al., 2012). There were a mix of fished sites and sites protected from fishing on the GBR and in Seychelles (Table

S2.1). Reef fisheries on the GBR mainly target coral trout (*Plectropomus* spp.) and red throat emperor (*Lethrinus miniatus*) with handlines (Welch et al., 2008). Inshore reef fisheries in Seychelles use mainly fish traps ("kazye") and handlines to target rabbitfish (Siganidae), snapper, emperor, and trevally (Carangidae) (SFA, 2023). Total human gravity estimates were used as a proxy for the level of human impact at each reef site (calculated as the total human population divided by the squared travel time within a 500 km radius of each site; Cinner and Maire, 2018).

Reef fish and benthic data were collected using underwater visual surveys in each location. Surveys took place on reef slopes between 4 and 9 m depth. The structural complexity of the reef in each replicate was recorded on a six-point scale, from 0 (sand or rubble with no vertical structure) to 5 (exceptionally complex with numerous caves and overhangs) (Polunin and Roberts, 1993), which correlates with other commonly used methods of estimating structural complexity on coral reefs (Wilson et al., 2007). This measure of structural complexity has proven to be a powerful predictor of reef trajectories post-disturbance (Graham et al., 2015) and of the biomass and trophic structure of reef fish assemblages (Darling et al., 2017).

Counts and length estimations of diurnally active, non-cryptic reef fish ≥8 cm were recorded to species level. In the Chagos Archipelago, GBR and Maldives, reef surveys were conducted on four replicate transects per site. Fish counts and total length estimates were recorded along 50 × 5 m (250 m^2) transects. Benthic data were recorded using point intercepts, by recording the substrate directly below the measuring tape every 50 cm. In Seychelles, eight point count replicates were conducted per site, each within a 7 m radius circle (154 m^2). Fish counts and length estimates were recorded within each point count area, with large fish surveyed first, followed by site attached species, to avoid double counting. Line intercepts were used to collect benthic data within each point count area, where the total length of each type of substrate along a 10 m transect was recorded. Hard corals and macroalgae were recorded to genus level and morphology for corals at all survey locations. In all locations, fish surveys were conducted by the same observer (Nicholas Graham) to avoid observer bias. There may be small amounts of variation associated with different survey techniques, however methods papers have found little difference between belt transects and point counts in estimating fish abundance and biomass (Samoilys and Carlos, 2000).

Analyses focused on four trophic groups of reef fish that are typically targeted by fisheries: herbivore/detritivores, macroalgal browsers, mobile invertivores, and piscivores (234 species in total; Table S2.2). Species from other trophic groups were not included in the study. Observations of species in the Pomacentridae family (damselfishes) were removed from the herbivore/detritivore group as they skewed productivity estimates due to high abundances, and they are not targeted by fisheries. Elasmobranch species were also omitted (<0.1% of observations in the Chagos Archipelago and the GBR) due to difficulties in accurately estimating biomass from underwater visual surveys (Ward-Paige et al., 2010).

Nutrient productivity

Biomass productivity (i.e. the rate somatic biomass is produced) of reef fish was estimated using a trait-based approach, developed by Morais and Bellwood (2020). Trait information was compiled for all species observed in surveys using published sources, including diet, reef position, and maximum total length (Morais and Bellwood, 2018, 2019; Benkwitt et al., 2020; Robinson et al., 2023; FishBase (and references therein; Froese and Pauly, 2023). Any individual fish with an estimated total length greater than or equal to the maximum species length (3.6 and 5.3% of observations, respectively) was assigned a length 0.1 cm below the maximum species length, with the assumption their lengths were overestimated in the field, to avoid numerical issues during productivity calculations. Using the adjusted individual length estimates, daily productivity (g day^{-1}) was estimated for every fish in the reef survey data using the *rfishprod* package (Morais and Bellwood, 2020) in R (version 4.3.1; R Core Team, 2023).

Firstly, K_{max}, a species-level growth coefficient (Morais and Bellwood 2018), was calculated using species traits (diet, reef position, maximum total length) and mean sea surface temperature (SST) over the survey period in each location. Daily SST data were obtained from NOAA Coral Reef Watch (2023) for an area encompassing all reef sites in each location. Traditionally, the growth coefficient of a population (K) as it approaches the population asymptotic size (L_{∞}) is used in models of fish growth; however, K_{max} combines K and L_{∞} for a species population into a single parameter, standardised to the maximum species size, L_{max}, by assuming $L_{\infty} = L_{max}$ (Morais and Bellwood 2018). By constraining estimates to each species' L_{max}, K_{max} allows growth rates to be compared between different geographies and habitats (Morais and Bellwood 2018). We assumed all individuals of the same species in each location were a single population with identical K_{max} values after bootstrapping over 1,000 iterations. Differences in SST between locations caused differences in K_{max} estimates within a species, as *rfishprod* predicts higher growth rates for fish in warmer temperatures (Morais and Bellwood, 2018).

The increase in total length after one day was estimated per individual by incorporating K_{max} and age estimates into the Von Bertalanffy Growth Function (Equation 1, **Chapter 1**, p36). Daily growth in length was then converted into daily accumulation of somatic mass using species-specific length–weight parameters (Froese, 2006; Equation 2, **Chapter 1**, p36). Daily productivity estimates assumed all fish survived until the following day; therefore, mortality was not incorporated into calculations and estimates represent the productivity potential of fish observed during reef surveys.

Productivity estimates were summed by species per transect and combined with nutrient concentrations from the FishBase Nutrient Analysis Tool (Froese and Pauly, 2023; MacNeil, 2023) to obtain nutrient productivity estimates. The Nutrient Analysis Tool provides global species-level predictions of nutrient concentration per 100 grams of white muscle tissue, from Bayesian hierarchical models that include information on fish species' phylogenetic, trophic, and metabolic traits. Due to the trait-based nature of the model that is based on empirical nutrient concentrations of <10% of species, model predictions are likely to be better for certain species and locations than others (MacNeil, 2023). For each of the six focal nutrients (calcium, iron, zinc, selenium, vitamin A, and omega-3 fatty acids), daily nutrient productivity was calculated per species per transect by scaling concentrations 100 g^{-1} to biomass productivity estimates. Nutrient productivity was then summed per trophic group for each nutrient.

Data analyses

Site-level means and standard errors were calculated across transects for biomass and nutrient productivity estimates, and for benthic variables (structural complexity, branching coral cover, and macroalgae cover), to compare between locations. Nutrient productivity means were also calculated across sites with the same structural complexity score (to the nearest 0.5) in each location to compare trends between trophic groups of fish across a reef complexity gradient.

A structural causal modelling approach (Arif and MacNeil, 2023) was used to estimate the effects of environmental and fish population variables on the biomass productivity of each trophic group of reef fish. Structural complexity, branching coral cover, and macroalgae cover were continuous predictors, while fishing was categorical ("fishing" or "no fishing"). Fish population variables were mean total length and species diversity per trophic group (both continuous). Mean total length was calculated per transect, weighted by the biomass of each species. Simpson's diversity index (D) was calculated per transect using Equation 5, where p_i = the number of individuals of each species (i) as a proportion of the entire trophic fish assemblage. Simpson's diversity index accounts for both species richness and evenness (Simpson, 1949).

$$\mathrm{D} = 1 - \sum {p_i}^2 \tag{5}$$

Directed acyclic graphs (DAG) were then created for each trophic group to visualise interactions between the response (biomass productivity) and predictor variables (Figs S2.2-S2.5). Each node in a DAG represents a variable with arrows (edges) between nodes indicating causal effects between variables, for example X → Y would mean X causes an effect in Y, while the absence of an arrow would mean there was no causal relationship between X and Y

(Greenland et al., 1999). DAGs were created by drawing on relevant literature to propose causal relationships between variables (Table S2.3).

A “backdoor criterion” was applied to determine if the inclusion of other variables was required in models to negate any non-causal paths between predictor and response variables, according to each DAG; this process resulted in only causal pathways remaining to avoid statistical biases such as confounding, overcontrol, and collider bias (Arif and MacNeil, 2023). To determine the necessary variables required (if any) to act as adjustments in each model, the software *DAGitty* was used (dagitty.net; Textor et al., 2016). Based on the finalised DAGs, hierarchical generalised linear mixed models (GLMM) were constructed for each predictor variable. The effect of fish biomass on productivity was not estimated due to high collinearity (Fig. S2.6), however biomass was included as an adjustment in other models when required. The top level of the model hierarchy provided global estimates across all study locations, while the second level provided estimates for each location (i.e. separate posterior distributions). Models were run on transect-level data using Bayesian methods in the *rethinking* package (McElreath, 2023). Logged biomass productivity estimates were used as the response in all models. All continuous variables were standardised by dividing each observation by the maximum value in the data (resulting in values from 0 to 1) to allow relative effect sizes to be compared among predictors. Reef site was included as a random effect (i.e. separate intercepts) in every model to account for any site-level variation in the survey data. The basic structure of each model is given in Equation 6, with “predictor1” representing the predictor of interest in each model. Other predictors that were required as causal adjustments based on our DAGs were also included (Table S2.4).

All models were initially run with four chains for 3000 iterations; however the number of iterations was increased for any model with poor Rhat values (i.e. >1.01) or with a total number of divergent transitions >5%. Model outputs were validated using traceplots to visualise chain performances.

$$LogProductivity \sim Normal(\mu\,, \exp(\sigma))$$

$$\mu = \alpha_{LOCATION[i]} + \beta 1_{LOCATION[i]} \times predictor1 + \cdots + \beta_{SITE[j]}$$

$$\alpha_{LOCATION[i]} \sim Normal(\alpha_{GLOBAL}\,, \sigma_{\alpha})$$

$$\alpha_{GLOBAL} \sim Normal(0\,, 1)$$

$$\beta 1_{LOCATION[i]} \sim Normal(\beta 1_{GLOBAL}\,, \sigma_{\beta 1})$$

$$\beta 1_{GLOBAL} \sim Normal(0\,, 1)$$

$$\ldots$$

$$\beta_{SITE[j]} \sim Normal(0\,, \sigma_{SITE})$$

$$\sigma \sim Normal\ (0\,, 1)$$

$$\sigma_{\alpha} \sim Exponential(1)$$

$$\sigma_{\beta 1} \sim Exponential(1)$$

$$\sigma_{SITE} \sim Exponential(1)$$

[6]

Results

Site-level reef structural complexity was highest in the Chagos Archipelago (median = 3.0, range = 1.5-3.6) and lowest in Seychelles (median = 2.1, range = 0.5-3.1), although there was high variability between sites, particularly in the Chagos Archipelago and GBR (Fig. 2.1 a). The GBR had the highest and most variable branching coral cover (range = 5-34%), while Maldives had the lowest and least variable (range = 0-5%) (Fig. 2.1 b). Seychelles had the most variable macroalgae cover, with a maximum of 78% at one site and little to no macroalgae cover at others (median = 2%) (Fig. 2.1 c). Macroalgae cover on the GBR was also highly variable (median = 12%, range = 1-42%). Mean macroalgae cover did not exceed 5% at any sites in the Chagos Archipelago or Maldives.

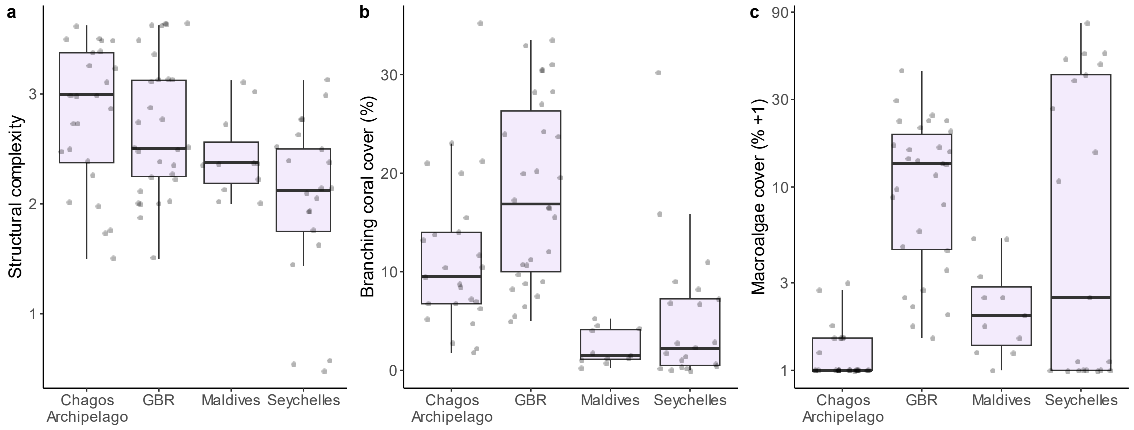

Figure 2.1: Boxplots of coral reef structural complexity (**a**), live branching coral cover (**b**), and macroalgae cover (**c**) across four study locations. Thick horizontal lines represent median values and points are site-level means across reef transects. Macroalgae values (+1) are plotted on a log scale for clarity.

The median biomass productivity of all trophic groups of fish was highest in the Chagos Archipelago compared to all other locations (Fig. 2.2 a). In all locations, herbivore/detritivores had the highest median productivity; 1.1 kg ha^{-1} day^{-1} in the Chagos Archipelago, 74% lower on the GBR (0.3 kg ha^{-1} day^{-1}), and 65% lower in both Maldives and Seychelles (0.4 kg ha^{-1} day^{-1}). Piscivores were the second most productive group in the Chagos Archipelago (median = 0.8 kg ha^{-1} day^{-1}, 75% of herbivore/detritivore productivity), whereas mobile invertivores were in all other locations, with piscivore productivity particularly low in Seychelles and equal with macroalgal browsers (medians = 0.02 kg ha^{-1} day^{-1}). Macroalgal browsers were the least productive group in all other locations and had the most variable productivity in all locations (Fig. 2.2 a).

Although the greatest contributions to nutrient productivity were generally from herbivore/detritivores in all locations (similar to biomass productivity trends), there were exceptions for certain nutrients. For example, in the Chagos Archipelago, the greatest contributions of selenium (44%), vitamin A (50%), and omega-3 fatty acid (47%) production were from piscivores, while the productivity of all other nutrients was mainly driven by herbivore/detritivores (Fig. 2.2 b). The largest calcium, iron, and zinc productivity contributions were from herbivore/detritivores in all locations, particularly for zinc (Chagos Archipelago = 61%, GBR = 71%, Maldives = 63%, Seychelles = 69%). Vitamin A productivity contributions were similar from herbivore/detritivores and invertivores on the GBR (39% and 36%) and in Seychelles (40% and 41%), and from piscivores and invertivores in Maldives (36% and 34%). In Seychelles, nutrient contributions from macroalgal browsers were slightly higher than

piscivores for all nutrients except vitamin A, even though biomass productivity estimates were similar (Fig. 2.2 a, b).

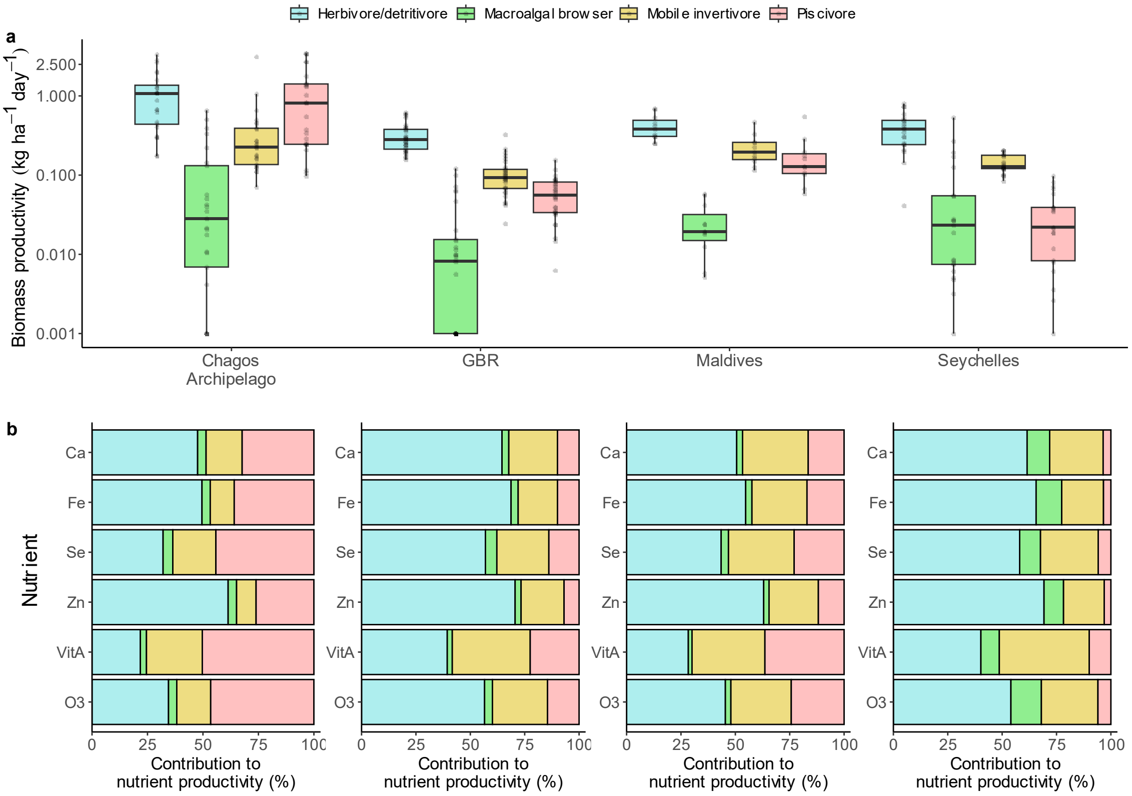

Figure 2.2: Total biomass productivity of four trophic groups of reef fish (**a**) and percentage contributions of trophic groups to the productivity of six nutrients (calcium (Ca), iron (Fe), selenium (Se), zinc (Zn), vitamin A (VitA), omega-3 fatty acids (O3)) (**b**) across study locations. Points in **a** are site-level productivity means across reef transects, presented on a log scale.

Although the greatest contributions to nutrient productivity were generally from herbivore/detritivores in all locations (similar to biomass productivity trends), there were exceptions for certain nutrients. For example, in the Chagos Archipelago, the greatest contributions of selenium (44%), vitamin A (50%), and omega-3 fatty acid (47%) production were from piscivores, while the productivity of all other nutrients was mainly driven by herbivore/detritivores (Fig. 2.2 b). The largest calcium, iron, and zinc productivity contributions were from herbivore/detritivores in all locations, particularly for zinc (Chagos Archipelago = 61%, GBR = 71%, Maldives = 63%, Seychelles = 69%). Vitamin A productivity contributions were similar from herbivore/detritivores and invertivores on the GBR (39% and 36%) and in Seychelles (40% and 41%), and from piscivores and invertivores in Maldives (36% and 34%). In Seychelles, nutrient contributions from macroalgal browsers were slightly higher than piscivores for all nutrients except vitamin A, even though biomass productivity estimates were similar (Fig. 2.2 a, b).

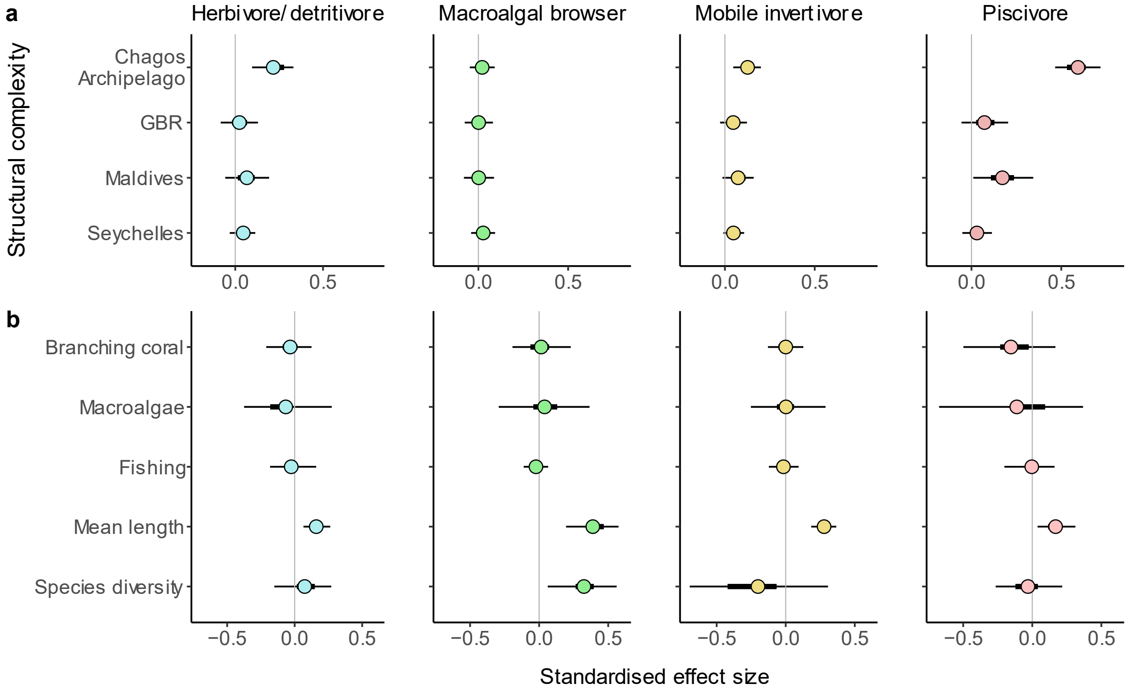

Figure 2.3: Causal effects of reef structural complexity (**a**) and other environmental and fish community variables (**b**) on fish biomass productivity across four trophic groups of reef fish. Points are standardised effect sizes from hierarchical models, with 50% (thick lines) and 90% (thin lines) highest posterior density intervals. Estimates for structural complexity (**a**) are per study location, all others (**b**) are global estimates across all four locations.

Causal models revealed that reef structural complexity generally had a positive effect on biomass productivity for all trophic groups other than macroalgal browsers, in all locations (Fig. 2.3 a). However, the effect of structural complexity varied between locations, with the strongest positive effects in the Chagos Archipelago for herbivore/detritivores (effect size = 0.22, 90% highest posterior density intervals (HPDI) [lower = 0.10, upper = 0.33]), mobile invertivores (0.13, $HPDI_{90\%}$ [0.05, 0.20]), and piscivores (0.59, $HPDI_{90\%}$ [0.47, 0.72]). Piscivore productivity was also higher on more structurally complex reefs in Maldives (0.17, $HPDI_{90\%}$ [0.01, 0.34]). Although all effect sizes were positive, structural complexity had little influence on the productivity of any trophic groups on the GBR and in Seychelles (Fig. 2.3 a).

Environmental variables such as branching coral cover, macroalgae cover, and presence of fishing activity had little effect on the productivity of any trophic group at a global level (Fig. 2.3 b). However, piscivore productivity was lower on reefs with greater branching coral cover in the Chagos Archipelago (Fig. S2.7). In Seychelles, macroalgae cover had a small positive effect on browser productivity (0.09, $HPDI_{90\%}$ [0.03, 0.16]) and a small negative effect for herbivore/detritivores (-0.09, $HPDI_{90\%}$ [-0.17, -0.02]) (Fig S2.7).

Productivity was highest on reefs where the mean fish length within each trophic assemblage was greater (herbivore/detritivore: 0.16, $HPDI_{90\%}$ [0.07, 0.26]; macroalgal browser: 0.39, $HPDI_{90\%}$ [0.19, 0.57]; mobile invertivore: 0.28, $HPDI_{90\%}$ [0.18, 0.37]; piscivore: 0.17, $HPDI_{90\%}$ [0.04, 0.31]) (Fig. 2.3 b), across all locations (Fig. S2.7). However, there did not appear to be any association between mean length and reef structural complexity across trophic groups or locations (Fig. S2.8). The effect of species diversity on productivity was variable both between and within trophic groups (Figs. 2.3 b and S2.7). Global estimates showed macroalgal browser productivity increased with Simpson's diversity index (0.32, $HPDI_{90\%}$ [0.06, 0.56]) (Fig. 2.3 b), although this was more variable in Maldives (0.32, $HPDI_{90\%}$ [-0.16, 0.81]) (Fig. S2.7). There was no clear influence of species diversity on the productivity of any other trophic group at the global level, however, in the Chagos Archipelago, higher species diversity was associated with lower productivity for piscivores (-0.30, $HPDI_{90\%}$ [-0.39, -0.23]) and especially invertivores (-0.93, $HPDI_{90\%}$ [-1.01, -0.86]), while more diverse herbivore/detritivore assemblages had slightly higher productivity in Seychelles (0.17, $HPDI_{90\%}$ [0.10, 0.24]) (Fig. S2.7).

To investigate nutrient production over a structural complexity gradient in more detail, we focused on calcium productivity at each location (Fig. 2.4), as all nutrients followed similar trends (Fig. S2.9). Calcium productivity increased from low to high structural complexity in the Chagos Archipelago (almost six-fold, from 0.02 to 0.11 mg m^{-2} day^{-1}), Maldives (by 22%, from 0.02 to 0.03 mg m^{-2} day^{-1}), and Seychelles (3-fold, from 0.01 to 0.03 mg m^{-2} day^{-1}) but decreased on the GBR (by 44%, from 0.03 to 0.02 mg m^{-2} day^{-1}) (Fig. 2.4 a). The particularly large increase in calcium productivity in Chagos was driven by increased production of all groups except macroalgal browsers (Fig. 2.4 b), while the smaller increases in Maldives and Seychelles were mainly from mobile invertivores and herbivore/detritivores, respectively (Fig. 2.4 d, e). Herbivore/detritivore calcium productivity was highest on the most complex reefs in Seychelles (63% of total; structural complexity = 3), on reefs with intermediate levels of complexity (structural complexity = 2.5) in Chagos (64% of total) and Maldives (53% of total), and on the least complex reefs on the GBR (77% of total; structural complexity = 1.5, however this was from one reef site only) (Fig. 2.4 b-e).

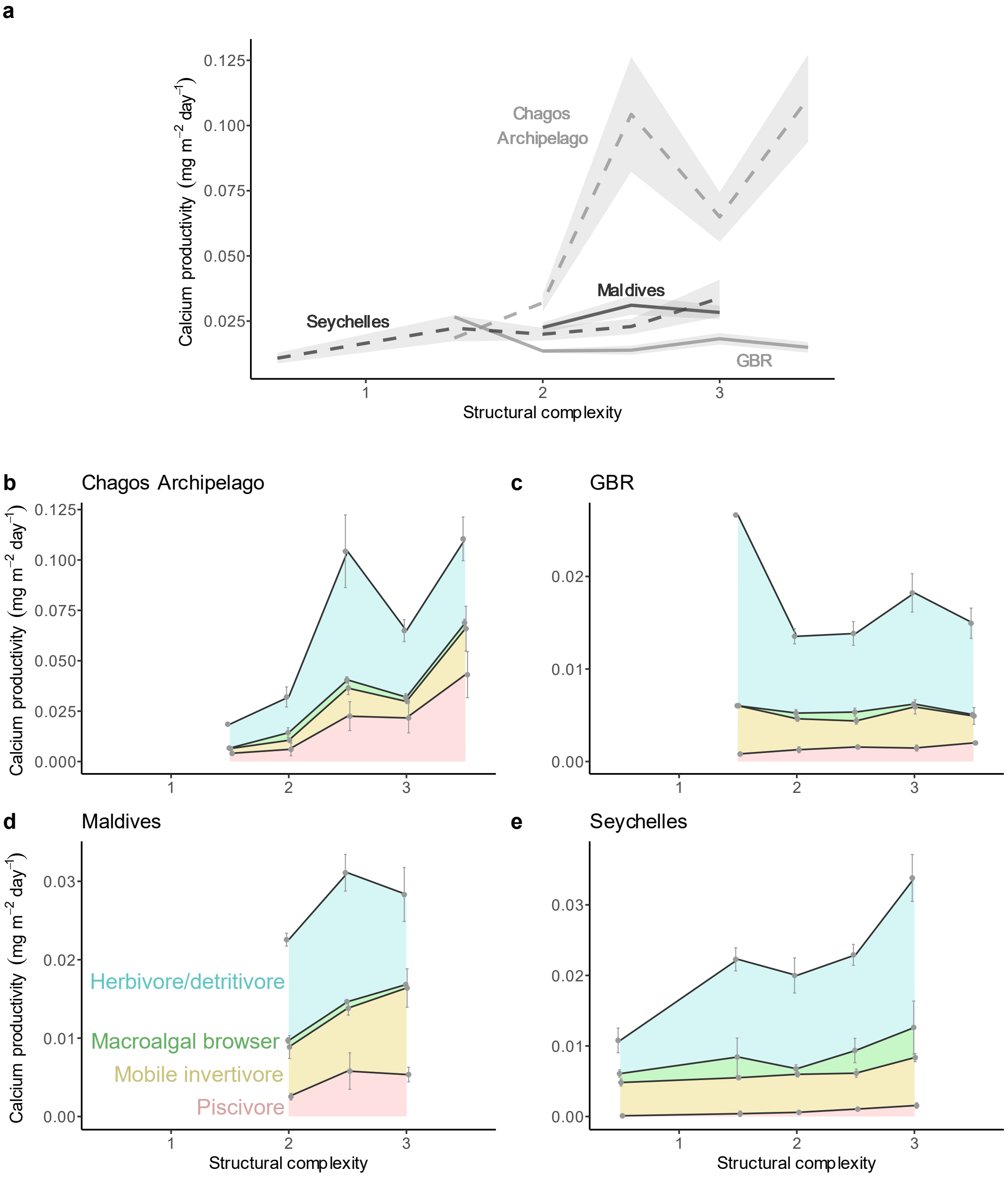

Figure 2.4: Calcium productivity from reef fish across a reef structural complexity gradient, presented as the total of all focal trophic groups at each study location (**a**) and as the cumulative total separated by trophic group for each location separately (**b-e**). Shading in **a** is standard error of the mean and grey points in **b-e** are mean calcium productivity values across structural complexity scores in 0.5 bins (± standard error of the mean). Note y-axis scales and structural complexity ranges differ between locations.

Discussion

This study investigated the production of nutrients that are vital for human health by coral reef fishes in relation to the benthic structure of coral reefs. Reef structural complexity was a positive predictor of biomass and nutrient production for all trophic groups except macroalgal browsers, suggesting that more complex reef habitats support fisheries nutrient productivity across multiple species. However, there were variations in how reef fish productivity responded to structural complexity among study locations, with a particularly positive effect in the unfished Chagos Archipelago. In fished locations, greater mean fish length was a more important driver of productivity than structural complexity across trophic groups (including macroalgal browsers). These results suggest that the topographic features of coral reefs, as well as average fish size, are important variables driving the production of biomass and nutrients across multiple fisheries target species.

Although the productivity of multiple trophic fish groups was generally positively affected by reef structure, groups in lower trophic levels such as herbivore/detritivores and invertivores are likely to be particularly important for nutrient yields in reef fisheries due to their high productivity across all locations. Causal models suggested that productivity of both trophic groups was slightly higher on more complex reefs at each fished study location (Fig. 2.3), indicating that reef structure may be important for maintaining catches of these fishes. Seychelles had the greatest fishing pressure across our study locations (consistent with human gravity estimates, Table S2.1) yet these reefs supported levels of nutrient production from herbivore/detritivores and invertivores comparable to other fished locations (Fig. 2.2), particularly on more complex reefs (Fig. 2.4). Herbivorous and invertivorous fishes have been found to make large contributions to nutrient productivity on tropical coral reefs elsewhere (Robinson et al., 2023) and are commonly targeted by small-scale reef fisheries (McClanahan and Mangi, 2001; SFA, 2023).

Although the abundance and productivity of reef fishes in lower trophic levels may increase on degraded reefs, this is dependent on reef structure being maintained (Rogers et al., 2018a). For example, scraping parrotfish can have higher feeding rates on more complex reefs that have experienced some losses in live coral cover (Robinson et al., 2020a), likely enhancing productivity, and can also have higher abundance on more complex macroalgal reefs (Moustaka et al., 2024). However, herbivore/detritivore species have also been found to have similar feeding rates across a range of reef habitat types and complexities (Richardson et al., 2020), which may explain why although herbivore nutrient productivity tended to be highest on more complex reefs, they made relatively large contributions to productivity across a gradient of reef complexity at all locations (Fig. 2.4). Herbivore/detritivore nutrient productivity appeared to be particularly high on the least complex reefs on the GBR (Fig. 2.4 and S2.9), however this low complexity was represented by only one site and therefore this level of productivity may not be typical on other reefs of similar complexity. Although the productivity of browsing herbivores was low compared to other trophic groups and was largely unaffected by reef complexity, these fishes have been found to have high rates of biomass turnover on macroalgal reefs in Seychelles and may be able to sustain catches by quickly replenishing biomass removed by fisheries (**Chapter 1**).

The large positive effect of reef structural complexity on nutrient production in the Chagos Archipelago compared to other fished locations suggests fish productivity may be more influenced by reef structure on unfished compared to fished reefs. Piscivore productivity in the Chagos Archipelago was particularly enhanced on more complex reefs (Fig. 2.3), presumably because protection from fishing promotes high abundances of piscivores, as even moderate fishing pressure can cause marked declines in targeted piscivore populations (Boaden and Kingsford, 2015). Piscivore productivity is expected to be highest at intermediate levels of prey refuge density (Rogers et al., 2018b), which may often be the case in the Chagos Archipelago as powerful wave action reduces fine-scale complexity (and therefore prey refuges) provided by branching corals on many reefs (Graham and McClanahan, 2013), however this will be dependent on wave exposure. This may also explain why piscivore productivity responded positively to structural complexity but negatively to branching coral cover (Fig. 2.3 and S2.7). Therefore, piscivores likely benefit from a combination of the absence of fishing pressure and good accessibility to smaller prey, resulting in relatively large contributions to the production of nutrients. Although more structurally complex reefs support greater small-bodied prey populations (Alvarez-Filip et al., 2011), predatory fishes are more vulnerable to removal by fisheries when the density of prey refuges is high (Rogers et al, 2018b), which may explain why increases in piscivore productivity with reef structural complexity were relatively low in locations with fishing activity.

Maintaining structural complexity on coral reefs appears to have benefits for the nutrient yields of reef fisheries. Nutrient productivity at all locations in the Indian Ocean increased with structural complexity (Figs. 2.4 and S2.9), which could be particularly important in this region where people in many coastal nations are at risk of nutrient deficiencies, for example calcium and zinc (Kumssa et al., 2015). Structural complexity supports the ecological functioning of reef ecosystems (Darling et al., 2017; González-Barrios et al., 2021) and the fisheries services they can provide people (Beese et al., 2023; Morais et al., 2023), indicating that maintaining reef complexity can have win-win outcomes for ecosystems and people. For example, more structurally complex reefs have a greater functional richness of fishes (the diversity of unique trait combinations amongst species; Richardson et al., 2017), which in turn may lead to a higher functional richness of species in catches that can buffer against climate-induced declines in fisheries yields (unlike the species richness of catches; Dee et al., 2016). Therefore, reef structural complexity can benefit a range of diverse fishes on reefs, supporting nutrient yields in climate-impacted reef fisheries.

These results are based on a six-point visual scale of reef complexity (Polunin and Roberts, 1993), however due to the patchiness and heterogeneity of benthic reef habitats (Karisa et al., 2020), the use of other metrics that describe reef topographical features may provide further insights into associations between reef structure and fish productivity. Causal models indicated that live branching coral cover had little effect on fish productivity compared to structural complexity and, although both variables can often be correlated (Graham and Nash, 2013), there appear to be discrepancies between branching coral and overall structural complexity across study locations (Fig. 2.1 a, b). Fishes utilise reef structure for feeding or shelter at fine scales such as individual coral colonies, overhangs, and grooves (Kerry and Bellwood, 2012; Urbina-Barreto et al., 2021), which can be difficult to represent in one metric over an entire transect area with a high degree of horizontal variation in topographic features (Duvall et al., 2019). Kochan et al. (2023) found that species in higher trophic levels were more abundant on fished reefs with greater vertical relief, measured as the maximum height of the benthos, while the increased abundance of herbivorous fishes in lower trophic levels on more complex reefs is dependent on a greater availability of suitable feeding substrate, specifically (Oakley-Cogan et al., 2020). The spatial scale of fish movement on and between reefs is influenced by foraging behaviour and reef habitat condition, and can also vary between and within trophic groups (Nash et al., 2012; Semmler et al., 2021). Given the importance of fish abundance and availability of food sources for estimating fish productivity (Rogers et al., 2018a; Morais and Bellwood, 2020), these nuances in how various trophic groups of reef fish interact with specific topographical features are likely to have implications for nutrient productivity and could be valuable considerations for future studies.

Trophic assemblages with a larger mean fish length had higher fisheries productivity, which had no clear link to reef structural complexity. This is presumably linked to the length-based method used to calculate biomass productivity, as body size is the primary predictor of reef fish productivity (Morais and Bellwood, 2018). However, by applying this theoretical framework to empirical data, the results of this study suggest that maintaining larger mean fish lengths on reefs is optimal for fisheries nutrient productivity. Fisheries management measures could potentially promote nutrient productivity on reefs by restricting the harvesting of individuals below a threshold length, thereby reducing growth overfishing (the removal of immature fish) and increasing the mean size of reef fish. In addition to having benefits for the size structure of reef fish communities, length-based management measures such as larger mesh sizes on fishing gear and minimum landing sizes can also increase fisheries yields and revenue (Mbaru and McClanahan, 2013; Ben-Hasan et al., 2021). It will be necessary to implement management measures that are specific to the context of fisheries in each location, which includes the challenge of taking a multi-species approach for each gear type when monitoring fish stocks due to the mixed nature of small-scale fisheries (Humphries et al., 2019). Length-based fisheries management in conjunction with the conservation of reef structural complexity may be of particular benefit to fisheries biomass and nutrient productivity on coral reefs.

This study links benthic reef characteristics and fisheries nutrient productivity from reef fish commonly targeted by small-scale fisheries. Conserving the structural complexity of reefs can provide nutritional benefits to tropical coastal communities and should be a key management consideration as climate change continues to impact coral reef ecosystems. Reef structure could be conserved by restricting activities that cause structural damage to the reef benthos such as anchoring and destructive fishing practices (Mangi and Roberts, 2006). In addition to providing fisheries benefits, strategically protecting highly complex reef areas may increase reef resilience to local stressors as well as future climate-driven disturbances (Randazzo-Eisemann et al., 2021). While this study focused only on the natural structure of reefs, future studies into the potential of artificial reef structures for boosting fisheries nutrient productivity could be useful (as suggested by Beese et al., 2023), particularly in areas where fisheries productivity is low on highly degraded reefs.

Chapter 3

Impacts of reef habitat disturbance on the Seychelles artisanal trap fishery

Abstract

As coral reefs face degradation from multiple stressors, reef fisheries must adapt to maintain yields and supply fish to local markets. Fishers witness the environmental conditions on their fishing grounds firsthand and adapt their fishing behaviour in response to catch trends. The collective responses across fishers can ultimately determine how a fishery adapts to environmental disturbances and habitat degradation, therefore engaging with fishers to obtain valuable local knowledge can inform fisheries management. Interviews with artisanal trap fishers on two islands in Seychelles were conducted to determine their perceptions and responses regarding the degradation of reef habitats. More causes of reef degradation were perceived by fishers on the larger island of Mahé, however coral bleaching was by far the most noticed cause of degradation on both islands, leading to short-term, sharp reductions in fisheries yields. Perceptions of catches were variable, however most fishers believed yields had worsened over time, in contrast to catch per unit effort data that had remained stable. One third of fishers stated reduced catches were caused by changing habitats, and perceived catch changes were associated with adaptations to fishing activity, such as increasing trap effort, changing gear type, and travelling further to fishing grounds. While it was clear that fishers valued the importance of reef habitats for fishing, there was evidence that direct human factors may have more of an impact on the trap fishery than coral bleaching in the long term. For example, increases in fishing effort and theft of fish traps were identified as issues negatively affecting yields, causing some fishers to fish with handlines more often or even stop trap fishing altogether. These findings highlight that multiple factors are impacting and changing the Seychelles trap fishery, and that fisheries management could benefit from including information from fishers to assess and address issues regarding overexploitation and habitat degradation.

Introduction

The impact of climate change on small-scale fisheries has been a growing research topic in recent years, with implications for fisheries resources and operations (Ilosvay et al., 2022). Small-scale coral reef fisheries provide food security and livelihoods to millions of people throughout the tropics (Teh et al., 2013; Kittinger et al., 2015), therefore adaptation to environmental change is necessary to avoid detrimental impacts to the socio-economic importance of reef fisheries. Small-scale fisheries that operate on inshore coral reef habitats provide people with a unique variety of fish species compared to other more industrialised fleets (Kuster et al., 2005; Yadav et al., 2021), and buying fish directly from landing sites and at small local markets is common in many areas (Nassiri et al., 2021), providing a culturally important means of food and nutrition security. As the species composition and overall yield of catches is determined by a combination of environmental and fishing factors (Pennino et al., 2016), changes in coral reef environments and the resulting adaptations within reef fisheries will impact the fish available to consumers in coastal communities and small-scale fisher revenue.

