Functional ecology of fish on coral reefs: the roles of seascape and subsistence fishing

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Abstract

Globally, fish are being removed from our oceans at unsustainable rates. This is particularly true for coral reef fish, which, in addition to overfishing, are also under threat from global warming, ocean acidification, and pollution. Current conservation strategies for coral reef fisheries either indirectly control the amount of fish caught through restrictions on fishing effort, techniques, and areas, or directly limit fish catch using quotas for each fishery. However, to ensure that these conservation strategies function to their utmost potential, we need to identify the fishing techniques and seascape characteristics that have the most impact on coral reefs and their associated fish assemblages.

This thesis used a field study on a group of remote Pacific atolls to establish how fishing using traditional techniques for food, not profit (subsistence fishing) affected coral reef fish assemblages. I demonstrate that subsistence fishing may be an effective way of providing food for small island communities, while also maintaining pristine reef fish assemblages. This thesis also investigated how connections in coastal seascapes affected crucial ecosystem functions on coral reefs. I show that connectivity can exert opposing effects on ecosystem functions, and that the distribution of fish and the ecosystem functions they provide may not align. I advocate that if marine spatial plans aim to incorporate ecosystem functions into their framework, they need to explicitly measure ecosystem function, rather than using proxies such as fish abundance. Finally, this thesis reports how the arrangement of mangroves and coral reefs in coastal seascapes varied globally, and how these differences affected the distribution of fish. I show that the configuration of coastal mangrove and coral reef seascapes, and their effects on fish, are correlated with tidal range, and I suggest that we cannot make global generalisations about the scale at which mangrove connections modify fish assemblages on coral reefs.

This thesis makes direct recommendations on how to improve the conservation of coral reef fish. By endorsing low-impact fishing techniques and improving our understanding of seascape ecology, we can expect to improve conservation strategies for coral reefs, making them as practical and effective as possible.
Statement of originality

This work has not previously been submitted for a degree or diploma in any university. To the best of my knowledge and belief, this thesis contains no material previously published or written by another person except where due reference is made in the thesis itself.

Tyson S. H. Martin    October 26, 2017
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Acknowledgement of co-authored papers

Included in this thesis is 1 published paper (Chapter 2) and 2 papers currently under review (Chapters 3 and 4). All are co-authored with other researchers and my contribution to these papers is outlined at the start of each relevant chapter. Each paper is formatted for its target journal. The bibliographic details for each paper are as follows:

Subsistence harvesting by a small community does not substantially compromise coral reef fish assemblages. ICES Journal of Marine Science, 74:2191-2200.

**Martin TSH, Olalde ABH, Olds AO, Gilby BL, Butler IR, Yabsley NA, Schlacher TS, Connolly RM**
(under review) Habitat connectivity exerts opposing effects on piscivory and browsing. Landscape Ecology.


Acknowledgement of contributions made by those who did not qualify for author status is included in each published paper.

Tyson S. H. Martin

Supervisor: Prof. Rod M. Connolly
Related publications

Peer reviewed publications:


Conference presentations based on this thesis:


Martin TSH, Olds AD, Connolly RM (2015) Fishing and seascape thresholds on coral reefs, Stockholm University, invited speaker (1 hour seminar).


Foreword: The busy lives of coral reef fish

Reef fish lead busy lives, often swept across large areas of open ocean as larvae before recruiting to reefs and other inshore habitats such as mangroves and seagrass beds. Then, as they age, their habitat requirements may change, causing them to move to new areas that better suit their lifestyles. As adults, they will eventually end up living on coral reefs, with herbivorous fish munching away on algae, and predatory fish lurking, ready to pounce on an unsuspecting meal. These fish are always very busy, connected through trophic interactions with other fish, and ecological interactions with their surrounding habitats. Whether assessing fishing impacts or designing conservation plans, it is crucial to remember these connections.
Chapter 1 Introduction to subsistence harvesting, seascape connections and the ecosystem functioning of coral reefs

Reef flat in the Republic of the Marshall Islands (Image: Daniela Ceccarelli)
The effects of fishing on coral reefs