Climate change influences the distribution of fish populations, fisheries yields, and therefore fisher incomes (Daw et al., 2009), with variation in the ability of different individuals and fishery sectors to adapt (Cinner et al., 2013). Choices made by individual fishers are important to consider when assessing the effects of climate change and other disturbances on fisheries, as fishers' actions in response to witnessing changes firsthand can mark the initial actions that lead to adaptation in a fishery (Ilosvay et al., 2022). Fishers generally choose where to fish based on the productivity of fishing grounds (Aswani, 1998), therefore climate-induced changes in the productivity across grounds and in the variability of catches (Daw et al., 2009) will likely lead to changes in fishing activity and behaviours. In addition to the decisions fishers make to optimise catches based on their previous experiences, exploitation of fishing grounds is also influenced by constraints, such as time, costs, and potential hazards (Abernethy et al., 2007). Climate-related changes that affect coral reef fisheries, such as benthic habitat shifts (Wilson et al., 2019; Rassweiler et al., 2022) and weather (Chollett et al., 2014; Etongo and Arrisol, 2021), may create or interact with existing constraints on fishing activity, resulting in the need for adaptations by fishers to maintain catches.

Fishers' local ecological knowledge (LEK), based on their perceptions of catches across fishing grounds, can complement fisheries management and provide useful context that augments scientific data (Silvano and Valbo-Jørgensen, 2008; Horta e Costa et al., 2013). LEK can be particularly useful in situations where other data are unavailable and can reveal insights into the spatiotemporal distributions of target species and productive fishing grounds, which can then give direction to management actions such as surveys in key fishing areas (Lima et al., 2007). Incorporating fishers' LEK in management and policy could aid the mitigation of potentially negative consequences of climate change (Savo et al., 2017) on coral reef fisheries. For example, by gaining insights into changing fish distributions and how adaptation of fishing strategies may alter the fishing pressure on species or areas that are particularly sensitive to climate change or local stressors. Information from fishers can provide useful inputs to an ecosystem approach to fisheries management, which aims to account for interactions between fish, fishers, and environmental conditions on fishing grounds (Garcia and Cochrane, 2005). Landings data alone do not always provide such detailed information, particularly for data-deficient fisheries or when collected at low spatial or temporal resolution. Therefore, the inclusion of LEK from fishers will be particularly important as reef habitats and fisheries respond to stressors such as climate change.

This study investigates the perceptions and responses of fishers to coral reef habitat degradation, using the artisanal fish trap fishery in Seychelles as a case study. The inclusion of LEK from fishers across the fleet based on their own fishing experiences allows changes in reef habitats and fish catches across fishing grounds to be documented, which can be used to assess the impacts of reef degradation on the fishery as a whole. Specifically, this study focuses on 1) fishers' perceptions of changes in reef habitats and how this affected fish catches, and 2) the implications of reef habitat changes for fishing activity and fisher livelihoods. By including the opinions of a range of fishers, trends and variation in responses to changing environmental variables on fishing grounds may be revealed, which may be relevant to the management of small-scale reef fisheries in Seychelles.

Methods

Study location

This study took place on Mahé and Praslin, the two most populated inner granitic Seychelles islands (Fig. S1.1). The artisanal fishing fleet in Seychelles operates on inshore reef habitats and grounds further offshore on the Mahé Plateau and provides a vital source of fresh fish to the population of Seychelles (Le Manach et al., 2015). Over 60% of artisanal fishing vessels in 2021 were small fibreglass boats with outboard engines (known locally as "Mini-Mahé"), with the rest of the fleet mainly comprised of other larger vessels (such as whalers and schooners) (Seychelles Fisheries Authority (SFA), 2023). The majority of artisanal fish landings in 2021 were from the handline fishery (71%; consisting mainly of species from Carangidae, Scombridae, Lethrinidae, and Lutjanidae families), followed by 14% from fish traps (12% from static traps, 2% from active traps) and 10% from gillnets (SFA, 2023). Landings from the trap fishery are dominated by the family Siganidae but include fishes from other families, such as Labridae (mainly parrotfishes, Scarinae), Lethrinidae and Mullidae (SFA, 2023).

Reefs around Mahé and Praslin experienced mass coral mortality in 1998 following a severe marine heatwave, causing some reefs to shift to a macroalgae-dominated state while others remained dominated by hard corals as colonies recovered (Wilson et al., 2019; **Chapter 1**). A second heatwave in 2016 reduced hard coral cover on recovering reefs and both bleaching events were associated in changes in the abundance of reef fish targeted by fisheries, particularly decreases in smaller size classes (Wilson et al., 2019).

Fisher interviews

Interviews with 34 artisanal fish trap fishers were conducted on Mahé (*n* = 23) and Praslin (*n* = 11) from May to June 2022 to gather perceptions of habitat changes and changes in fishing activity. Interviews consisted of a semi-structured questionnaire with closed questions to provide quantitative data as well as open-ended questions to provide complementary qualitative data (Chapter 3 supplementary material, p134). The semi-structured format allowed interviews to remain focused on the topics of interest while also being flexible enough to explore any points made by respondents further (Adeoye-Olatunde and Olenik, 2021). The first section of the questionnaire was designed to collect information relating to personal and fishing characteristics, for example age, number of years fished, frequency and duration of fishing trips, and types of fishing gears used. The remainder of the questionnaire related to fishers' perceptions of change in reef habitats and fish catches, and how this related to impacts and alterations to their fishing activity.

To gather perceptions of habitat change, fishers were first asked if they had noticed any changes on reefs in general, as well as on any of their fishing grounds, at any time. Fishers were prompted to give descriptions of their observations and provide estimates of when the changes occurred, how long they took to occur, and if they were temporary or permanent changes. Fishers were asked about any general changes first to avoid leading questions that may have produced biased responses (Adeoye-Olatunde and Olenik, 2021). Due to the history of coral bleaching on reefs surrounding the inner granitic islands in Seychelles (Wilson et al., 2019), fishers were then specifically asked about coral bleaching events in 1998 and 2016 (or prompted for more information if they had already mentioned coral bleaching) (Table 3.1). Fishers were asked which types of fish they regularly caught before being asked if they had noticed changes in the catches of any type and, if so, what the reasons for changes may be. If reef habitat conditions were not mentioned, fishers were asked if they thought catch changes could be linked to habitat change. In addition to each type of fish, fishers were asked if they thought overall yields had changed over time.

Fishers were asked about changes in their fishing activity and if any of their responses were related to reef habitat changes. Specifically, fishers were asked about changes in fishing grounds (including increasing their travel distance), changes in fishing effort (gear number, gear types, technique), and changes in landing or selling their catch (Table 3.1). Additional questions explored other factors that may have influenced fishing activity, such as temporal changes (fish prices, tourism, religious holidays, COVID-19 restrictions) or interactions with other fishers. Fishers were also asked if there were any other influences on their fishing activity that had not been raised in the interview so far, or if they had any other general comments to add.

Table 3.1: Topics and corresponding question numbers included in the questionnaire used to investigate the perceptions and responses of trap fishers in Seychelles in relation to reef habitat change (questionnaire in Chapter 3 supplementary material).

Perceptions		
Topics		**Question numbers**
Reef habitats		Q4 a, b
Habitat changes	Degradation Recovery	Q4 c-e; Q13 a, b
	Coral bleaching	Q4 f
	Fishing grounds	Q8 a-d
Fish catches		Q5
Catch changes	General	Q6 a, b; Q7 a, b; Q13 c
	Habitat related	Q6 c; Q7 c, d
Responses		
Topics		**Question numbers**
Change in grounds	General	Q8 e-h
	Travelling further	Q9
Change in fishing effort	Gear number Gear type	Q10 a, b
	Fishing technique	Q10 c; Q11 c, d; Q12
	Fishing less	Q18
Change in landing/selling fish		Q7 f; Q13 d
Responses to other factors		Q14; Q15; Q16

We followed a purposive snowball sampling approach (Ayhan, 2011) on each island to identify fishers who fished with fish traps (“kazye” in Seychellois creole/Kreol). Due to limited information on the exact number and location of trap fishers on each island, an opportunistic approach to sampling was used rather than a stratified approach. Initially, a few known fishers were identified for interview through contacts at SFA, and subsequent interviews were then based on recommendations from fishers who were interviewed (either specific individuals or fish landing sites to visit). Fishers who had never fished with fish traps were not interviewed. In situations where multiple fishers operated the same vessel, only one fisher per vessel was interviewed. Interviews were conducted in either English or Kreol (or a mix of both) with a translator, depending on each fisher’s preference, and recorded verbatim. Median interview length was 42 minutes (minimum = 19 minutes, maximum = 1 hour 18 minutes). Two of the fishers on Mahé and three on Praslin had retired and all others had active licences from SFA. Retrospective statistics from SFA revealed the sample of licensed trap fishers (i.e. excluding those who had retired) constituted 30% and 44% of active vessels in 2022 on Mahé (n = 69) and Praslin (n = 18), respectively (pers. comm., SFA, 2024). The use of interview data in this study was approved by the Faculty of Science and Technology Research Ethics Committee, Lancaster University (reference: FST-2022-2207-RECR-1).

As the main researcher who developed the questionnaire used in this study and conducted interviews, it is necessary to state my positionality. I have experience working with trap fishers in the United Kingdom, including a research project where I interviewed fishers about interactions between the natural marine environment and their catches. I have also conducted research into the impacts of coral bleaching on the benthos and fish populations on Seychelles reefs (Chapters 1 and 2). As a result, I am familiar with some considerations made by fishers when choosing where and how to fish, as well as the ecology of coral reefs in Seychelles. These past experiences influenced the questions I chose to ask, my interactions with fishers, and interpretation of results during this study.

Trap fishery landings

Monthly landings data from the trap fisheries around Mahé and Praslin from January 2017 to December 2021 were obtained from the SFA catch assessment survey. Monthly SFA sampling effort is randomly distributed among landing sites on Mahé and Praslin, within geographic strata per island based on the number and type of boats active at the sites (Robinson et al., 2006). Landing site observers subsampled catches to estimate the weight of each species landed per vessel, as well as fishing effort (e.g. number of traps) and the number of active fishing vessels per site (by gear type). Weights of different species may be estimated from the taxonomic composition of mixed fish packets. After filtering the available data to include landings from fish traps only, data from 14 landing sites on Mahé and two sites on Praslin were used in this study.

Data analyses

Quantitative data generated from questionnaires were collated and used to calculate medians of fisher characteristics (age, number of years fished, boat length, and fishing trips per week). Categorical responses (e.g. “yes”/”no”) were summarised and percentages of responses across fishers on each island were calculated. Responses relating to macroalgae or sea grass habitats were grouped into one category (“macroalgae/sea grass”) due to ambiguity of the terms used to describe these habitats when translating from Kreol to English. Quantitative data were also generated from the qualitative information provided by fishers. First, qualitative data were separated into two broad categories relating to the research questions: 1) fisher perceptions (Table S3.1), and 2) responses and/or outcomes of changes in fishing activity (Table S3.2). Quotes from fishers were organised by topic and coded to determine the themes that emerged from fishers' collective responses (Tables S3.1 and S3.2). Thematic coding involved identifying key words or phrases that were relevant to a particular topic and summarising responses to generate common themes. Fishers often referred to environmental variables when discussing fish populations and catches, and vice versa, therefore certain quotes were included multiple times in thematic coding tables.

Fish trap landings data were used to visualise catch per unit effort (CPUE), from 2017 to 2021 on Mahé and Praslin, focusing on the families Siganidae and Labridae, as these were the two main species groups (rabbitfish and parrotfish, respectfully) caught by fishers. Landings data from static and active fish traps were not separated during analyses, as both gear types are often hauled during the same fishing trip but data are assigned to only one gear type by observers at landing sites (pers. obs.). First, the total weight of each fish species landed per fishing trip per vessel was calculated. Then species weights were aggregated to obtain totals per fish family. CPUE for each family was calculated per fishing trip by dividing the landed weight (kg) by the number of fish traps hauled. Landings weights without effort estimates (30% of observations) could not be included in analyses. Monthly CPUE means and standard errors per family were then calculated across all fishing trips and landing sites per island. Monthly coefficients of variation were calculated per family per island by dividing the standard deviation of CPUE by mean CPUE. All quantitative analyses were performed using R (version 4.3.1; R Core Team, 2023).

Results & discussion

There were several similarities in fishers' characteristics between islands, including median age (Mahé = 54, Praslin = 52) and years fished (Mahé = 17, Praslin = 20) (Table 3.2). However, there was a large difference in the minimum age of respondents (Mahé = 21, Praslin = 40). Approximately three quarters of respondents on each island depended on fishing as their main source of income (Mahé = 78%, Praslin = 73%). The median number of fishing trips per week was slightly higher in Praslin (6) compared to Mahé (4.5) with three fishers on Praslin (including two who had retired from trap fishing) stating they fished approximately twice every day of the week. The use of "active traps" that are strategically set for short periods of time and hauled multiple times per day to target rabbitfish are common in Seychelles, particularly for *Siganus sutor* spawning aggregations (Robinson et al., 2011). The higher number of weekly fishing trips on Praslin suggests the use of active traps may be more common there.

Table 3.2: Descriptive statistics of fisher characteristics by island, from interviews on Mahé and Praslin.

	Mahé (*n* = 23)	Praslin (*n* = 11)
Age (years)		
Median	54	52
Minimum	21	40
Maximum	69	72
Years fished		
Median	17	20
Minimum	3	5
Maximum	50	43
Retired (trap fishing)	*n* = 2	*n* = 3*
Is/Was fishing main source of income?		
Yes	*n* = 18 (78%)	*n* = 8 (73%)
No	*n* = 5 (22%)	*n* = 3 (27%)
Boat length (m)		
Median	5.9	5.8
Minimum	4.9	4.9
Maximum	7.0	6.7
Number of fishing trips per week		
Median	4.5	6
Minimum	3	2
Maximum	14	11

* two fishers had retired from commercial trap fishing but still fished with handlines; one fisher still fished recreationally with traps.

Fishers' perceptions of change

Reef habitats

Fishers described multiple causes of degradation on coral and macroalgae/sea grass habitats, with a similarly high proportion of fishers on each island mentioning degradation of coral habitats (91%) and specifically coral bleaching as the main cause (Mahé = 74%, Praslin = 73%) (Table 3.3). More fishers on Mahé also mentioned other causes of coral degradation, such as land reclamation (35%), sedimentation (17%), and wave action (17%), as well as degradation of macroalgae/sea grass habitats (43%), mainly from wave action (Table 3.3). This suggests the inshore reef habitats around Mahé have been more exposed to a wider range of disturbances compared to Praslin. For example, extensive land reclamation during infrastructure development has destroyed reefs close to Victoria, the capital city on Mahé, and further south to create the international airport and luxury residences (Jennings et al., 2000), while coastal development on such a scale has not occurred on Praslin and was not mentioned by any fishers there.

Due to the widespread coral mortality on reefs around Mahé and Praslin following coral bleaching events in 1998 and 2016, and the resulting benthic regime shifts from hard coral dominance to fleshy macroalgae dominance on several reefs (Wilson et al., 2019), fishers were specifically asked if they had noticed reef habitat changes in relation to either bleaching event, which likely explains why the total proportion of fishers to mention coral bleaching on each island was so high. However, several fishers mentioned coral bleaching without being prompted during interviews, especially on Praslin (Mahé: unprompted = 22%, prompted = 57%; Praslin: unprompted = 55%, prompted = 18%). Two fishers specified high sea temperature as the cause of coral bleaching, with other reasons given including a change in the climate and too much freshwater from rainfall (Table S3.1). Five fishers mentioned "*algae blooms*", referring to rapid growth of benthic macroalgae, with two fishers (one per island) stating that they followed the 2016 bleaching event, which is in agreement with previous scientific surveys (Wilson et al., 2019).

Table 3.3: Types of marine habitat degradation and their causes as stated by fishers during interviews on Mahé ($n = 23$) and Praslin ($n = 11$). Values are the percentage of fishers on each island that identified types of reef degradation and the cause(s), with the number of respondents given in brackets. If fishers did not mention coral bleaching of their own accord, they were asked if they noticed the 1998 or 2016 bleaching events.

Perceived habitat degradation (bold) and causes	Mahé	Praslin
Hard coral	**91% (21)**	**91% (10)**
Bleaching	74% (17)	73% (8)
Land reclamation	35% (8)	0
Sedimentation	17% (4)	0
Wave action	17% (4)	9% (1)
Other	9% (2)	27% (3)
Macroalgae/Sea grass	**43% (10)**	**27% (3)**
Wave action	36% (4)	0
Other	13% (3)	9% (1)

Perceptions of the time taken for reefs to recover following coral bleaching varied between fishers on each island. On Mahé, four fishers (17%) described the recovery of coral following bleaching in 2016 as "*quite fast*", with time estimates for recovery ranging from six months to two years. However, two fishers on Praslin (18%) said the coral had taken five to six years since bleaching in 2016 to recover, with another fisher noting that since 2016, coral was "*quicker to recover than in 1998*" and that recent coral bleaching "*started about 6 months ago and reefs are already getting back to normal*" (Table S3.1). These perceptions of relatively faster reef recovery after the 2016 coral bleaching are aligned with data from reef surveys conducted in 2022 which indicate the rate of coral recovery following the 2016 bleaching event has indeed been faster compared to the 1998 event (Graham et al., in review). A possible contributing factor to this was the additional reef disturbance from the 2004 tsunami which fishers on both islands recalled during interviews. One fisher stated the reef was "*completely destroyed*" following the tsunami, and another said, "*the coral was very nice before* [the tsunami] *but after it was dead and white*", suggesting that such a large-scale disturbance likely impacted coral recovery following bleaching in 1998. The tsunami is estimated to have hindered recovery from bleaching by six years, with reefs more directly exposed to the tsunami trajectory damaged most (especially carbonate reefs; Obura and Abdulla, 2005). The general agreement among fisher perceptions and fisheries-independent surveys, as well as the additional context from fishers regarding the history and relative levels of impact of different types of reef disturbances, highlights fishers' awareness of reef habitat changes and the value of their LEK to science and management.

Fish trap catches

Several fishers stated that trap catches were severely reduced during and immediately after coral bleaching (48% of fishers on Mahé, 45% on Praslin), and that fish moved elsewhere when the water temperature was too high. One fisher said coral bleaching was "*really bad for fishing*" and another said, "*I wouldn't fish on a bleached reef, it's not worth it as you won't catch anything*". Like perceptions around recovery of the reef, there was variation in perceptions of the time taken for catches to recover following coral bleaching. Some fishers (24%) believed catches had remained lower than they were prior to bleaching, with some noting high sea temperatures and dead coral as the reason, although there was some acknowledgement that catches were "*starting to get better*" again six years post-bleaching (Table S3.1). Other fishers described faster catch recovery times but only on Mahé (17% of Mahé fishers); one fisher said, "*catches were very bad at the time of coral bleaching, but quite quick to come back*". It is clear from fishers' perceptions that climatic shocks, such as widespread coral bleaching, have the potential to negatively impact fish yields from traps. Multiple studies have estimated the effects of coral bleaching on trap fishery yields in Seychelles using data collected in years before and after bleaching events (Grandcourt and Cesar, 2003; Graham et al., 2007; Robinson et al., 2019b), however these did not show such extreme immediate reductions in fish abundances or catches when bleaching occurred, as mentioned by fishers in this study. In fact, fisheries statistics presented in six-monthly intervals indicate the Seychelles trap fishery CPUE peaked in 2016 (SFA, 2023), even though fishers described a period of very low catches as a result of coral bleaching in this year. Given that coral bleaching can severely disrupt trap fisheries yields in the short-term, a higher temporal resolution of data could better document these effects on landings.

Most fishers perceived a declining trend in total catches from traps, particularly on Praslin (64%), while just over a quarter of fishers on each island said catches had generally remained the same (Fig. 3.1 a). Similarly, most fishers perceived decreases in rabbitfish catches, particularly on Praslin (64% of fishers; Fig. 3.1 b), suggesting trends in rabbitfish catches may have driven fishers' overall impression of their catches over time. All fishers said they targeted

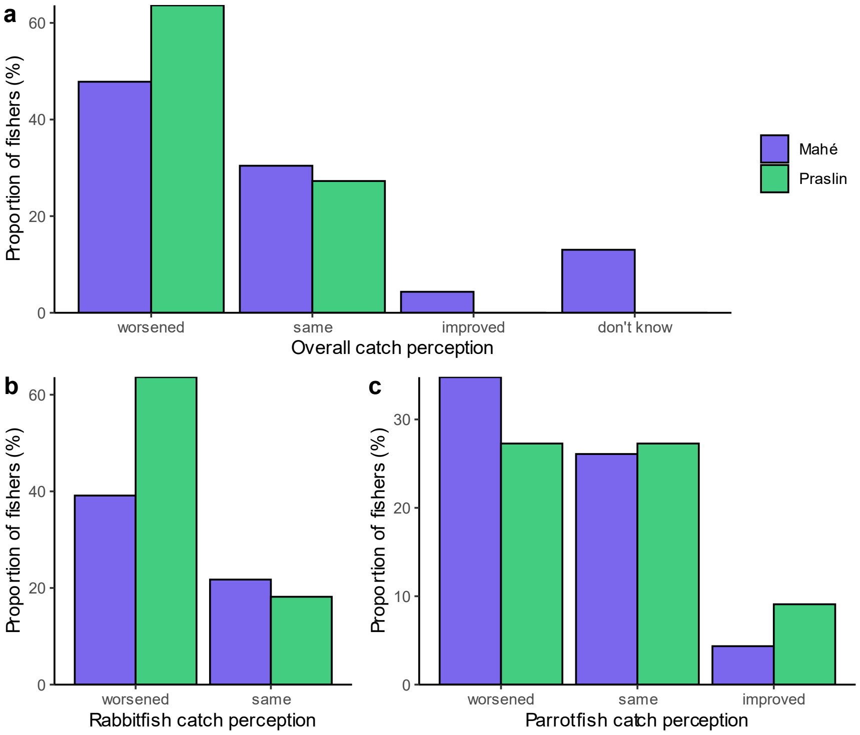

Figure 3.1: Fisher perceptions of changes in their catches from fish traps, for total catch (**a**), rabbitfish (**b**), and parrotfish (**c**). Responses per island do not add to 100% as some fishers gave no opinion, particularly for specific types of fish (**b** and **c**).

rabbitfish and several described being able to catch rabbitfish "*anywhere*" and "*all year round*", highlighting the importance of these fishes to the Seychelles trap fishery (Robinson and Shroff, 2004). Landings data suggest total rabbitfish catches decreased from 2016 to 2020, which is aligned with fisher perceptions, however catches then increased sharply in 2021 (SFA, 2023). However, rabbitfish CPUE from fish traps increased slightly from January 2017 to December 2021 on both islands (Mahé: 2.3 to 4.0 kg trap^{-1}, Praslin: 2.3 to 3.2 kg trap^{-1}; Fig. 3.2 c), although catches were variable, particularly during the early southeast monsoon season (SEM, the south-easterly trade winds during the austral winter) in 2019 (May/June; Fig. 3.2 d). A previous study estimated rabbitfish CPUE fluctuated between 2.5 and 3.5 kg trap^{-1} from 1994 and 2016 (Robinson et al., 2019b) which is comparable to CPUE estimates in this study following bleaching in 2016 (Fig. 3.2 c), suggesting long-term rabbitfish catches can be relatively resilient to coral bleaching (likely due to their high rates of biomass turnover on macroalgal reefs in Seychelles; **Chapter 1**). Previous research has found fisher perceptions of declining catches were more negative than fisheries landings data suggested (Daw et al., 2011), however CPUE of some species groups (e.g. lethrinids) was declining prior to bleaching in 2016 (Robinson et al., 2019b), which may have influenced fishers' perceptions of overall yields. Several fishers (26%) mentioned that catches could be highly variable, which may make it more difficult to notice longer term catch trends, particularly when catching a high diversity of species in a multispecies fishery (Pet-Soede et al., 2001). It should be noted that CPUE estimates may be biased towards vessels with larger landings that sell catch at designated landing sites, while vessels with smaller landings or those that send rabbitfish to be salted (bypassing landing sites) may be missed by catch assessment surveys.

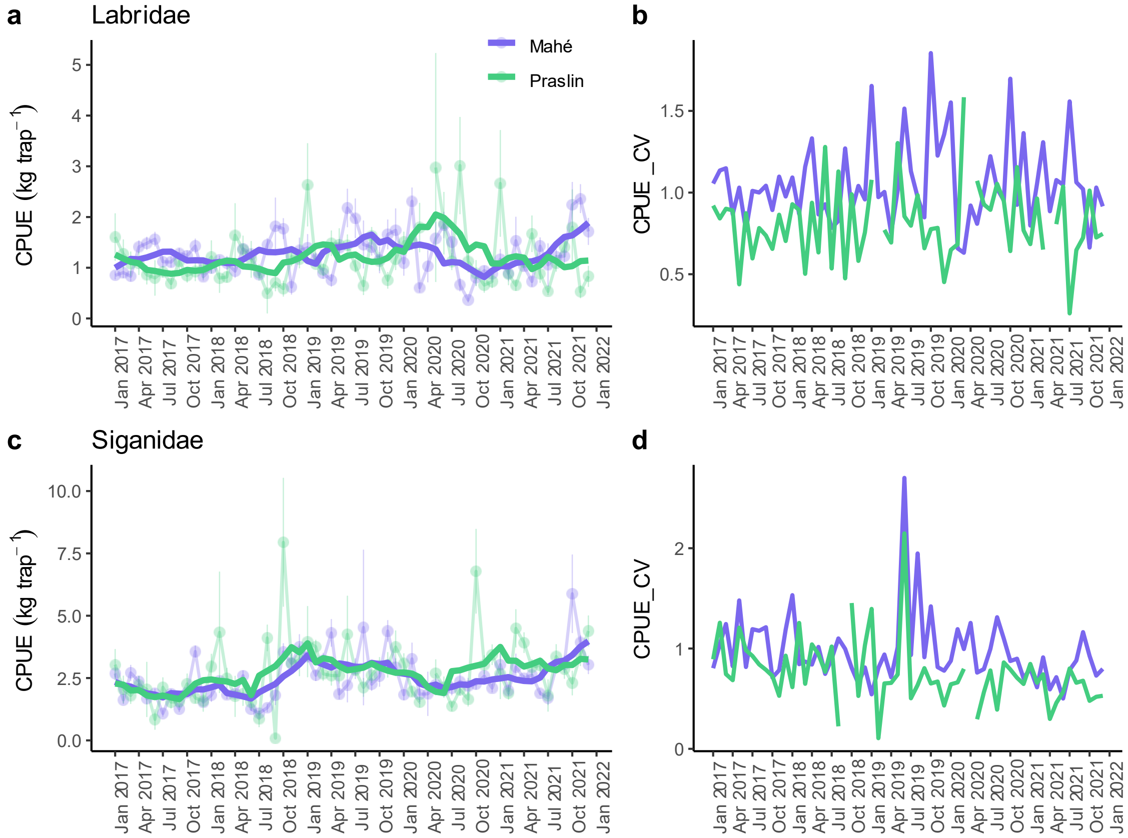

Figure 3.2: Monthly catch per unit effort (CPUE) for trap fish landings of fishes in the families Labridae (predominantly parrotfish; **a**) and Siganidae (rabbitfish; **c**), from Seychelles Fishing Authority landings sampling across multiple sites on Mahe and Praslin. Data are plotted as monthly means (points) with the standard error of the mean (whiskers), with 6-month moving averages plotted as thick lines. The coefficient of variation (CV = standard deviation/mean) is plotted per island for Labridae (**b**) and Siganidae (**d**).

Almost half of the fishers we interviewed (47%) said rabbitfish catches were highest when they formed spawning aggregations in sync with the lunar cycle during and in the months prior to the northwest monsoon (NWM, the north-westerly trade winds during the austral summer) (Table S3.1). The timing and locations of *Siganus sutor* aggregations have been documented in waters around Praslin and the abundance and CPUE of this species were markedly higher in the days immediately following the full moon (Bijoux et al., 2013; Robinson et al., 2017). According to fishers, rabbitfish are caught on healthy coral reefs when spawning and mainly on seaweed habitats at other times (Table S3.1). Such habitat- and time-sensitive changes in catches linked to spawning behaviour would not necessarily be detectable from monthly landings data.

Therefore, it is possible that fishers' perceptions of decreasing rabbitfish catches, particularly in Praslin, could be in relation to a specific time or place, for example catches on coral reefs during spawning aggregations or catches on algal reefs during the times between spawning, even when average catches over longer periods are stable. One fisher on Mahé said that rabbitfish had "*changed spawning grounds*" and another on Praslin said they were scarcer now, "*even during the spawning season*", suggesting spawning aggregations may be smaller than they once were. There were also signs from three fishers on Praslin that the catchability of rabbitfish had changed. One fisher said, "*there are more rabbitfish on the reefs now, but I am catching the same amount as before. This year is different. Rabbitfish are not going in the traps so there are fewer packets to land*". The more common use of active traps on Praslin may also have influenced fishers' perceptions of rabbitfish catches, as hauling traps multiple times per day may improve a fisher's understanding of where and when the best catches occur.

All but three fishers (91%) said they target parrotfish. The proportion of fishers who perceived decreases in parrotfish catches and those who thought they had remained the same between islands was similar (Fig. 3.1 c), although a higher proportion of fishers on Mahé (35%) said parrotfish catches had decreased compared to Praslin (27%). Although few fishers specified that parrotfish catches had improved (Fig. 3.1 c), anecdotal information from other fishers indicated their perceptions of parrotfish yields were generally positive. For example, one fisher on Mahé said parrotfish catches were "*good to average all year*" and another on Praslin said, "*catches are variable, but you get larger groups more often than rabbitfish*". Similar to rabbitfish, multiple fishers (24%) indicated that parrotfish could be caught across habitats and seasons (although especially in the NWM and on coral reef habitats; Table S3.1). One fisher said, "*Since the corals died in 2016, catches have been ok. Algae grows and parrotfish come in to feed on it and catches are fruitful*", which is aligned with studies suggesting parrotfish may be an important group of species for maintaining catches on reefs impacted by coral bleaching (**Chapter 1**; Graham et al., 2020; Morais et al., 2020b). Landings data suggest parrotfish CPUE from fish traps remained relatively stable in years following beaching (2017-2021) on both islands (long-term means: Mahé = 1.3 kg trap^{-1}, Praslin = 1.2 kg trap^{-1}; Fig. 3.2 a), which corroborates the general perception amongst fishers that parrotfish could be reliably caught. It is possible that abundant herbivorous species maintaining catches affected some fishers' perceptions of reef habitat recovery, with relatively favourable fishing yields giving the impression that the reefs themselves had recovered.

Even though most fishers noticed habitat and catch changes, only one third believed catch changes were linked to the changes in reef habitat (Fig. 3.3). Interestingly, almost all fishers (89%) who thought catch changes were linked to habitat felt their catches had worsened over time, while the catch perceptions of those who did not make a connection between habitat and catch were more evenly split between worsening catches (53%) or otherwise (42% who noticed changes in catch composition but not total yields, 5% who thought catches had improved; Fig. 3.4). Of the fishers who noticed changes in their catches, a higher proportion on Mahé (37%) said this was linked to habitat changes compared to Praslin (22%), therefore it is possible that the higher prevalence of habitat stressors around Mahé (Table 3.3) may have resulted in more obvious links between habitat effects and reduced catches. Figure 3.4 confirms that most fishers who did change their fishing activity thought catches had worsened, suggesting that a decrease in yields was the main motivation for adaptation.

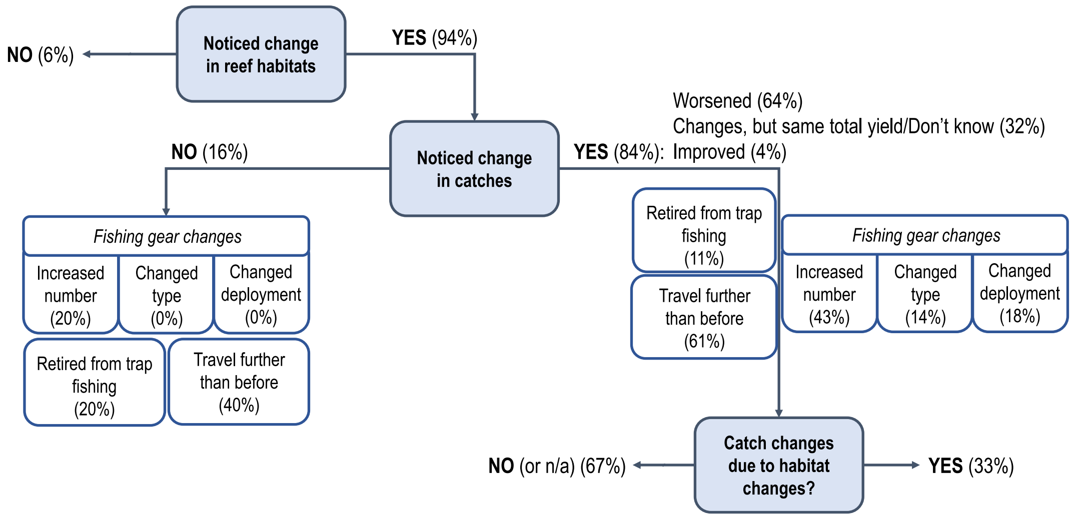

Figure 3.3: Flow chart of fisher perceptions regarding changes in reef habitats and catches, with details of changes to fishing activity made by fishers. Responses relating to perceptions ("yes"/"no") sum to 100%, while responses regarding changes in fishing activity do not as some respondents did not make any changes and other fishers made more than one change.

Relationships between fisher responses and perceptions

Most fishers who noticed environmental changes to reef habitats also noticed changes in their trap catches (84%) with the majority believing catches had worsened (64%; Fig. 3.3). Fishers who had altered their fishing activity in some way tended to perceive more catch changes than those who had not. Only one fisher who did not perceive catch changes increased the number of fish traps they used, compared to 12 fishers (43%) who had perceived changes. Of the fishers who did not perceive catch changes, none had altered the types of fishing gear they used or how they deployed them, compared to four and seven fishers who did perceive changes, respectively (Fig. 3.3).

Two out of five fishers who did not perceive catch changes said they now travelled further to fishing grounds, compared to 61% (*n* = 17) of those who did notice catch changes. This could be expected, as altering fishing activity tends to be an adaptation in response to the changing

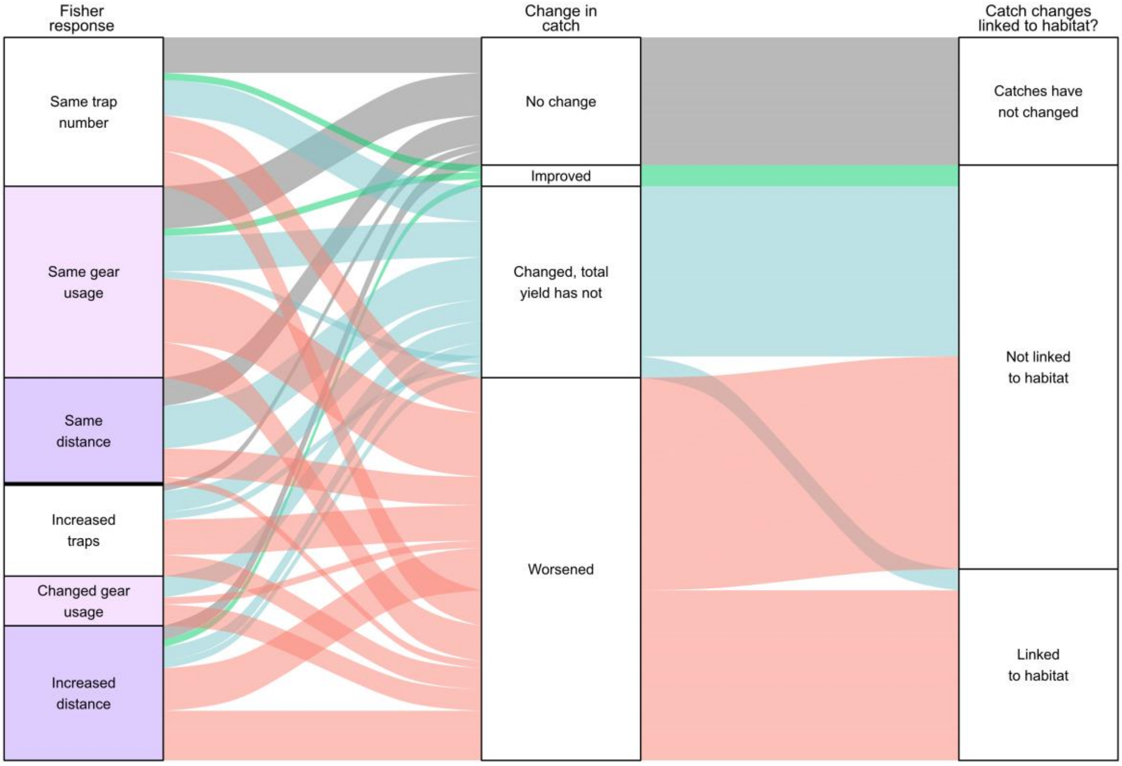

Figure 3.4: Sankey diagram of relationships between changes in fishing activity (left), fisher perceptions of trap catches (centre), and perceived associations between catch changes and reef habitat changes (right). Flows are coloured by perceptions of change in catches (grey = no change, green = improved, blue = catches of some species changed but total yield did not, pink = worsened). Every fisher (*n* = 34) is represented in each type of fishing response on the left (number of traps (white), gear usage (lighter purple), and distance travelled (darker purple)), therefore the number of data points used to generate flows on the left side of the plot is three times higher compared to the right, however both sides are proportionally comparable. Gear usage refers to changes in gear type and/or deployment of gear.

abundance of target species (Abernethy et al., 2007), therefore fishers who did not notice catch changes may be less likely to adapt. Although the two fishers who did not perceive catch changes travelled further, their reasons for doing so were related to land reclamation and leaving "*fish closer to shore to reproduce*" during the NWM (Table S3.2). Travelling further to fish was the most common adaptation (Fig 3.3), generally in response to insufficient yields on grounds closer to shore (including due to land reclamation; Table S3.2). Of the fishers who estimated the extra distance they needed to travel each day to maintain their catches, the median distance was 8.25 miles further (minimum = 0.25 miles, maximum = 30 miles), while the median increase in travel time was 2.5 hours (minimum = 2 hours, maximum = 8 hours). Due to the bathymetry of the inner Seychelles islands, there is a vast area of the Mahe Plateau that is relatively shallow, giving small-scale fishers some flexibility in exploiting potential fishing grounds further offshore compared to other island nations (Graham et al., 2007). However, the distance fishers can travel is constrained by weather and sea conditions associated with monsoon seasons (Table S3.2).

Implications of changes for the trap fishery

Habitat factors

Although most fishers did not relate long-term changes in trap catches to reef habitat changes (Fig. 3.3), there was general acknowledgement amongst fishers on each island of the importance of reef habitats for the fishery. As one fisher succinctly put it: "*fish feed people and they need habitats*", reflecting the opinions of many other fishers regarding their reliance on suitable inshore habitats for fishing (Table S3.1; Woodhead et al., 2021) and highlighting the vital role of fish for food and nutrition security in Seychelles (Bonham et al., 2009; Conway et al., 2018). There was a consensus among fishers regarding the importance of healthy coral habitats for target species and as fishing grounds, for example for parrotfish and for rabbitfish spawning aggregations (Table S3.1). One fisher said, "*I don't set traps on coral but it's important for fish to travel between coral habitat, so I still depend on healthy coral when fishing on seaweed*", highlighting the importance of live corals for trap fishing across multiple habitats, particularly for species such as *S. sutor* (Ebrahim et al., 2020a). Considering the importance of coral reefs for the Seychelles trap fishery and the widespread degradation caused by coral bleaching across islands compared to other more localised stressors (Table 3.2), climate-induced bleaching is likely the primary cause of habitat degradation that will negatively impact yields in the future. Although herbivores can be highly productive fisheries targets on coral reefs recovering from bleaching (**Chapter 1**), due to the increasing frequency of marine heatwaves in the Western Indian Ocean (Saranya et al., 2022), the time between successive bleaching events is expected to be reduced (Hughes et al., 2018), which would be problematic for Seychelles reefs and trap fishery yields if hard corals are unable to recover.