Coral reefs are under increasing pressure from pollution, global climate change and overharvesting (Harborne et al. 2017, Hughes et al. 2017). These stressors exert negative impacts on reefs over a variety of temporal and spatial scales (Nystrom & Folke 2001, Wilson et al. 2006, Hoegh-Guldberg et al. 2007, Pandolfi et al. 2011). In many cases the most direct and ubiquitous impact is that of overfishing (Jackson et al. 2001, Valentine & Heck 2005). Overfishing usually results in the systematic removal of larger-bodied predatory fish, and this loss of top-down predation pressure can upset the balance of reef food webs via altered trophic cascades (Pauly et al. 1998, Mumby et al. 2006, Fenner 2014, McClanahan & Muthiga 2016). In addition, overfishing of herbivorous fish can also affect the health of corals and food web structure (Edwards et al. 2014). By consuming the corals main competitor, algae, herbivorous fish promote coral growth and recruitment, helping reefs to resist and recover from disturbances (Adam et al. 2011, Edwards et al. 2014, Heenan et al. 2016). Understanding and managing fishing across all trophic levels, is therefore critical to promote the healthy functioning and longevity of coral reef ecosystems (Foley 2013).

The effects of fishing also depend of the type of fishing practised. Commercial fishing regularly targets large predators such as tuna, sharks and groupers which are of high value (Mumby et al. 2012, Burgess et al. 2013, Clarke et al. 2013). The monetary incentive to capture these particular types of fish results in increased fishing effort, as well as the use of specialised technology and fishing gear, so that even as fish stocks decline, short-term catch rates can remain high (Burgess et al. 2013). This overfishing eventually results in the collapse of the target species, causing the industry to change target species and/or fish increasingly remote locations (Fabinyi 2012). However, despite the increasing reach and impacts of commercial fishing, people in many island nations still rely on subsistence fishing, where fish are captured using traditional equipment for food, not profit (Berkes 1988). This practice has been ongoing for hundreds of years and rather than specifically targeting certain high-value species, subsistence fishers usually catch a wide variety of fish, placing importance on obtaining enough protein, rather than on monetary value (Dalzell 1996). Due to our long history of overharvesting reef fish, and the fact that the majority of coral reefs are now in a heavily degraded state (Hughes et al. 2010), opportunities to compare the effects of commercial and subsistence fishing with pristine baselines are rare.
Recent studies on remote coral reefs have provided a baseline of the fish assemblage structure and functioning of coral reefs in the absence of human impacts (e.g. Sandin et al. 2008, Houk & Musburger 2013). Fish assemblages on healthy coral reefs are dominated by sharks and other large fish from higher trophic levels, including: trevally (Carangidae), snapper (Lutjanidae), grouper (Serranidae) and large-bodied wrasse (Labridae) (Friedlander & DeMartini 2002, Stevenson et al. 2007, DeMartini et al. 2008, Sandin et al. 2008). However, these large reef fish are prime targets for coral reef fishers, and are usually the first to be harvested, with fish communities becoming progressively smaller in size as these large animals are systematically removed (Pauly et al. 1998, Fenner 2014). In many cases, these large fish that dominate untouched reefs are wide-ranging, using multiple habitats throughout their lifecycles (Huijbers et al. 2015), and conservation initiatives that do not account for the mobility of these species throughout reef seascapes may not perform to their full potential.