The degradation and recovery of seagrass and algae habitats mentioned by fishers was typically seasonal and caused by water motion (Table S3.1), which may not be an issue unless these habitats are further impacted by additional disturbances (Orth et al., 2006; Fulton et al., 2019). Increased damage to algae and sea grass habitats may affect catches on these fishing grounds, particularly as several fishers noted the importance of these habitats for rabbitfish (Table S3.1). For example, one fisher said, "*the seaweed is disappearing. This is very concerning as there is a lack of habitat for fish*". As well as being important fishing grounds (Wilson et al., 2022), macroalgae habitats are also a nursery ground for many species targeted by reef fisheries (Fulton et al., 2020), therefore degradation of these habitats may eventually impact the recruitment of target species to the Seychelles trap fishery. Another consequence of degraded algae habitats is losing access to bait sources. Half of the fishers interviewed said they baited traps with algae (mainly "*lanmous ver*", a *Gracilaria* species), however some fishers indicated land reclamation and sedimentation has destroyed much of the suitable shallow water habitats where algae can be harvested (Table S3.1), suggesting that coastal infrastructure development may be impacting traditional trap fishing methods in Seychelles, at least in some areas around Mahé.

Human factors

Fishers indicated that multiple human factors were impacting the trap fishery, such as increases in the amount of fishing effort. Few fishers explicitly mentioned the issue of increasing effort but one fisher on Mahé said, "*Now there are more fishers with more traps, so fewer fish per fisher*", and others mentioned overfishing of certain areas. However, this was partially verified by 38% of fishers who said they had increased the number of traps they use. One fisher said, "*I use more traps when there are fewer fish*", and another said, "*I used to use two to three traps, now I need about thirty*", indicating that increasing the number of traps is a common strategy used to maintain yields, which was clearly the most common gear adaptation among fishers from qualitative data (Table S3.2). Four fishers described having to leave traps for a longer soak time (the time between setting and hauling) to catch the same amount of fish they used to get in a shorter time (Table S3.2). This is also an example of increasing fishing effort for static gears such as fish traps (Mendo et al., 2023) and may result in discrepancies with CPUE data that only describe catch per trap without accounting for soak time (Daw et al., 2011).

Previous studies involving hypothetical scenarios of declining catches found that fishers were less likely to continue fishing at the same intensity as catches worsened (Cinner et al., 2011; McClanahan et al., 2016), as some fishers fished more intensively while a similar proportion reduced fishing intensity (Cinner et al., 2011). From this empirical study, increasing fishing intensity was a common response of trap fishers, which is aligned with a large increase in trap effort from 2017 (the year after severe coral bleaching; SFA 2023). It is expected that a reduction in fishing effort would be required following an environmental shock that reduces fisheries resources (such as coral bleaching) to allow resources to rebuild (Cinner et al., 2011). However, that does not seem to be the case with the Seychelles trap fishery as a large increase in fishing effort occurred shortly after bleaching, yet CPUE remained stable in the following years (Fig. 3.2). It should be noted that CPUE can be misleading, particularly when environmental conditions or fishery characteristics change (both of which occurred around the time of coral bleaching), as well as for species that aggregate (such as rabbitfish) which can sustain relatively high CPUE estimates even when population sizes have been reduced (Maunder et al., 2006). Therefore, the general perception of fishers that catch rates had declined (Fig. 3.1) could indicate that more careful management is needed for the Seychelles trap fishery than CPUE data would suggest, especially given the increased fishing effort in recent years (Robinson et al., 2020b; SFA, 2023).

Six trap fishers said they fished with handlines more often due to poor trap catches, including one fisher who retired from the trap fishery to focus only on handlining (Table S3.2). The retired fisher also increased the number of traps prior to leaving the fishery and said, "*I stopped fishing with traps because I was getting a small amount of fish and there's a big demand for jacks. So, I still fish with handline*". Market demand for demersal and pelagic species caught with handlines may incentivise fishers to increase handline fishing effort to maintain catches and a source of income, perhaps acting as a mechanism to reduce fishing pressure on reef species targeted by the trap fishery, at least by some fishers. Targeting a diverse range of species can protect fishers' incomes against declines in certain species populations (Robinson et al., 2020b) and fishing with handlines more may be a way for trap fishers to increase the diversity of their catches, especially when coral bleaching occurs and trap catches are extremely poor. However, a similar increase in fishing effort following bleaching in 2016 was seen in both the artisanal trap and handline fisheries (SFA, 2023), suggesting fish populations associated with both fisheries experienced increased fishing pressure. A combination of increased fishing pressure and post-bleaching habitat effects may make it difficult to assess the independent impacts of these factors on fish populations, therefore more detailed analyses of fish stocks following bleaching that include information from fishers regarding changes in fishing effort could be useful in the management of the trap fishery (Daw et al., 2011).

Over half of the fishers interviewed (56%) said they had to travel further to maintain catches (Table S3.2). Travelling further to exploit new fishing grounds has been linked to increasing fishing effort in Seychelles, due to a combination of more fishers and a higher demand for fish (Etongo and Arrisol, 2021). The extra travelling distance increased fishing time by multiple hours for most fishers and increased fuel consumption. Additional costs included purchasing more rope and buoys for fishing in deeper water further offshore, as well as replacing lost traps (Table S3.2). A previous study of Seychelles fishing fleets found that the greater expenditure associated with increased mileage was not necessarily recouped by fish sales (Robinson et al., 2020b), however some trap fishers said they had increased the price of fish packets to offset rising fuel costs. Fuel costs may restrict the distance some fishers are able to travel (Abernethy et al., 2007), as well as vessel size as larger vessels are able to travel further in a shorter time and continue to fish in less favourable sea conditions (Woodhead et al., 2021). Fishers' rising expenses as they have progressively travelled further from the shore to maintain catches will affect their net income or pass the additional costs onto buyers which may create financial barriers that restrict poorer people's access to fish.

Fishing further from the shore was also associated with more difficult fisheries operations and safety risks. Fishing difficulty was mainly linked to adverse weather and sea conditions, for example fishers said hauling traps was "*more tiring*" in deeper water and took "*more time*" (Table S3.2). However, two fishers thought fishing was easier further offshore as they were able to catch more fish. Of the fishers who travelled further, over half (53%) described risks to their safety while fishing further from the shore, related to sea conditions (waves and currents) and fishing alone (Table S3.2). As climate change can cause storms and sea conditions to worsen, the safety of fishers fishing offshore may be compromised, especially if fishers continue to fish using their traditional knowledge of conditions on fishing grounds (Daw et al., 2009). The necessary trips to fishing grounds further from shore to earn a fishing livelihood appears to be increasing the likelihood that fishers may encounter dangerous situations. Schemes that provide safety training and equipment for fishers may be useful for the Seychelles artisanal fleet, as was mentioned by five fishers during interviews.

Fishing gear is also at risk when fishing further from shore. Losing traps to currents and large waves was mentioned by four fishers, however a greater risk of trap theft further offshore was also identified as an issue by four fishers (Table S3.2). The general problem of trap theft was mentioned by nine fishers in total (26%), including one retired fisher who said theft was the main reason he quit trap fishing and he "*would still fish if there was no theft because trap fishing is fun*". A trap fisher on Praslin had most of his traps stolen and said, "*many fishers have stopped fishing because of this*", while another on Mahé had all traps stolen. Replacing traps is difficult due to a lack of suitable materials and skilled trap makers in Seychelles, and is also expensive (Nageon de Lestang, 2005) which makes traps more attractive to thieves. Due to the number of traps some fishers have had stolen, replacing lost traps can be a large expense which may be difficult when a fisher's yields and income have been negatively affected by lost fishing gear. Having all or almost all fish traps stolen also forces fishers to completely shift their way of fishing, generally switching to using handlines instead, and may lead to a loss of traditional knowledge in the trap fishery. Small-scale fishers often face constraints on their ability to change the fishing gears they use or the grounds they fish (Abernethy et al., 2007), and in Seychelles, the risk of theft appears to influence where fishers choose to set traps, although there were also trade-offs between a higher risk of theft and greater catches further offshore (Table S3.2). Although gear theft was prevalent in the Seychelles trap fishery and appeared to have a large influence on some fishers' fishing activity and livelihoods, a lack of information means that attempting to manage this issue could be challenging.

Conclusion

This study adds to research into the changing artisanal fishing sector following multiple climate impacts on inshore coral reefs in Seychelles (Etongo and Arrisol, 2021; Woodhead et al., 2021) and demonstrates fishers' ability to provide information on a range of environmental and human factors affecting the trap fishery. Fishers revealed that trap catches are extremely poor when coral bleaching occurs but recover relatively quickly, which is in general agreement with scientific data that suggest populations of herbivorous fishes (the main targets for fish traps) increased on Seychelles reefs following bleaching in 2016 and may have sustained fisheries yields (**Chapter 1**; Robinson et al., 2019a). Fishers also provided information on their fishing activity based on the spatiotemporal movements of fish, for example targeting rabbitfish spawning aggregations on coral reefs at the full moon but targeting them on macroalgal reefs at other times. Such information on fishing effort could be useful to include in fisheries management to add relevant context to monthly landings statistics, particularly for species such as rabbitfish that depend on multiple habitats. Considering the contrasting trends in CPUE between landings data and fisher perceptions, consulting fishers and working collaboratively to reach a collective understanding of changes in resource status may be wise before management decisions are made based on CPUE data alone (Hoyle et al., 2024). Fishers' LEK may be an essential component of fisheries management, complementing fisheries-dependent and fisheries-independent data sources, and highlights the importance of using multiple sources of evidence in fisheries research (Mendoza et al., 2022).

This study demonstrates that fisher responses to perceived changes can alter how a fishery operates. A combination of increased trap effort, travelling to different fishing grounds, and focusing effort on other fisheries (e.g. handlines) are changing the Seychelles trap fishery, and have the potential to alter the amount and composition of fish landed to local markets. Fishers' adaptation strategies to maintain fishing livelihoods are often different to what those in a management or policy position may predict (Savo et al., 2017), therefore further and continued engagement with fishers could inform managers about how particular responses to changing marine resources could impact the supply of fish from the Seychelles trap fishery. Human factors such as overfishing and theft were identified as potential threats to the trap fishery, however the relative contributions of habitat degradation and changes in fishing effort to the perceived declines in catches are unknown, and further research that attempts to disentangle these impacts on the fishery could be useful.

Chapter 4

Drivers of nutrient intakes from fisheries in French Polynesia

Abstract

Small-scale fisheries provide nutrients to hundreds of millions of people worldwide, with yields in many tropical nations dependent on the condition of coral reef habitats. Small-scale fisheries are a particularly important food source in societies with nutrient deficiencies and where unhealthy food alternatives are widely available. Using data from coral reef surveys around two islands in French Polynesia (Moorea and Raiatea), this study shows how the availability of nutrients to fisheries changed in relation to the condition of coral habitat. Fish biomass and nutrient availability were highest when coral cover was low around both islands, driven predominantly by abundant herbivorous reef fish. The importance of fish in people's diets was also investigated, to determine if fish consumption was aligned with available fisheries resources on local reefs and if nutrient intakes from fish could be explained by people's socioeconomic background. People ate a higher diversity of reef fish in Raiatea, however nutrient intakes from fish were higher in Moorea. Most people ate more fish than meat on both islands, however fish consumption declined over generations. People from fishing households had higher nutrient intakes from reef and pelagic fish, and people from farming households had higher intakes from reef fish. Preference for reef fish over pelagic fish in diets was also associated with higher total nutrient intakes. Promoting traditional diets rich in fish could be key to meeting people's nutritional needs in French Polynesia while reducing diet-related health issues linked to the overconsumption of fat.

Introduction

Small-scale fisheries provide a wide diversity of food fish in many countries across the tropics (Belton and Thilsted, 2014) and often provide an accessible and affordable animal-based source of protein and key micronutrients that are lacking in people's diets (Kawarazuka and Béné, 2011; Hicks et al., 2019). Tropical fisheries vary in their vulnerability to environmental stressors, such as climate change, as well as in the nutrient density of yields (Maire et al., 2021). Therefore, tropical fisheries have the potential to remain an important source of human nutrition as marine environments are altered (Hicks et al., 2021; Robinson et al., 2022a), although changes in the availability of fisheries resources may lead to changes in people's fish consumption patterns.

Marine fisheries are sensitive to the condition of key habitats of targeted fish populations (Brown et al., 2019), for example the condition of coral habitat influences the productivity, availability, and long-term sustainability of reef fisheries (**Chapters 1** and **2**; Cruz-Trinidad et al., 2014; Morais et al., 2020b). Currently, there is little understanding of how reef habitat condition impacts the provisioning of nutritious seafood through fisheries (Hicks et al., 2021). Existing literature show variable responses of fishery catches to changes in coral reef condition. For example, an increased abundance of herbivorous fish following coral mortality maintained small-scale fisheries yields on some degraded reefs in Seychelles (Robinson et al., 2019b), while reef fisheries in the Pacific are expected to become less productive as coral cover is progressively lost (Bell et al., 2013). The impacts of reef habitat condition on the composition and size of fisheries catches may therefore influence the food provisioning services provided by coral reefs (Woodhead et al., 2019). Decreases in fish catches would be expected to reduce fish consumption, increasing risks of nutrient deficiencies in tropical coastal communities (Golden et al., 2016). Reef-associated fish have relatively high concentrations of zinc and vitamin A, while small pelagic (open-ocean) species have high calcium and omega-3 fatty acid concentrations (Robinson et al., 2022b), therefore changes in seafood composition, for example through projected catch increases of pelagic fisheries (Bell et al., 2013), would alter people's nutrient intakes from fish.

People's dietary choices are influenced by many factors beyond availability, including culture, price, demographics, and convenience (Tilman and Clark, 2014). For example, increasing availability of imported "Western" foods across the coastal tropics, driven by the globalisation of food trade systems (Thow et al., 2011), has facilitated dietary transitions away from traditional diets of nutritious local fish and plants, towards energy-dense and high-fat foods (Hughes and Marks, 2009). The nutritional implications of moving away from traditional diets are a public health concern, as diets may become deficient in essential nutrients, leading to micronutrient deficiencies, or contain excess nutrients contributing to health conditions such as obesity and diabetes (Hughes and Marks, 2009; Sahal Estimé et al., 2014; Stevens et al., 2022). For example, in the Peruvian Amazon, replacing wild caught freshwater fish with chicken and farmed fish reduced intakes of essential fatty acids and iron; nutrients that were already deficient in people's diets (Heilpern et al., 2021). If there is a shift away from traditional fish-based diets towards modern diets with high fat content, it is important that people balance local produce and imported foods in a way that minimises diet-related ill-health (Parry et al., 2010). Nutrition and diet-related health issues are unequally distributed within societies (Friel and Baker, 2009), therefore it is imperative to determine which groups of people may be most at risk from eating fewer traditional foods.

This study focuses on French Polynesia as a case study to examine linkages between ecological conditions (coral reef habitat and fisheries resources), socioeconomic factors, and people's diets (Fig. 4.1). Specifically, the research objectives are to: 1) assess the availability of nutrients from reef fish in relation to changes in coral reef habitat condition, and 2) investigate the importance of reef and pelagic fish for people's nutrient intakes in relation to their socioeconomic background.

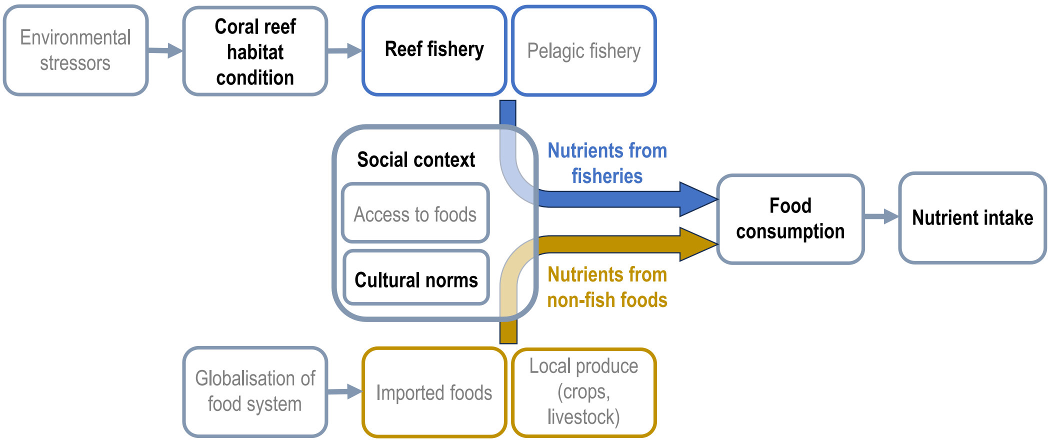

Figure 4.1: Conceptual diagram of links between coral reefs, fisheries, food supply, and dietary nutrition. Environmental stressors (e.g. climate change, crown-of-thorns sea star outbreaks) affect coral reef habitat condition, which in turn affects reef fisheries catches. People's nutrient intakes are determined by their consumption of foods from reef and pelagic fisheries (blue) and other sources (orange). Food consumption is influenced by social context, including culture and access to foods. Variables in grey text were not measured in the current study (e.g. availability of reef fishery resources was estimated, but pelagic resources were not).

Methods

Study area

This study focuses on two islands, Moorea and Raiatea, within the Society Archipelago, French Polynesia (Fig. S4.1). Moorea is the second most inhabited island in French Polynesia after Tahiti, with a population of 17, 463, while Raiatea has a population of 12, 291 (Institute of Statistics of French Polynesia, 2017). Obesity is an urgent health concern in French Polynesia, with 68% of men and 67% of women estimated to be overweight or obese in 2008 (Daigre et al., 2012). French Polynesia has become dependent on Western imports of high-calorie foods since the 1980s, such as chicken which has a particularly high fat content when fried (World Health Organisation (WHO), 2003). Food imported into French Polynesia is mainly sourced from Europe, and the volume of unhealthy imported foods has increased over time (Andrew et al., 2022).

Small-scale fisheries in French Polynesia use traps, hook and line, gillnets, and spearguns to catch reef-associated and pelagic fish, of which a large proportion is consumed locally (Chauvet and Galzin, 1996; Leenhardt et al., 2016). Reef and pelagic fish are sold at the roadside in Moorea, which provides an income for fishing families and a local supply of fish for islanders (Nassiri et al., 2021). A large proportion of fish caught around Raiatea is sold at a large market (Uturoa) at the north of the island (Chauvet and Galzin, 1996). It is also common for islanders to order fish directly from fishers (Leenhardt et al., 2016).

Ecological data

Live coral cover on reefs around Moorea and Raiatea was reduced to almost zero by 2010 after crown-of-thorns sea star (*Acanthaster planci*; “taramea” in Tahitian) outbreaks, before being further impacted by a cyclone and coral bleaching (Pérez-Rosales et al., 2021). Underwater visual surveys were conducted to collect data on live coral cover (photo-quadrats) and abundances and sizes of reef fishes (belt transects). Surveys were conducted every second year, in even years (2010-2020) at one site in Raiatea and two sites in Moorea, and in odd years (2011-2019) at another site in Moorea (Fig. S4.1).

Photo-quadrats were used to record images along a 20 × 1 m section of the outer reef slope (between 7 and 13 m depth). Reef sites were sampled using a metal frame secured between two permanent metal stakes to ensure the same section of reef was sampled each year. Twenty replicate 1 m^2 photo-quadrats were completed along the frame, resulting in the entire 20 m^2 reef section being sampled. Photo-quadrat images were analysed using point intercept estimates, where 81 evenly spaced points were systematically overlaid onto each 1 m^2 quadrat image. Live coral at each point was recorded to genus level and coral cover was calculated as: 100 × number of points with live coral / 81. A total of 1620 points were analysed per 20 m^2 reef section. Live coral cover (%) was estimated by summing across all hard coral genera.

Fish data were collected along three belt transects of 50 × 5 m (250 m^2) at each site. All fish within the transect area were recorded to species level and their sizes estimated to the nearest cm. All three transects per site were conducted at the same depth, with one transect overlapping the coral photo-quadrat area and the other two 25 m away on either side, parallel to the first. Fish lengths were converted to weights using species-specific length-weight parameters (Froese, 2006) (Equation 2, **Chapter 1**, p36).

Fish species were classified into three trophic groups: “herbivore” (including detritivores and microvores), “mobile invertivore” (including microinvertivores and macroinvertivores), and "piscivore" (Parravicini et al., 2020) (Table S4.1). Fish weights were summed per trophic group to estimate the total biomass per transect in kilograms per hectare. Mean biomass and standard error were calculated across transects for each survey year.

Socioeconomic and dietary surveys

A semi-structured questionnaire was created to gather socioeconomic and dietary data in Moorea and Raiatea (Chapter 4 supplementary material, p157). The questionnaire was piloted in both islands, alongside informal discussions, to create a final version that incorporated island-specific context while still allowing comparisons to be made between islands. In total, 183 household interviews were conducted in Raiatea, between June and September 2019 and 96 in Moorea in September 2019. A purposive snowball sampling approach (Ayhan, 2011) was used for interviews, stratified across administrative districts, targeting fishing and non-fishing households (Table S4.2). Initially, a few influential people in a district were identified for interview, and subsequent interviews were then based on their recommendations and introductions. People who had not lived on either island for at least five years were not interviewed. Sample sizes satisfied the chosen 95% confidence level given the population of each island (with 10% margin of error as only one person per household was sampled, even though households often contained multiple people). Approximately two thirds of respondents on each island were women as they were most commonly at home during the day to answer questions (Table S4.2). Interviews were conducted in either French or Tahitian with a translator. Interviews were conducted with approval of the Faculty of Science and Technology Research Ethics Committee, Lancaster University (reference: FST18040).

Data on the frequency of consumption of various food groups in people's diets were collected (based on the Global Individual Food consumption data Tool, GIFT; Food and Agriculture Organisation (FAO), 2022; Table S4.3) and the types of fish people ate. Options for the frequency of consumption were: "never", "1-2 times per month", "3-4 times per month", "1-2 times per week", "3-5 times per week" and "6 or more times per week". All responses were standardised by converting to number of times per week. Some food categories were grouped together prior to analyses using a similar approach to Kennedy et al (2011), for example "nuts/seeds" and "legumes" were separate questionnaire responses but were combined to give a total consumption frequency (Table S4.3).

The types of fish eaten were identified to species level where possible, otherwise to taxonomic family level. Fish names given in Tahitian were matched to scientific taxa based on local knowledge and FishBase (Table S4.1). Frequency of consumption was not collected for each type of fish, only for fish in general. Respondents were also asked about their fish consumption in comparison to their meat consumption and their fish and meat consumption in comparison to previous generations (parents/grandparents).

Nutrient content of fish

Fish nutrient estimates were obtained from the Nutrient Analysis Tool in FishBase (Froese and Pauly, 2022; MacNeil, 2023), developed by Hicks et al. (2019). Nutrient prediction updates from August 2022 were used. Nutrient concentrations in a 100 g portion of muscle tissue were estimated for five nutrients (calcium, Ca; iron, Fe; zinc, Zn; vitamin A, Vit A; omega-3 fatty acids (eicosapentaenoic acid (EPA) + docosahexaenoic acid (DHA)), O3) that are highly concentrated and bioavailable in fish and lacking in diets across the tropics (Beal et al, 2017; Ferguson et al, 2019; Golden et al, 2021). Nutrient content data were extracted for each species observed in reef surveys and for species mentioned by respondents during interviews. When fish were not identified to species level, or when nutrient estimates were not available for a particular species, genus or family level estimates were used by taking medians across species belonging to the same taxonomic grouping also found in French Polynesia (according to FishBase).

Nutrient concentrations (100 g^{-1}) per individual fish were scaled up to reef survey biomass estimates to represent the total quantity of each nutrient per hectare (i.e. the potential nutrient yield for fisheries). Only fish $\geq$15 cm in total length were included to represent the nutrients within fish deemed large enough to be captured by fisheries (i.e. the minimum fishable size; Rassweiler et al, 2020). Values were then summed per trophic group in each transect and then the mean calculated across transects at each survey site.

We then estimated the mean nutrient concentration of a 100 g fish portion for each respondent, by averaging nutrient concentrations across all fish species they provided during interviews. Nutrient estimates per person were then expressed as the percentage contribution to daily recommended nutrient intakes (RNIs) or equivalent for adult women (Ca = 1000 mg, Fe = 19.6 mg, Zn = 4.9 mg, Vit A = 270 µg; WHO/FAO, 2004) (O3 = 250 mg; European Food Safety Authority, 2010) (Table S4.4).

Calculating nutrient density and intakes

The nutritional quality of different food groups was assessed by calculating the nutrient density based on the five focal nutrients (Drewnowski, 2009). Nutrient density was defined as the sum of percentage contributions to RNIs for all five nutrients in a 100 g portion of food, with the maximum possible value for each nutrient capped at 100%, or a maximum of 500% when all five nutrients are fully meeting dietary needs. The nutrient contents of 100 g food portions were obtained from Pacific Island food composition tables (FAO, 2004) by taking a median across all food items within each food group (Table S4.3) for each nutrient. Specific food items were removed from the composition tables if they were not eaten in the form given, for example raw flour or raw plant-based foods that were toxic unless cooked prior to consumption (e.g. taro leaves/stalks). The total fat content of 100 g food portions was also obtained from food composition tables and expressed as a percentage of the maximum recommended daily fat allowance (65 g; Drewnowski, 2009).

Each respondent's average diet was represented by calculating the total nutrient density across all food groups, weighted by frequency of consumption for each food group, i, up to the total number of food groups eaten by a respondent, *n* (Equation 7).

$$NutrientDensity_{weighted} = \frac{\sum(NutrientDensity \times ConsumptionFrequency)_{i \ldots n}}{\sum ConsumptionFrequency_{i \ldots n}} \quad [7]$$

These weighted nutrient density scores represented the nutritional value of each person's diet, based on the content of the five nutrients. As frequency of fish consumption was across all species eaten per respondent, we estimated separate weighted nutrient densities for reef and pelagic fish by equally splitting consumption frequency.

In addition to nutrient density of diets, people's nutrient intakes were estimated using information on typical portion sizes from the food composition tables (FAO, 2004), as these data were not collected during interviews. The nutrient content in 100 g of each food item was rescaled to estimated portion sizes. Medians across food items were then used to represent the nutrients in a typical portion for each food group. Nutrient values were multiplied by the frequency each food group was consumed in a week and divided by seven to give a daily estimate of nutrient intake per respondent. It should be noted that foods eaten more than once per day were not captured during interviews, for example the most frequent response for consumption for any food was "every day", without indicating whether a particular food was eaten multiple times a day or not. As such, nutrient intake estimates are not intended to be a complete daily profile of people's nutrition, but rather a representation of which foods people tended to eat on a regular basis, allowing comparisons to be made between people eating more or less of various foods.

Data analyses

All analyses were run in R (version 4.2.2; R Core Team, 2022). Associations between the nutrient density of fish consumed and socioeconomic backgrounds of respondents were investigated by conducting a redundancy analysis (RDA) for each island using the "*easyCODA*" package (Greenacre, 2018). Response variables were the percentage contributions to RNI for each of five nutrients and the total nutrient density estimate of each respondent's diet. Explanatory variables were gender (man or woman), age, education level (at least high school level or lower), wealth, ability to speak at least one Polynesian language (yes or no), fisher or farmer households (both, fisher only, farmer only, or neither), preference for reef or pelagic fish (based on the number of fish families eaten), how often takeaway food was eaten, and how often traditional Tahitian dishes ("Maa Tahiti") were eaten.

Wealth was determined using a principal component analysis (PCA) that included details of each respondent's home ownership (own house, renting or lodger), financial difficulties (yes or no) and vehicle ownership. Each respondent was given a vehicle score, calculated by multiplying each item by a score that reflected its value (bicycles = 0.1, pirogues (small boats) = 0.2, motorcycles = 0.5, cars and motorboats = 1) and summing scores for all vehicles owned. Some households may have had shared access to certain items, for example pirogues, however this was not accounted for in the analysis. Values from PCA axis 1 explained 39% of variation in the data and were used as a wealth indicator in analyses, with higher values indicating higher wealth (Fig. S4.2). All numerical explanatory variables in the redundancy analyses (age, wealth, fish preference, takeaway food, and Maa Tahiti frequencies) were scaled, with mean = 0 and standard deviation = 1, to allow the effects of variables to be examined relative to one another.

Variance explained by each variable, the global significance of the model, and the significance of axes and terms in the model were examined for each redundancy analysis. Variance inflation factors for model terms were assessed using the "*vegan*" package (Oksanen et al., 2022) to ensure that none had a value >2.

Generalised linear models (GLM) were used to investigate the effects of various socioeconomic variables on nutrient intakes. Separate models were used to analyse nutrient intakes from entire diets, reef fish only, and pelagic fish only (for *i* questionnaire respondents; Equation 8), all with Gaussian distributions.

$$\begin{aligned} NutrientIntake_i \sim \alpha + gender_i + \beta_1 \times age_i + education_i + language_i \\ + fishing\_farming_i + \beta_2 \times wealth_i + \beta_3 \times takeaway\_food_i \\ + \beta_4 \times Maa\_Tahiti_i + \beta_5 \times fish\_preference_i + island_i \end{aligned} \tag{8}$$

Model assumptions of each GLM were verified using the protocol described by Zuur and Ieno (2016), by plotting residuals against fitted values and each covariate in the model. Residuals were assessed to confirm there were no temporal or spatial dependencies.

Results

Availability of reef fish biomass and nutrients to fisheries

Coral cover increased from ~0-33% between 2010 and 2020 in Raiatea and, in Moorea, from 2-47% between 2010 and 2018 before declining to 28% by 2020 (Fig. 4.2 a). Over this period of coral recovery, reef fish biomass generally decreased (Fig. 4.2). In Moorea, biomass of all trophic groups decreased from 2010 to 2020 (by 37% for both herbivores and invertivores, 33% for piscivores) (Fig 4.2 b). A 54% decrease in herbivore biomass occurred in Raiatea from 2010 to 2020 (2444.9 ±310.4 to 1126.0 ±296.2 kg ha^{-1}), while invertivore and piscivore biomass gradually declined from 2010 to 2018 before biomass for all trophic groups rose from 2018 to 2020 (Fig. 4.2 c). Fish biomass was higher in Raiatea than Moorea, particularly for herbivores and mobile invertivores.

Nutrient availability from reef fish was similar to biomass trends for most nutrients and was also higher in Raiatea than Moorea (Fig. S4.3). Availability of all five nutrients from mobile invertivores and piscivores were at similarly low levels in Moorea over the time series, however in Raiatea, nutrient quantities from invertivores were higher than piscivores. Vitamin A availability from invertivores in Raiatea was particularly high (and variable) in 2010 and 2020 compared to other trophic groups (Fig. S4.3).

Fish consumption and nutrient intakes

The reef fish families eaten by most respondents were herbivores on both islands; Scaridae in Moorea (72% of respondents) and Acanthuridae in Raiatea (60% of respondents) (Fig. 4.3 a). With the exceptions of Scaridae and Mullidae, all reef fish families were eaten by a higher proportion of respondents in Raiatea compared to Moorea. Three reef fish families were typically eaten in Raiatea, compared to two in Moorea (Fig. 4.3 b). The pelagic fish families eaten by most respondents were Scombridae in Moorea (64% of respondents) and Carangidae in Raiatea (71% of respondents) (Fig. 4.3 c). The proportion of respondents who ate each pelagic family was more similar between islands than for reef fish, although a lower proportion of people ate carangids in Moorea (57%; Fig. 4.3 c). The median number of pelagic families consumed was two on both islands (Fig. 4.3 d).

On both islands, around half of respondents said they ate more fish than meat (Moorea = 50%, Raiatea = 55%) (Fig. 4.3 e). The second most popular response in Moorea was eating equal amounts of fish and meat (31%), while in Raiatea it was eating more meat (30%). Although most people ate more fish than meat, the majority of people on both islands said they ate less fish (Moorea = 69%, Raiatea = 53%) and more meat (Moorea = 46%, Raiatea = 47%) compared to previous generations (Fig. 4.3 f, g). A higher proportion of people in Raiatea (28%) said their fish consumption was equal to their elders (18% in Moorea), while a higher proportion in Moorea (29%) said their meat consumption was equal to their elders (17% in Raiatea). 14% of respondents in Raiatea did not eat meat, as they were pescatarian (compared to only 1% in Moorea) (Fig. 4.3 g).

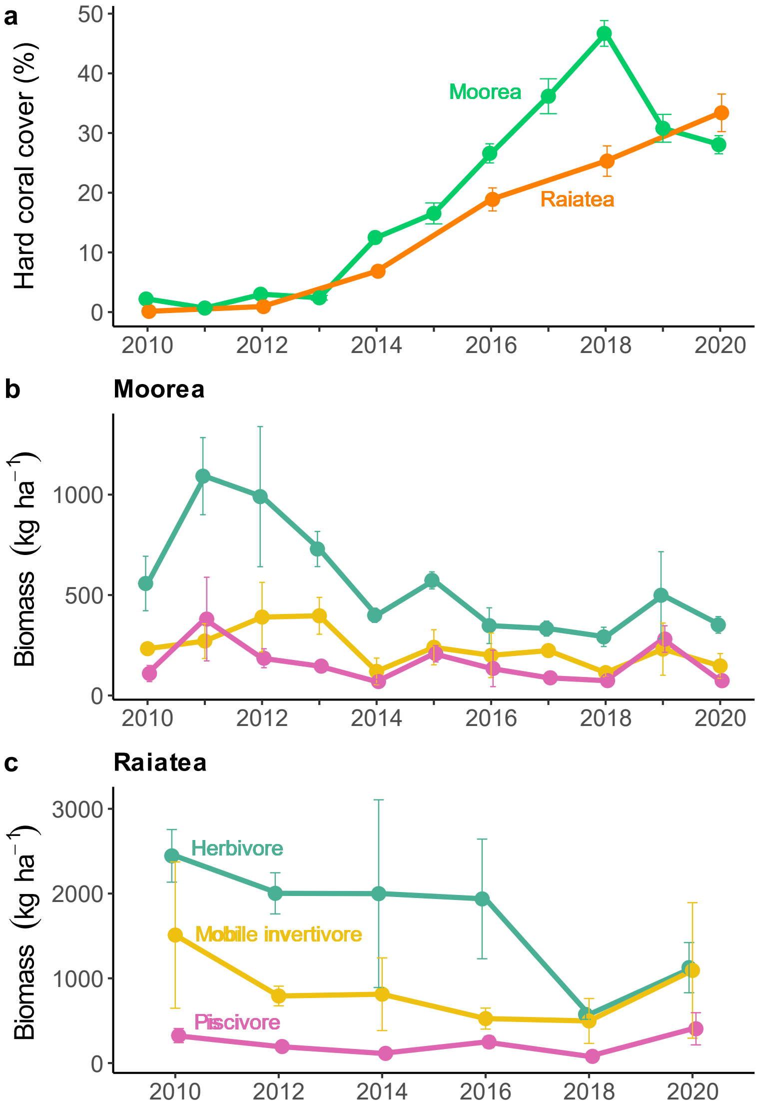

Figure 4.2: Trends of hard coral cover (**a**) and fish biomass on reefs in Moorea (**b**) and Raiatea (**c**) from 2010 to 2020. Biomass trends are for three trophic groups of reef fish (herbivore, mobile invertivore and piscivore). Only fish above the minimum fishable size (≥15 cm) with the potential to contribute to human nutrition were included. Errors bars are the standard error of the mean across transects. Note y-axis scales for biomass differ between islands (**b** and **c**).

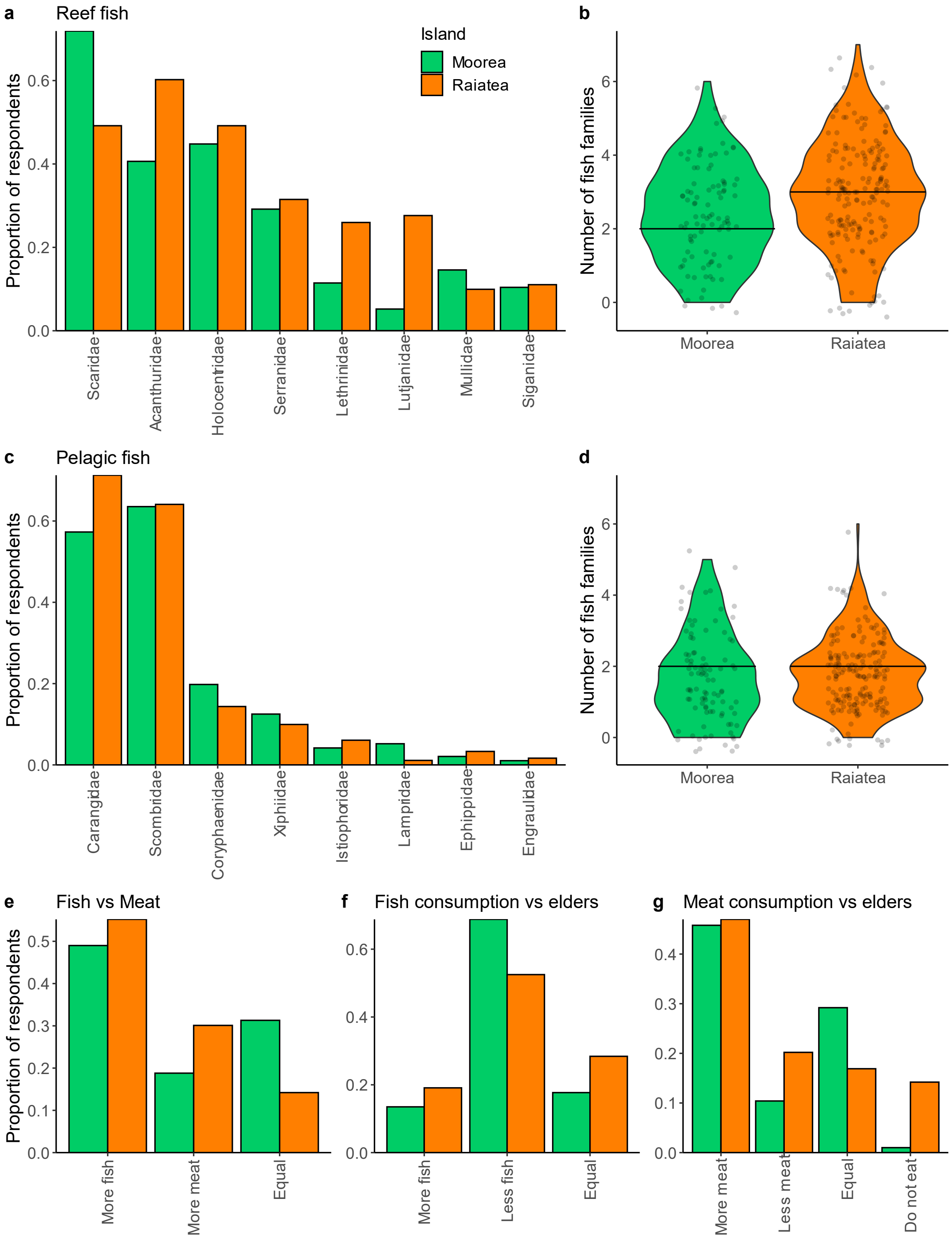

Figure 4.3: Proportion of respondents who ate the top eight reef (**a**) and pelagic (**c**) fish families, as stated during interviews in Moorea (green, *n* = 96) and Raiatea (orange, *n* = 181, two respondents who did not eat fish were not included). The total number of fish families consumed by each respondent is shown for reef (**b**) and pelagic (**d**) fish, with medians represented as solid horizontal lines. A comparison of fish to meat consumption per respondent (**e**), as well as perceptions of fish (**f**) and meat (**g**) consumption compared to their elders are also shown.

Out of the top five fish families eaten (reef: Holocentridae, Scaridae and Acanthuridae; pelagic: Carangidae and Scombridae), Carangidae was the most nutrient dense (153% in total across all five nutrients; Fig. 4.4 a). Both pelagic fish families had the highest concentrations of omega-3 (Carangidae: 86% of RNI, Scombridae: 99%) and iron (Carangidae: 12%, Scombridae: 10%) compared to reef fish families. Calcium concentrations were variable between pelagic families, with Carangidae having the highest (20%), whereas Scombridae was more similar to reef fish (<5%). Reef fish families had higher zinc concentrations, particularly Scaridae (52%) and Acanthuridae (45%). Vitamin A concentrations were variable among reef and pelagic families, and highest in Holocentridae (34%) (Fig. 4.4 a).

Pelagic fish was the most nutrient dense of all food groups for these five nutrients (137%) and reef fish was second (118%) after eggs and dairy (Fig. 4.4 b). The five most nutrient dense food groups were all animal-based, though there was considerable variation in the concentration of each nutrient between food groups. Dairy foods had the highest calcium concentration (22% of RNI) but the lowest iron concentration (1%), whereas iron-rich foods were pelagic fish (11%) and meat (including chicken and tinned meat, 10%). Meat had the highest zinc concentration (59%) followed by reef fish (35%), and foods with high vitamin A content were eggs (73%), dairy (55%), and reef fish (29%) (Fig. 4.4 b).