**Improving marine reserve design using seascape characteristics**

Marine reserves are now a common tool for conservation, and have been widely implemented to restore biodiversity and promote healthy functioning of ecosystems (Sala et al. 2002, Foley et al. 2010). The large body of work examining the effectiveness of marine reserves has shown that they can significantly enhance the biomass of harvested fish (e.g. Alcala 1988, Halpern 2003, McClanahan et al. 2006, Emslie et al. 2015), particular if they are well-enforced, no-take, large (>100 km²), old (>10 years) and isolated by deep water or sand (Edgar et al. 2014). The effectiveness of marine reserves can also be improved through the adoption of smart design principles that draw from the discipline of landscape ecology (Wedding et al. 2011). Connectivity links populations and habitats through the movement of organisms (Massol et al. 2011, Olds et al. 2012a), and is a function of the spatial configuration of habitats, as well as the mobility and dispersal capabilities of the organisms that use them (Hodgson et al. 2009, Sheaves 2009). Landscape ecology has long recognised the importance of connectivity between habitats, which is critical to the distribution, demography and persistence of organisms (Lundberg & Moberg 2003, Lindenmayer et al. 2008). The use of connectivity to improve reserve design, however, has only recently been
applied to the sea (Wedding et al. 2011, Olds et al. 2017). For example, the performance of marine reserves on coral reefs can be improved by modifying their design to incorporate connections with neighbouring ecosystems, such as seagrass and mangroves, that are critical for the nutrition and recruitment of exploited fish species (e.g. Grober-Dunsmore et al. 2009, Nagelkerken et al. 2012, Olds et al. 2013, Martin et al. 2015). This growing body of literature demonstrates that the performance of marine reserves is contingent on the configuration of the surrounding seascape (Olds et al. 2016), and that incorporating these connections into conservation planning may enhance the ecological outcomes they provide (Magris et al. 2016).

The function of reserves, however, is not only to increase the biomass and diversity of fish assemblages, but to also promote healthy ecosystem functioning (Olds et al. 2012c, Yabsley et al. 2016). Fish provide crucial ecosystem functions such as predation and herbivory. Depending on the resources that they consume, the feeding behaviour of fish can alter basal communities either directly (e.g. by consuming benthic algae) or indirectly (by consuming herbivores) (Yabsley et al. 2016). Consequently, the importance of connectivity for fish distribution and abundance is also likely to extend to the ecosystem functions they provide (Edwards et al. 2010).

**The effects of connectivity on ecosystem functions**

Empirical tests that assess the effects of connectivity on marine ecosystem function are rare, with most studies using patterns in species richness and abundance as surrogates for ecological functions (Olds et al. 2016). In tropical seascapes, most research has focussed on quantifying the effects of seascape connectivity, that is, connections between reefs and other habitats (generally mangroves and seagrass beds), on the abundance and distribution of important functional groups of fish (Mumby et al. 2004, Nagelkerken 2009, Kimirei et al. 2011, Berkstrom et al. 2012). Some studies have shown that the effects of seascape connectivity can extend to the relevant ecosystem functions that animals provide (Olds et al. 2012c, Yabsley et al. 2016), however, no research has yet quantified the simultaneous effects of connectivity on multiple ecosystem functions in coastal seascapes. In addition, for the vast majority of coastal ecosystem processes, it is unknown if habitat connections
(between habitats of the same type) or seascape connections (between habitats of different types) are more important, or if they are overridden or modified by within-habitat characteristics such as depth, topography and rugosity, or anthropogenic influences such as fishing impacts (Figure 1.1). Further, as ecosystem functions operate simultaneously, and are provided by organisms that likely respond differently to habitat and landscape connectivity, what may adversely affect one ecosystem function may be beneficial for others (Beger et al. 2010).

Figure 1.1: Schematic of the different types of connections; habitat (e.g. reef - reef), landscape and seascape (e.g. reef - seagrass/mangrove), anthropogenic (e.g. reef - fishing access points) that can influence animal distributions and the functions they perform.
Do seascapes differ in configuration and size and how does this affect fish?

Mangroves, seagrasses and coral reefs are important fish habitats in tropical and subtropical seascapes, and each has specific geographical requirements. For example, coral reefs must lie in sufficient water to avoid prolonged exposure to the sun as the tide rises and falls, mangroves require low-energy shorelines, and seagrasses need shallow, clear water for photosynthesis. The distribution of these habitats throughout seascapes is, therefore, likely to be driven by three main factors: (1) tidal range, which impacts both the depth and clarity of the water; (2) local topography, which affects the bathymetry, prevailing winds, and waves of the local area; and (3) marine bioregion, which determines the climate, and therefore species of corals, mangroves, and seagrasses available to colonise the area (Spalding et al. 2007, Igulu et al. 2014). The resulting spatial configuration of these habitats is likely to affect how local fish use them. For example, mangroves that are only accessible at high tide to fish are more likely to be used for brief tidal feeding migrations (Olds et al. 2012a, Martin et al. 2015), rather than the ontogenetic use as nurseries common throughout the Caribbean where mangroves are permanently submerged (Nagelkerken 2007, Jaxon-Harm et al. 2012, Huijbers et al. 2015).