As with nutrient density, the food groups with the highest fat content were from animal sources, the highest being dairy (33% of the recommended daily total fat intake in 100 g) (Fig. 4.4 b). Pelagic fish had more fat content (16%) than reef fish (4%) and compared to other animal-based food groups, reef and pelagic fish were relatively nutrient-dense and low in fat (Fig. 4.4 b).

People on Moorea generally ate each food group more frequently compared to Raiatea (Fig. S4.4). Fish was one of the food groups with the largest difference in frequency of consumption between Moorea (median = 4.0) and Raiatea (median = 1.5). Most food groups were commonly eaten every day in Moorea, however on Raiatea, few people stated they ate any food group every day (Fig. S4.4).

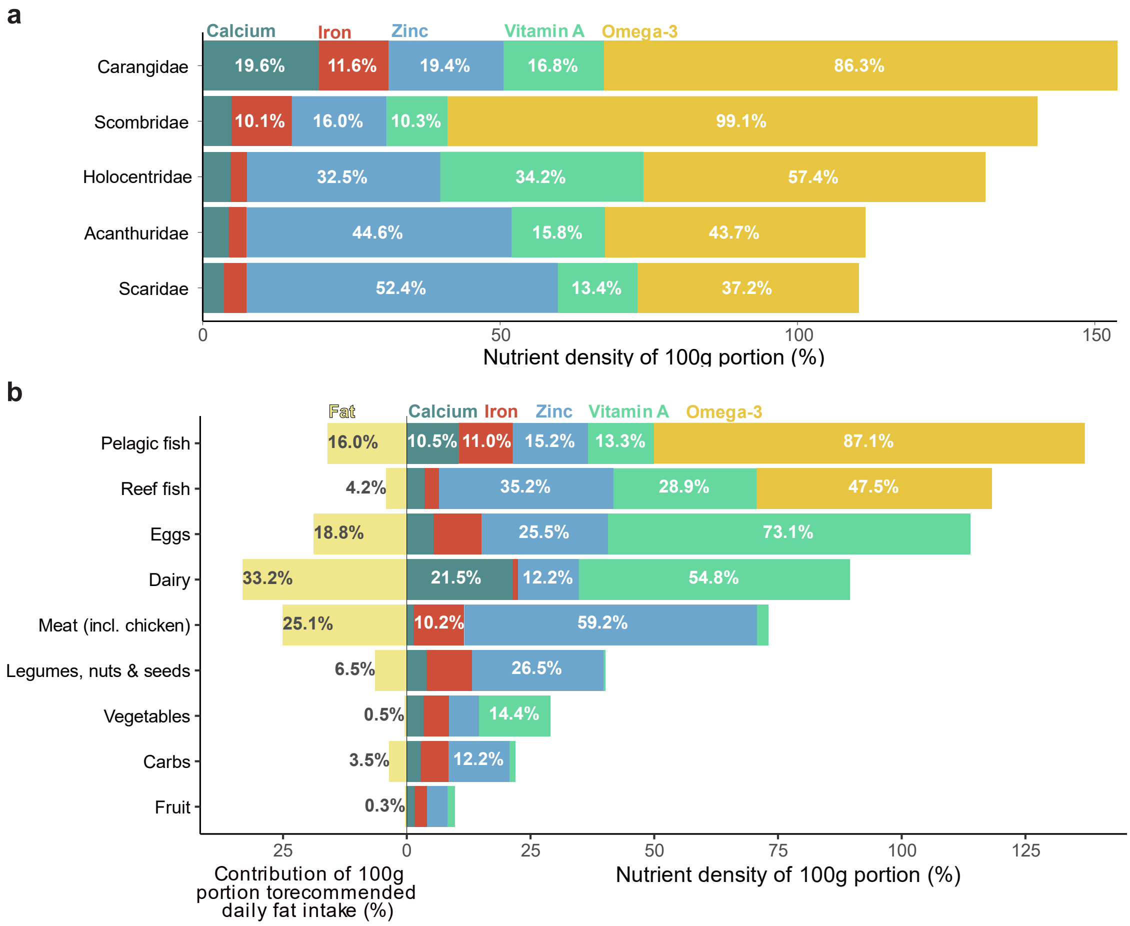

Figure 4.4: Nutrient densities of 100 g portions of the top five fish families eaten (**a**) and of food groups (**b**), calculated as the sum of contributions to daily recommended nutrient intakes (RNI) across five nutrients (calcium, iron, zinc, vitamin A, and omega-3 fatty acids). The contributions of 100 g portions to the maximum recommended daily fat intake (65 g, Drewnowski, 2009) are also shown for each food group (**b**, left). Values for fish families (**a**) are means of all fish species in each family mentioned by respondents during interviews. Nutrient estimates for reef and pelagic fish groups (**b**) are means of all fish species eaten by respondents. Omega-3 fatty acids (eicosapentaenoic acid (EPA) + docosahexaenoic acid (DHA)) were assumed to only be present in fish. Nutrient contents of food portions were obtained from Pacific Island food composition tables (FAO, 2004), except fish which were obtained from the Nutrient Analysis Tool in FishBase (Froese and Pauly, 2022).

Redundancy analyses of the relationships between respondents' characteristics and nutrient density of their diets revealed which people tended to get more of certain nutrients from fish. Preference for reef fish had the strongest effect on the nutrients people received from fish on both islands (Moorea: $F = 31.9$, $p = 0.001$; Raiatea: $F = 28.7$, $p = 0.001$) (Fig. 4.5 a, b). People who preferred to eat reef fish had higher intakes of zinc and vitamin A and, conversely, those who ate more pelagic families had higher intakes of calcium, iron, and omega-3, consistent with the nutrient concentrations for those fish groups (Fig. 4.4 b).

On Moorea, older people and those from farming (but not fishing) households had diets that consisted of more nutritious foods, although effects were small (age: $F = 2.4$, $p = 0.074$), while those with a higher level of education had less nutritious diets ($F = 5.7$, $p = 0.005$) (Fig. 4.5 a). People from households involved in fishing and farming got fewer nutrients associated with pelagic species (calcium, iron, omega-3 fatty acids) and were more aligned with nutrients from reef fish (zinc and vitamin A) (fishing and/or farming: $F = 3.5$, $p = 0.002$). On Raiatea, those who spoke Tahitian had more nutrient-dense diets ($F = 5.1$, $p = 0.003$) and women to a lesser extent ($F = 2.2$, $p = 0.066$) (Fig. 4.5 b). People from fishing households (including those who also farmed) got more nutrients associated with reef fish, while people from farming only households got more nutrients from pelagic fish (fishing and/or farming: $F = 4.3$, $p = 0.001$).

Models were fitted to estimate the relative strength of the drivers identified in redundancy analysis on people's nutrient intakes. People from fishing households and people in Moorea had higher total nutrient intakes (fishing: effect size = 27.9 ±8.0 standard error, $t = 3.5$, $p < 0.001$; Moorea: 49.5 ±7.3, $t = 6.8$, $p < 0.001$), as well as nutrient intakes from reef (fishing: 9.8 ±2.4, $t = 4.0$, $p < 0.001$; Moorea: 10.9 ±2.2, $t = 5.0$, $p < 0.001$) and pelagic fish (fishing: 10.2 ±4.7, $t = 2.2$, $p = 0.030$; Moorea: 15.6 ±4.2, $t = 3.7$, $p < 0.001$) (Fig. 4.5 c, d, e). However, for people from fishing households that were also involved in farming, this was not significant for nutrient intakes from pelagic fish (total nutrient intake: 31.1 ±10.1, $t = 3.1$, $p = 0.002$; reef fish: 16.7 ±3.1, $t = 5.4$, $p < 0.001$) (Fig. 4.5 e). People from farming households with no involvement in fishing also had higher nutrient intakes from reef fish (9.5 ±4.3, $t = 2.2$, $p = 0.027$). People who preferred to eat reef fish had higher nutrient intakes from reef fish, which could be expected, however they also had higher total nutrient intakes in their diets (7.8 ±3.4, $t = 2.3$, $p = 0.022$). Older people and wealthier people had slightly lower total nutrient intakes (age: -8.8 ±3.4, $t = -2.6$, $p = 0.010$; wealth: -6.6 ±2.9, $t = -2.3$, $p = 0.021$) (Fig. 4.5 a). Eating Maa Tahiti more often was associated with slightly higher nutrient intakes from reef fish (2.3 ±1.0, $t = 2.2$, $p = 0.027$). Women had higher nutrient intakes, while more educated people and those who ate more takeaway food had lower nutrient intakes, however these effects were weak and non-significant (Fig. 4.5 c, d, e).

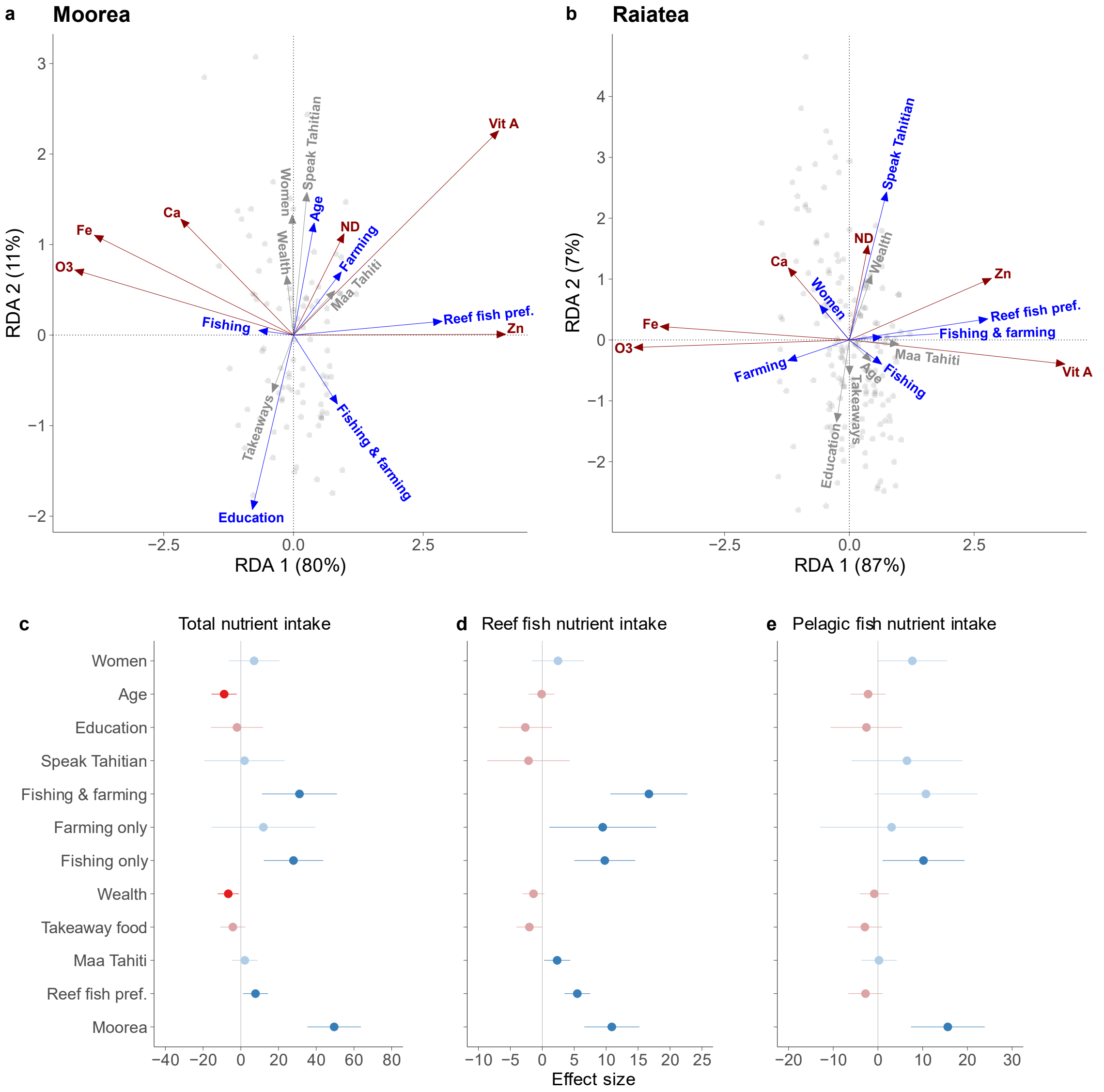

Figure 4.5: Analyses of socioeconomic effects and dietary habits on the nutrients in people's diets. Redundancy analyses for Moorea (**a**) and Raiatea (**b**) show associations between people's background (blue and grey arrows) and the nutrient density (ND) of five nutrients received from fish, as well as the ND across all food groups in their diet (red arrows). Explanatory variables with a significance level of $p < 0.1$ are shown in blue, others are shown in grey. Axis percentages are the variance explained by the data (note different axis scales for RDA 2 between islands). Generalised linear model estimates for the effect of socioeconomics on nutrient intakes are shown for total dietary intakes (**c**), and from reef (**d**) and pelagic (**e**) fish only, with confidence intervals (1.96 × standard error). Significant terms ($p \leq 0.05$) are shown in solid colour and non-significant terms are faded. Nutrient estimates for fish species were obtained from the Nutrient Analysis Tool in FishBase (Froese and Pauly, 2022).

Discussion

This study investigated the resources available to coral reef fisheries and the importance of fish in islander diets through a nutrition lens. Nutrient availability to reef fisheries was highest when live coral cover was low, mainly due to the high biomass of herbivorous fishes, suggesting that nutrient provisioning services can be maintained on these reefs despite periods of habitat degradation. Reef and pelagic fish were key components of people's diets on both islands (despite differences in available reef fish biomass), although there was evidence that the amount of fish people were eating had decreased over time while meat consumption had increased. Socioeconomics were a major driver of fish consumption, for example people from fishing and farming households had higher nutrient intakes from fish. Collectively, these results suggest local food cultures and norms may be stronger drivers of nutrition from fisheries, relative to ecological factors on coral reefs.

High herbivorous fish biomass when live coral cover was low underpinned large contributions of nutrients from reefs. Herbivorous fishes important to fisheries, such as parrotfish, often increase in biomass and productivity following reductions in live coral due to greater benthic algal and detrital food sources (Rogers et al., 2018; Morais et al., 2020a; Rassweiler et al., 2020). In Moorea, the initial increase in herbivore biomass following a prolonged crown-of-thorns sea star outbreak and a cyclone facilitated the recovery of hard corals through the removal of competitive algae, leading to altered compositions of reef fish assemblages as corals recovered (Lamy et al., 2016). Herbivore biomass (and nutrients) also increased in Moorea in 2019 (Figs 4.2 and S4.3) after coral cover was reduced once more following a coral bleaching event (Speare et al., 2022). Thus, low trophic-level fishes (e.g. herbivores) can provide nutrients to small-scale fisheries on low-coral cover reefs, which will likely continue to be important for food provisioning if reefs become degraded again in future. Comparatively low reef fish biomass in Moorea could potentially be linked to higher fishing pressure in response to high fish consumption and thus market demand for reef fish, particularly as larger fish are preferentially targeted by spearfishers (Rassweiler et al., 2020). Fish biomass trends can help inform if the fish consumption patterns on Moorea and Raiatea may be sustained and continue to provide essential nutrients, given the level of reef resources available. These results suggest careful management may be necessary when fisheries become more dependent on low trophic-level fishes to maintain a plentiful supply of nutrients from these species, particularly when coral cover is relatively high.

As multiple reef and pelagic fishes were important components of diets, it is likely that many islanders receive nutritional benefits from reef and pelagic fisheries. For example, people in fishing households had high nutrient intakes from both fish groups (Fig. 4.5) and would have had high zinc and vitamin A intakes from reef fish, and iron, calcium, and omega-3 intakes from pelagic fish. This could explain why people who were less wealthy (for example from lower income households, such as fishers and farmers) had slightly higher nutrient intakes, if their diets contained plenty of locally produced foods, such as fish and vegetables they harvested themselves. For example, it is common for fishers to keep a share of their catch to eat within their household (Kawarazuka and Béné, 2010). The popularity of carangid and scombrid fishes on both islands (Fig. 4.3 c) suggests islanders received health benefits associated with eating pelagic fish rich in omega-3, calcium, and iron. Adequate omega-3 intakes can help to prevent obesity-related health issues, which are particularly prevalent in French Polynesia (Inamo et al., 2011), and so pelagic fish could be hugely beneficial to those who regularly eat them, for example fishing households and Mooreans (Fig. 4.5). Fish is available at many roadside points around Moorea, whereas in Raiatea, fish and other foods tend to be sold at a large market in the north of the island, which would have influenced people's access to fish and could explain the higher frequency of fish consumption in Moorea.

Although fisheries in French Polynesia were important for supporting people's nutritional needs, there was also evidence that fish consumption may have decreased from one generation to the next, along with an increase in meat consumption. Meat is nutrient-dense and could provide people with higher zinc intakes compared to reef fish, but with the added cost of having a higher fat content (Fig. 4.5 b). Globalisation of French Polynesia's food system may have contributed to the loss of some traditional food cultures (Hughes and Lawrence, 2005), with an increase in Western, industrialised food imports, particularly processed meat high in saturated fat and foods with high amounts of added sugar (Brewer et al., 2023). The increasing reliance on imported food in French Polynesia has corresponded to the high proportion of overweight and obese adults (Hawley & McGarvey, 2015), therefore promoting traditional Polynesian diets and reducing reliance on imported foods could help to address these diet-related health issues (DiBello et al., 2009; Thow et al., 2011). In 2001, French Polynesia introduced excise taxes on refined carbohydrates, processed foods and high-fat foods, however food taxation policies could be strengthened with the aim of improving diets and reducing the prevalence of common non-communicable diseases (Walby et al., 2024). As omega-3 fatty acids can counteract the negative health effects of saturated fat found in red meat and many other Western foods (Shahidi and Ambigaipalan, 2018), locally caught fish (especially pelagics) may be a particularly important food source alongside meat for those with a high reliance on imported foods.

The varying effects of people's socioeconomic attributes on their consumption habits indicates social norms, habit, and identity can have a large influence on their nutrition (Baumhofer et al., 2020). Aspects of Polynesian culture, such as regularly eating Maa Tahiti, and speaking Tahitian in Raiatea, had positive effects on nutrition, suggesting traditional customs may be associated with health benefits. Lower total nutrient intakes in the elderly could be of concern, however this has previously been observed in French Polynesia as food intakes decrease with age (WHO, 2003). Although there were no strong effects, results indicated women may have had more nutritious diets and had higher nutrient intakes compared to men, which is typical worldwide (Miller et al., 2022). Therefore, efforts to promote nutritious diets in French Polynesian men could result in health benefits. The causes of the large differences in nutrient intakes between people in Moorea and Raiatea are presumably due to Mooreans generally consuming foods more frequently. It is unclear from these results whether this is an indication of overconsumption in Moorea or of limited nutrient intakes in Raiatea. This island effect on nutrition may stem from differences in food culture and warrants further investigation.

Conclusion

This study highlights the importance of nutrient-dense reef and pelagic fish from local fisheries to societies in French Polynesia. The nutrient provisioning services provided by coral reef ecosystems can be maintained when the condition of coral habitat is reduced. Despite the globalisation and industrialisation of the food system increasing reliance on imported food, it was apparent that traditional diets rich in nutritious fish had persisted in French Polynesia. While more research is needed into specific drivers of people's food acquisition and consumption habits, this study highlights which demographics benefited most from fisheries-derived nutrition and reveals those where potential improvements to nutrition could be made. Time series of social data alongside ecological data would be immensely valuable for similar studies in the future to more closely connect reef ecosystems and their influence on human nutrition, particularly as islander diets transition over time.

General discussion

In this thesis, I investigated the impacts of coral reef degradation on small-scale tropical reef fisheries from ecological and social perspectives. The strong influence of reef habitat condition on the ecology and composition of fish assemblages affects fisheries productivity and therefore the food and nutrient provisioning services of coral reefs. The adaptations trap fishers in Seychelles made in response to reef habitat degradation and direct human impacts sustained fishing livelihoods but also led to changes in fishing effort and yields. The availability of fish on reefs in French Polynesia decreased as hard corals recovered, yet reef fisheries continued to make important contributions to people's nutrition alongside pelagic fisheries. Collectively, my thesis demonstrates how multiple aspects of small-scale fishery food systems can be influenced by reef degradation, from production to consumption.

Chapter summary

Chapter 1

In **Chapter 1**, I demonstrated how fisheries biomass productivity and turnover differed between post-bleaching habitats in Seychelles. Productivity increased on reefs where hard corals were recovering resulting in higher productivity almost 20 years after bleaching on both fished and protected reefs compared to pre-bleaching levels. Additionally, by approximately 10 years after bleaching, productivity was no longer elevated on protected reefs in marine reserves, suggesting productivity increases were not affected by fishing. Multiple trophic groups of reef fish contributed to the productivity increases on recovering reefs, although herbivore/detritivores predominantly drove this trend, resulting in the elevated standing biomass on these reefs (Graham et al., 2020). Previous studies have also found that productivity increased in the short term after coral bleaching, however turnover was reduced suggesting productivity was mainly due to the growth of existing larger fish on reefs with limited recruitment of smaller individuals to reefs (Morais et al., 2020a, 2020b). However, my results show simultaneous increases in productivity and turnover on reefs recovering from bleaching, with increases in the abundance of key fisheries target species, especially smaller individuals, which has positive implications for recruitment to fisheries.

On regime-shifted reefs, despite notable shifts in benthic and fish species composition, and a reduction in species richness (Chong-Seng et al., 2012), productivity returned to pre-bleaching levels on fished reefs, driven mainly by macroalgal browsers and mobile invertivores. Larger productivity increases occurred on reefs protected from fishing, suggesting marine reserves on macroalgal habitats can remain a useful management strategy to enhance fisheries productivity and standing biomass. Rates of biomass turnover for multiple trophic groups were elevated on macroalgal reefs compared to recovering reefs, indicating that biomass removed by fisheries can be relatively quickly replenished. My results suggest that the macroalgal habitats that developed following coral bleaching in 1998 can not only remain productive fishing grounds, but can also sustain fisheries yields due to the high turnover of fast-growing, highly reproductive species such as *Siganus sutor* that are of commercial importance in Seychelles (SFA, 2023).

Chapter 2

My results from **Chapter 2** indicate that reef structural complexity promotes the production of nutrients available to fisheries in multiple locations, to a greater extent than hard coral cover. This effect was greatest in the unfished Chagos Archipelago, however on reefs with low complexity, nutrient productivity was comparable to other fished locations, suggesting the absence of fishing pressure in wilderness areas enables elevated productivity on more complex reefs. Larger average fish length was also associated with higher nutrient productivity levels, therefore without fisheries selectively removing larger individuals, it is possible this also contributed to the much higher nutrient productivity estimates on more complex reefs in the Chagos Archipelago. Herbivore/detritivores made large contributions to nutrient productivity over a gradient of different reef complexities, suggesting species in this group will be of high importance for supplying nutrients to fisheries if reef structure becomes degraded. However, herbivores have relatively low concentrations of some nutrients important to human health compared to fish in other trophic groups, for example vitamin A. Therefore, maintaining reef complexity can supply more and different nutrients to fisheries from other trophic groups such as piscivores, which will be particularly important in areas where coral reef fisheries make substantial contributions to the nutrient security of people, for example Maldives (Yadav et al., 2021) and Seychelles (Conway et al., 2018).

Chapter 3

In **Chapter 3**, I interviewed artisanal trap fishers in Seychelles to investigate their perceptions of reef degradation caused by climate change and other stressors, and their fishing responses. Coral bleaching events, such as the one in 2016, greatly reduced catches from fish traps, however several fishers stated catches recovered relatively quickly following bleaching. Fishers on the more densely populated island of Mahé identified more causes of reef habitat degradation, such as land reclamation and sedimentation, suggesting direct human impacts on reef ecosystems have more of an influence on the trap fishery there than on Praslin. Despite the indication from fishers that trap catches could recover following coral bleaching, most fishers perceived a reduction in catches over time and had adapted their fishing activity as a result. Although overfishing was identified as a problem for the trap fishery, many fishers had increased fishing effort and the distance travelled to maintain trap catches, while others focused more on handline fishing. My findings demonstrate that collecting fishers' LEK and information on adaptation strategies can provide valuable insights into the interactions between marine habitats and fishing activity that could be integrated into management. For example, changes in fishing activity in response to declining yields alter the fishing pressure different fish stocks and grounds are subjected to, as well as the species composition of fish landed to markets. Previous interview-based studies with artisanal fishers in Seychelles have harnessed fisher LEK to gain insights into the spatiotemporal ecology of reef fishes (for example, spawning aggregations of commercial species; Robinson et al., 2004) and which aspects of habitat change are most influential to fishing livelihoods (Woodhead et al., 2021). In addition to gathering perceptions of changing inshore reef habitats and fish catches, my research also includes empirical information on fisher responses related to their perceptions of fishing grounds, highlighting the factors that shape fishing behaviour and what the implications may be for the Seychelles trap fishery.

Chapter 4

In **Chapter 4**, I investigated the influence of coral reef condition on the availability of biomass and nutrients to fisheries, as well as the contributions fisheries make to people's nutrient intakes in French Polynesia. My results indicated that reef fishes in low trophic levels were more available to fisheries on reefs with reduced coral cover. These species were also popular among consumers when coral cover was high, providing nutritional benefits to islanders alongside species caught in pelagic fisheries. Although fish was a major source of protein and nutrients in most people's diets, people generally ate less fish and more meat compared to their elders, indicative of a transition away from traditional fish-based diets towards diets consisting of imported foods. Households that were involved in traditional livelihoods, such as fishing and farming, had higher nutrient intakes from fish, suggesting urbanisation may be associated with lower levels of fish consumption. As reef and pelagic fish were the most nutrient-dense foods in my study, with a low fat content compared to other animal-based foods, small-scale fisheries in these islands constitute a healthy local source of nutrition that could be beneficial in tackling the high prevalence of overweight and obesity stemming from high-calorie imported foods in French Polynesia. This chapter is a rare example of a case study that links ecological reef data, nutrient content of foods, and socioeconomics to highlight the importance of local fisheries for public nutrition and health.

Synthesis

My thesis demonstrates that degraded coral reef habitats can continue to sustain fisheries yields and provide nutritious food to people, although with altered species composition of catches. As fisheries yields from degraded reefs become more dominated by fishes in lower trophic levels, the nutrient composition of catches is also altered, with increases for some nutrients and decreases for others. Therefore, the quantity and nutritional quality of fish reef fisheries supply to people are influenced by coral reef degradation.

A common theme throughout my thesis is the importance of herbivorous reef fishes to coral reef fisheries on degraded reefs throughout the tropics. Not only did herbivorous fishes make large contributions to biomass and nutrient productivity (**Chapters 1** and **2**), but they were also primary targets for trap fisheries in Seychelles (**Chapter 3**) and the most popular reef fish among consumers in French Polynesia (**Chapter 4**). Herbivores benefitted from post-bleaching reef habitats and were also relatively resistant to decreases in reef structural complexity, making herbivores a key group for sustaining fisheries productivity following reef disturbances. Theory suggests herbivore productivity can be reduced by approximately half on reefs after dead coral structures are completely eroded (Rogers et al., 2018a), which is similar to my nutrient productivity estimates in Seychelles in **Chapter 2** (Fig. 2.4 e), the only study location where there were reefs with zero complexity. This suggests if future reef degradation results in greater reef complexity losses and reef flattening, large declines in fisheries nutrient productivity can be expected across study locations. Structural complexity had no effect on macroalgal browser productivity in **Chapter 2** yet had a large positive influence in **Chapter 1**. These contrasting results from the same study location could be due to the models in **Chapter 1** including multiple survey years and capturing changes in structural complexity and browser productivity over time, while the models in **Chapter 2** included data from only one survey year (2011), when browsers like *S. sutor* were recorded in low numbers in Seychelles (Fig. 1.5 e). It is possible that data across multiple years give a more accurate representation of the importance of structural complexity on the productivity of this group of fishes, particularly as the movement and shoaling behaviour of *S. sutor* can cause high variability in underwater visual survey observations (Kruse et al., 2016). Trap fishers in Seychelles also noted the importance of prominent coral or rock structures for *S. sutor* spawning aggregations (**Chapter 3**), suggesting these particular forms of reef structure are important for the life history of this species, and therefore recruitment to fisheries. As such, the benthic structure of reefs is likely key for maintaining productive reef fisheries on degraded reefs, and the increased biomass productivity and turnover seen on recovering coral and macroalgal reefs, respectively (**Chapter 1**), is likely dependent on reef structural complexity.

Herbivorous reef fish assemblages responded differently to benthic disturbances on reefs between some study locations. For example, there were differences in herbivore standing biomass trends over several years in the Seychelles (**Chapter 1**) and French Polynesia (**Chapter 4**). Herbivore biomass was lower than pre-bleaching estimates seven years after the 1998 coral bleaching event in Seychelles, but by ten years after bleaching, biomass was greatly enhanced and remained high as hard corals recovered (Fig. 1.2 a). This contrasts with herbivore biomass in French Polynesia, which increased following coral mortality and then generally decreased as hard corals recovered (Fig. 4.2). Although reefs in Seychelles and French Polynesia experienced severe coral mortality, the stressors leading to coral loss differed between locations; coral bleaching in the Seychelles (Wilson et al., 2019) and crown-of-thorns sea star outbreaks and a tropical cyclone in French Polynesia (Pérez-Rosales et al., 2021). Therefore, the different drivers of reef degradation between these locations may have led to different responses of reef fish in subsequent years. Responses of coral communities to disturbances can exhibit consistent differences between geographic regions over time (Mellin et al., 2024), therefore differing characteristics of benthic communities between study locations in my thesis could also contribute to different reef fish responses. Additionally, differing fishery characteristics, as well as demand for reef fish, could influence the fish community trends observed between study locations. For example, parrotfish are caught with fish traps in Seychelles (SFA, 2023) while they are often targeted by more size-selective gears such as spearguns in French Polynesia (Rassweiler et al., 2020), which could lead to differences in the size structure of targeted parrotfish species between locations and affect productivity estimates.

My results indicate herbivores can sustain fisheries following climatic disturbances on reefs and supply markets with species highly concentrated in nutrients such as zinc (Fig. 4.4 a). In areas where reef fish consumption is declining and the consumption of high-calorie imported foods has increased, for example French Polynesia (**Chapter 4**) and Seychelles (Cardoso et al., 2013), herbivorous fish that are already commonly harvested and part of traditional food cultures (such as parrotfish and rabbitfish) could be particularly good food choices for people. Fish species that are already part of traditional dishes are likely easier to promote in diets than less familiar species, therefore dietary health schemes should take advantage of the fact that productive reef fish species available from local markets can contribute to healthy diets. As reef degradation may cause inshore fisheries landings to be dominated by herbivores, the reduced diversity of species may also reduce the availability of reef fish rich in nutrients such as vitamin A. However, invertivores also made significant contributions to fisheries following coral bleaching (Fig. 1.3 c; Fig. 2.2 a) and have relatively high vitamin A concentrations (Fig. 4.4 a), and could therefore be an important source of this nutrient from fisheries on degraded reefs. Pelagic fish are highly concentrated in calcium, iron, and omega-3 fatty acids compared to reef fish (Fig. 4.4), therefore eating a range of fish from reef and pelagic fisheries can maximise nutrient intakes from small-scale fisheries (Robinson et al., 2022a). Pelagic fisheries are likely to remain an important food source alongside reef fisheries, as the biomass of some pelagic fish species is expected to increase in future climate projections (Bell et al., 2018) and because market demand for pelagic fish has made these species popular fisheries targets in multiple areas (**Chapters 3** and **4**).Although habitat disturbances can reorganise reef benthos and fish assemblages and affect fisheries productivity potential, fishing activity and people's situational circumstances also play a large part in the benefits people receive from reef fisheries. For example, in **Chapter 3**, several fishers increased their fishing effort in response to declining yields, creating a situation where fish populations are at risk of being overfished. Some species were highly productive on post-bleaching reef habitats (**Chapter 1**) which can buffer against biomass declines as fishing effort increases, however the overall biomass and productivity of exploited fish populations still decreases with fishing intensity (Morais et al., 2020b, 2023). Therefore, the increased fishing pressure in the Seychelles trap fishery may compromise the supply of certain species to markets. Many trap fishers had also expanded the areas they fished, travelling further offshore and fishing with handlines more often, which not only has the potential to change the composition of species landed but may also raise fish prices for consumers as fishers try to offset the rising costs of fuel. Management efforts that aim to maintain sustainable supplies of fish from reef and pelagic fisheries will be important for providing a variety of fish to local markets, particularly as a decline in fish supplies may lead to people finding alternative sources of protein, such as terrestrial-sourced meats that could be detrimental to people's dietary health (**Chapter 4**).

Thesis limitations and future considerations

My thesis used existing datasets in three of four data chapters and some methodological techniques that can be broadly applied to reef fish data. While the use of existing data was necessary due to the COVID-19 pandemic, data collection that was more tailored to specific research questions may have led to results that provided further insights into the effects of coral reef degradation on different aspects of small-scale fisheries. For example, collection of different reef structural complexity metrics during surveys may have allowed the effect of structure loss on different groups of reef fish in different locations to be inferred in more detail.

Chapter 2 used a six-point visual assessment of structural complexity (Polunin and Roberts, 1993), which can capture large scale complexity better than finer scale complexity that may be more relevant to smaller fish species or individuals. Reef fishes typically interact with reef structure on scales smaller than that of the visual assessment used in my thesis (Kerry and Bellwood, 2012; Urbina-Barreto et al., 2021), therefore examining reef complexity at varying scales is recommended to capture variability across reefscapes (Duvall et al., 2019). An inclusion of multiple complexity metrics could improve our understanding of which types of complexity are important to the nutrient productivity of different reef fishes. For example, piscivore productivity is linked to reef structure that can provide suitable refuges for prey populations (Rogers et al., 2014) and a more detailed investigation into the contributions of different reef features to specific types of complexity (such as rugosity or fractal dimensions; Knudby and LeDrew, 2007) may help to explain which complexity metrics led to enhanced nutrient productivity of piscivores in the Chagos Archipelago and Maldives (Fig. 2.3 a). Similarly, using only live coral cover in analyses conceals nuances in benthic reef community responses to disturbance, for example responses of different coral genera or growth forms (Mellin et al., 2024), therefore including coral traits could be useful in future studies relating reef recovery trajectories to fish populations and fisheries productivity.

The fish productivity calculations in **Chapters 1** and **2** used a trait-based approach developed by Morais and Bellwood (2020). As species traits are global, this framework for estimating fish productivity does not account for geographical differences in growth rates between study locations (or between reefs within locations). Therefore, although sea surface temperature is taken into account, other environmental variables that influence fish populations and growth rates, such as food availability and quality (Jones, 1986; Ruttenberg et al., 2005), are not accounted for in the productivity estimates in my thesis, which would need to be considered to more accurately capture regional differences in fisheries productivity (Williams et al., 2007). This also applies to the fish nutrient concentration estimates used in **Chapters 2** and **4**; the nutrient content of fish varies based on the nutritional quality of food sources between reefs, even within species (Robinson et al., 2022a), however the estimates used in my analyses were global averages per species. Separating fish species into more detailed trophic groups could also reveal more nuanced responses to reef degradation. For example, the herbivore/detritivore trophic group in my analyses contained a vast number of species, however parrotfish can be grouped into several functional groups based on feeding behaviour that respond differently to habitat change, as well as susceptibility to fishing varying between species (Molina-Hernández and Alvarez-Filip, 2024). Given that my analyses were conducted across different reef habitats with different levels of fishing pressure, a more in-depth examination of the variation between habitats and responses of fish taxa may have highlighted important implications for specific fisheries targets that were masked by coarse-taxonomic groupings in my analyses (Ceccarelli et al., 2016).

Studies that investigate how the connectivity between reefs affects fisheries productivity could add further insights to my results. As many coral reef fishes, including fisheries targets, undergo ontogenetic shifts from macroalgae habitats to coral habitats (Fulton et al., 2020), the elevated biomass turnover on macroalgal reefs may eventually lead to enhanced recruitment to fisheries on coral reefs. Information on the movement of fish between reefs could help to develop management strategies, such as protecting key nursery grounds for fished species. An improved understanding of the energy inputs and primary productivity of different reef systems could also lead to more accurate nutrient productivity estimates in reef fish. As reef fish productivity can be enhanced by pelagic energy inputs (Morais et al., 2019) and the nutrient content of fish is also influenced by the nutritional quality of benthic energy sources (Robinson et al., 2022a), research into the effects of varying nutrient sources on reefs could improve nutrient productivity estimates between different areas.

Three of my data chapters use data from the Seychelles inner granitic islands, particularly **Chapters 1** and **3**. The disturbance history of these reefs and resulting recovery trajectories are somewhat unique compared to other coral reef systems in the Indo-Pacific. The dominance of fleshy macroalgae at some reef sites as a result of regime-shifts following coral bleaching in 1998 led to two distinct reef categories: coral-dominated and algae-dominated. This was not the case at other study locations in my thesis (Fig. 2.1 c), therefore my interpretation of results regarding fisheries productivity (**Chapter 1**) and fisher responses (**Chapter 3**) are not generalisable to most other coral reef fisheries. As such, the example of Seychelles reefs is not representative of all other Indo-Pacific reef systems, and therefore the implications of my results (for example high rates of biomass turnover sustaining fisheries catches on macroalgal reefs) may not be relevant in other geographies. Additional case studies would be needed elsewhere to account for context-specific reef and fisheries characteristics, particularly if results are used to inform management (Côté et al., 2013).

My results from **Chapter 3** highlight the vast amount of information that fishers can provide on fishing grounds, fish species, and fishing activity. Future research and fisheries management could benefit from including local knowledge from fishers regarding specific topics of interest, such as catch recovery timeframes of different species following coral bleaching. The information collected during interviews could be maximised when interviewers are able to have in-depth conversations with fishers in their first language, for example Kreol in Seychelles.

In **Chapter 4**, I made linkages between reef condition and people's nutrient intakes from reef fish, however studies that involve time series of reef and dietary data would be extremely useful to strengthen our understanding of the implications of changing reef fisheries resources for people's nutrient intakes over time. Fish sales data could also be used to add information on the intermediate link between fish landings and fish consumption. Furthermore, information on the frequency of consumption of each type of fish would greatly improve nutrient intake estimates and highlight the nutritional and cultural importance of different species.

Recommendations and concluding remarks

From my research into the impacts of coral reef degradation on ecological and social aspects of small-scale fisheries, I would recommend the following action points to improve the food and nutrient provisioning services coral reefs can provide to people:

1) *Restrict activities that cause physical damage on reefs to maintain structural complexity and promote fisheries productivity.*

Reef structure is important for supporting productive fish communities that supply biomass and nutrients to fisheries. The maintenance of natural reef structures and potentially the addition of artificial structures could be particularly important to promote the productivity of fisheries-derived nutrients in areas where nutrient deficiencies are prevalent in diets. Reducing human activities that compromise reef structure, such as anchoring and destructive fishing practices (Mangi and Roberts, 2006), should be included in fisheries and conservation management. Urgent global action to drastically reduce greenhouse gas emissions and reliance on fossil fuels is also needed to limit global heating as much as possible and minimise the intensity of widespread climate-induced disturbances on coral reefs (Wolff et al., 2015). As climate impacts are expected to result in unprecedented coral mortality, shortened coral recovery periods, and eventually reduced structural complexity through erosion of the reef matrix (Perry and Alvarez-Filip, 2019), the climate crisis is a threat to the food provisioning services of coral reefs.

2) *Integrate LEK from fishers into fisheries management.*

> To effectively monitor and manage the interactions between marine habitats and fisheries, information from those who regularly witness these interactions firsthand can be hugely beneficial. Fishers are well-placed to provide information on fishing grounds across space and time, as well as any adjustments they have made in response to change (or other factors), therefore revealing changes in both reef habitats and fishing pressure. It is possible to gather LEK relatively quickly, which can be valuable when assessments are time-sensitive, such as following environmental shocks. Such fisheries-dependent data can be considered alongside other data types in ecosystem-based fisheries management to assess the sustainability of various fisheries as reef habitats continue to change.

3) *Promote traditional diets, including fish from sustainable reef and pelagic fisheries, in areas where globalisation has impacted food systems and public health.*

> Reef and pelagic fisheries provide coastal communities with nutrient-rich food sources that are healthier than many other animal-sourced foods that have become more common through dietary transitions. While food taxation policies could help to reduce less healthy foods in diets (Walby et al., 2024), educational programmes that highlight locally caught fish as sustainable and healthy food options that also honour traditional cultures could be an effective way to improve diets. Balancing the nutritional needs of people with the ecological state of marine habitats and fish stocks is necessary to ensure reef fisheries can sustainably provide nutritional benefits into the future.