The distance between reefs, mangroves and seagrasses may also affect how far fish are willing to swim to utilise multiple habitats. For example, a coral reef that lies as close as possible to mangroves in a ‘broad’ seascape (where reefs and other habitats are separated by hundreds of metres), may be regarded as ‘distant’ from mangroves in another, more compressed, seascape where habitats are much closer together (Figure 1.2) (Martin et al. 2015). Thus, what constitutes ‘high connectivity’ may vary between seascapes of different sizes. These varying thresholds of connectivity may also affect the distribution of fish, and the ecosystem functions they provide, across the seascape. For species of fish that perform either ontogenetic or diurnal movements between reefs and mangroves, the closest reefs to mangroves may have special importance, either as a stepping stone for juveniles as they migrate further offshore (e.g. snappers, sweetlips) (Huijbers et al. 2015), or a home base to launch tidal feeding forays into the mangroves (e.g. sparids) (Olds et al. 2012a, Martin et al. 2015). Consequently, some species may position themselves to be as close to mangroves as the configuration of the seascape allows (Figure 1.2) (Martin et al. 2015). By improving our understanding of the impact of seascape configuration on connectivity, we may enhance
our capacity to identify priority areas for conservation across tropical seascapes around the globe (Olds et al. 2016).

Figure 1.2: Generalised conceptual diagram illustrating the importance of scale when incorporating mangrove-reef connectivity into conservation planning. Fish may position themselves to be as close as possible to mangroves. Modified from Martin et al. (2015). Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/)

**Thesis scope, rationale and objectives**

This thesis compares fish and coral assemblages in subsistence, commercially harvested and near-pristine areas, and explores how we can improve coral reef conservation by promoting subsistence-based harvesting and incorporating connectivity between habitats into marine spatial planning. I use field and desktop experiments to investigate fishing and seascape connectivity, and explore how they affect the trophic and ecological interactions that govern the health of corals and associated fish assemblages.

To assess the effects of subsistence and commercial fishing against a near pristine baseline, I compare fish and coral assemblages at three remote atolls in the Republic of the Marshall Islands (RMI) (Figure 1.3). The atolls of the RMI are surrounded by deep water (thousands of metres) and separated by hundreds of kilometres. They have similar biogeography, ocean currents and water temperatures, and differ only in the fishing methods and pressure exerted on each atoll. Therefore, they provide an ideal opportunity to test how various types of fishing affects the trophic dynamics of fish and corals.
To measure how different types of connectivity impact ecosystem function, I used a measurative field experiment in Hervey Bay, Queensland (Figure 1.4). Hervey Bay contains fringing coral reefs, mangrove forests and seagrass beds which are linked hydrologically and biologically by daily tidal and fish movements (Martin et al. 2015). Connectivity between reefs, mangroves and seagrass beds affects predatory and herbivorous fish distribution in the region (Olds et al. 2012b, Engelhard et al. 2016), but, it is unknown if the effects of connectivity are consistent across the multiple functions they provide. I counted fish and deployed assays measuring herbivory and predation on reefs with varying levels of habitat and seascape connectivity to (i) ascertain whether connectivity exerts similar effects on multiple ecosystem functions, and (ii) establish whether patterns in ecological functions align with those of the animals that provide them.
To test for global and regional differences in the spatial configuration of mangroves and coral reefs in coastal seascapes, I performed a global meta-analysis which quantified differences in the spatial properties of these adjoining ecosystems in 25 tropical and subtropical locations, spanning three marine realms (Spalding et al. 2007). I then collected fish data from 12 locations (a subset of the original 25), representative of the typical seascape types and sizes found around the world. To investigate how differences in the configuration of mangroves and reefs affected fish distribution, and measure how quickly the effects of mangrove-reef connectivity diminish as distance from mangroves increase, I modelled the distribution of fish in each location against seascape variables collected in the meta-analysis.