These recommendations highlight the need for ecological, fisheries, and human health considerations for the management of coral reef social-ecological systems. The appropriateness of any conservation or fisheries management strategy depends on the context of specific systems, for example the type and severity of reef degradation, the type of fisheries involved, and the reliance of people on reefs for food and livelihoods. Taking Seychelles as an example, fisheries productivity was enhanced on coral reefs and biomass turnover was enhanced on macroalgal reefs following coral bleaching, however artisanal fishing effort also increased. Considering the rates of fisheries production in relation to specific habitats and comparing to rates of biomass extraction by fisheries could help to monitor the sustainability of reef fisheries. Sustainable fisheries are particularly important for the continued provision of essential nutrients to people, particularly in areas where high-calorie foods are causing transitions to less healthy diets (for example, the widespread increase in the availability of fried chicken in Seychelles; Cardoso et al., 2013). The increase in fishing effort towards pelagic species influences the species and nutrient composition of landings, however this will also alter the fishing pressure on particular species or habitats, which should also be taken into account in fisheries management. Regardless of geographic location, assessing multiple dimensions of reef fisheries over space and time may be intensive but is necessary when attempting to capture the complex interactions between the environmental and social elements of coral reef fisheries as reef habitats change.

An ecosystem-based fisheries management approach, that incorporates human dependency on reefs, could be an effective strategy that considers environmental, social, and economic elements of sustainability. Of course, a desirable outcome would be reefs where the ecological conditions create suitable habitats for diverse reef fish communities which can provide a plentiful supply of fish for human needs. However, there will be trade-offs between conserving coral reef ecosystems and meeting human demand for resources. For example, if the nutritional benefits of a fishery are derived from unsustainable practices that cause harm to reef ecosystems, sourcing nutrients from other fisheries species or nutrient-rich foods may need to be considered. This may result in a reliance on imported foods in some regions, however efforts to promote healthy and nutritious foods will be needed to avoid situations where unhealthy alternatives lead to increases in non-communicable diseases (**Chapter 4**). Alternatively, in areas where reef conservation measures are required for reef recovery or protection, there should also be considerations for allowing some level of fishing where people are dependent on fisheries for protein and nutrients. Rather than creating large no-take areas that prioritise ecological conservation goals and exclude small-scale fisheries, well-designed and well-managed marine protected areas could provide benefits for biodiversity as well as food security and human health (Viana et al., 2024). Fishing restrictions, such as limits on the number or type of fishing gears and vessels, may also allow certain fishing practices to take place while protecting reef ecosystems from overfishing or habitat damage (Roberts et al., 2024). Such restrictions could be relevant in Seychelles, where increased fishing effort on climate-impacted reefs (SFA, 2023) may compromise fisheries productivity gains on these reefs.

While results from observational studies in my thesis may suggest win-win outcomes in terms of the increased productivity of some species that are also popular food fish (assuming fisheries are well-managed), it is important to acknowledge that reef fisheries may not respond to future coral bleaching events as they have previously. This is especially true considering the expected increases in the frequency and intensity of future coral bleaching events (Hughes et al., 2018), meaning the baselines used to assess reef health and fisheries will likely need to be reassessed. Globally, structurally complex reefs with many small planktivorous fishes are becoming less common as they are replaced by reefs with higher macroalgal cover and large-bodied fishes, affecting both fish species composition and nutrient pathways (Brandl et al., 2024). Indeed, my results suggest productive species in lower trophic levels will remain particularly important fisheries targets and nutrient sources following severe coral bleaching, while species in higher trophic levels may be more vulnerable to climate-induced reef degradation (Obura et al., 2022). Therefore, baselines used to manage fisheries and nutrient yield expectations of reef fisheries must also change. Geographic, environmental, and anthropogenic context all influence reef habitats (Brandl et al., 2024), which may explain some of the differences observed between study locations in my thesis, therefore regional baselines should be used in future research and management of coral reef fisheries. Ultimately, the conservation and management actions needed for coral reef social-ecological systems must be evidence-based, with realistic considerations of the services reef fisheries can provide in a changing world and our ability to achieve desired goals in different contexts (Streit et al., 2024).

Monitoring and managing fisheries ecology and the impacts on human wellbeing in an ever-changing world is challenging due to the balance required between environmental and socioeconomic dimensions (Roberts et al., 2024). Ongoing collection of multiple data types, such as those in my thesis (ecology, fisheries, socioeconomic, nutrition), is necessary to identify patterns of change on coral reefs and identify potential opportunities for management to help devise adaptation strategies (Edmunds, 2024). My research has shown that degraded coral reefs can still provide valuable fisheries and nutrition services to people, however as these ecosystems continue to change into the future, the food provisioning services of reefs and efforts to sustain them will also need to change.

Appendices

Chapter 1 supplementary material

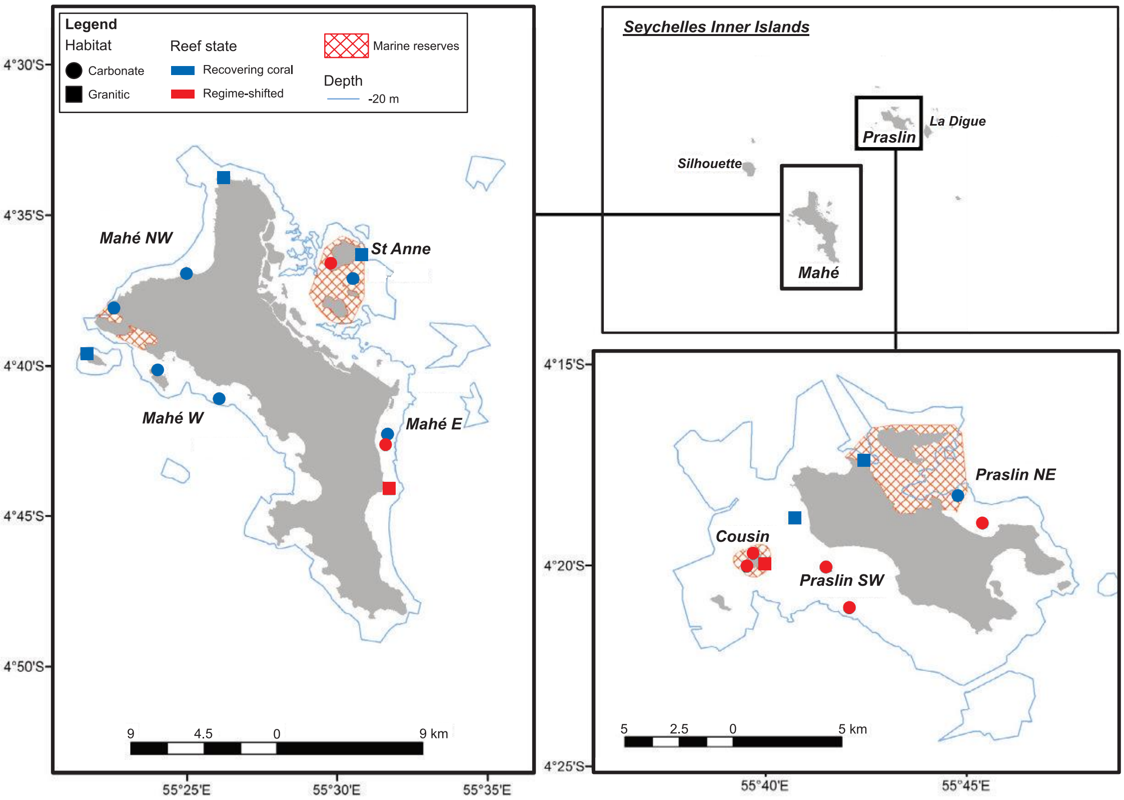

Figure S1.1: Reef survey sites around the islands of Mahé (left) and Praslin (bottom right) in the Seychelles Inner Islands. Reefs that were recovering to a coral-dominated state following the 1998 bleaching event are shown in blue, reefs that regime-shifted to a macroalgae-dominated state are shown in red. Reef sites with a carbonate substrate are shown as circles, sites with a granitic substrate are shown as squares. No-take areas are marked with red crosshatches. Cousin marine reserve is managed by an NGO (Nature Seychelles), all other reserves are government managed.

Table S1.1: All fish species observed during underwater visual surveys from 1994 to 2017, classified into trophic groups. The total number of species within each trophic group is given and species are presented by taxonomic family. Species considered primary, important, and occasional targets in the Seychelles trap fishery are marked with ^{P}, ^{I}, and ^{O}, respectively (according to Graham et al., 2007 and Seychelles Fishing Authority). Columns continue from left to right.

Herbivore/detritivore (*n* = 30)

- Acanthuridae
  - *Acanthurus leucosternon*^{O}
  - *Acanthurus lineatus*^{O}
  - *Acanthurus nigrofuscus*^{O}
  - *Acanthurus tennentii*^{I}
  - *Acanthurus triostegus*^{O}
  - *Ctenochaetus binotatus*^{O}
  - *Ctenochaetus striatus*^{I}
  - *Ctenochaetus truncatus*
  - *Zebrasoma desjardinii*
  - *Zebrasoma scopas*
- Pomacentridae
  - *Pomacentrus trilineatus*
- Scarinae
  - *Calotomus carolinus*^{I}
  - *Cetoscarus bicolor*^{I}
  - *Chlorurus atrilunula*^{O}
  - *Chlorurus sordidus*^{P}
  - *Chlorurus strongylocephalus*
  - *Hipposcarus harid*^{O}
  - *Scarus caudofasciatus*^{I}
  - *Scarus falcipinnis*^{I}
  - *Scarus frenatus*^{I}
  - *Scarus ghobban*^{P}
  - *Scarus globiceps*^{I}
  - *Scarus niger*^{I}
  - *Scarus prasiognathos*^{I}
  - *Scarus psittacus*^{I}
  - *Scarus rubroviolaceus*^{P}
  - *Scarus scaber*^{I}
  - *Scarus tricolor*^{I}
  - *Scarus viridifucatus*^{I}
- Siganidae
  - *Siganus stellatus*^{I}

Macroalgal browser (*n* = 4)

- Acanthuridae
  - *Naso elegans*^{O}
- Scarinae
  - *Leptoscarus vaigiensis*^{I}
- Siganidae
  - *Siganus argenteus*^{I}
  - *Siganus sutor*^{P}

Mobile invertivore (*n* = 46)

- Balistidae
  - *Sufflamen chrysopterum*
- Chaetodontidae
  - *Chaetodon auriga*
- Haemulidae
  - *Diagramma pictum*^{O}
  - *Plectorhinchus gibbosus*
  - *Plectorhinchus orientalis*^{I}
  - *Plectorhinchus schotaf*^{I}
- Labridae
  - *Anampses meleagrides*
  - *Bodianus axillaris*
  - *Cheilinus fasciatus*^{I}
  - *Cheilinus trilobatus*^{I}
  - *Coris formosa*
  - *Gomphosus caeruleus*
  - *Halichoeres cosmetus*
  - *Halichoeres hortulanus*
  - *Halichoeres marginatus*
  - *Halichoeres scapularis*
  - *Hemigymnus fasciatus*
  - *Hemigymnus melapterus*
  - *Labroides bicolor*
  - *Labroides dimidiatus*
  - *Macropharyngodon bipartitus*
  - *Novaculichthys taeniourus*
  - *Stethojulis albovittata*
  - *Thalassoma hardwicke*
  - *Thalassoma hebraicum*
  - *Thalassoma lunare*
- Lethrinidae
  - *Lethrinus enigmaticus*^{I}
  - *Lethrinus harak*^{I}
  - *Lethrinus lentjan*^{I}
  - *Lethrinus mahsena*^{I}
  - *Lethrinus nebulosus*^{I}
  - *Lethrinus obsoletus*^{I}
  - *Lethrinus rubrioperculatus*^{O}
  - *Monotaxis grandoculis*^{I}
- Lutjanidae
  - *Lutjanus fulviflamma*^{I}
  - *Lutjanus gibbus*^{I}
  - *Lutjanus kasmira*^{I}
- Mullidae
  - *Mulloidichthys flavolineatus*^{I}
  - *Parupeneus barberinus*^{I}
  - *Parupeneus ciliatus*^{I}
  - *Parupeneus macronemus*^{I}
  - *Parupeneus rubescens*^{I}
  - *Parupeneus trifasciatus*
- Nemipteridae
  - *Scolopsis frenata*^{O}
- Epinephelidae
  - *Epinephelus fasciatus*^{I}
  - *Epinephelus merra*^{I}

Omnivore (*n* = 11)

- Chaetodontidae
  - *Chaetodon guttatissimus*
  - *Chaetodon lunula*
  - *Chaetodon xanthocephalus*
- Monacanthidae
  - *Cantherhines pardalis*
  - *Chaetodon lunula*
  - *Chaetodon xanthocephalus*
- Pomacanthidae
  - *Pomacanthus semicirculatus*
- Pomacentridae
  - *Neoglyphidodon melas*
  - *Plectroglyphidodon dickii*
  - *Plectroglyphidodon johnstonianus*
  - *Plectroglyphidodon lacrymatus*
  - *Stegastes nigricans*
- Siganidae
  - *Siganus puelloides*^{I}

Piscivore (*n* = 19)

- Labridae
  - *Epibulus insidiator*
  - *Oxycheilinus digramma*
- Lethrinidae
  - *Lethrinus olivaceus*^{I}
- Lutjanidae
  - *Aprion virescens*^{P}
  - *Lutjanus argentimaculatus*
  - *Lutjanus bohar*^{P}
  - *Lutjanus monostigma*
  - *Macolor niger*^{I}
- Mullidae
  - *Parupeneus cyclostomus*^{I}
- Epinephelidae
  - *Aethaloperca rogaa*^{O}
  - *Anyperodon leucogrammicus*^{I}
  - *Cephalopholis argus*^{I}
  - *Cephalopholis leopardus*^{P}
  - *Cephalopholis miniata*^{I}
  - *Cephalopholis urodeta*^{O}
  - *Epinephelus coeruleopunctatus*^{O}
  - *Epinephelus hexagonatus*^{O}
  - *Epinephelus spilotoceps*
  - *Epinephelus tukula*

Planktivore (*n* = 6)

- Acanthuridae
  - *Paracanthurus hepatus*
- Pomacentridae
  - *Amblyglyphidodon leucogaster*
  - *Chromis atripectoralis*
  - *Chromis ternatensis*
  - *Chromis weberi*
  - *Dascyllus trimaculatus*

Sessile invertivore (*n* = 13)

- Chaetodontidae
  - *Chaetodon kleinii*
  - *Chaetodon lineolatus*
  - *Chaetodon melannotus*
  - *Chaetodon meyeri*
  - *Chaetodon trifascialis*
  - *Chaetodon trifasciatus*
  - *Chaetodon zanzibarensis*
- Labridae
  - *Labrichthys unilineatus*
- Monacanthidae
  - *Oxymonacanthus longirostris*
- Pomacanthidae
  - *Apolemichthys trimaculatus*
  - *Centropyge multispinis*
  - *Pomacanthus imperator*
- Zanclidae
  - *Zanclus cornutus*

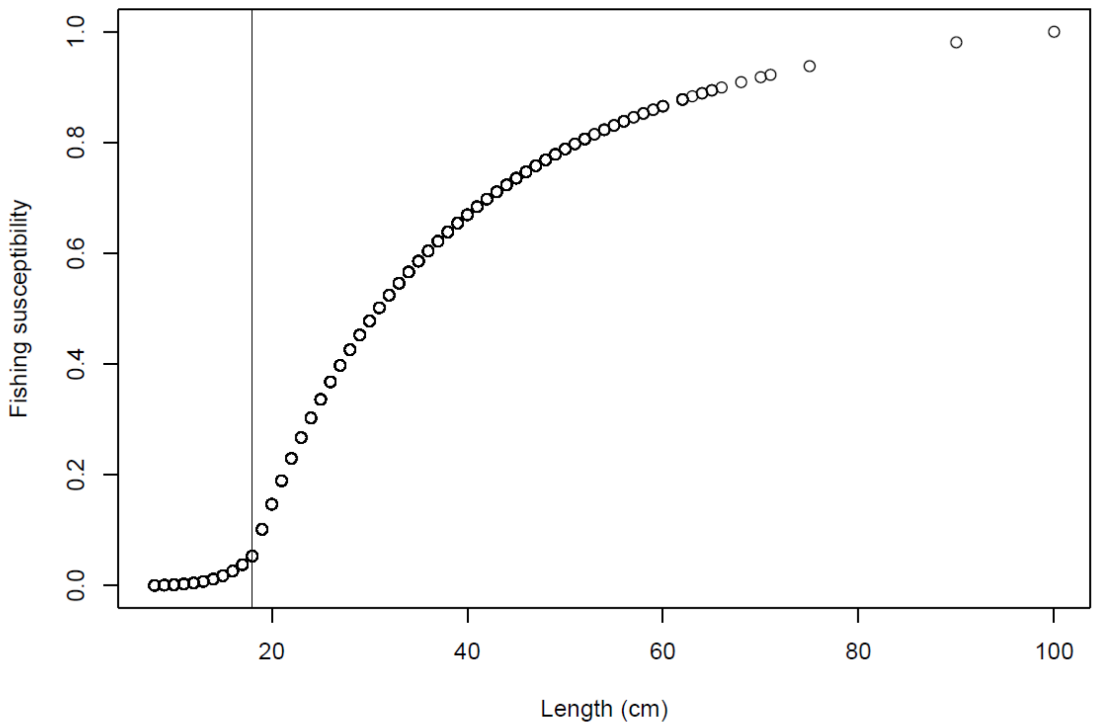

Figure S1.2: Fishing probability distribution (adapted from Morais et al., 2020b) for the target fish assemblage on fished reefs, showing susceptibility to fishing for each cm length. The vertical line at 18 cm represents the target length above which individuals were considered fishable.

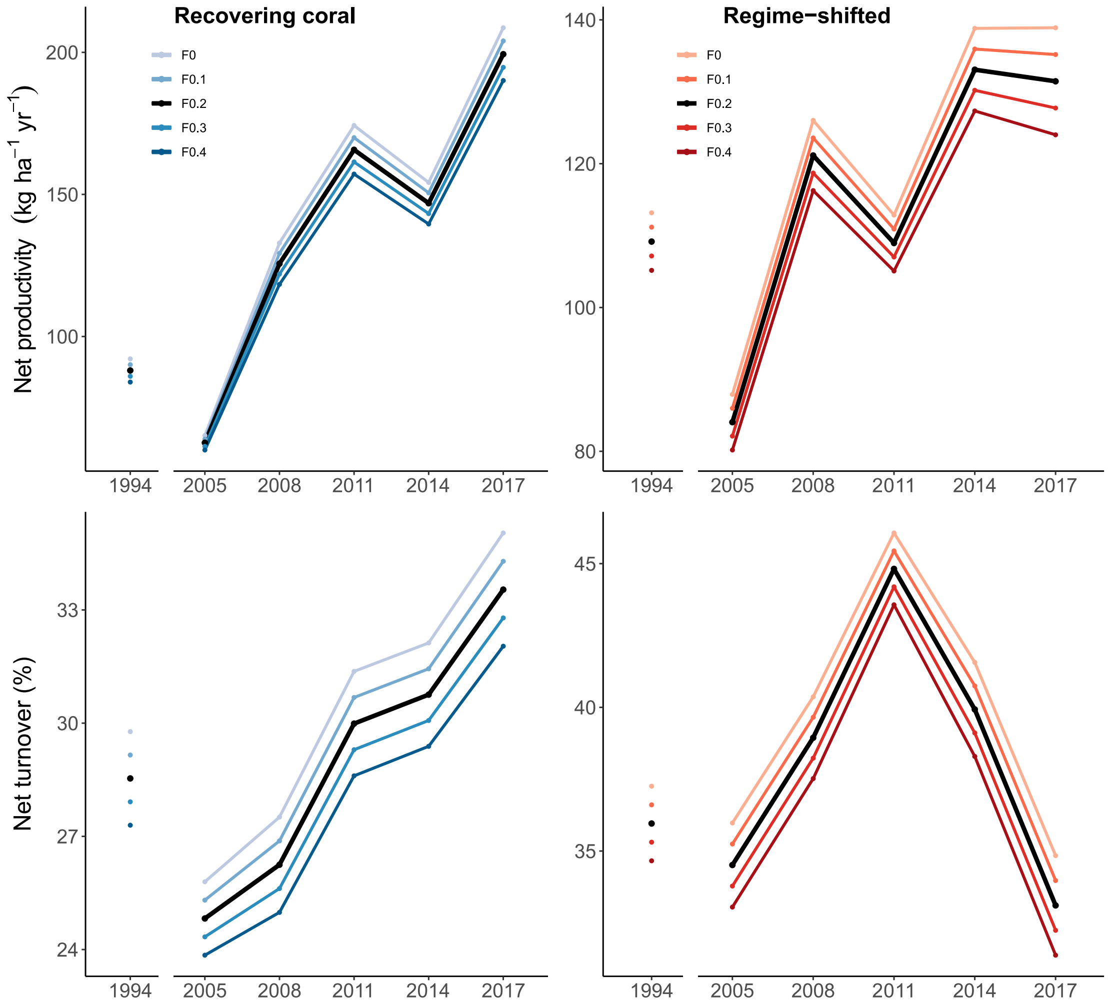

Figure S1.3: Effect of differing fisheries capture rates on whole fish assemblage net productivity (top) and net turnover (bottom) on fished reefs. Recovering coral reefs are shown on the left and regime-shifted reefs on the right (note the differences in y-axis scales between reef states). Estimates at a fishing capture rate of 0.2 are shown as thick black lines and are used throughout the main text of Chapter 1. It should be noted that when calculating net turnover (net productivity divided by standing biomass), productivity estimates changed between capture rates while biomass estimates remained the same. Breaks in the x-axes represent an eleven-year gap between surveys, during which the 1998 coral bleaching event occurred.

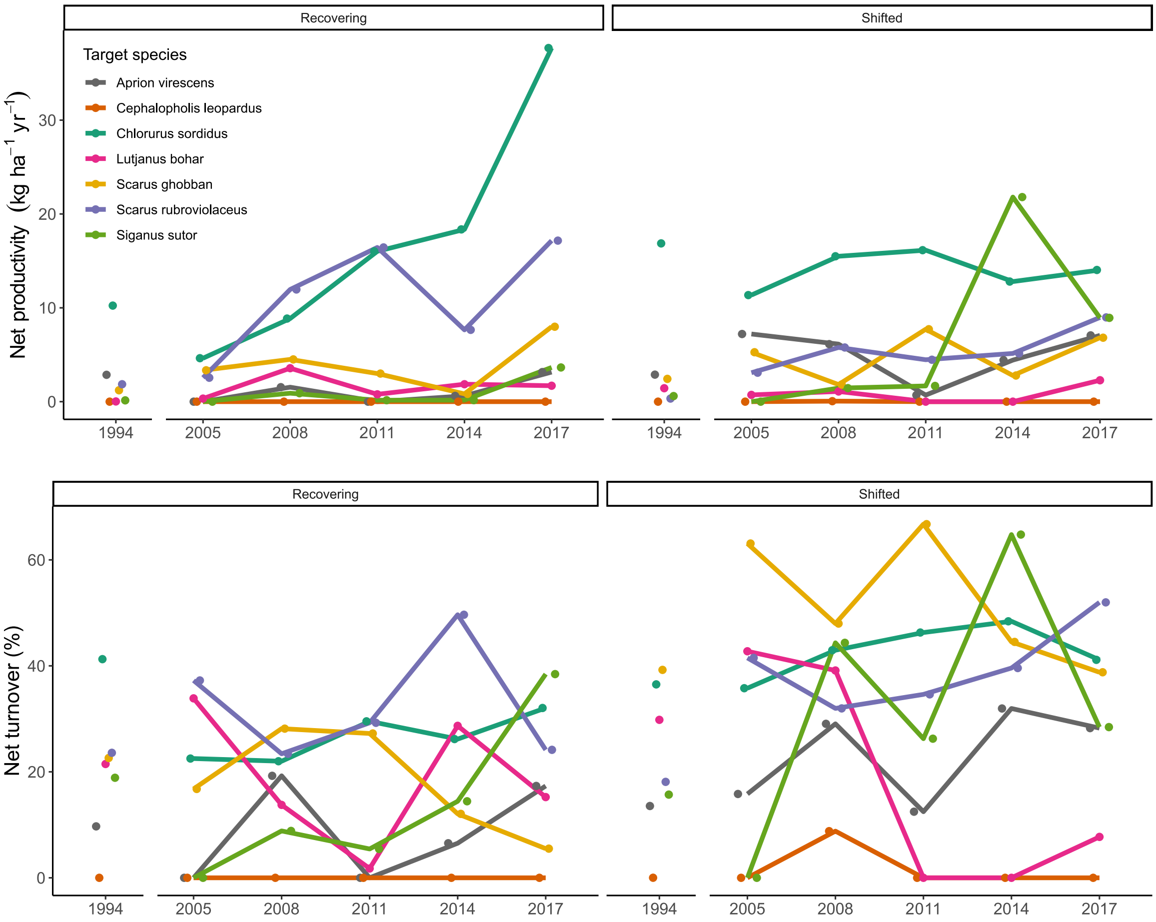

Figure S1.4: Mean net productivity (top) and net turnover (bottom) for primary trap fishery target species on recovering coral (left) and regime-shifted (right) reefs following coral bleaching in 1998. 1994 points are pre-bleaching estimates. Breaks in the x-axes represent an eleven-year gap between surveys, during which the 1998 coral bleaching event occurred. A second bleaching event occurred in 2016.

Table S1.2: Generalised linear model (GLM) results for fish assemblage biomass, net productivity, and net turnover estimates between fished reefs and reefs within protected marine reserves in 1994. Responses (biomass, productivity, and turnover) were all log-transformed.

	Effect size	Standard error	*t*-value	*p*-value
Biomass				
Intercept	5.63	0.05	119.27	<0.001
Marine reserve	0.55	0.07	7.68	<0.001
Productivity				
Intercept	4.48	0.05	93.68	<0.001
Marine reserve	0.44	0.07	6.03	<0.001
Turnover				
Intercept	0.28	0.01	42.04	<0.001
Marine reserve	-0.03	0.01	-2.94	0.004

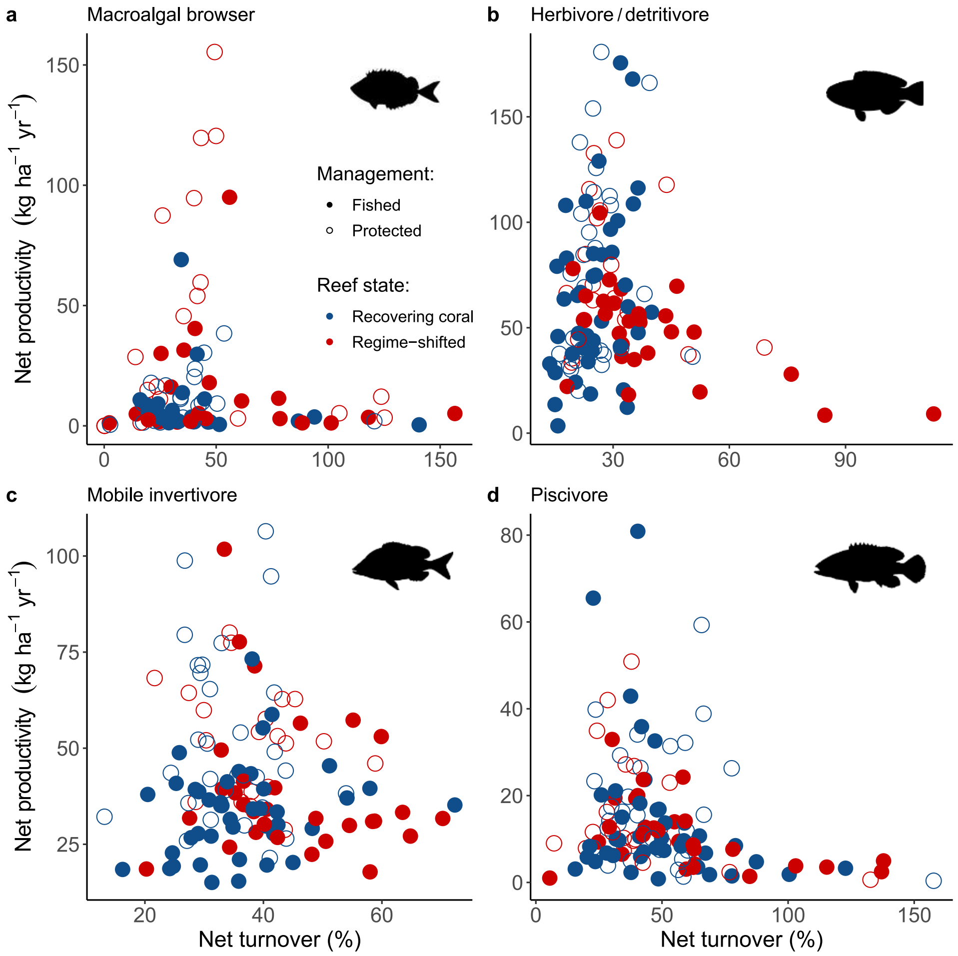

Figure S1.5: Net productivity plotted against net turnover using site-level values across all survey years for macroalgal browsers (**a**), herbivore/detritivores (**b**), mobile invertivores (**c**), and piscivores (**d**) on recovering coral (blue) and regime-shifted (red) reefs. Filled circles are fished sites, open circles are protected sites within marine reserves. Note that axes scales differ between trophic groups. Fish silhouettes are from the *fishualize* R package (Schiettekatte et al., 2019).

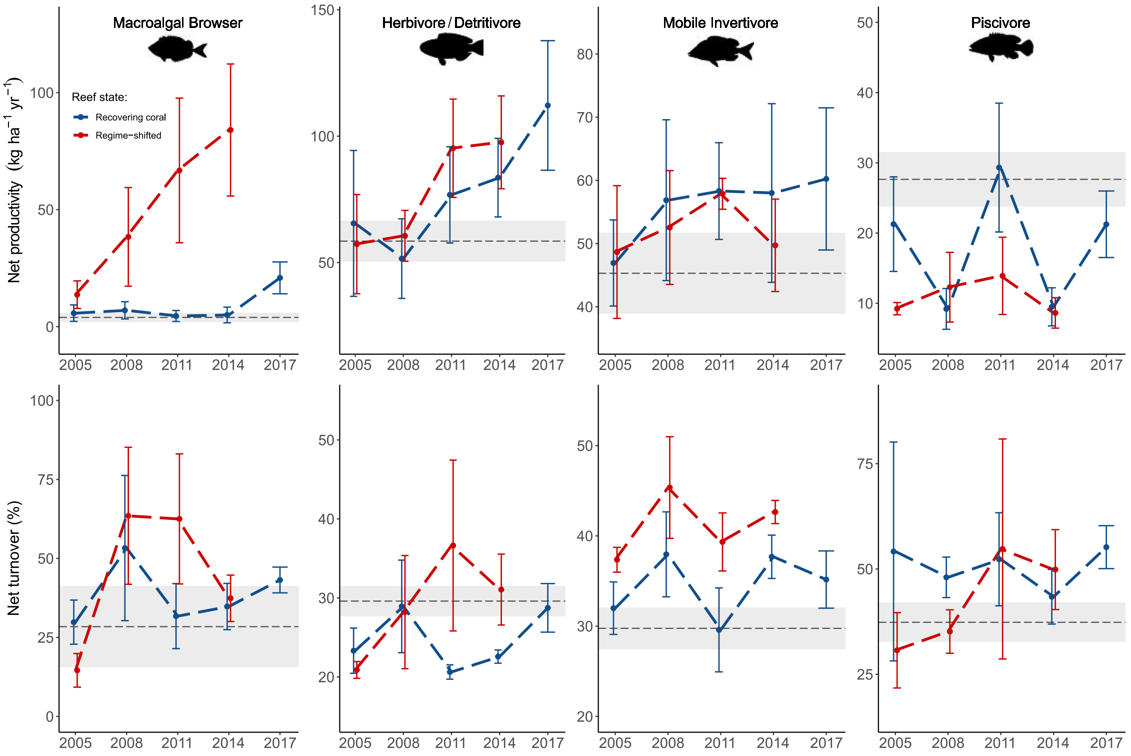

Figure S1.6: Mean net productivity (top) and net turnover (bottom) for selected fish diet groups on reefs protected from fishing following recovering (blue) and regime-shifted (red) trajectories after a major coral bleaching event in 1998. Error bars represent ±1 standard error of the mean across all reef locations surveyed each year. Pre-bleaching estimates are shown as grey horizontal lines (with shading for ±1 standard error of the mean). Protected regime-shifted reefs are not presented for 2017 as three of four reef locations were not sampled. Note that y-axis scales differ between diet groups. Fish silhouettes are from the *fishualize* R package (Schiettekatte et al., 2019).

Table S1.3: Generalised linear mixed model (GLMM) results for four trophic groups of reef fish. Reef site and survey year were included as random intercepts in each model (given by Equation 4).

	Macroalgal browser			**Herbivore/detritivore**			**Mobile invertivore**			**Piscivore**		
	Estimate	Standard error	*t*	Estimate	Standard error	*t*	Estimate	Standard error	*t*	Estimate	Standard error	*t*
Intercept	1.19	0.29	4.07	3.88	0.22	17.94	3.57	0.10	37.16	2.23	0.15	15.02
Structural complexity	0.68	0.16	4.35	0.11	0.09	1.31	0.05	0.05	0.94	0.32	0.11	2.83
Depth	-0.24	0.13	-1.84	0.01	0.08	0.08	-0.04	0.04	-1.02	0.06	0.09	0.68
Live coral cover	-0.48	0.18	-2.71	0.03	0.09	0.37	0.05	0.06	0.90	0.03	0.13	0.22
Dead coral cover	0.07	0.12	0.63	0.10	0.06	1.81	0.05	0.04	1.15	0.19	0.10	2.02
Macroalgae cover	0.68	0.15	4.48	-0.06	0.08	-0.70	0.02	0.05	0.30	0.01	0.11	0.09
Management (protected)	0.59	0.27	2.18	0.30	0.21	1.45	0.35	0.09	3.76	0.24	0.18	1.39
Habitat (granite)	0.70	0.30	2.32	0.28	0.23	1.23	0.12	0.10	1.17	0.22	0.20	1.08

Chapter 2 supplementary material

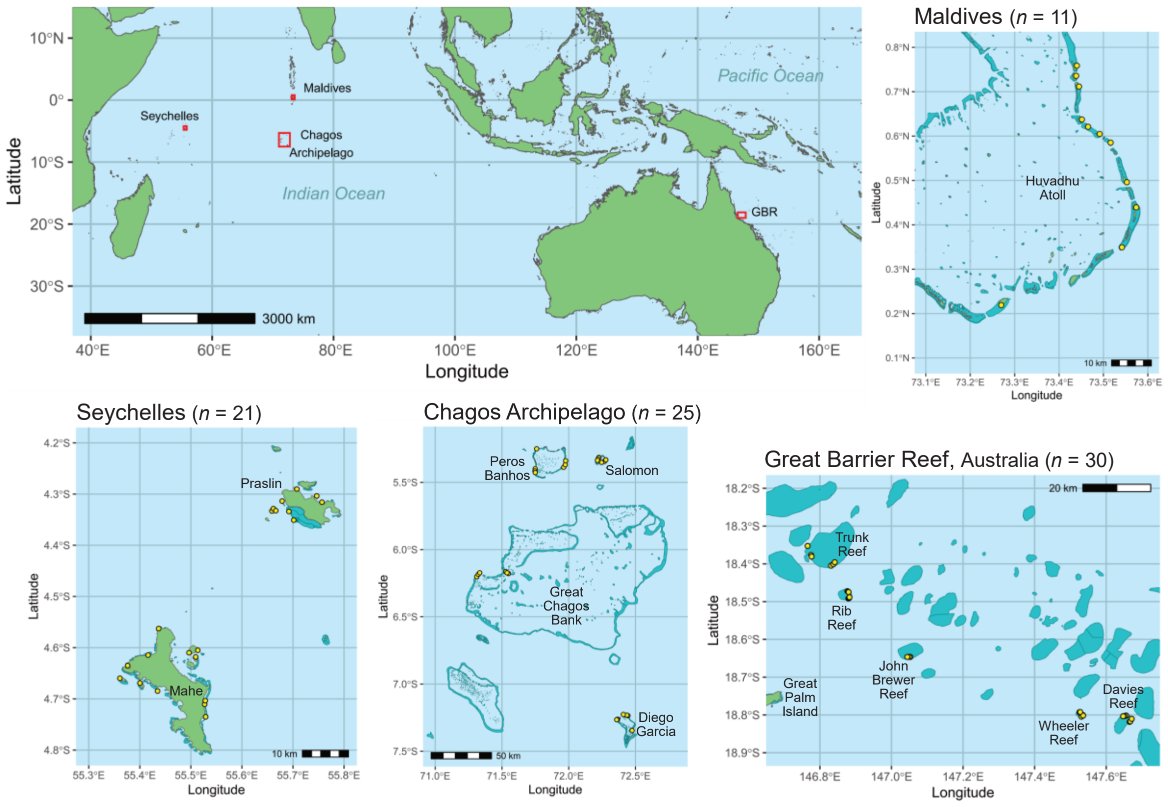

Figure S2.1: Map of study locations across the Indo-Pacific (top left). Reef sites within each study location where underwater visual surveys took place are shown as yellow points: Maldives (top right), Seychelles (bottom left), Chagos Archipelago (bottom middle), Great Barrier Reef (bottom right). Note latitude and longitude scales differ between panels.

Table S2.1: Summary of reef site details across four study locations. Human gravity estimates were obtained from Cinner and Maire (2018).

	Chagos	GBR	Maldives	Seychelles
Total reef sites	25	30	11	21
Fished	0	6	11	12
Unfished	25	24	0	9
Recovering coral, after coral bleaching	25	30	11	12
Regime shift to macroalgae	N/A	N/A	N/A	9
Human gravity				
Mean (std. deviation)	0 (0)	3.1 (0.6)	9.4 (3.0)	442.1 (601.2)
Minimum	0	2.4	5.2	32.5
Maximum	0	4.0	13.8	2111.7

Table S2.2: Families of reef fish per trophic group included in our study from underwater visual surveys in the Chagos Archipelago, the Great Barrier Reef, Maldives, and Seychelles. The number of species within each family is given in brackets. All species in the Pomacentridae family (*n* = 17) were omitted from the herbivore/detritivore group to prevent high abundances of non-fisheries targets skewing productivity estimates.

Herbivore/detritivore	**Macroalgal browser**	**Mobile invertivore**	**Piscivore**
Acanthuridae (*n* = 17)	Acanthuridae (*n* = 6)	Apogonidae (*n* = 2)	Bleniidae (*n* = 2)
Balistidae (*n* = 1)	Ephippidae (*n* = 2)	Balistidae (*n* = 6)	Carangidae (*n* = 7)
Pomacanthidae (*n* = 2)	Kyphosidae (*n* = 1)	Chaetodontidae (*n* = 6)	Cirrhitidae (*n* = 2)
Scarinae (*n* = 32)	Scarinae (*n* = 1)	Cirrhitidae (*n* = 2)	Epinephelidae (*n* = 26)
Siganidae (*n* = 6)	Siganidae (*n* = 2)	Epinephelidae (*n* = 3)	Labridae (*n* = 3)
		Haemulidae (*n* = 8)	Lethrinidae (*n* = 3)
		Holocentridae (*n* = 3)	Lutjanidae (*n* = 9)
		Labridae (*n* = 46)	Mullidae (*n* = 1)
		Lethrinidae (*n* = 9)	Muraenidae (*n* = 1)
		Lutjanidae (*n* = 4)	Scombridae (*n* = 1)
		Mullidae (*n* = 8)	Sphyraenidae (*n* = 1)
		Nemipteridae (*n* = 3)	Synodontidae (*n* = 1)
		Pempheridae (*n* = 1)	
		Pinguipedidae (*n* = 2)	
		Tetraodontidae (*n* = 4)	

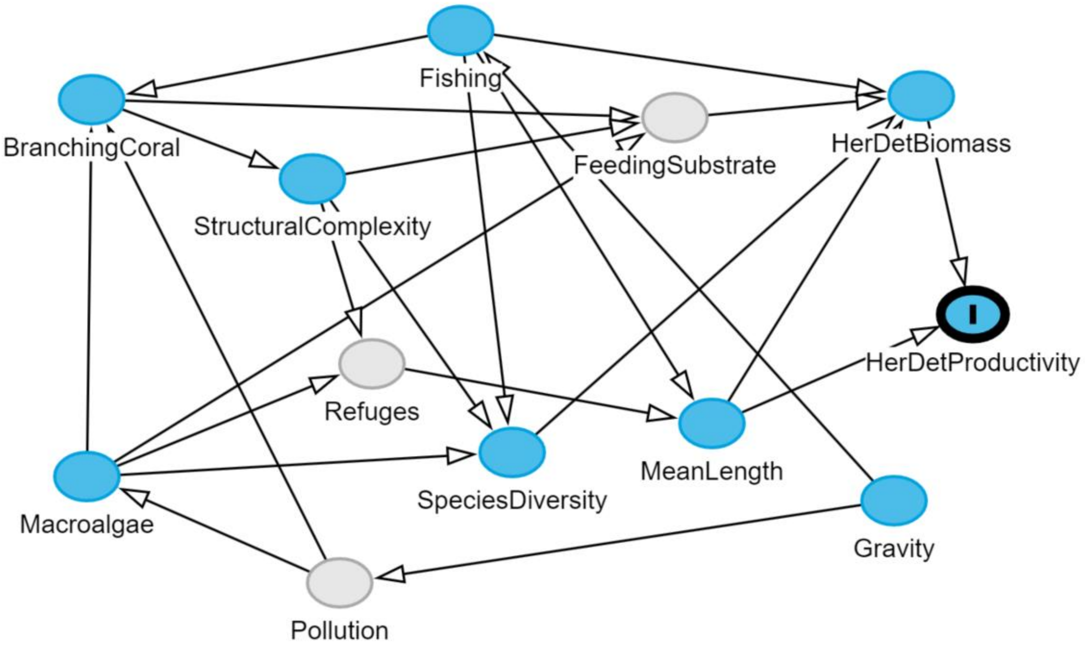

Figure S2.2: Directed acyclic graph (DAG), representing the causal relationships between variables used in analyses for the herbivore/detritivore trophic group. Biomass productivity ("HerDetProductivity") was the response variable in each model, outlined in bold. Unmeasured variables that were contextually important are shown in grey. Justifications for causal relations are given in Table S2.3. Made with DAGitty (Textor et al., 2016).