Specifically, this thesis:

- provides evidence of how low-pressure subsistence fishing of relatively pristine systems affects the trophic structure and biodiversity of coral reefs (**Chapter 2**)
- examines how habitat and seascape connectivity shapes multiple ecosystem functions across seascapes (Chapter 3)
- quantifies global differences in the configuration of mangroves and coral reefs in coastal seascapes (Chapter 4)
- tests how quickly the effects of mangrove-reef connectivity on fish diminish as the distance between mangroves and reefs increases (Chapter 4)
References


Foley CMR (2013) Management implications of fishing up, down, or through the marine food web. Mar Policy 37:176-182


Chapter 2 Subsistence harvesting by a small community does not substantially compromise coral reef fish assemblages

This chapter is a co-authored published paper formatted for the ICES Journal of Marine Science. My contribution involved: designing the study, conducting the fieldwork, data analysis, interpretation of results, writing the manuscript and submission to the journal. The bibliographic details of the paper, including all authors, are:

Subsistence harvesting by a small community does not substantially compromise coral reef fish assemblages. ICES Journal of Marine Science, 74: 2191-2200

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Abstract

Fisheries usually first remove large predators before switching to smaller species, causing lasting changes to fish community structure. Reef fish provide essential protein and income for many people, and the impacts of commercial and high-intensity subsistence fishing on reef fish are well documented. However, how fish communities respond to low levels of subsistence fishing using traditional techniques (fishing for food, few fishers) is less well understood. We use three atolls in the Marshall Islands as a model system to quantify effects of commercial and subsistence fishing on reef fish communities, compared to a near-pristine baseline. Unexpectedly, fish biomass was highest on the commercially-fished atoll where the assemblage was dominated by herbivores (50% higher than other atolls) and contained few top predators (70% lower than other atolls). By contrast, fish biomass and trophic composition did not differ between pristine and subsistence-fished atolls—top predators were abundant on both. We show that in some cases, reefs can support fishing by small communities to provide food but still retain intact fish assemblages. Low-intensity subsistence fishing may not always harm marine food webs, and we suggest that its effects depend on the style and intensity of fishing practised and the type of organisms targeted.
Introduction

Excessive hunting or harvesting can have detrimental effects on animal populations in all biomes (Jackson et al., 2001; Myers et al., 2007; Estes et al., 2011; Ripple et al., 2014). Typically, the first animals removed by hunting are large, long-lived species (Pauly et al., 1998; Alroy, 2001; Myers and Worm, 2003). These are often top-predators and their removal by humans for trophy hunting, food, or livestock protection can result in substantial changes to entire ecosystems via altered trophic cascades (Pace et al., 1999; Babcock et al., 2010; Brashares et al., 2010). Well-known examples of this phenomenon from around the globe include: hunting of lions and leopards in Africa (Brashares et al., 2010); shooting of wolves in America (Ripple and Beschta, 2004); exclusion of dingoes in Australia (Letnic and Koch, 2010); and fishing of sharks in the North-west Atlantic (Myers et al., 2007).

Top predators are harvested heavily in all marine ecosystems, and cascading effects of fishing are documented for kelp forests (Steneck et al., 2004), seagrass beds (Atwood et al., 2015), estuaries (Atwood et al., 2015), and coral reefs (Dulvy et al., 2004). Yet, many studies of the effects of fishing focus solely on commercially valuable species such as Atlantic cod (Myers et al., 1997), tuna (MacKenzie et al., 2009) and sharks (Baum et al., 2003). Despite the encroaching footprint of commercial fishing, people in less developed countries continue to rely on subsistence fishing, where fish are captured by small communities for food (Berkes, 1988) and they can often exert considerable fishing pressure on local systems (e.g. McClanahan et al., 2011; Allen, 2013; Zeller et al., 2015). These fishers frequently use traditional equipment (often without modern fishing technology), catching fish from all trophic levels whilst rarely specifically targeting top-predators (although this does depend on the cultural context, for exception see Glaus et al., 2015) (Dalzell, 1996). Subsistence harvesting over long periods can alter food web dynamics (e.g. Simstead et al., 1978), with strongly negative ecological effects of extensive subsistence harvesting reported on land (Fitzgibbon, 1998) and for some marine ecosystems (Dulvy et al., 2004; Mann and Powell, 2007; Peckham et al., 2007; Drew et al., 2013).

Reef fish are the primary source of protein for millions of people that live on tropical islands and coral atolls, and reefs provide approximately 10% of all fish consumed by humans (Moberg and Folke, 1999; Albert et al., 2015). The effects of fishing on coral reef ecosystems
have been comprehensively assessed. Heavy fishing negatively impacts reefs by altering the structure and function of reef food webs (e.g. McClanahan, 1995; Friedlander and DeMartini, 2002; Stevenson et al., 2007; D’Agata et al., 2014; Fenner et al., 2014). The majority of studies, however, have not differentiated between small-scale artisanal fishing (small commercial operations fishing for profit), and subsistence fishing (fishing only for food, no monetary incentive to capture or refrigeration to store excess fish) that is still practised by many small coastal communities. A potential reason for this is the difficulty of quantifying fishing effort for coral reefs, it can be hard to tell if people are fishing for food, local barter or in small-scale commercial operations (Teh et al., 2013). Where fishing for profit occurs, distance to the nearest market is often shown to be the strongest driver of patterns in fish assemblages (e.g. Cinner and McClanahan, 2006; Brewer et al., 2012; Cinner et al., 2013). Studies investigating subsistence fishing have concluded that at high levels, it can affect the size and structure of reef fish communities (Jennings and Polunin, 1996 & 1997; Dulvy et al., 2004a,b; Graham et al., 2005). However, less is known about how subsistence fishing at very low levels compares to reefs that are truly pristine (Sandin et al., 2008; Graham & McClanahan, 2013). Instead, studies often assess fishing impacts by comparing reef fish assemblages between reserve and fished areas (McClanahan et al., 2011). It is, therefore, unclear if low-pressure subsistence fishing by small communities using traditional gear alters coral reef food webs from a pristine state in the same way that small and large scale artisanal fishing does.

Here we explore how pristine reef communities are modified by fishing with respect to structure and biomass, including the entire communities of large non-cryptic species. We contrast three differently exploited remote coral atolls in the Republic of the Marshall Islands, central Pacific Ocean, to quantify the effect of low-impact subsistence harvesting on reef fish biomass and trophic composition, compared to commercial fishing and a near pristine baseline. By comparing differences in fish communities in a rare system containing pristine (inaccessible or uninhabited) reefs, low historical pressure, and contrasting modern fishing patterns, we provide evidence of how low-pressure fishing of relatively pristine systems affects the trophic structure and biodiversity of coral reefs. It is clear that high biomass indicates near-pristine conditions (Graham and McClanahan, 2013), however here we provide evidence that high biomass may not necessarily indicate intact community
structure, and that the low pressure exerted on reefs by small numbers of subsistence fishers does not dramatically alter reefs from a pristine state.