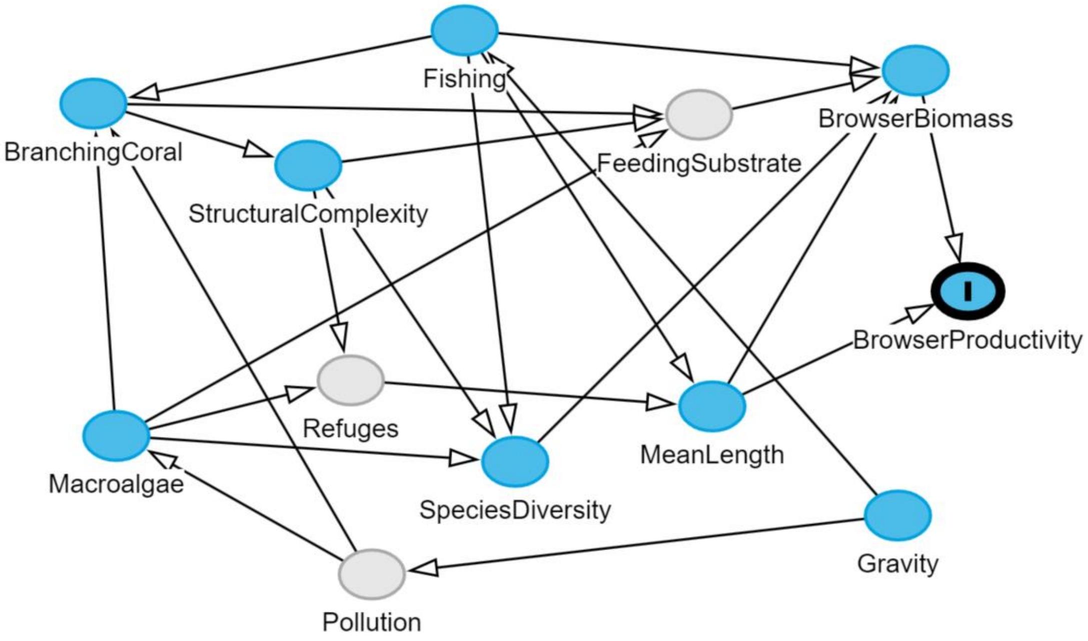

Figure S2.3: Directed acyclic graph (DAG), representing the causal relationships between variables used in analyses for the macroalgal browser trophic group. Biomass productivity (“BrowserProductivity”) was the response variable in each model, outlined in bold. Unmeasured variables that were contextually important are shown in grey. Justifications for causal relations are given in Table S2.3. Made with DAGitty (Textor et al., 2016).

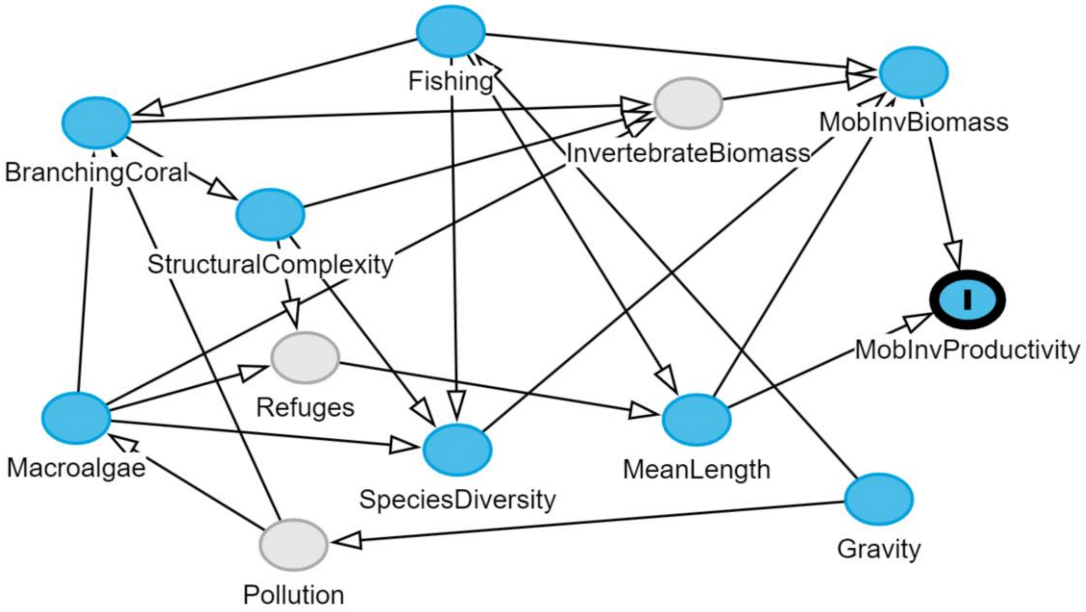

Figure S2.4: Directed acyclic graph (DAG), representing the causal relationships between variables used in analyses for the mobile invertivore trophic group. Biomass productivity (“MobInvProductivity”) was the response variable in each model, outlined in bold. Unmeasured variables that were contextually important are shown in grey. Justifications for causal relations are given in Table S2.3. Made with DAGitty (Textor et al., 2016).

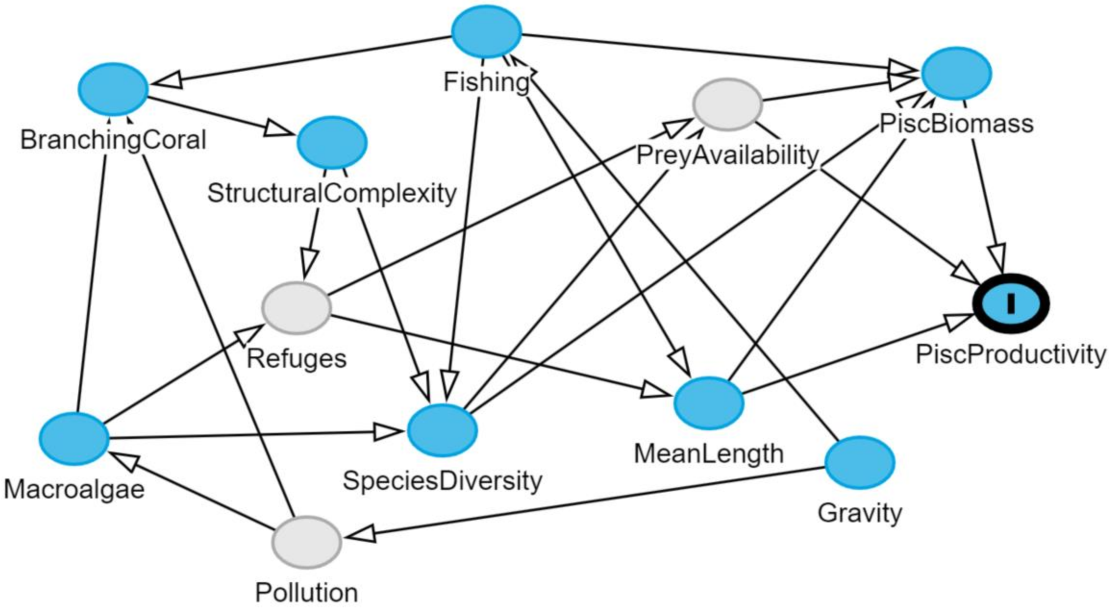

Figure S2.5: Directed acyclic graph (DAG), representing the causal relationships between variables used in analyses for the piscivore trophic group. Biomass productivity ("PiscProductivity") was the response variable in each model, outlined in bold. Unmeasured variables that were contextually important are shown in grey. Justifications for causal relations are given in Table S2.3. Made with DAGitty (Textor et al., 2016).

Table S2.3: Justification of causal relationships between variables included in directed acyclic graphs (DAGs). Relationships specific to particular trophic groups are included at the bottom of the table.

Direction of effect	**Proposed relationship**	**References**
Structural complexity → Refuges	Reef complexity influences the density of prey refugia.	Rogers et al. (2014)
Structural complexity → Species diversity	Reef complexity had a positive effect on the species richness of reef fish.	Darling et al. (2017)
Branching coral → Structural complexity	Branching coral cover was positively correlated with reef structural complexity, more so than total live coral cover.	Graham & Nash (2013)
Macroalgae → Branching coral	Macroalgal overgrowth has an influence on coral growth rates (both increase in cover and individual colonies). Macroalgal overgrowth can reduce the health, recruitment, and survival of hard corals.	Tanner (1995) Ceccarelli et al. (2018)
Macroalgae → Refuges	Macroalgae habitats act as nursery grounds for several families of reef-associated fishes due to refuges provided by algal canopies.	James & Whitfield (2023)
Macroalgae → Species diversity	Reefs with higher macroalgal cover were associated with reduced diversity of reef fish species.	Chong-Seng et al. (2012)
Refuges → Mean fish length	Larger fish are less sensitive to reductions in reef structure and loss of live coral cover.	Pratchett et al. (2014)
Pollution → Macroalgae	Nutrient pollution that leads to nitrogen and phosphorus enrichment on coral reefs can enhance macroalgal growth.	Zhao et al. (2021)
Pollution → Branching coral	Increased nutrient pollution on reefs hinders calcification rates of hard corals and can lead to dissolution and erosion of carbonate reef structures.	Silbiger et al. (2018)
Human gravity → Pollution	Local pressures on coral reefs, such as wastewater pollution and nutrient runoff, are elevated close to large human populations.	Burke et al. (2011)
Human gravity → Fishing	Human gravity incorporates human population sizes and the travel time in relation to coral reef locations, with higher gravity sites theoretically more accessible to fisheries.	Cinner et al. (2018)
Species diversity → Fish biomass	Biodiversity was a positive predictor of tropical fish biomass, and across multiple trophic groups.	Duffy et al. (2016)
Mean fish length → Biomass productivity	Productivity estimates are based on fish lengths, with species of different sizes differing in their growth coefficients.	Morais & Bellwood (2020)
Mean fish length → Fish biomass	Larger fish lengths result in larger biomass estimates, following Equation 2.	Froese (2006)
Fish biomass → Biomass productivity	Productivity (i.e. the production of somatic biomass) estimates are largely dependent on the existing fish biomass on the reef.	Morais & Bellwood (2020)
Fishing → Fish biomass	Marine protected areas with fishing bans had higher fish biomass.	Strain et al. (2019)
Fishing → Branching coral	Coral cover and recovery was higher in marine protected areas with no fishing.	Wilson et al. (2012)

Fishing → Mean fish length	Mean length of targeted reef fishes was lower at sites with higher fishing intensity.	Pet-Soede et al. (2001)
Fishing → Species diversity	Negative relationship between reef fish species diversity and fishing pressure.	Jennings et al. (1995)
Herbivore/detritivore; Macroalgal browser		
Structural complexity → Feeding substrate	Structural complexity determines the spatial patterns of fish herbivory. Feeding rates of scraping parrotfish were higher on more complex reefs.	Vergés et al. (2011) Robinson et al. (2020a)
Branching coral → Feeding substrate	Feeding rates of herbivorous fishes were lower in habitats dominated by branching corals. The feeding habits of herbivores such as parrotfish change in relation to live coral cover.	Bennett et al. (2010) Nash et al. (2012)
Macroalgae → Feeding substrate	Browsing herbivores feed on macroalgae and have specific physiological adaptations allowing them to target algal resources. Grazing and browsing herbivores avoided very dense macroalgal growth, and preferred feeding where macroalgal density was low.	Choat et al. (2004) Hoey & Bellwood (2011)
Mobile invertivore		
Branching coral → Invertebrate biomass	Higher abundance and productivity of invertebrates on dead coral compared to live coral.	Fraser et al. (2021)
Structural complexity → Invertebrate biomass	As reef structure degrades into rubble, many invertebrate taxa become more abundant and more productive.	Wolfe et al. (2021)
Macroalgae → Invertebrate biomass	Macroalgae habitats have higher invertebrate abundance and biomass compared to other tropical coastal habitats.	Tano et al. (2016)
Piscivore		
Refuges → Prey availability	As refuges from predation increase, reef habitats become more favourable for prey species and prey become more abundant.	Rogers et al. (2018b)
Prey availability → Piscivore productivity	When prey is easily accessible to predatory fish, their productivity is high. When access to prey is limited (e.g. when refuge density is high), hunting efficiency and therefore productivity is reduced.	Rogers et al. (2018b)

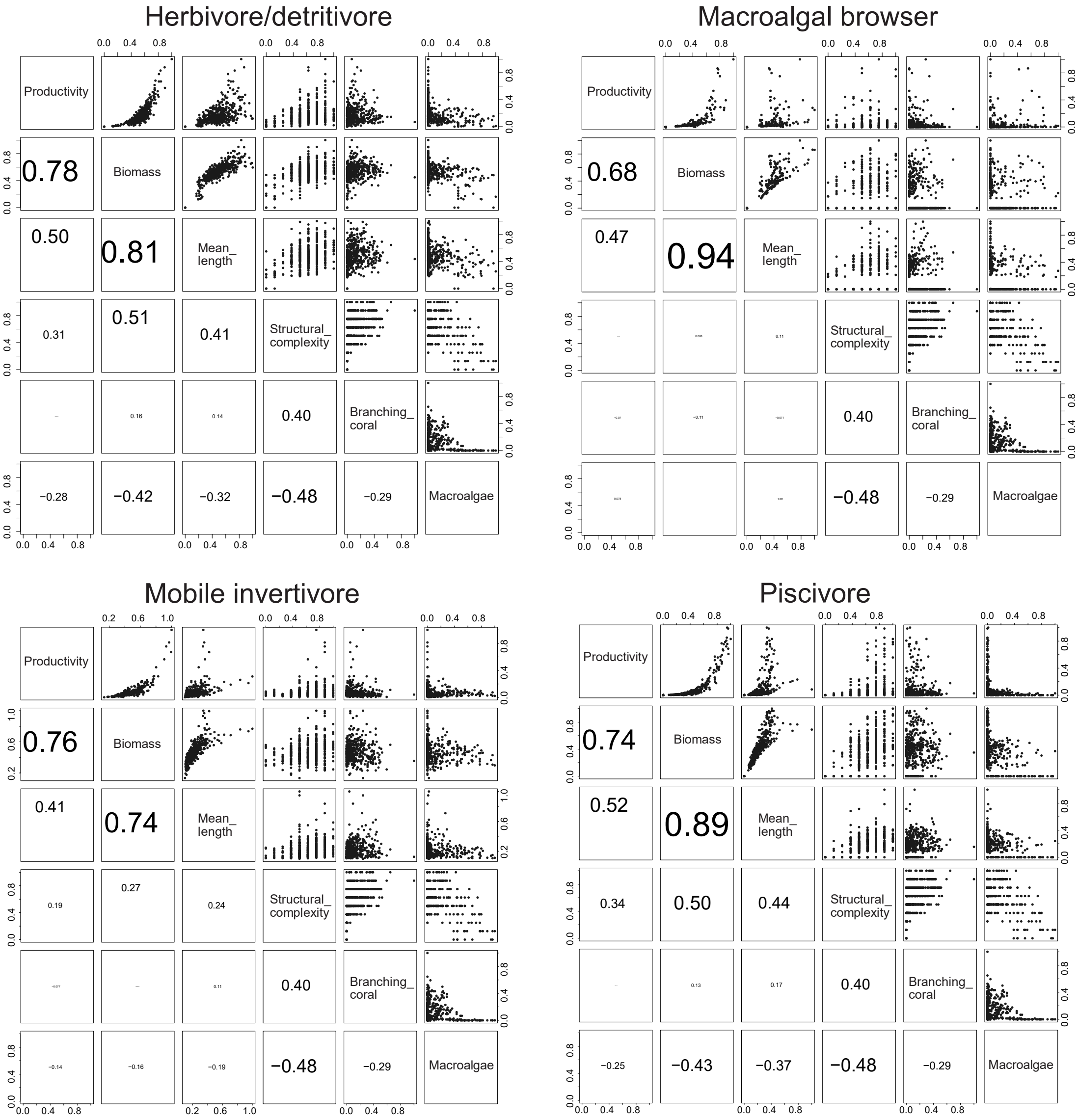

Figure S2.6: Pairs plots of continuous covariates used in causal models for each trophic group of reef fish. Covariate names are given along the diagonal with Pearson correlation coefficients shown in the bottom left half of each grid (font sizes are proportional to correlation values). All covariates were standardised (*x*/maximum(*x*)). Productivity was the response variable in all models.

Table S2.4: Predictors included as adjustments in each causal model depending on the predictor of interest, based on DAGs for each trophic group of reef fish (Figs S2.2-S2.5). Adjustments were the same across all trophic groups for all predictors of interest, except mean length which required no adjustments for piscivores.

Predictor of interest	**Predictors required as adjustments**
Structural complexity	Branching coral
Branching coral	Fishing; Macroalgae
Macroalgae	[*No adjustments required*]
Fishing	Human gravity
Mean length	Fishing; Macroalgae; Structural complexity; [*No adjustments required for piscivores*]
Species diversity	Fishing; Macroalgae; Structural complexity

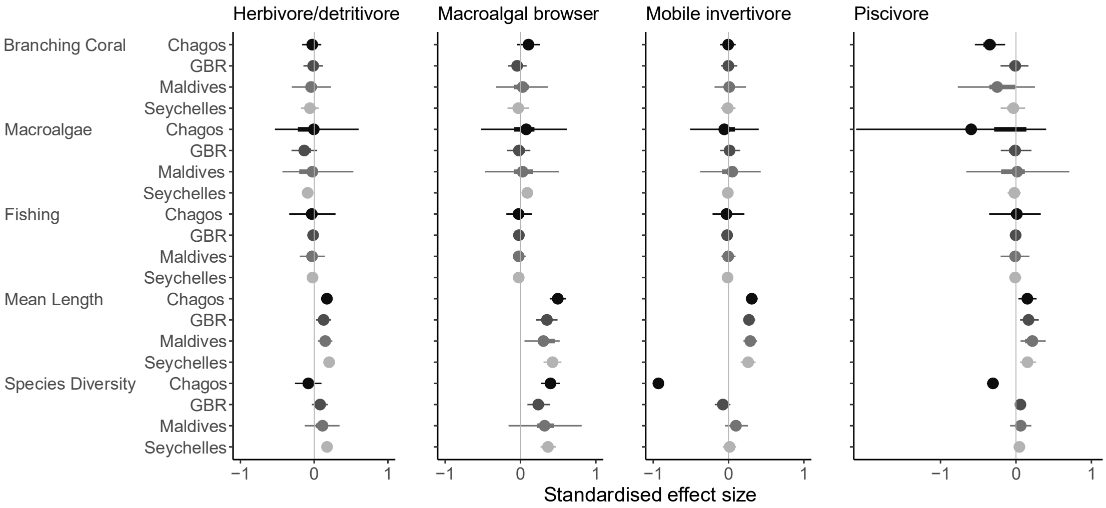

Figure S2.7: Location-level effect size estimates of covariates from hierarchical generalised linear mixed models (GLMM). Separate models were used for each covariate per trophic group of reef fish. Points are standardised effect sizes, with 50% (thick lines) and 90% (thin lines) highest posterior density intervals (HPDI). Note x-axis scale differs for piscivores due to wide HPDI for macroalgae in the Chagos Archipelago.

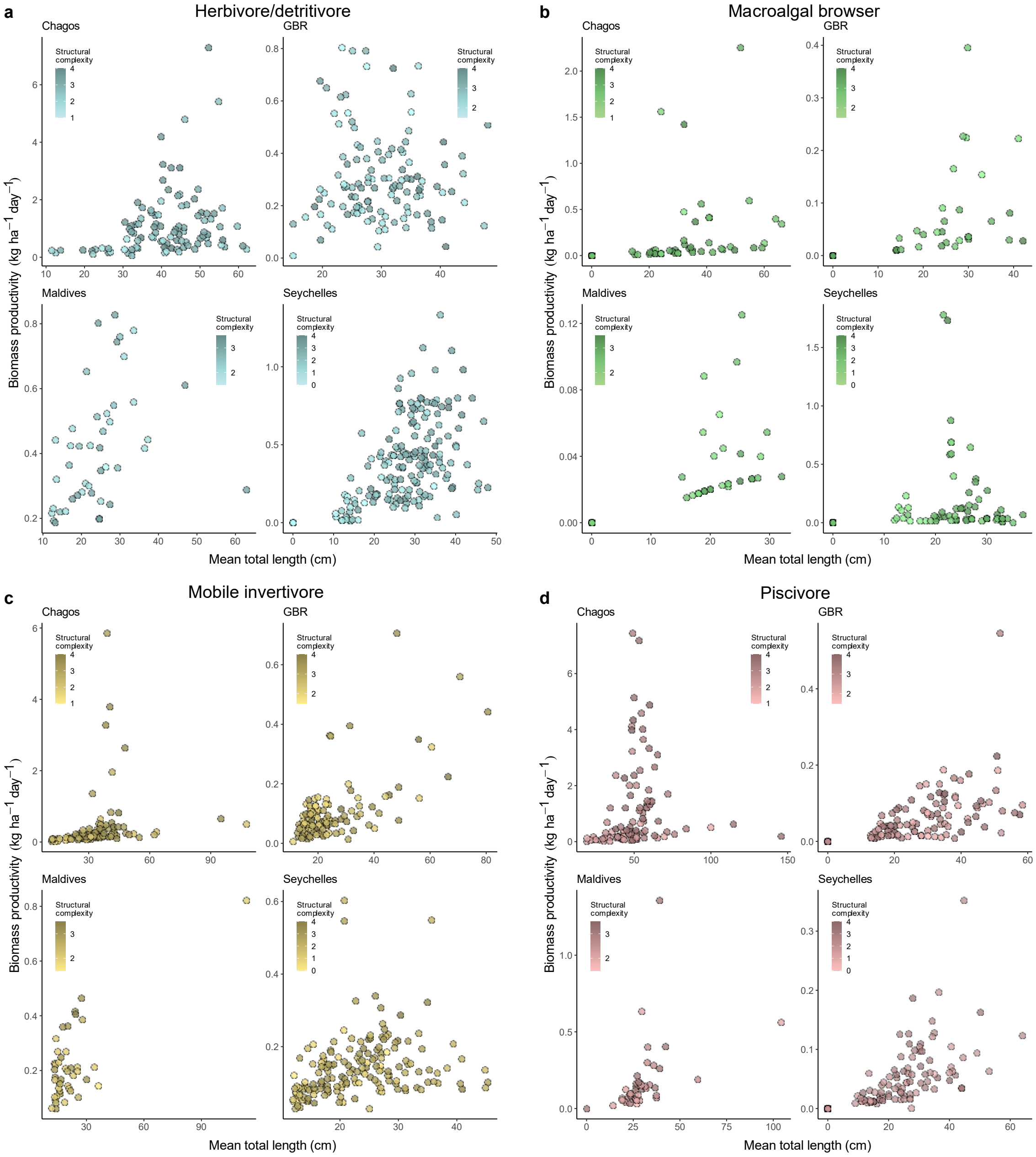

Figure S2.8: Mean total fish length against biomass productivity per transect across survey locations for herbivore/detritivores (**a**), macroalgal browsers (**b**), mobile invertivores (**c**), and piscivores (**d**). Points per transect are shaded by structural complexity estimates (darker points = more complex). Note x- and y-axes differ between trophic groups and locations; structural complexity ranges differ between locations.

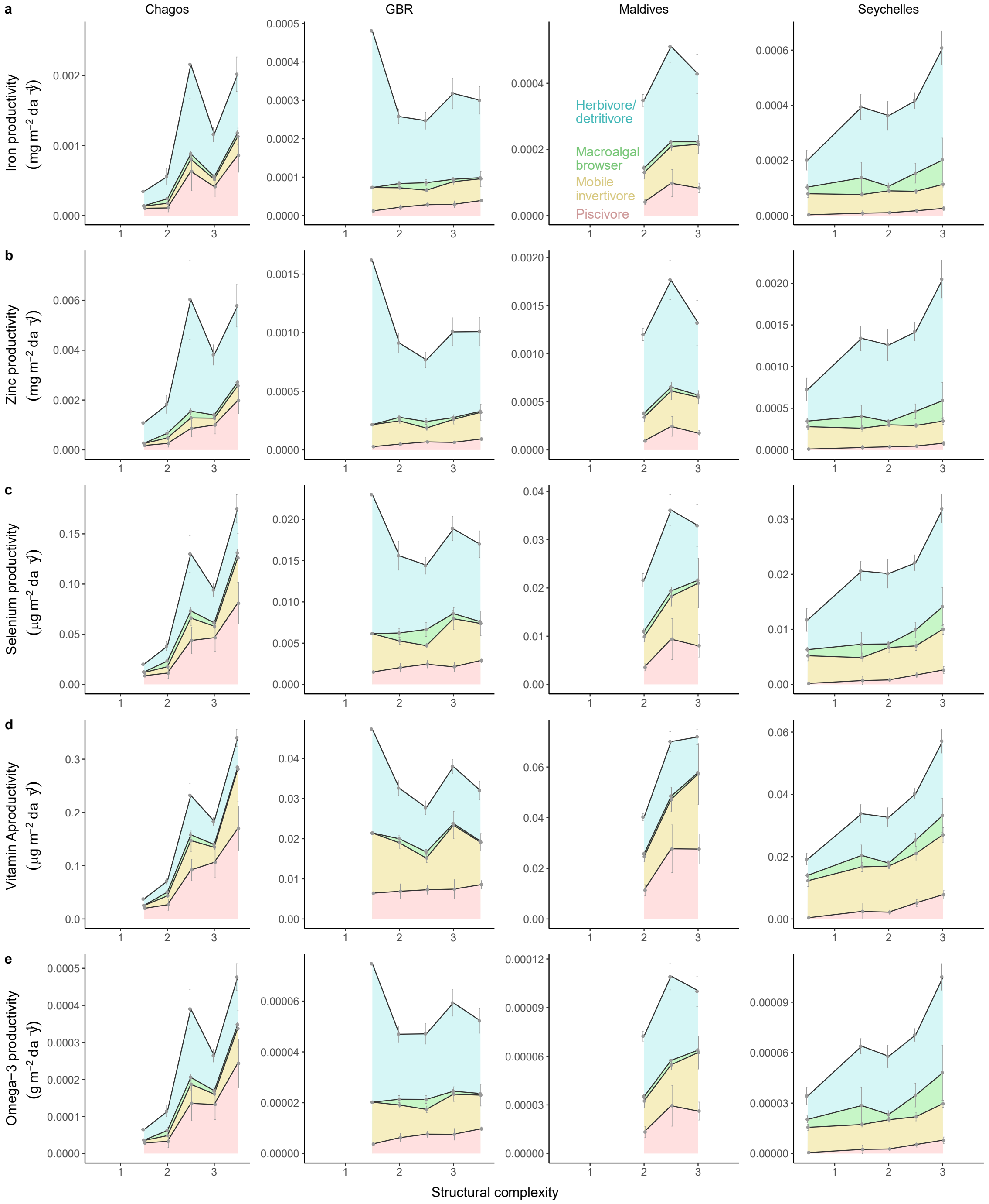

Figure S2.9: Nutrient productivity from reef fish across a reef structural complexity gradient, presented as the cumulative total separated by trophic group per location (columns) for five nutrients: iron (**a**), zinc (**b**), selenium (**c**), vitamin A (**d**), omega-3 fatty acids (**e**). Values are means across reef sites with the same structural complexity score (rounded to the closest 0.5) ± standard error of the mean. Note y-axis scales and structural complexity ranges differ between locations.

Chapter 3 supplementary material

Questionnaire

All information given will be treated in complete confidentiality. No individuals will ever be identified in any material published by Lancaster University or Seychelles Fishing Authority as a result of this survey nor will any of the data obtained be passed on to any other party.

LOCATION OF SURVEY: .... DATE: .... QUESTIONNAIRE #:.........

START TIME: …………………. END TIME: ……………………

Q.1 a) How long have you fished on reefs in Seychelles? ....…...…… years
b) What is your age? ………………………. years
c) Is fishing your main source of income? Yes □ No □
d) Do you fish all year round? Yes □ No □ If not, when?...

e) In a typical week, how many fishing trips do you do? ………………………………
f) How long is a typical fishing trip? ……………………………………………….
g) Do you fish with a crew? If yes, how many? ……………………………………..

Q.2) Could you please give some details about your boat:

a) Length? .... m / feet **b)** Type? (e.g. Mini-Mahe) …………………….
c) Power? .... kW / HP (ask units) outboard / inboard

d) How far is your boat from where you live? …………………………………. (km/miles, or minutes travel)
e) Where do you keep your boat? ……………………………………………………………………

Q.3 a) What gear types are you using at the moment? (if traps, ask static or active)

1) kazye (bamboo)	☐	*2) kazye (metal)*	☐	*3) other*	☐
4) other ………………	☐	*5) other* ……………….	☐	*6) other* ……………….	☐

b) What kinds of bait do you use? (if applicable) ………………………………………………………………
c) What type of reefs/seabed do you fish with each gear type? Please give details of how this changes with season throughout the year.
Gear:
1________________________ …………………………………………………………………………
2________________________ …………………………………………………………………………
3________________________ …………………………………………………………………………

Q.4 a) How important is the seabed habitat for fishing, on a scale of 1 to 5?
Not important **1 2 3 4 5** Very important
b) Why is that? ……………………………………………………………………………………….
c) Have you ever noticed the reef environments changing during your time as a fisher? (not fish yet!)
Yes □ No □
d) If yes, how? ……………………………………………………………………………………...
e) What was the timescale? For example, when did it start? How long did it last? How quickly has it progressed?
…………………………………………………………………………………………………
f) What about after coral bleaching in 1998 and 2016? (if already mentioned, ask for more details)
…………………………………………………………………………………………………

Q.5) What are the main types of fish you catch? Start with the species you catch the most:

a) *Species*	b) *How much on a good day?*	c) *How much on average day?*	d) *How much does it sell for?*	e) *Actively target species?*	f) *Effort & Gear used*	g) *Fishing grounds/ Habitat/ Season*
1st : ………						
2nd : ………						
3rd : ………						
Others: ………						
………						
………						
………						

Q.6 a) Have you ever noticed any changes in your catches of each species? When did you notice this happening? *(Please note if catches have improved/worsened, or become less predictable/more variable. Include amount caught, fish size, value, season)*

1st: ……………………………………………………………………………………………………

2nd: ……………………………………………………………………………………………………

3rd: ……………………………………………………………………………………………………

Others: ………………………………………………………………………………………………

………

b) Why do you think these changes happened? ……………………………………………………

………

………

c) Do you think these changes could be linked to the state of the reef/seabed? ………………………

………

Q.7 a) Are there any species you used to catch often that you no longer or rarely catch? Yes ☐ No ☐

b) Which species? And why do you think that is? ……………………………………………………

………

c) Do you think there is a time lag between changes in the reef environment and changes in fish catches?
Yes ☐ No ☐

d) If yes, how long? And for which species? ……………………………………………………

………

e) Are there differences between the fish species you catch now and the general demand for fish at markets?
Yes ☐ No ☐

f) If yes, does this lead to a lot of waste from your catch? How much and how do you deal with this?

………

Q.8 a) What proportion of your fishing time do you think is spent on each type of habitat that you have mentioned? Why?

Habitat 1 ______________________

………

Habitat 2 ______________________

………

Habitat 3 ______________________

………

b) Are you willing to give the names of your fishing grounds and the habitat types there? We are more interested in the kind of seabed there, rather than exact locations

Name	Habitats
___________________________________	……………………………………………………….
___________________________________	……………………………………………………….

c) Are there areas you fish where you do not know the type of seabed? Yes ☐ No ☐

d) Do you fish these areas based on good catches you have had previously? Please give details of species/gear types/season ……………………………………………………………………………

……

e) Are there any types of fishing grounds/habitats you used to fish on, but no longer do? Yes ☐ No ☐

f) If yes, which grounds and why? ……………………………………………………………………

……………………………..……………………………………………………………………………

g) Are there any fishing grounds where you spend longer fishing than you used to, to get the same amount of fish? Where? Please give details of species /seasons /habitat change.

……

……

h) What about the opposite: grounds where you can spend less time to get the same amount of fish you used to?

……

…….

Q.9 a) Do you travel further than you used to while fishing? Yes ☐ No ☐

b) If yes, approximately how much further? ………………………………………………………………

c) Why is that necessary?…...……………………………………………………………………………

d) When did you make this change? ………………………………………………………………….

e) How does that affect any of the following:

Fishing time ……………………………………………………………………………….
Depth ……………………………………………………………………………………..
Sea conditions ..……………………………………………………………………………
Access to grounds ………………………………………………………………………….
Fishing difficulty ...…………………………………………………………………………
Risks to self …………...…………………………………………………………………
Risks to gear …………………...…………………………………………………………
Fuel ……………………………………………………………………………………………
Boat/engine maintenance …………………………………………………………………

Q.10 Have changes in reef environments ever caused you to change any of the following:
(Please give details for each)

a) Number of fishing gears (e.g. number of traps) Yes ☐ No ☐
b) Type of fishing gears Yes ☐ No ☐
c) Deployment of fishing gears (e.g. soak time) Yes ☐ No ☐

Q.11 a) Do you rely on technology while fishing? (e.g. fish finder/GPS) Yes ☐ No ☐

b) Which kinds, and when do you use them?

……………………………………………………………………………………………………….

c) Has this changed due to changes in reef habitats? Yes ☐ No ☐

d) If yes, how? *(please specify grounds/species)*

………………………………………………………………………………………………..

…………………………..………………………………………………………………………

Q.12 a) Have you had to develop new skills/expertise because of changing reef conditions? Yes ☐ No ☐

b) If yes, which skills and why?

……

……

Q.13 a) Have changes in the habitat conditions of your fishing grounds ever made you feel concerned as a fisher? Yes ☐ No ☐

b) In what way?

……

c) In general, do you think fish catches have: ☐ improved ☐ worsened ☐ stayed the same ☐ don't know ?
(*Prompt for timescales, e.g. may have worsened a while ago and then stayed the same for a long time*)
Comments:

………

………

d) Have fish packets/landings changed in any way? How? *(species composition)*

…………………………..………………………………………………………………………………

Q.14 a) Have you relocated your boat due to fishing conditions/fish catches? Yes ☐ No ☐

b) If yes, how far? ……………………………. (km/miles) (or in minutes travel time)
c) and why? ………………………………………………………………………………………

Q.15 a) Does information or catches from other fishers ever influence where or how you fish? Yes ☐ No ☐
b) If yes, how? If no, why not?
……

Q.16) Please comment if any of the following affect (or have ever affected) where and how you fish:
a) fish prices ..………………………………………………………………………………………
b) tourist industry ……………………………………………………………………………………..
c) holidays (Easter/Xmas) ……………………………………………………………………………..
d) COVID-19 ……………………………………………………………………………………………
e) marine protected areas ……………………………………………………………………...…….
f) other fishers …………………………………………………………………………………………
g) anything else (health, boat) ………………………………………………………………………

Looking forward…

Q.17 a) Do you think learning/improving the following skills would improve your fishing ability because of changes in reef habitats?: (please state why/why not)
Fishing gear/techniques: ……………………………………………………………………………
Navigation: ……………………………………………………………………………………………
Safety at sea: ..………………………………………………………………………………………
Boat handling: …………………………………………………………………………………………

b) Which skills (if any) would you be willing to invest time learning?
Fishing gear/techniques: ……………………………………………………………………………
Navigation: ……………………………………………………………………………………………
Safety at sea: ……………………………………………………………………………………..
Boat handling: …………………………………………………………………………………………

c) Which of the above skills would you consider the biggest priority to learn right now? Why?
……

Q.18 a) Have you ever considered stopping fishing for another career, or reducing the amount of fishing you do? Yes ☐ No ☐
b) If yes, why was this?
...……..……………………………………………………………………………………………………
c) (if not already mentioned) Did this have any link to the state of the habitats you fish? (Please give details of which reefs/habitats)
……
……

Q.19) Is there anything else you would like to add about changes in your fishing activity?
……

End of interview

- Thank you very much for taking part. Do you have any questions for us?
- If you wish to withdraw your data from the study, please let me know within 14 days (*give contact number/email*)

Reliability of interview - For interviewer to complete after interview.

Indicate to what degree you feel the respondent was reliable in answering the survey:
☐ reliable ☐ moderately reliable ☐ not very reliable

If answers were unreliable, explain why below and, if possible, state which questions:
……

Table S3.1: Quotes from fishers relating to perceptions of changing reef habitats or catches. Quotes are organised by topics and sub-topics on the left, with themes within each topic defined on the right. Note that quotes may be paraphrased due to translation from Kreol to English. Interview IDs containing "M" = Mahé, "P" = Praslin, "R" = fishers who had retired from trap fishing (but not necessarily all types of fishing). IDs are coded to contain information on habitat and catch perceptions (h = noticed reef habitat changes, c = noticed catch changes; when bold and linked with ">" (**h>c**) = catch changes due to habitat changes), and fisher responses (T = travelling further, G = increased number of traps, G = changed gear type, G = changed gear deployment).