**Methods**

We consider three remote coral atolls in the Republic of the Marshall Islands on a gradient from unexploited to heavily fished (Figure 2.1). These atolls are exposed to similar environmental conditions (e.g. biogeography, ocean currents, and water temperatures) (Tables 2.1 & 2.2); therefore, if they were left undisturbed, they are likely to support analogous fish communities and vary only according to the size, and fishing techniques, of local human populations (Aswani and Sabetian, 2010; Cinner et al., 2013; Guillemot et al., 2014). Consequently, these atolls provide a natural laboratory ideal for examining fishing impacts. We surveyed complete large non-cryptic fish assemblages at three atolls: 1. a near-pristine atoll (Rongelap) that has been largely uninhabited for 60 years (Pinca et al., 2004); 2. an atoll (Ailuk) with a small human population that uses traditional subsistence fishing techniques to catch fish (mostly herbivores) from low trophic levels (Pinca, 2006); and 3. an atoll (Majuro) with a large human population where fishing is intense (compared with other atolls in the republic) and commercial fishers target large, predatory fishes (Pinca, 2005) (Table 2.1). Historically, all atolls have supported small human populations of around 100 inhabitants for centuries.
Fish Surveys

Coral reef fish assemblages were surveyed in July and August of 2014 with visual census surveys. Surveys were conducted on SCUBA at depths of both 3 m and 10 m at 17 haphazardly selected outer reef crest sites spread evenly between the three atolls (Majuro: n = 6, Ailuk: n = 5, Rongelap: n = 6). These sites were spaced approximately 10 km apart. For each site and depth, we identified, counted and recorded the size of all fish larger than 10
cm along three replicate belt transects (250 m long x 5 m wide, 102 transects in total). Belt transects are known to occasionally overestimate the abundance of large, mobile macrofauna such as sharks (Ward-Paige et al., 2010), and underestimate timid or heavily fished species (Kulbicki et al., 1998; MacNeil et al., 2008). For these reasons, we use longer 250 m transects to better estimate large species (Choat and Pears, 2003) instead of the 50 m long transects more typically used in coral reef fish surveys. The three SCUBA transects (10 m depth) were conducted on the same dive, with transects following the reef edge and separated by 50 m. The time required to complete transects is not reported as this varied according to the amount of fish in the area (Jennings & Polunin, 1996). Three matching transects (3 m depth) were conducted on the return swim. All counts were made by the same diver. We visually estimated fish size (to the nearest centimetre) and converted these to biomass values using published length-weight relationships (Froese and Pauly, 2000; Kulbicki et al., 2005). Fishes were placed into three non-overlapping trophic groups according to trophic level values and published literature: top predators, mesopredators and herbivores (Froese and Pauly, 2000; Palomares, 2000; Choat et al., 2002; Stevenson et al., 2007) (for species list see Appendix A). Qualitative benthic assessments were made at 50 m intervals along each transect using visual estimates and included data on hard coral and algal cover (%), coral diversity and reef complexity (where 0 = no vertical relief, 1 = sparse low profile relief, 2 = widespread low profile relief, 3 = moderately complex, 4 = very complex with numerous cracks and caves, 5 = exceptionally complex with numerous caves, cracks and overhangs) (Polunin and Roberts, 1993).