Topic		**Quotes**	**Theme**	**Interview IDs**
Habitat				
Coral reef	***Degradation***			
	Coral bleaching	"Noticed coral bleaching in 2016 (M1)"; "Lots of rain this year – too much freshwater maybe caused bleaching? (M10)"; "When the water temperature is too hot, it causes coral bleaching (M11)"; "Sometimes coral dies. Sometimes the climate changes and changes the coral (M12)" "Coral goes slightly green first, then white (M16)"; "Coral was grey, now white (M18)"; "Bleaching happens every year, but it changes slowly over time. It is getting worse (M19)"; "Now, at some lobster fishing grounds, coral bleaching started about 6 months ago (P1)"; "There was coral bleaching about 5-6 years ago (P8R)"; "The coral started to change, usually when the water was hot (P10R)"; "the reefs have changed since the coral bleaching (P10R)";	Coral bleaching in 2016 was noticeable. There has also been more recent bleaching. High sea temperature is the main cause of bleaching.	M1_hc-T, M10_hc, M11_**h>c**-TG, M12_h-TG, M16_h, M18_**h>c**-TG, M19_hc-TG, P1_hc-GGG, P8R_h, P10R_hc-GG
	Other	"Tsunami in 2004 caused damage to the reef (M1)"; "Reclaimed land destroyed a granite reef (M2)"; "Reclaimed land changed the reef a lot and resulted in dead coral (M3)"; "doesn't fish outside the reef anymore because during spring tides, traps damage the reef (especially metal traps) (M3)"; "Waves break and kill corals in some seasons (M7)"; "Land reclamation caused coral to die. The inward side of the reclamation was worse (M8)"; "Desalination plant discharged chemicals into the sea - affects the reef. The main problem here is red soil washing into the sea and affecting corals (M9R)"; "Metal traps from other fishers are damaging the reefs (M9R)"; "Weather brings in sand which covers coral, then in the other season the sand goes back out and the coral grows better (M10)"; "used to fish where land was reclaimed (M11)"; "Sometimes corals are exposed at low tide (M12)"; "Land reclamation is a problem because it took away lots of reef area (M12)";	Land reclamation has destroyed reefs and sedimentation damages corals. Fishing practices damage corals (especially metal traps). Waves and currents can damage the reef (e.g. storms, tides, tsunami in 2004).	M1_hc-T, M2_h-T, M3_hc-TG, M7_hc-T, M8_hc-G, M9R_hc, M10_hc, M11_**h>c**-TG, M12_h-TG, M15_**h>c**-T, M16_h, M20_hc-TG, P1_hc-GGG, P3_h, P4_hc-G, P5R_hc,

Coral reef (continued)		“Reef was completely destroyed after the tsunami (M15)”; “Pumping sand when they deepened the seabed by a couple of metres killed coral. Also land reclamation (M16)”; “on usual fishing sites, coral breaks off every year due to bad weather in the SEM - attracts more fish (M20)”; “Some fishers break coral (P1)”; “Other fishers are damaging coral with their fish traps, which is concerning (P3)”; “In December, the tides are lower so coral dies each year, then recovers. The cycle repeats each year (P4)”; “The reef is different every day! Sometimes coral is broken, sometimes it’s white, sometimes there are no fish (P5R)”; “After the tsunami in 2004, the coral changed position. We marked coral locations with a GPS but the coral was gone after tsunami. The coral was very nice before but after, it was dead and white (P6)”; “I’ve noticed coral dying (P7)”; “Coral is dead – it happened about 2 months ago (P9)”; “Metal traps last longer - you can leave on the reef for 3-4 days but they can scrape against the reef in the swell. This kills coral polyps and damages the ecosystem (P10R)”;		P6_**h>c**-TGGG, P7_hc-G, P9_**h>c**-TGGG, P10R_hc-GG
	Recovery			
	Coral bleaching	“Quite fast recovery after bleaching (M1)”; “After bleaching in 2016, the whole reef took about one year to grow back. It is OK now (M3)”; “Coral can grow back in six months to a year (M4)”; “Takes about two years for the reef to recover from coral bleaching, sometimes more (M8)”; “Takes a long time to recover – years (M18)”; “Coral is growing perfectly now after coral bleaching five years ago (M21)”; “coral bleaching started about 6 months ago - already getting back to normal (P1)”; “1998 bleaching was different to 2016 bleaching. 2016 was quicker to recover than in 1998 (P1)”; “coral bleaching didn’t last long. Strong currents cleaned the corals and then it went back to normal, but it took some time (P8R)”; “After bleaching, it took 5-6 years until now for reefs to recover (P10R)”; “after coral bleaching 5-6 years ago, the coral is getting back to normal now. Some places are recovering better than others (P11)”	Recovery from bleaching was relatively fast (6 months to 6 years).	M1_hc-T, M3_hc-TG, M4_**h>c**-TG, M8_hc-G, M18_**h>c**-TG, M21_**h>c**-T, P1_hc-GGG, P8R_h, P10R_hc-G, P11_hc-T
	Other	“When there is no construction, not many problems, but when it starts, it can take 3-5 years for the reef to recover (M9R)”; “recovers in 2-3 months (M12)”; “Has seen corals growing at reef restoration sites (M15)”;	Coral recovery can be within months to multiple years, depending on cause.	M9R_hc, M12_h-TG, M15_**h>c**-T, M16_h,

Coral reef (continued)		“Coral took about two years to recover from sand from human activities (M16)”; “After breaking in the SEM, it recovers bit by bit until the next year (M20)”; “The seabed changes between coral and seaweed every 6 months over the monsoon season – damage then regrowth (P3)”; “Corals have gotten bigger (P4)”; “After the tsunami, it took a long time for coral to recover, but can’t remember (P6)”; “Some places recovered after the coral died 2 months ago, some places are still dead (P9)”		M20_hc-TG, P3_h, P4_hc-G, P6_**h>c**-TGGG, P9_**h>c**-TGGG
Macroalgae/ seagrass	***Degradation***	“Spaghetti-like seagrass reduced in density in the last 3-4 years, especially in August/SE monsoon (M1)”; “Water motion churns up algae with the changing seasons (M1)”; “Land reclamation caused seaweed to die (M8)”; “After heavy rains, seaweed dies - source of bait and fishing grounds are affected (M8)”; “Desalination plant discharged chemicals into the sea - kills seaweed and fish don’t have anything to eat (M9R)”; “sometimes seaweed gets ripped out (M12)”; “the tsunami killed seagrass (removed the roots) (M16)”; “on usual fishing sites, seaweed breaks off every year due to bad weather in the SEM - attracts more fish (M20)”; “The sand has covered seaweed, seagrass and lanmous - not able to set traps there anymore (M22)”; “the seaweed is disappearing. This is very concerning as there is a lack of habitat for fish (M23)”; “Seaweed has gotten thinner, and is different now. This happens every December (P4)”; “Long sea grass kills seaweed, and then there are fewer fish (P7)”; “sometimes concerned about sand erosion or lack of algae (P11)”	Bad weather and sea conditions damage macroalgae/seagrass, generally associated with seasons. Other human and ecological factors can affect macroalgae/seagrass habitats.	M1_hc-T, M8_hc-G, M9R_hc, M12_h-TG, M16_h, M20_hc-TG, M22, M23_hc-TG, P4_hc-G, P7_hc-G, P11_hc-T
	Recovery/ growth	“Algal blooms can be up and down (M4)”; “recovers in 2-3 months (M12)”; “After breaking in the SEM, it recovers bit by bit until the next year (M20)”; “After 2016 bleaching there was an algae bloom (M20)”; “algae bloom on seabed happened 2-3 years ago. It is still happening now (P1)”; “there was an algae bloom after coral bleaching about 5 or 6 years ago (P8R)”	Algae blooms (benthic macroalgae) tend to follow coral bleaching.	M4_**h>c**-TG, M12_h-TG, M20_hc-TG, P1_hc-GGG, P8R_h
Other		“Too much construction, waste goes into sea (M8)”; “During southeast monsoon there is a major change along the coastline. There is a reduction of sand, rocks become visible across beaches (M13)” “There have been changes in the amount of sand accumulated on or near the reefs (M14)”; “Stop land reclamation everywhere. It destroys habitat and reduces the number of fish (M14)”; “Used to fish in an area that is now reclaimed land (M15)”; “the tsunami changed the tides for a long time (M16)”;	Land reclamation and sedimentation have impacted reef environments.	M8_hc-G, M13_hc-GG, M14_**h>c**-TGG, M15_**h>c**-T, M16_h, M22

Other (continued)		"There has been reclaimed land. The sand used to be a bit deeper - sand is going further offshore now (M22)"		
Fish				
Habitat	***Coral***	"coral bleaching probably caused a decrease in the amount of fish (M4)"; "[following reef degradation,] changes in fish are immediate. Fish move to feed on "live" reef (M4)"; "if the coral dies, fish move somewhere else, especially parrotfish (M4)"; "remembers there were fewer fish during coral bleaching (M5)"; "Sometimes on corals there are fish, sometimes not, e.g. if corals are clean, there is food for fish, but when sand comes in and covers the coral, fishing is bad. Depends on the weather (M9R)"; "Fish slowly went deeper after 2016 bleaching, little by little (M17)"; "there are fewer fish around corals now compared to three years ago (M19)"; "If coral breaks (e.g. because of anchors), it attracts a lot of parrotfish (P1)"; "If there is no coral, there are no fish (P2)"; "Fish stay where there is shelter and food. Fish swimming in schools move between coral areas (P6)"; "Fish were slightly deformed after coral bleaching in 2016 (P6)";	Fish depend on coral habitat. There were fewer fish on reefs during and after coral bleaching.	M4_**h>c**-TG, M5_**h>c**, M9R_hc, M17_hc, M19_hc-TG, P1_hc-GGG, P2_c-T, P6_**h>c**-TGGG
	Macroalgae/ sea grass	"Habitats provide nutrition for the fish, which helps to concentrate fish there. Fish eat the seaweed when it breaks (M20)"; "Reef fish were the worst affected by the algae bloom after 2016 coral bleaching, rather than bourgeois (M20)"; "Freshwater and saltwater mix and makes places different, e.g. longer sea grass, and changes the fish species. Not the ones I want to catch (P1)"; "Algae is a problem. When it blooms, there are no fish or octopus or anything (P6)"; "Algae blooms kill fish (P7)";	Fish feed on algae but are negatively affected by algal blooms.	M20_hc-TG, P1_hc-GGG, P6_**h>c**-TGGG, P7_hc-G
	Other/general	"There are too many carang [jacks] now (M7)"; "there are no mackerel in the SEM (M7)"; "fish inside the reef are smaller now than before (M7)"; "Sometimes see dead fish. The sea used to be richer [more fish] (M8)"; "Noise and oil released from people's boat engines affects fish (M9R)"; "When there is too much rain, there is nothing for fish to eat so they leave. Also when the temperature is too high (M10)"; "The moon has an effect on fish, e.g. low/high tide. Fish can be there on the grounds, but are not biting - another day they will (M10)"; "Tide is rising higher than before and when it does, you don't catch as many fish (M15)"; "There are fewer jacks this year. Everything else is stable (M17)"; "Fish feed people and they need habitats (M17)"; "Used to be more fish about 10 years ago, but less now because it is too hot (M18)"; "Have not noticed any species reducing in number. There are more wrasse now - don't catch them but seeing more of them when diving to see where to place traps (M22)"; "Last year there were almost no fish but starting to come back now (M23)";	Multiple environmental variables are impacting fish populations. Amounts of different types of reef and pelagic fish are variable.	M7_hc-T, M8_hc-G, M9R_hc, M10_hc, M15_h>c-T, M17_hc, M18_**h>c**-TG, M22, M23_hc-TG, P1_hc-GGG, P11_hc-T

Habitat (continued)		“I don’t see many sharks while diving anymore (P1)”; “There is some ghost fishing from other people’s lost traps (P1)”; “if the habitat is damaged, the fish won’t come (P11)”;		
Catch	***Rabbitfish***	“spawning is the best time to catch rabbitfish. From September-February, at full moon (M2)”; “can catch rabbitfish anywhere, all season (M3)”; “There are more rabbitfish at the full moon, and when they are spawning in October (M6R)”; “There are more in October/November when they are spawning. I catch more on algae reefs (M7)”; “In the NWM, they spawn at the full moon and catches are better. Can be caught everywhere (M8)”; “Only noticed a difference in rabbitfish catches – they have changed spawning grounds (M8)”; “From October onwards you get them near big rocks while spawning at the full moon. Spawning aggregations last 2-3 days, then they leave (M10)”; “You get more on seaweed. You get lots in the NWM but not in SEM (M11)”; “Landings have changed but it depends - you might get a lot of rabbitfish but sometimes not (M12)”; “I mainly catch rabbitfish on coral but also on seaweed. Catches are variable between coral and seaweed (M12)”; “best catches are in the vann swet [SEM] (M13)”; “Seaweed grows on traps and helps to catch rabbitfish (M16)”; “Can catch a lot of rabbitfish in a short time when they are spawning (M16)”; “they can be caught all year round (M16)”; “If there is no sea grass, then there are no rabbitfish (M18)”; “you get more in the NWM and where there is seagrass with rock (M18)”; “Rabbitfish are smaller now, but catch the same number (M19)”; “the best catches are after the full moon. I catch more where there is more seaweed (M19)”; “There are more rabbitfish on seaweed. The time depends, it varies whether I catch more in the SEM or NWM. August-October is best in the SEM, February-March is best in the NWM, when fish are spawning (M20)”; “Sometimes catches are better just before high tide (M21)”; “The best catches are when they are spawning in March/April. They like seaweed and very green areas (M22)”; “Rabbitfish are more scarce and smaller now (M23)”; “just before the full moon is best, on seaweed (M23)”; “Rabbitfish move a lot and catches are variable. They aggregate, but not always in the same place. Sometimes they are in smaller groups (P1)”; “Catches depend on the moon. The best catches are in November/December (NWM). Best on rock and seaweed (P1)”;	Rabbitfish catches are better when spawning at full (and new?) moon. Can be caught all year round, but best in NWM. Mostly caught in macroalgae habitats, except when spawning when they are caught on coral reefs. Rabbitfish yields have decreased. Possibly from reduced abundance, smaller size, or reduced catchability.	M2_h-T, M3_hc-TG, M6R_hc-TG, M7_hc-T, M8_hc-G, M10_hc, M11_**h>c**-TG, M12_h-TG, M13_hc-GG, M16_h, M18_**h>c**-TG, M19_hc-TG, M20_hc-TG, M21_**h>c**-T, M22, M23_hc-TG, P1_hc-GGG, P3_h, P4_hc-G, P5R_hc, P6_**h>c**-TGGG, P7_hc-G, P8R_h, P9_**h>c**-TGGG, P10R_hc-GG, P11_hc-T

Catch (continued)		“there are more rabbitfish on the reefs now, but I am catching the same amount as before (P3)”; “This year is different. Rabbitfish are not going in the traps so there are fewer packets to land (P3)”; “catches are best at full moon when they are spawning, on coral mainly (P3)”; “In October and March, I catch more rabbitfish (P4)”; “It is best to catch rabbitfish on seaweed when there is not full moon. At full moon, they go on coral (P4)”; “This year, rabbitfish are a little rarer than before, even during the spawning season (P5R)”; “rabbitfish maybe haven’t reduced in number, but I am catching fewer in traps (P5R)”; “Before, if you were only using one trap baited with papaya leaf, you got so many rabbitfish you didn’t know what to do with them. But not now (P6)”; “Before coral bleaching in 2016, rabbitfish catches were decreasing (P7)”; “I catch most inside the reef, on seaweed (P7)”; “I caught younger, smaller rabbitfish in March/April (P8R)”; “Higher catches in the NWM, rare in SEM (P8R)”; “When the water is too hot, you can’t even catch rabbitfish. Happens every year but it’s worse this year (P9)”; “The number of rabbitfish in catches is declining. Maybe they are moving somewhere else, maybe because of hot water and dead coral (P9)”; “catches are good at the new moon, outside the reef (not on the reef) (P9)”; “the best catches are at full moon and new moon on corals. At other times, on seaweed everywhere (P10R)”; “Rabbitfish catches are not good this year. No difference in any other species (P11)”; “Rabbitfish are getting used to the traps and not going in (P11)”; “sometimes I have to spend a longer time fishing now to catch the same amount, depending on the season. Mainly for rabbitfish (P11)”		
	Parrotfish	“more parrotfish now (M1)”; “Catches don't change much. Usually good to average all year (M2)”; “there are more parrotfish overall now (M3)”; “can catch parrotfish anywhere, all season (M3)”; “Can catch parrotfish all year. Catches are best on corals (M7)”; “catches are better where there are more corals, but they are caught everywhere. When traps are left more than one day, I get good parrotfish catches. There are more in the NWM, the SEM is too rough on some grounds (M8)”; “best catches are around rocks and coral (M11)”; “The best catches are on coral, especially in the NWM (M12)”; “Catches are best on coral reefs and in the NWM (M14)”; “Seaweed grows on traps and helps to catch parrotfish (M16)”; “catches depend on the currents. Best catches are November-April (M16)”; “you get more in the NWM and near coral (M18)”;	Can be caught all year round, but best in NWM. Can be caught across different habitats, but mostly on coral reefs. Catches are generally reliable, with some increases in recent years.	M1_hc-T, M2_h-T, M3_hc-TG, M7_hc-T, M8_hc-G, M11_**h**>**c**-TG, M12_h-TG, M14_**h**>**c**-TGG, M16_h, M18_**h**>**c**-TG, M19_hc-TG, M20_hc-TG, M21_**h**>**c**-T, M22,

Catch (continued)		“Parrotfish are smaller now, but catch the same number (M19)”; “Can spend less time now to catch the same amount of fish on corals - mainly for parrotfish (M19)”; “parrotfish can be caught any time of the year. There are none on seaweed, you get more around rock (M19)”; “I catch more in the SEM, also when they are spawning. When the sea is rough, the fish come inside the reef. I catch more on coral (M20)” “Since corals died in 2016, catches have been ok. Algae grows and parrotfish come in to feed on it and catches are fruitful (M21)”; “there are more parrotfish in seaweed environments. Catches drop when the tide is too rough (M22)”; “during the algae bloom (Mar/Apr) the fish changed instantly: caught more fish as a lot of them came inside the reef (e.g. big parrotfish). But the advice was not to eat fish, so struggled to sell anything (M23)”; “Parrotfish move a lot and catches are variable, but you get larger groups more often than rabbitfish, especially at the start of SEM (P1)”; “Catches are best in NWM, around mixed corals (P1)”; “I was catching a lot of parrotfish before coral bleaching in 2016 but not now (P7)”; “I catch most [parrotfish] inside the reef, on seaweed (P7)”; “Didn’t ever notice any change in parrotfish catches (P8R)”		M23_hc-TG, P1_hc-GGG, P7_hc-G, P8R_h
	Other species	“There are few fish close to shore (e.g. grouper), mainly due to dredging/land reclamation (M3)”; “catching more karang [jacks] in a shorter time on coral now than before (M7)”; “Used to catch more zekler [*Lethrinus lentjan*] but now catch sousout [*Gymnocranius elongatus*]. With traps, don’t get [*Lutjanus mahsena*] anywhere (M8)”; “catching the same fish, but not the same quantity as before. But mackerel has stayed the same (M10)”; “[*Lutjanus gibbus*] has increased in numbers. There weren’t many when I started fishing. Lots on outer islands now, which is a good sign (M10)”; “I sometimes catch snapper now, but got more before (M12)”; “In 10 years of fishing, surgeonfish have decreased (M14)”; “sweetlips are smaller now, and I see fewer while diving (M21)”; “used to catch a lot of sweetlips in traps but not anymore (M22)” “There are more jobfish and jacks than before. Mackerel attracts jacks (P1)”; “At high tide, you can catch a lot of jacks on coral (P1)”; “Used to catch sharks with nets. There were seasons when I caught a lot of sharks, but there aren’t many now - purse seiners destroyed the fishery (P2)”; “I don’t catch as many marar [*Leptoscarus vaigiensis*] now. There used to be plenty. Maybe they have been overfished. They are slow to reproduce (P3)”;	Catches of most species have declined. Catches of pelagic species like jacks and mackerel are good.	M3_hc-TG, M7_hc-T, M8_hc-G, M10_hc, M12_h-TG, M14_**h>c**-TGG, M21_**h>c**-T, M22, P1_hc-GGG, P2_c-T, P3_h, P6_**h>c**-TGGG, P8R_h, P11_hc-T

Catch (continued)		“Much less octopus now (P6)”; “Because of purse seiners, there is less tuna. Tuna used to chase smaller fish inside the reef that I could catch (P6)”; “It is difficult to find bordomar [*Lutjanus sanguineus*] in fish traps now (P6)”; “used to get a lot of rouze kapisen [*Mulloidichthys* sp.] but nothing now. Germans liked it! (P6)”; “There are some places where I used to get bourzwa with a handline but not anymore (P8R)”; “I am maybe catching fewer snappers and groupers now (P11)”;		
	Coral	“catch decreased significantly around time of coral bleaching – water was too warm (M2)”; “reefs have changed a lot. Fish is limited now. At one time, you could fish only on coral and get plenty of fish, but now you need to search different habitats (M6R)”; “Fishing was better before coral bleaching. It is starting to get better now (M6R)”; “catches are up and down, so keep good coral patches secret (M6R)”; “Coral bleaching causes fish to leave. The habitat has changed and fishing grounds are not as good (M8)”; “when fishing with traps, things aren’t living on sand - more on coral where they feed (M10)”; “[Coral bleaching] happens sometimes, depends on month (usually Mar-Apr). Really bad for fishing. After 2016 bleaching, fish went deeper. Caught nothing at 60m, but at 66m it was ok (M10)”; “After 2016 bleaching, octopus fishing was good (M10)”; “Still caught fish after coral bleaching (M11)”; “When the coral died, I didn’t catch any fish (M15)”; “When 2016 bleaching happened, it was difficult to catch fish - had to go deeper. Lasted around 6 months, then things stabilised slowly (M17)”; “If coral is dead, then there are no fish. About one week after bleaching, there are no more fish. Takes years for fish to come back. (M18)”; “After bleaching, caught smaller fish so there were more in each packet. Maybe bigger fish were leaving and going deeper? (M18)”; “Catching fewer red snapper and grouper now because the coral is dead (M18)”; “if you damage corals with traps then fish won’t go in (M21)”; “changes in catch are instant when the reef bleaches. I wouldn’t fish on a bleached reef, it’s not worth it as you won’t catch anything (M21)”; “coral bleaching means no more fish and no more food for people (M21)”; “Catches were very bad at the time of coral bleaching, but quite quick to come back (M23)”; “When fishing with traps. it’s best in areas without too much coral - a mix of seaweed and coral is best and set traps on the white sand (P1)”; “Maybe climate change is affecting catches. Hotter weather makes fish move deeper, or to where corals are easier to feed on (P1)”; “Changes in fish catches happen at the same time as reef environment changes. Hot water means no fish. When coral is starting to bleach, fish traps can be empty (P1)”; “there are fewer fish than before bleaching. The reef did recover (P5R)”;	Coral bleaching drastically reduced fish catches. The best catches are on healthy coral reefs. It took some time for fish catches to return to pre-bleaching levels.	M2_h-T, M6R_hc-TG, M8_hc-G, M10_hc, M11_**h>c**-TG, M15_**h>c**-T, M17_hc, M18_**h>c**-TG, M21_**h>c**-T, M23_hc-TG, P1_hc-GGG, P5R_hc, P6_**h>c**-TGGG, P7_hc-G, P10R_hc-GG

Catch (continued)		“If the coral is dead, you won’t catch fish (P6)”; “I don’t set traps on coral but it’s important for fish to travel between coral habitat, so I still depend on healthy coral when fishing on seaweed (P7)”; “I caught less fish when coral bleaching happened in 2016 (P7)”		
	Macroalgae/ sea grass	“I fish on seaweed. Traps near coral catch fewer fish (M3)”; “I can catch more fish in a shorter time than before, on algae only (P4)”	Yields can be better on macroalgae reefs.	M3_hc-TG, P4_hc-G
	Other/general	“Hard to notice any differences between years – just have to go to the right place at the right time (M2)”; “Fish spawn more or less in different years, leading to good or bad fishing (M4)”; “fish catches have stayed the same but fluctuate (M4)”; “I catch fewer fish inside the reef compared to outside. They are also smaller (M4)”; “there have been long-term decreases in the quantity and quality of fish (M5)”; “in Jan/Feb, fish are rare and catches are low (M8)”; “Catches are up and down (M10)”; “I am now catching less of everything. The fish just left (M11)”; “Catches have gotten worse because of rising sea temperatures (M13)”; “Catches have been up and down in terms of bigger/smaller fish (M16)”; “less of all species, each year (M18)”; “you don’t catch anything on sand (M20)”; “Inside the reef, fish are scared so catch fewer. They are also smaller (M21)”; “All species have decreased over the last 30 years (M21)”; “two weeks ago, I hauled 18 traps and didn’t even get one packet of fish (M23)”; “All species have become smaller and there are fewer of them. Five years ago in May/June you got a lot of juveniles. Now you don’t see many (M23)”; “Only gets about one packet per trap - used to be more before (M23)” “When the water is clean, it is not good for fishing (P1)”; “Sometimes can spend all day searching for fish and then the next day will get a lot. I used to go fishing with my father so I know some good spots (P1)”; “I get roughly one packet of fish per trap (P2)”; “There are more fishers now, so I catch fewer fish (P4)”; “Spending more time fishing and getting nothing is more common now (P4)”; “Before, you caught more fish than now (P5R)”; “There are fewer of all species compared to before (P6)”; “From July to September, the water is dirty and catches are worse (P6)”; “There has been overfishing on the reef because of technology, e.g. echosounders and GPS (P6)”; “the amount of fishing time on different grounds depends on the tide and temperature (P6)”; “When it is hotter, habitat is less important for fishing (P7)”; “In some places I could catch more in a shorter time than before. I was not expecting it but started fishing and caught lots quickly (P8R)”;	Catches can be highly variable. Trap catches have worsened. Habitat, fish behaviour, and overfishing contribute to lower catches.	M2_h-T, M4_**h>c**-TG, M5_**h>c**, M8_hc-G, M10_hc, M11_**h>c**-TG, M13_hc-GG, M16_h, M18_**h>c**-TG, M20_hc-TG, M21_**h>c**-T, M23_hc-TG, P1_hc-GGG, P2_c-T, P4_hc-G, P5R_hc, P6_**h>c**-TGGG, P7_hc-G, P8R_h, P10R_hc-GG

Catch (continued)		“Didn’t notice many changes in catches but fish were not going in the traps. They are getting cleverer! (P10R)”; “sometimes you can leave traps for one hour and they’re full. Other times you leave them for five hours to get the same amount. I don’t know why (P10R)”; “trap catches have worsened but the fish are still there - all species (P10R)”;		

Table S3.2: Quotes from fishers regarding their responses to changing reef habitats or catches, and associated outcomes. Quotes are organised by topics and sub-topics on the left, with themes within each topic defined on the right. Note that quotes may be paraphrased due to translation from Kreol to English. Interview IDs containing "M" = Mahé, "P" = Praslin, "R" = fishers who had retired from trap fishing (but not necessarily all types of fishing). IDs are coded to contain information on habitat and catch perceptions (h = noticed reef habitat changes, c = noticed catch changes; when bold and linked with ">" (**h>c**) = catch changes due to habitat changes), and fisher responses (T = travelling further, G = increased number of traps, G = changed gear type, G = changed gear deployment).

Topic		**Quotes**	**Theme**	**Interview IDs**
Fishing effort	***Grounds***	"coral reef, macroalgae, and rock are all important for fishing, so I spend an equal amount of time on each (M1)"; "I have had to learn to fish on the changing reefs and explore new grounds (M1)"; "I won't fish on grounds for a while to let the fish recover, then I return (M1)"; "I know from experience when and where to put traps to catch the most fish (M2)"; "I fish mainly in seaweed areas (M3)"; "I spend equal time fishing on coral, seaweed, and seagrass (M4)"; "I leave grounds dormant for two to three months to allow fish to increase, then return (M4)"; "In the NWM, I set traps outside the reef (6 - 10 miles). In the SEM, I move traps inside the reef and get fewer fish (8 - 10 packets) (M4)"; "I spent more time on coral than on seaweed (M6R)"; "Even when coral bleaching happened, I kept my routine (M6R)"; "At one time, you could fish only on coral and get plenty of fish, but now you need to search different habitats (M6R)"; "I put traps around the edge of the marine park (M15)"; "When 2016 bleaching happened, it was difficult to catch fish - had to go deeper (M17)"; "I move away from grounds if I am getting bad catches, then return after a time (M23)"; "I can look into the water with my mask to see if coral looks normal (P1)"; "I sink a camera down to look at seabed when fishing deeper, e.g. red snapper fishing at a depth of about 40-45 m. I don't fish directly on the coral (P1)"; "I spend more time fishing on coral (P3)"; "I rotate between fishing grounds based on season to leave grounds to recover (P3)"; "I rotate between fishing grounds (P6)"; "I went to fish in areas where the coral is healthy (P10R)"; "I would stop fishing on the reef about now [May] as we are coming into the bad season [SEM] (P10R)"; "I fish on the reefs most of the time (P11)"	Common for fishers to focus effort on coral habitat. Fishers manage their fishing activity by monitoring habitat condition and catches on grounds.	M1_hc-T, M2_h-T, M3_hc-TG, M4_**h>c**-TG, M6R_hc-TG, M15_**h>c**-T, M23_hc-TG, P1_hc-GGG, P3_h, P6_**h>c**-TGGG, P10R_hc-GG, P11_hc-T
	Fishing gear	"I need to increase the number of traps to get an average catch (M4)"; "I increased the number of fish traps I had, only because of trap theft (M6R)"; "I use fewer traps in the SEM (M11)"; "I use more traps when there are fewer fish (M12)";	Many fishers increased the number of fish traps they used to maintain catches.	M4_**h>c**-TG, M6R_hc-TG, M11_**h>c**-TG, M12_h-TG, M14_**h>c**-TGG,

Fishing effort (continued)		"Compared to when I started, I can now set multiple traps instead of just one in a day (M14)"; "when trap catches were bad I fish with handlines more (M18)"; "since all of my traps were stolen 6-8 months ago, I fish with handlines/trolling (M18)"; "I use more traps now. I had 5 traps, then 10, and now 15 (M19)"; "I did more handline fishing when trap catches were poor (M20)"; "Before, less than 10 traps was enough but now I have 18. I only get about one packet per trap but used to get more before (M23)"; "When fishing is bad on the reefs I switch to handline instead of traps (P1)"; "I bring my fish traps inside the reef more now (P1)"; "I don't fish to my maximum. I can always reduce number of traps if I need to (P1)"; "I was using six traps, but now ten (P4)"; "I used to use two to three traps, now I need about 30 (P6)"; "If I don't catch enough fish for the hotel with traps one day, I will go and fish with handlines the next day. It depends (P6)"; "I need to use my echosounder to find fish now (P6)"; "I had six traps before but now have twelve (P7)"; "I have ten traps now. I had six before (P9)"; "I do more handline fishing now, as trap catches aren't good (P9)"; "I increased the number of traps I used to 20 or 25 (P10R)"; "I stopped fishing with traps because I was getting a small amount of fish and there's a big demand for jacks. So I still fish with handline (P10R)"	Changing fishing gears, from traps to handline, as a result of poor trap catches is common.	M18_**h>c**-TG, M19_hc-TG, M20_hc-TG, M23_hc-TG, P1_hc-GGG, P4_hc-G, P6_**h>c**-TGGG, P7_hc-G, P9_**h>c**-TGGG, P10R_hc-GG
	Fishing time	"with handlines, I don't waste time. I will just move on if the fish are not biting (M2)"; "I leave traps longer now before hauling (M3)"; "I sometimes haul 15 out of 20 traps, for example, and leave 5 traps longer to get more fish (M8)"; "Having to fish longer than before to catch the same amount, mainly on coral (M10)"; "Nowadays, I am catching less. Before, could leave the traps for a shorter period of time, but nowadays need to leave them longer to catch the same amount and species. Probably because of land reclamation and climate change (M14)"; "I have to leave traps longer now. Before, I hauled traps within a few hours. Now, I leave them for one to two days usually (M23)" "I had to spend longer with handlines to catch the same amount as before (P8R)"; "before I could set traps for about two hours, but now I set them for 4-5 hours (P9)"; "in some places I have to fish longer to catch enough fish. I have to set traps several times, and keep trying (P9)"; "sometimes I have to spend a longer time fishing now to catch the same amount, depending on the season. Mainly for rabbitfish (P11)"	Traps are left in the water for longer to catch enough fish.	M2_h-T, M3_hc-TG, M8_hc-G, M14_**h>c**-TGG, M23_hc-TG, P8R_h, P9_**h>c**-TGGG, P11_hc-T
	Other fishers	"catches have worsened because there are more fishers (M1)"; "Each fisher used to have about three traps. You could set traps for one hour and would catch enough. Now there are	An increase in the number of fishers	M1_hc-T, M3_hc-TG,

Fishing effort (continued)		more fishers with more traps, so fewer fish per fisher. I used to catch about 50kg from those traps, now I would only get about 5kg (M1)"; "I avoid other fishers if possible (M3)"; "fish traps get stolen (M11)"; "Maybe overfishing the exact same grounds closer to shore has resulted in fewer fish there. Most fishers target the shore (M20)"; "Lots of people are stealing boat engines. I build and fix boats. Fishers from Mahé come to steal traps, I only have 3 traps left! Many fishers have stopped fishing because of this (P2)"; "other fishers noticed where I was fishing. If you get fish, people go to that spot so I don't go there anymore (P8R)"; "Other fishers will follow me to see where I am fishing (P9)"; "Fishers are coming from Mahé and stealing traps (P10R)"	and traps has caused catches to decline. Fishers try to keep their best fishing grounds secret. Theft of fish traps/fishing assets are a common issue.	M11_**h>c**-TG, M20_hc-TG, P2_c-T, P8R_h, P9_**h>c**-TGGG, P10R_hc-GG
	Continuing to fish	"My father and grandfather were fishers, I won't do anything else (P2)"; "I wouldn't stop fishing. It's the only thing I know (P3)"	Alternative jobs are not an option for some.	P2_c-T, P3_h
	Reducing effort/ Retirement	"I had to change to handlines and then to trolling instead of fishing with traps – better for my back health. But theft of traps is the main reason I quit. Traps cost a lot to make. I would still fish if there was no theft because trap fishing is fun - pulling up traps to see what's there (M6R)"; "I stopped fishing because of my bad knee (M9R)"; "I want to go into tourism and also do some farming. That would reduce fishing pressure on the ocean and lead to more fish and more tourists. Tourists are very happy when they see fish, like parrotfish, and pay to do that. Sometimes you can make the same amount of money in one day as you do when fishing (P1)"; "I studied agriculture at school and have thought about switching from fishing to farming. I maybe will in a year (P4)"; "I have thought about stopping fishing for 6 months or so, not permanently. This should be enforced for all fishers (P7)"; "I have thought about doing another job because sometimes it is not easy to catch fish and you don't always earn enough money (P9)"; "If I was offered a better job, of course I would stop fishing (P11)"	Several trap fishers have considered alternative livelihoods (some have already retired).	M6R_hc-TG, M9R_hc, P1_hc-GGG, P4_hc-G, P7_hc-G, P9_**h>c**-TGGG, P11_hc-T
	Other	"During COVID-19 there were fewer buyers. I fished just as often but used fewer traps (P3)"; "During COVID, restrictions made it difficult to go fishing. Fish sales were also reduced (P5R)"; "COVID affected fishing a lot. Everyone had to stay inside (P9)"	COVID-19 restrictions resulted in reduced fishing effort.	P3_h, P5R_hc, P9_**h>c**-TGGG

Travelling further	***Distance/time***	“I used to travel one mile when trap fishing about two years ago, now I travel three miles. With handlines I used to travel six miles but now it’s 15 miles, and a trip is overnight which I never used to do (M1)”; “I used to travel less than one mile but since the land reclamation, I have to travel up to 21 miles. Sometimes I stay overnight in Praslin. I need to go further so other fishers can’t see where I go (M2)”; “I sometimes travel about three miles more because of dredging and land reclamation, which takes about 3 hours extra. But not for rabbitfish (M3)”; “Sometimes I have to go five or six mile further to catch enough fish, which takes 2-3 hours longer. But in some years I don’t have to go that far, catches are up and down (M4)”; “I had to travel about 14 to 16 miles further, to Praslin, as there were fewer fish closer to Mahé than that. It adds 3 hours to my fishing time (M6R)”; “I travel 10 extra miles now because the fish inside the reef have gotten smaller. This has added 4 hours to my fishing time (M7)”; “I have to travel 4-5 miles further since the land reclamation 30 years ago. About 2 hours longer (M11)”; “I travel further during the NWM, which used to be about 5 miles, but now 7 miles. This leaves the fish closer to shore to reproduce (M12)”; “I need to go 400 m further now to avoid putting traps in the marine park (M14)”; “I have to travel about 30 miles more to get enough fish. Fishing time has increased from 4 hours to 8-10 hours (M15)”; “I travelled about 20 miles before, but now 40-50 miles because there are no fish closer to shore. It took me 1-2 hours to get back to shore before but now takes 3-4 hours – I can’t go fast in my boat (M18)”; “I travel further now, about 2-5 miles, but only because I am searching for new fishing grounds to catch enough fish (M19)”; “I have to go 10 – 15 miles further to catch enough fish. Before I could catch fish very close to the shore. It takes 2-3 hours longer (M20)”; “I now fish up to 12 miles away. Before it was 6-8 miles. I spend an extra 1-2 hours looking for my traps. But it depends on catches, I go further to maintain catches. The distance has increased gradually over time. Sometimes I still fish very close to shore (M21)”; “I go to a different bay now to catch fish, which takes 2-3 hours longer (M23)”; “I have to travel 15 – 20 miles more to catch enough fish. Fishing takes 2.5 hours longer now (P2)”; “With traps, I have to go 16 miles offshore to catch fish. I fished almost at the shore before. The distance increased slowly over time, I have to go further each year (P6)”; “I used to do multiple shorter fishing trips and go in and out but this year I have started doing one longer trip for the whole day when going further (P9)”;	Many fishers are having to travel further to maintain their catches, with traps and handlines. The extra distance adds multiple hours to fishing time.	M1_hc-T, M2_h-T, M3_hc-TG, M4_**h>c**-TG, M6R_hc-TG, M7_hc-T, M11_**h>c**-TG, M12_h-TG, M14_**h>c**-TGG, M15_**h>c**-T, M18_**h>c**-TG, M19_hc-TG, M20_hc-TG, M21_**h>c**-T, M23_hc-TG, P2_c-T, P6_**h>c**-TGGG, P9_**h>c**-TGGG, P11_hc-T

Travelling further (continued)		"I only have to travel further for handlines – before it was 9-10 miles, now it is 17 miles. The distance has increased slowly over the years (P11)"		
	Fuel/costs	"I use the same amount of fuel but the price is higher now (M1)"; "I need 10-15 extra litres of fuel (M3)"; "more mileage means more fuel and maintenance expenses (M4)"; "expenses have increased (M5)"; "I use 20-40 litres more fuel (M7)"; "My fuel has increased from 50 litres to 100 litres. Before I had to do boat maintenance maybe every 3 months, but now every month (M11)"; "fuel was 400 SCR before, but now 600-700 SCR (M15)"; "the amount of fuel has doubled to 50 litres now. And it is more expensive now (M18)"; "the amount of fuel I use has doubled; I used to use 24 litres, but now I use 48 litres (M20)"; "You can lose gear to the currents. I also need more buoys, 3-4, when further out (M20)"; "I use double or more fuel now. Before it was about 25 litres and now it is over 50 litres (M23)"; "before I had a 25 HP engine. Now I have a 40 HP engine because I need to come back faster to sell fish (M23)"; "Fuel has doubled from 25 litres to 50 litres per day. It cost 500-600 SCR before but now it is 1200 SCR (P2)"; "My traps are in deeper water now, up to 40 m, so more rope is needed (P6)"; "I use more fuel now, about 75 litres in the SEM. I also have more engine maintenance now as it gets more use every day (P6)"; "I no longer fish near Aride Island because fuel is too expensive now and it is too far (P9)"; "trap can be stolen further out, especially if left too long (P9)"; "I used to use 25 litres of fuel, now I use up to 50 litres. I need to do boat maintenance more often (P9)"; "Fuel is 2000 SCR per day but before it was 1000 SCR. I have to change oil and everything sooner than before as well, my boat needs servicing more often (P11)"	The extra fuel and engine maintenance needed to travel further is greatly increasing running costs. There are additional costs associated with setting traps further from shore.	M1_hc-T, M3_hc-TG, M4_**h>c**-TG, M5_**h>c**, M7_hc-T, M11_**h>c**-TG, M15_**h>c**-T, M18_**h>c**-TG, M20_hc-TG, M23_hc-TG, P2_c-T, P6_**h>c**-TGGG, P9_**h>c**-TGGG, P11_hc-T
	Safety/risks/ difficulty	"It is windier at times further out, plus the current. I have to stay closer to the coast in the SEM (M2)"; "traps are more likely to be stolen further out (M3)"; "it is risky further out. I have a lifejacket and a knife in case I get stuck in rope (M3)"; "There are more risks because of bad weather – the currents are worse and you are more exposed to winds (M4)"; "Fishing is more difficult because of the current and buoys can be submerged – you can lose days of fishing searching. Traps can be lost as well (M4)"; "fishing is easier further away because there are more fish there (M6R)"; "Fishing is more difficult now and larger waves can be dangerous for me and my fish traps (M11)"; "bigger boats sometimes cut trap ropes (M12)";	Weather and sea state can cause risks to fishers when fishing further offshore. There are risks of fish traps being damaged or stolen further offshore. There are difficulties associated with the practicalities	M2_h-T, M3_hc-TG, M4_**h>c**-TG, M6R_hc-TG, M11_**h>c**-TG, M12_h-TG, M15_**h>c**-T, M18_**h>c**-TG, M20_hc-TG, M21_**h>c**-T, M23_hc-TG, P2_c-T, P6_**h>c**-TGGG,

Travelling further (continued)		"NWM is calmer. I go further out during the SEM but it's rougher. Risks are not a problem. Sometimes it's windy but I force myself to go fishing. Traps can move in the swell, moving against rocks (M15)"; "fishing is easier further out, but it is very risky. When trolling, giant fish jump and could hit the boat. The boat is rocky. Fishing line needs to be stronger than shoreline (M18)"; "It is more tiring fishing further offshore in deeper water. If I was injured, it would take longer to get to hospital, and it can be risky if there is a sudden change in sea state while out there (M20)"; "There are a lot of currents offshore and sometimes the water is murky, so fishing is more difficult (M21)"; "There are more safety risks inside the reef when there are big waves, compared to further out. But there is more risk of trap theft and damage from other people further out (M21)"; "It is riskier further out because there are big waves. There are also thieves over in the other bay who steal traps. Traps can also be lost to currents (M23)"; "fishing is more difficult (P2)"; "there are more risks fishing alone. Young people aren't interested in crew jobs because there is no fixed salary (P2)"; "there is more chance traps will be stolen closer to Mahe (P2)"; "It can be windy, and takes more time to haul traps (P6)"; "I fish alone and would prefer to have a crewman but they are difficult to get (P9)"; "It is more difficult to catch the amount of fish you want (P11)";	of fishing further offshore.	P9_**h>c**-TGGG, P11_hc-T
Selling fish		"I send rabbitfish to Praslin to be salted if I catch too much (M2)"; "In the SEM, the fish prices rise so I go out fishing (M2)"; "when there were COVID restrictions, sales went down. I still fished though (M2)"; "There are some seasonal changes in fish packet composition (M2)"; "when there are more tourists and hotels are open, it helps with selling fish (M4)"; "I put fewer fish in each packet now (M5)"; "fuel and gear prices have increased, so I have more expenses while earning less (M5)"; "During the COVID lockdown, I didn't sell fish (M7)"; "if the price of fish goes up, I make bigger fish packets (M8)"; "The price of fish has gone up in the last 5 years. Fuel price goes up, so does the fish price (M10)"; "I still sold fish and fished the same during COVID (M10)"; "The species in my catch has changed so packets are more mixed now. I used to have all the same species in a packet more often (M11)"; "fish sells well around Christmas because people are at home then (M12)"; "fish are cheap for people to buy, but fuel is expensive (M13)"; "Traps are set further away so I would increase the price of fish packets, but some people will not buy fish at 150 SCR per packet. Some hotels buy the fish (M14)"; "The amount of buyers has reduced because of COVID (M14)";	Fish packets can be adjusted to account for changes in catch (e.g. season, size of fish) or demand (e.g. buyer preference). Unsold fish can be salted. Fish prices change seasonally but are generally rising to offset fishing costs. COVID-19 restrictions made selling fish difficult.	M2_h-T, M4_**h>c**-TG, M5_**h>c**, M7_hc-T, M8_hc-G, M10_hc, M11_**h>c**-TG, M12_h-TG, M13_hc-GG, M14_**h>c**-TGG, M15_**h>c**-T, M16_h, M17_hc, M18_**h>c**-TG, M19_hc-TG, M21_**h>c**-T, M22, M23_hc-TG, P1_hc-GGG,

Selling fish (continued)		"I target fish with higher value, so I go further for red snapper for example (M15)"; "fish packets are bigger in the NWM, but sold for the same price (M15)"; "Packets are bigger than before. Used to get around 10 packets, now 7-8 with same amount of fish (M16)"; "During COVID I sold for a cheaper price (M17)"; "In the NWM the price goes down because there are more fish then (M18)"; "People buy more red snapper and bordmar near Christmas, so I fish with traps less at that time (M18)"; "I sold fish the same during COVID (M18)"; "I catch bigger fish with handlines so there are fewer fish in packets (M18)"; "fish are smaller now so I put more in a packet (M19)"; "I target red snapper more at Christmas (M19)"; "COVID didn't affect fishing, but selling was a problem (M21)"; "There were restrictions during COVID. I couldn't move around as easily so selling dropped (M22)"; "A tax will be introduced in 2025 and all fishers will be taxed 15% on their earnings. This will discourage fishers and they will leave the fishery (M22)"; "Movement was restricted during COVID, so it was difficult for people to come and buy fish, and it was hard to fish (M23)"; "I sometimes put more fish in a packet (e.g. during COVID lockdown, people didn't want smaller packets) (P1)"; "Now I put about 2.5 kg of parrotfish in each packet. It weighs less when filleted but is almost the same value. I fillet fish more often now because people like to buy it that way (P1)"; "I target jobfish more when the price is good (P1)"; "At the start of the pandemic, there was a problem with fishers from Mahe selling fish in Praslin so fish prices went down (P1)"; "the composition of fish packets has not changed but I will increase the price to sell packets for 150 SCR because fuel prices have risen (P2)"; "I used to salt rabbitfish when I had lots of traps, but not anymore (P2)"; "Before, I used to sell fish in Baie St Anne but now I just salt fish at home (P5R)"; "COVID caused problems selling fish (P7)"; "I salted the rabbitfish I caught (P8R)"; "I didn't fish during COVID as there was no market and there was a curfew (P8R)"; "I can salt fish if it is not sold (P9)"; "people want a variety of fish (P9)"; "fuel prices are higher, so fish prices have gone up (P9)"; "tourists don't want fish from fish traps (P9)" "whenever I was catching fish during COVID, no one was buying it. I salted it when not sold (P10R)"; "I have to make fish packets smaller to make up for extra costs (P11)"; "jack prices go up when the weather is bad so I target them more (P11)"; "During COVID, it was hard to sell fish because no one had money to spend and hotels were closed (P11)";	Demand for fish is influenced by holidays and tourism.	P2_c-T, P5R_hc, P7_hc-G, P8R_h, P9_**h>c**-TGGG, P10R_hc-GG, P11_hc-T

Chapter 4 supplementary material

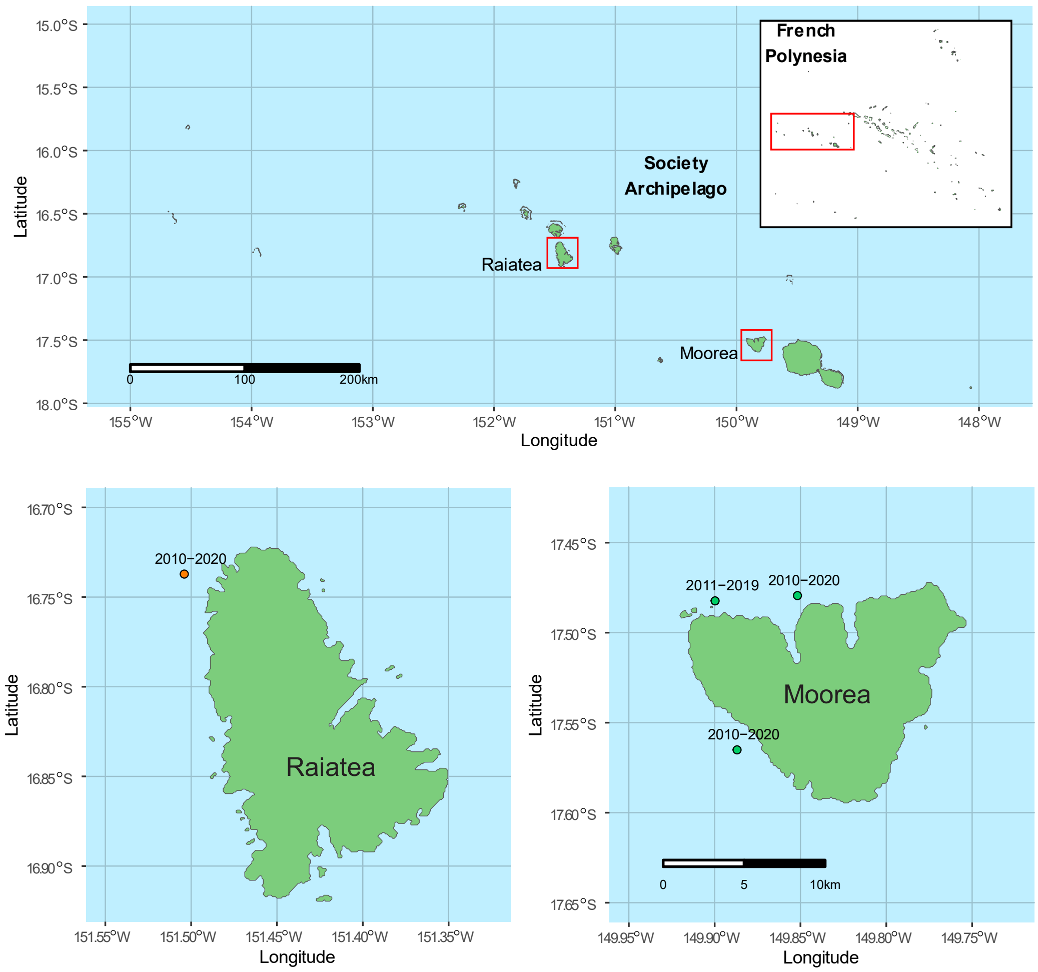

Figure S4.1: Map of Moorea and Raiatea within the Society Archipelago, French Polynesia (top). Reef survey sites are shown as points for each island (Raiatea: bottom left; Moorea: bottom right). Each reef site was surveyed every two years from 2010 to 2020, in even years except one site on Moorea which was surveyed in odd years, as shown by point labels. Bottom panels for each island are displayed at the same scale.

Table S4.1: Fish species observed during reef surveys in Moorea and Raiatea, from 2010 to 2020, classified into three trophic groups: Herbivore (including microvores and detritivores), Mobile invertivore and Piscivore. Species are listed by family with the number of species given for each family. Only species with individuals ≥15 cm observed during surveys are listed. Tahitian/local fish names for some families and species are included below in brackets.

Herbivore

- **Acanthuridae** (*n* = 18)
  - *Acanthurus mata*
  - *Acanthurus nigricans*
  - *Acanthurus nigricauda*
  - *Acanthurus nigrofuscus*
  - *Acanthurus nigroris*
  - *Acanthurus olivaceus*
  - *Acanthurus pyroferus*
  - *Acanthurus triostegus*
  - *Ctenochaetus binotatus*
  - *Ctenochaetus flavicauda*
  - *Ctenochaetus striatus*
    - (maito)
  - *Naso annulatus*
    - (ume/nason)
  - *Naso brevirostris*
    - (tatihi/tatii/herepo ti)
  - *Naso lituratus*
    - (ume tare)
  - *Naso unicornis*
  - *Zebrasoma rostratum*
  - *Zebrasoma scopas*
  - *Zebrasoma velifer*
- **Balistidae** (*n* = 2)
  - *Melichthys niger*
  - *Melichthys vidua*
- **Chanidae** (*n* = 1)
  - *Chanos chanos*
- **Scarinae** (*n* = 16)
    - (pehoro/deng deng)
  - *Calotomus carolinus*
  - *Cetoscarus ocellatus*
  - *Chlorurus frontalis*
  - *Chlorurus microrhinos*
    - (tegatega)
  - *Chlorurus sordidus*
    - (paati/ufu)
  - *Hipposcarus longiceps*
  - *Scarus altipinnis*
  - *Scarus forsteni*
  - *Scarus frenatus*
  - *Scarus ghobban*
  - *Scarus globiceps*
  - *Scarus niger*
  - *Scarus oviceps*
  - *Scarus psittacus*
    - (hou ninamu)
  - *Scarus rubroviolaceus*
  - *Scarus schlegeli*
    - (kukina)
- **Siganidae** (n = 1)
  - *Siganus argenteus*
    - (marava)

Mobile invertivore

- **Balistidae** (*n* = 7)
  - *Balistapus undulatus*
  - *Balistoides viridescens*
    - (oiri)
  - *Odonus niger*
  - *Pseudobalistes flavimarginatus*
  - *Rhinecanthus lunula*
  - *Rhinecanthus rectangulus*
  - *Sufflamen bursa*
- **Chaetodontidae** (*n* = 3)
    - (korei)
  - *Chaetodon lunula*
  - *Forcipiger flavissimus*
  - *Forcipiger longirostris*
- **Epinephelidae** (*n* = 3)
  - *Cephalopholis leopardus*
  - *Cephalopholis urodeta*
  - *Epinephelus fasciatus*
- **Holocentridae** (*n* = 9)
  - *Myripristis berndti*
    - (iihi/u'u)
  - *Myripristis murdjan*
    - (peti)
  - *Myripristis violacea*
    - (iihi/u'u)
  - *Neoniphon opercularis*
  - *Neoniphon samara*
  - *Sargocentron caudimaculatum*
  - *Sargocentron microstoma*
  - *Sargocentron spiniferum*
    - (apai/rukeruke)
  - *Sargocentron tiere*
- **Labridae** (*n* = 18)
  - *Anampses caeruleopunctatus*
  - *Anampses melanurus*
  - *Anampses twistii*
  - *Bodianus axillaris*
  - *Cheilinus chlorourus*
    - (papae)
  - *Cheilinus trilobatus*
    - (papae)
  - *Cheilinus undulatus*
    - (Napoleon/tapiro)
  - *Coris aygula*
  - *Coris gaimard*
  - *Epibulus insidiator*
  - *Gomphosus varius*
  - *Halichoeres hortulanus*
  - *Hologymnosus annulatus*
  - *Novaculichthys taeniourus*
  - *Oxycheilinus unifasciatus*
  - *Pseudocoris aurantiofasciata*
  - *Thalassoma lutescens*
  - *Thalassoma quinquevittatum*

Mobile invertivore (cont.)

- **Lethrinidae** (*n* = 2)
    - (oeo/bec de canne)
  - *Gnathodentex aureolineatus*
    - (maene)
  - *Monotaxis grandoculis*
- **Lutjanidae** (*n* = 4)
  - *Lutjanus bohar*
  - *Lutjanus fulvus*
    - (toau)
  - *Lutjanus gibbus*
    - (taea)
  - *Lutjanus monostigma*
    - (tanifa)
- **Mullidae** (*n* = 5)
  - *Mulloidichthys vanicolensis*
    - (vete)
  - *Parupeneus barberinus*
    - (ahuru/takire)
  - *Parupeneus cyclostomus*
    - (atiata)
  - *Parupeneus insularis*
    - (atiata)
  - *Parupeneus multifasciatus*
    - (atiata)

Piscivore

- **Carangidae** (*n* = 3)
  - *Carangoides orthogrammus*
  - *Caranx melampygus*
    - (paihere)
  - *Scomberoides lysan*
- **Epinephelidae** (*n* = 2)
  - *Cephalopholis argus*
    - (roi/merou celeste)
  - *Variola louti*
- **Labridae** (*n* = 1)
  - *Cheilio inermis*
- **Lethrinidae** (*n* = 2)
    - (oeo/bec de canne)
  - *Lethrinus olivaceus*
  - *Lethrinus xanthochilus*
- **Lutjanidae** (*n* = 1)
  - *Aphareus furca*
    - (paru)
- **Sphyraenidae** (*n* = 1)
  - *Sphyraena barracuda*
    - (tapito)

Questionnaire

Number ______________________ District and km___________
Sea/lagoon side ☐ Mountain/ocean side ☐
Male ☐ Female ☐ Other ☐

Socio-economic survey

Ask whether they have lived on island for >5 years. If not, do not do questionnaire.

FAMILIAL CHARACTERISTICS

1. How many people do you live and share meals and expenses with (you included)? _______
2. How many generations live in your house? _______
3. How many children are dependent on you? _______
3b. Are there other dependent persons (disabled adult, elderly…) living with you? how many? ___
4. Do you:
   ☐ Live in couple/family? ☐ Live alone? ☐ Share house with housemates?
   ☐ other _____________ ☐ Don’t want to answer
5. When were you born? _______
6. Do you make big decisions for the family?
   ☐ yes ☐ no ☐ one of several people deciding

6b. if not, who is it?

7. Who generally decides what people in the household eats during the day?
   ☐ you ☐ your partner ☐ someone else (who? ____________)
   ☐ It depends ☐ Each person decides for themselves, you don’t eat together
8. Are you:
   ☐ Owner of the house? ☐ Tenant?
   ☐ You are accommodated freely by a relative/friend?
9. Do you have easy access to the sea? yes ☐ no ☐
10. [material capital] Which methods of transportation do you own? : (specify how many)
    ☐ a. bicycles ☐ b. bike/scooter ☐ c. car
    ☐ d. truck/van ☐ e. motor boat ☐ f. boat without motor
    ☐ g. vaa (traditional boat)

HUMAN CAPITAL

11. What is the highest education level within your household? (Check the highest)
    ☐ Primary school ☐ Secondary school (brevet) ☐ Baccalauréat
    ☐ University degree☐ Other
12. Where were you born
13. [if the person doesn’t come from here] : How long have you lived on XXX? ____________
14. [if the person doesn’t come from here] : You moved on XXX because of
    ☐ Familial reasons? ☐ Work?
    ☐ Need of change? ☐ Other? ______
15. Does most of your family (uncles/aunt/cousins) live here, on XXX? Yes ☐ No ☐
16. With your family, which language do you speak mostly (several answers possibles)
    ☐ Tahitien? ☐ Paumotu?
    ☐ Marquisien and/or language from Australes? ☐ French? ☐ Tinto?
17. Did you parents used to do coprah or farming? Yes ☐ No ☐
18. Did your parents used to fish? Yes ☐ No ☐

SOCIAL CAPITAL

19. If there has to be a decision taken on the district, do you generally feel involved in the decision-making process? Yes ☐ No ☐ ; How? ____________________________
20. Do you feel involved in local life (sport, culture, church…)? Yes ☐ No ☐

If yes, how:
To check: are they involved in cultural activities, environment protection, fishing management?

FINANCIAL CAPITAL

Job and income
21. Do you (or anyone in your household) fish ? yes ☐ no ☐
20b. if yes, do you sell your catch ?
☐ Never, it's only for your personal consumption ☐ exceptionally (irregular and/or less than once a month)
☐ often (once or several times a month) ☐ every time you go to fish or almost
20c. if you or a relative fish to sell, do you have a CAPL card? yes ☐ no ☐
22. does anyone in your family do farming? yes ☐ no ☐
21b. if yes, do you sell your produce?
☐ never, it's only for personal consumption ☐ sometimes (irregular and/or less than once a month)
☐ often (once or several times a month) ☐ always
23. does anyone in your family harvest coprah ☐; vanilla☐; pearls☐
24. among your household, what is the part of food that you produce yourself (faaapu, fishing)?
☐ You don't produce anything ☐ You produce less than half of what you produce
☐ You produce more than half of what you produce
☐ You produce everything or almost everything of what you eat
25. Among your household, who is working and bringing back money to your family? what job do they do? (specify whether it is public or private sector, and whether it is a temporary or permanent work)?
25b. Are there retired people with pensions? how many? what did they use to do?
26. Are there financial difficulties in your household? yes ☐ no ☐
27. Are you doing other small jobs to bring back more money in your family? yes ☐ no ☐;
if yes, what? (e.g.: selling food, cakes, cleaning, gardening…)
28. Over the last month, what were your biggest expenses? (several answers possible specify the order)
☐ a-food ☐ b-house (electricity, water, rent…) ☐ c-fuel
☐ d-Entertainment-drinks ☐ e-health ☐ f-other ________

If it is a family that fish:
28. How many times do you go to fish?
☐ Rarely (less than once a month) ☐ occasionally (at least once a month)
☐ often (at least once a week)
29. Where do you fish? (several answers possible)
☐ offshore ☐ coastal fishing ☐ within lagoon
30. Are there periods of the year when you fish more often? when?
31. [Only for fishers who sell] – I realise that some days you fish a lot and other days, much less. If you think of a good day of fishing, what does that represent (number of coolers or number of fishes)? (ask whether it is the catch of one person or a team)
32. [Only for fishers who sell] – During a good month, how much would you say that you earn?
☐ between 0 and 9 999F (lire 10 000) ☐ between 10 000 and 39 999F (lire 40 000)
☐ between 40 000 and 74 999F (lire 75 000) ☐ between 75 000 and 99 999F (lire 100 000)
☐ between 100 000 and 150 000F ☐ more than 150 000F
33. [Only for fishers who sell] – where do you sell your fish generally? (several answers possible)
☐ a- shop/supermarket ☐ b- on the side of road ☐ c- on the quay
☐ d- door-to-door ☐ e- to the people who ordered before
☐ f- on the market ☐ g- from your house
☐ h- to Tahiti/other islands ☐ i- to hotels ☐ j-other (explain)
34. [Only for fishers who sell] – if you can't go to fish, how do you earn money instead?
☐ farm ☐ coprah ☐ Other activity
☐ from your savings ☐ dependent on family/others ☐ other
35. [Only for fishers who sell] – What complicates earning money from fishing? (open question) _________

MATERIAL CAPITAL

[for fishers only]
36. Do you have a boat for fishing? yes ☐ no ☐
If yes, what type of boat do you have:
☐ a. Poti marara ☐ b. Thonier ☐ c. Bonitier
☐ d. Kau ☐ e. Vaa ☐ f. other ______
37. What fishing material do you own?

☐ a. Parc a poisons ☐ b. net ☐ c. spear gun
☐ d. Harpon à dent ☐ e. Double crochet/griffe (tarau)
☐ f. Canne à pêche bamboo ☐ g. Moulinet ☐ h. Nylon
☐ i. Sondeur ☐ j. Nasse ☐ k. Cage
☐ l. Palme-masque-tuba ☐ m. cooler ☐ n. plastic box
☐ o. Tournevis ☐ p. Autre _______

DIET

38. If you think of a real meal that you’d eat with your family, and for which you would have no constraints in terms of money, weather, material, time, where everything would be available… what would you eat? how would it be prepared?

39. Generally, how many meals do you eat each day? at what time?

39b. Generally, do you eat something else during the rest of the day (in addition to what you indicated just before)? e.g. breakfast, snacks…

40. Think of your diet habits over the last year. Approximately how often did you eat the following types of food?

	Never or < once a month **1**	1-2 times a month **2**	3-4 times a month **3**	1-2 times a week **4**	3-5 times a week **5**	Everyday or almost **6**
a. Carbs (rice, pasta, bread, uru, tarot, fe’i, plantain, cassave, sweet potato, potatoes…)						
b. legumes (beans, peas, lentils, soya, chickpeas)						
c. nuts and grains (pistachio, almonds, cashew, macademia, sunflower seeds…)						
d. dairy (cheese, cream, milk, yoghurt, butter…)						
e. eggs						
f. vegetables (carrots, courgettes, cabbage, cucumber, onion…)						
g. fruits (mango, soursop, papaya, passion fruit, lemon, orange, pineapple, guava, noni…) (including fresh juice)						
i. fish						
j. clams/urchins						
k. chicken						
l. meat						
m. meat tins (punu puaatoro, corned beef..)						

41. Would you say that :
☐ You eat more fish than meat/chicken ☐ You eat more meat/chicken than fish
☐ You eat about the same amount of fish, chicken and meat

42. Compared to your parents, would you say that you eat
The same quantity of fish ☐ ; less fish ☐ ; more fish ☐ ; you don’t eat fish ☐

43. Compared to your parents, would you say that you eat
The same quantity of chicken ☐ ; less chicken ☐ ; more chicken ☐ ; you don’t eat chicken ☐

44. Compared to your parents, would you say that you eat:
The same quantity of meat ☐ ; less meat ☐ ; more meat ☐ ; you don’t eat meat ☐

45. How often do you eat crayfish/mantis shrimps/crabs?
☐ Several times a week ☐ Once a week ☐ 1-3 times a month
☐ Less than once a month ☐ Never or rarely

46. Thinking about your fish consumption, do you eat:
☐ Only lagoon fish or almost ☐ Only pelagic fish or almost
☐ As much as pelagic and lagoon fish

47. Can you name the main fish that you often eat?

48. Would you say that:
☐ You always eat the same fish ☐ You eat between 2-6 types of different fish per month
☐ You eat more than 7 types of different fish per month

49. You’d say that you get your fish mainly from (rank by importance order):
☐ From your own fishing ☐ From the catch given by a friend or relative
☐ From the catch of a local fisher (bought fish)
☐ From shop/supermarket ☐ Variable

50. [if you regularly buy your fish to a local fisher], how do you generally buy your fish?
☐ As tui ☐ Already cut/cleaned
☐ As unit ☐ It depends, variable

51. [if you regularly buy fish from a local fisher] what is the reasons justifying your choice?
☐ a-You know him, so it is normal to buy the fish from him
☐ b-his fish is good ☐ c-his fish is cheap
☐ d-it is the most practical (place and location)
☐ e- other. explain ______________

52. [if you regularly buy your fish to a local fisher], what make you decide to choose one fish over another?

53. When you buy your fish at the shop/supermarket, what types of fish do you buy mostly?
☐ Lagoon fish – name the main ones: ☐ Pelagic fish – name the main ones:
☐ both – name the main ones:

54. Where do you do your main grocery (except fresh products as bread…) (several answers possible)
☐ At the supermarket ☐ At the district shop ☐ At the moving market
☐ At the market of Uturao/Avera [for Raiatea only]
☐ On the side of the road ☐ other ____________

55. How often do you go to the shop for groceries (except fresh products like bread)
☐ everyday ☐ Several times a week ☐ Once a week
☐ 2-3 times a month ☐ Once a month ☐ Less than once a month

56. How do you go for groceries (except bread/fresh products)?
☐ By foot ☐ By bicycle ☐ By scooter/bike
☐ By car ☐ By public transportation

57. How long do you need to go for groceries? ________

58. At home, who cook mainly?
☐ yourself ☐ your partner
☐ someone else - who _____ ☐ nobody
☐ several people/everybody indifferently

59. What are the products that are essential/indispensable in your kitchen?

60. If you cook daily, what is the average time for preparation?

61. How often do you buy take-away meals
☐ Several times a week ☐ Several times a month, but less than once a week
☐ Once a month ☐ Less than once a month
☐ Never or almost never

62. How often do you go to eat at the snack/restaurant
☐ At least once a day ☐ 3-6 times a week
☐ 1-2 times a week ☐ 2-4 times a month
☐ Once a month ☐ Less than once a month
☐ Never or almost never

63. [depending on previous answer] When don’t you buy take-away food more often and rather privilege home-cooked food?

64. How often do you eat the Maa Tahiti with family?
☐ Several times a week ☐ Every Sunday – or once a week
☐ 2 to 3 Sunday a month ☐ Once a month
☐ Less than once a month ☐ Never or very rarely

65. [if they don’t eat the Maa tahiti every sunday] why not more often? ___________

Table S4.2: Descriptive statistics from interviews in Moorea and Raiatea. Interviews collected information from individual respondents, with some questions relating to their household (only one person per household was interviewed). Interviews took place on Moorea in September 2019 and on Raiatea from June to September 2019. Percentages relate to the total sample size per island.

	Moorea (*n* = 96)	**Raiatea** (*n* = 183)
Respondents per district*		
Taputapuatea	-	*n* = 55 (30.1%)
Tumaraa	-	*n* = 41 (22.4%)
Uturoa	-	*n* = 87 (47.5%)
Women	*n* = 64 (66.7%)	*n* = 126 (68.9%)
Median age	40.5	44
Minimum age	18	13
Maximum age	84	83
Men	*n* = 30 (31.3%)	*n* = 54 (29.5%)
Median age	45.5	42
Minimum age	20	18
Maximum age	77	81
Other gender	*n* = 2 (2.1%)	*n* = 3 (1.6%)
[Ages redacted for anonymity]	-	-
Household information		
Median persons per household	5	4
Fishing only	*n* = 42 (43.8%)	*n* = 93 (50.8%)
Farming only	*n* = 10 (10.4%)	*n* = 8 (4.4%)
Fishing and farming	*n* = 30 (31.3%)	*n* = 24 (13.1%)
Neither fishing nor farming	*n* = 14 (14.6%)	*n* = 58 (31.7%)
Easy access to the sea		
Yes	*n* = 93 (96.9%)	*n* = 125 (68.3%)
No	*n* = 3 (3.1%)	*n* = 13 (7.1%)
NA	*n* = 0	*n* = 45 (24.6%)
Highest education in household		
High school+	*n* = 62 (64.6%)	*n* = 110 (60.1%)
Lower	*n* = 33 (34.4%)	*n* = 71 (38.8%)
NA	*n* = 1 (1.0%)	*n* = 2 (1.1%)
Main language spoken with family		
French	*n* = 11 (11.5%)	*n* = 19 (10.5%)
At least one Polynesian language	*n* = 85 (88.5%)	*n* = 162 (89.5%)

* Population sizes for administrative districts in 2017 were as follows: Moorea = 17,463; Taputapuatea = 4,792; Tumaraa = 3,721; Uturoa = 3,778 (Institute of Statistics of French Polynesia, 2017). Uturoa was considered an urban district, all other districts were rural.

Table S4.3: Food groups used in this study (right), based on the Global Individual Food consumption data Tool (GIFT; FAO, 2022) (left). GIFT food groups in grey text were not included in this study.

GIFT food group		**Food groups in present study**
1)	Cereals and products (rice, maize, wheat, sorghum, millet, other grains)	**1) Carbohydrates (Carbs)**
2)	Roots, tubers and products (potato, sweet potato, cassava, taro, yam, plantain, other starchy roots/tubers)	
18)	Savoury snacks (crisps, cereal-based, other)	
3)	Pulses, seeds, nuts and products (includes soybean)	**2) Legumes, nuts & seeds**
4)	Milk and products (yoghurts, kefir, cream, whey, cheese)	**3) Dairy**
5)	Eggs and products	**4) Eggs**
6)	Fish, shellfish and products (including pickled or dried)	**5) Fish (incl. other seafood)**
7)	Meat and products (offal, processed/tinned/dried meats)	**6) Meat (incl. chicken & tinned)**
8)	Insects, grubs and products (including spiders and worms)	-
9)	Vegetables and products (leafy veg/salad, fungi, canned/pickled/fermented veg, dairy/meat imitates)	**7) Vegetables**
10)	Fruits and products (dried, canned/jarred)	**8) Fruits**
11)	Fats and oils (vegetable/animal fat and oil)	-
12)	Sweets and sugars (sweet bakery/pastry products, chocolate, jams, syrups/honey, dairy-based sweets)	-
13)	Spices and condiments (herbs, sauces/relishes)	-
14)	Beverages (alcohol, water, tea/coffee, soft drinks)	-
15)	Foods for particular nutritional uses (weight loss, sport supplements, medical, other)	-
16)	Food additives (sweeteners/flavourings, additives, microbiological/yeasts)	-
17)	Composite dishes (meals based on foods listed above)	-

Table S4.4: Recommended nutrient intakes (RNI) and equivalents per day for the five nutrients included in this study. Recommendations for adult, pre-menopausal women were used for all respondents in our study, regardless of age or gender.

Nutrient	**Daily Recommended Nutrient Intake (RNI)**	**References**
Calcium, Ca	1000 mg	WHO/FAO, 2004
Iron, Fe	19.6 mg§	WHO/FAO, 2004; FAO, 1988
Zinc, Zn	4.9 mg‡	WHO/FAO, 2004
Vitamin A	270 µg†	WHO/FAO, 2004; FAO, 1988
Omega-3 fatty acids (DHA + EPA)	250 mg*	European Food Safety Authority, 2010

§ Iron RNI estimate is for a dietary iron bioavailability of 15%.

‡ Zinc RNI estimate is for a dietary zinc bioavailability of 30%.

† Vitamin A requirements given as retinol equivalents (RE): 4.8 µg per kg body weight.

* Adequate Nutrient Intake (AI) used for omega-3 fatty acids, as RNI cannot be defined.

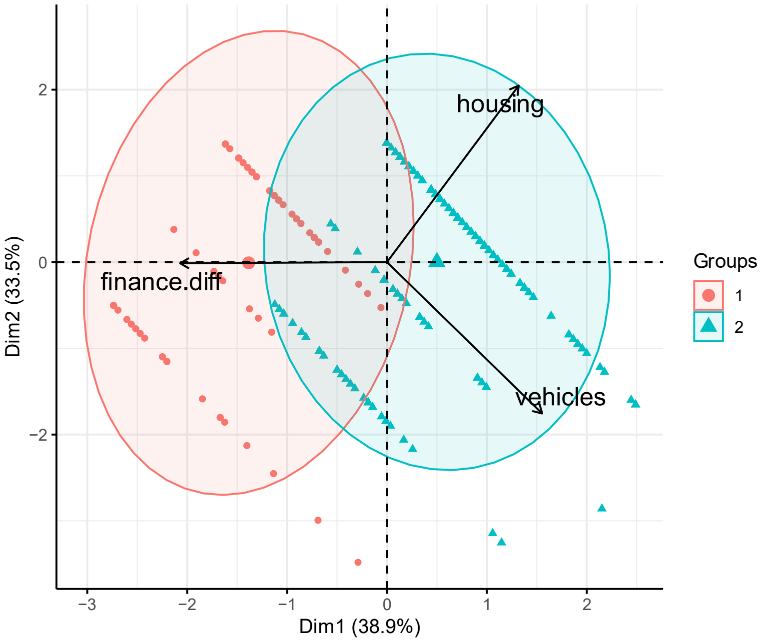

Figure S4.2: Principal component analysis (PCA) of variables used as a proxy for interview respondents' wealth ("finance.diff" = financial difficulties, "housing" = house ownership, "vehicles" = vehicle score). Arrows are loading vectors, representing the strength of each variable's association with principal components 1 (Dim1) and 2 (Dim2). Axis percentages correspond to the amount of variation in the data explained by each principal component. Values from principal component 1 were used to represent respondents' wealth in analyses. Points represent individual respondents, arranged into two groups: red (lower wealth on PC1) and blue (higher wealth on PC1), with large points indicating a typical respondent at the centre of each group.

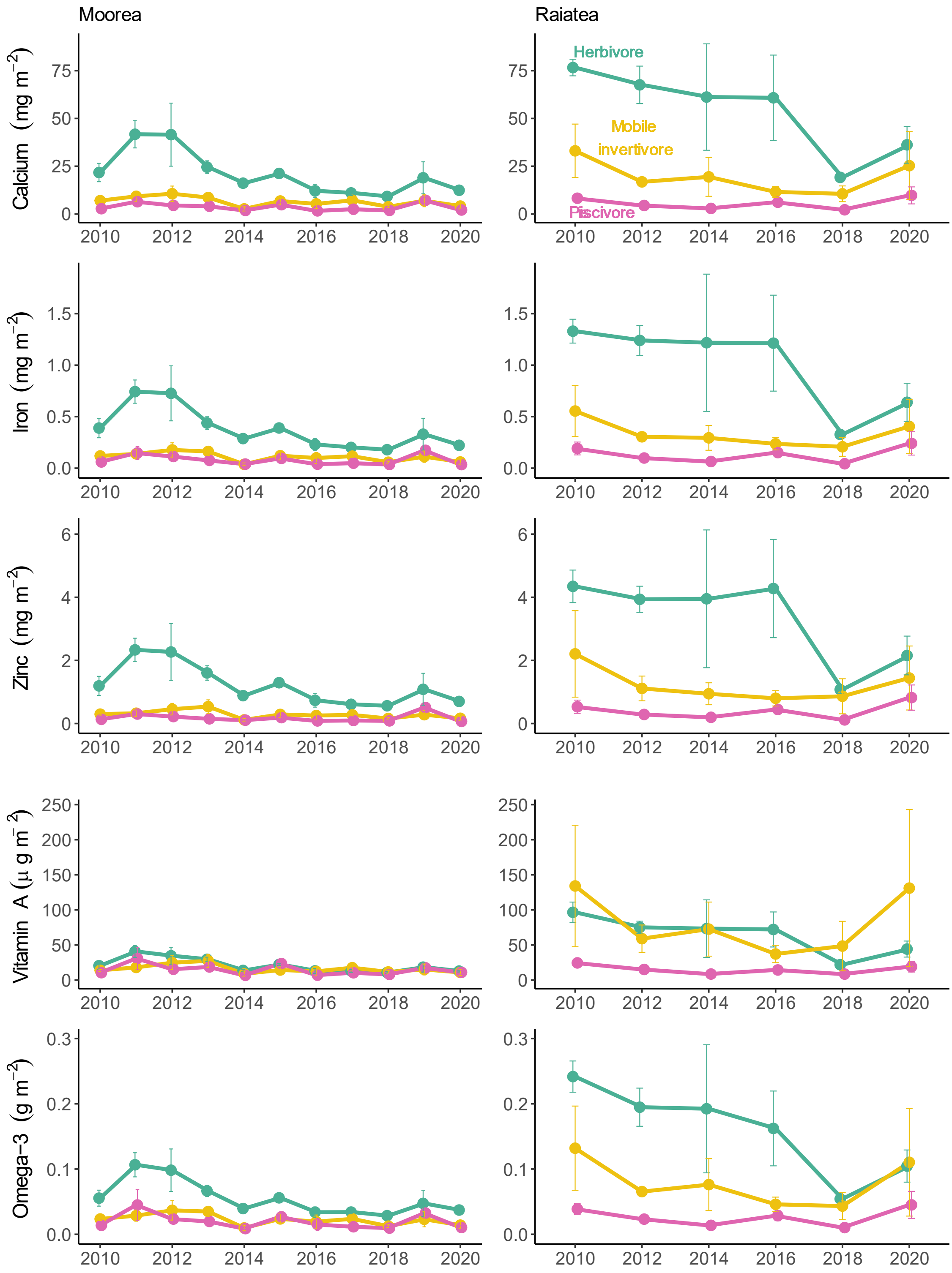

Figure S4.3: Estimated availability of five nutrients from fish on coral reefs around Moorea (left) and Raiatea (right) from 2010 to 2020. Only fish above the minimum fishable size (≥15 cm) with the potential to contribute to human nutrition were included, from three trophic groups: herbivores, mobile invertivores and piscivores. Errors bars are the standard error of the mean across transects. Species nutrient estimates are from FishBase (Froese and Pauly, 2022).

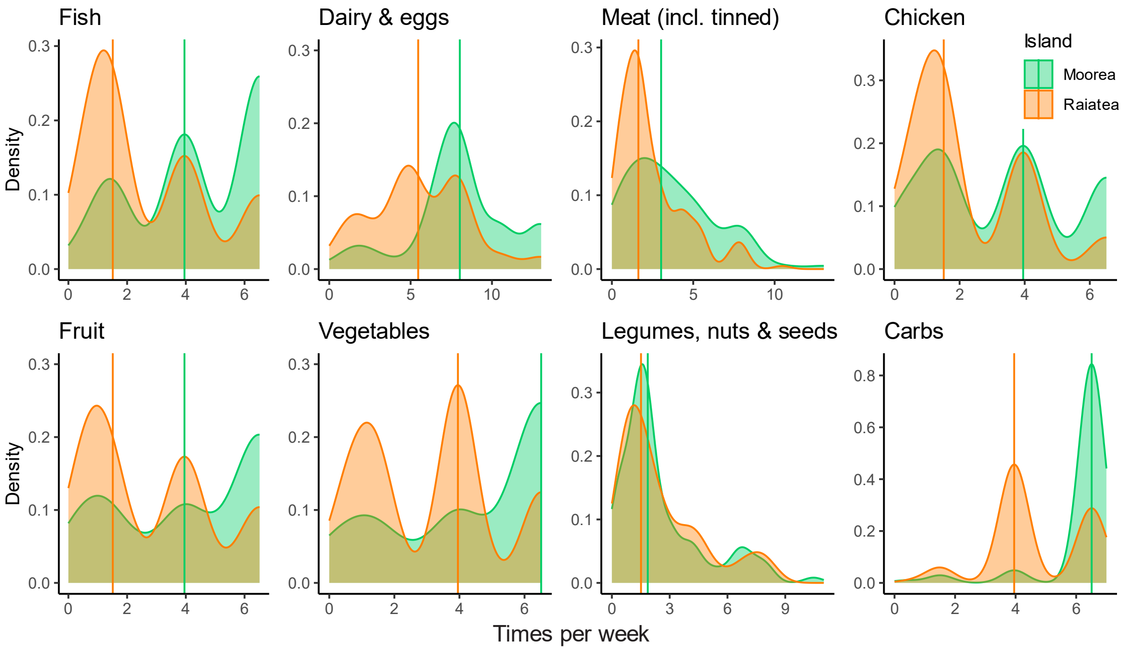

Figure S4.4: Frequency of consumption for each food group (times eaten per week) shown as the density of responses given by respondents during interviews in Moorea (*n* = 96) and Raiatea (*n* = 183) in 2019 (total density in each panel sums to 1 per island). Some food items have a maximum of 7 as the most frequent option was "every day" (fish, chicken, fruit, vegetables, and carbs). Other food items have values >7 as foods that were separate responses during interviews were combined: dairy + eggs, meat + tinned meat, and legumes + nuts/seeds. Vertical lines display the median frequency of consumption for each island.

Abbreviations

Ca	calcium
CPUE	catch per unit effort
CRIOBE	Centre de Recherches Insulaires et Observatoire de L'Environnement
CV	coefficient of variation
DAG	directed acyclic graph
DHA	docosahexaenoic acid (a type of omega-3 fatty acid)
EPA	eicosapentaenoic acid (a type of omega-3 fatty acid)
FAO	Food and Agriculture Organisation of the United Nations
Fe	iron
GBR	Great Barrier Reef
GIFT	Global Individual Food Consumption Data Tool
GLM	generalised liner model
GLMM	generalised linear mixed model
HPDI	highest posterior density interval
LEK	local ecological knowledge
ND	nutrient density
NGO	non-governmental organisation
NOAA	National Oceanic and Atmospheric Administration
NWM	Northwest Monsoon: season characterised by the north-westerly trade winds during the austral summer
O3	omega-3 fatty acids
PCA	principle component analysis
RDA	redundancy analysis
RNI	recommended nutrient intake (daily)
Se	selenium
SEM	Southeast Monsoon: season characterised by the south-easterly trade winds during the austral winter (not to be confused with the standard error of the mean, which is written in full wherever it appears)
SFA	Seychelles Fishing Authority
SST	sea surface temperature
VitA	vitamin A
WHO	World Health Organisation
Zn	zinc

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