**Natural environment and human impacts on the atolls**

Several recent studies have shown that fish assemblages may change between islands with different geomorphologies (e.g. Taylor et al., 2015; Heenan et al., 2016). Our islands, however, all have very similar geomorphologies. This is likely to have only minor effects on fish assemblages when compared to the pervasive impacts of fishing. In fact, most studies testing assembly patterns in coral reef assemblages over large geographical distances assume that changes in environmental conditions are negligible compared to the human or other drivers being tested (e.g. Jennings et al., 1996; Friedlander & DeMartini et al., 2002;
Stevenson et al., 2007; Sandin et al., 2008). To confirm that this approach is indeed valid for our three target atolls, we quantified geographic and environmental attributes for each atoll (Tables 2.1 & 2.2) (sensu Sandin et al., 2008). Key environmental attributes, sea surface temperature, chlorophyll a concentrations, pH and salinity were extracted from BioORACLE (a global environmental dataset), with averages taken from 2002-2009 for each (Tyberghein et al., 2012). The range in environmental variables among atolls in the current study was less than or equal to that for other island/atoll groups in the Pacific, including those previously used to test the effects of fishing such as the Line Islands (Stevenson et al., 2007; Sandin et al., 2008) and Hawaiian Islands (Friedlander & DeMartini, 2002). The atolls we surveyed are located within 4° of latitude, average monthly water temperature differs by less than 1°C, and they are all predominantly affected by the eastward flowing North Pacific Equatorial Countercurrent. They are also relatively isolated from other nearby other atolls, and are fished primarily by local communities (although some illegal fishing does occur in the remote areas of the RMI by boats operating from Guam and the Philippines (Viegas, 2016)). There are no confounding influences from land-based runoff, as the low-lying coral atolls of the RMI (average height is less than 2 m above sea level) are too small and porous to generate terrestrial sediment run-off (Table 2.2). The level of fishing pressure present at each atoll was determined from informal field interviews with local fisheries management staff and published data on the type of fishing, amount and species of fish harvested, and human population size at each atoll (Pinca et al., 2004; Pinca, 2005; Pinca, 2006; Beger et al., 2008) (Table 2.2). The small population (~144) on Rongelap Atoll was evacuated on March 3, 1954, because of fall-out from nuclear testing on nearby Bikini Atoll (Castle Bravo detonation, March 1, 1954). With the resulting lack of fishing pressure, diverse assemblages of fish and coral populations have thrived (Beger et al., 2008; Houk and Musburger, 2013). The atoll has been largely uninhabited for the last 60 years except for an unsuccessful attempt at resettlement between 1957 and 1984. A small group of approximately 10-40 construction workers has worked intermittently on the atoll since 2002, but fishing pressure has remained very low because construction workers relied primarily on imported food. Ailuk Atoll currently supports a steady population of approximately 350 people who practise subsistence fishing using traditional vessels and techniques typically used in the Marshall Islands, such as throw nets, drag nets, scoop nets, hook and line, and fish traps (although gear used to make this equipment has been supplemented by modern materials) (Petrosian-
Husa, 2004). Fishermen on this atoll predominantly target small siganids known locally as “Mole” (*Siganus argenteus*), although any fish they catch will be consumed immediately, there is no refrigeration on the island. Majuro has a growing population of ca. 30,000 residents (EPPSO, 2011). Its reefs experience intense commercial fishing across all trophic levels, but especially targeting large predators using modern equipment such as powered vessels and depth sounders. The targeted fishing of sharks is now banned in the RMI, however many are still caught as bycatch from longline vessels which operate throughout the entire region (Bromhead *et al.*, 2012).
Table 2.1: Environmental similarities between atolls in the Marshall Islands relative to those in other Pacific island groups previously used to compare human drivers across islands/atolls.

<table>
<thead>
<tr>
<th>Environmental Variable</th>
<th>Marshall Islands</th>
<th>Line Islands (Stevenson et al., 2007; Sandin et al., 2008)</th>
<th>Hawaiian Islands (Friedlander and DeMartini, 2002)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>SST (°C)</strong></td>
<td>Majuro vs. Rongelap 0.8</td>
<td>Kingman vs. Tabuaeran 0.4</td>
<td>Hawaii vs. Kure 2.2</td>
</tr>
<tr>
<td>Chl a (mg/m³)</td>
<td>Ailuk vs. Rongelap 0.09</td>
<td>Kingman vs. Palmyra 0.08</td>
<td>Hawaii vs. Kure 0.08</td>
</tr>
<tr>
<td>pH</td>
<td>Ailuk/Rongelap vs. Majuro 0.01</td>
<td>Kingman vs. Kiribati 0.01</td>
<td>Hawaii vs. Kure 0.02</td>
</tr>
<tr>
<td>Salinity (PSS)</td>
<td>Ailuk vs. Majuro 0.1</td>
<td>Kingman vs. Kiribati 0.4</td>
<td>Hawaii vs. Kure 0.5</td>
</tr>
</tbody>
</table>

Quantitative environment data are presented as means. Abbreviations are as follows: SST, Sea surface temperature; Chl a, Chlorophyll a; pH, potential hydrogen. Details on calculations are provided in the methods.
Table 2.2: Human population density, geography, fishing pressure and environmental differences across atolls

<table>
<thead>
<tr>
<th>Atoll</th>
<th>Reef area (km²)</th>
<th>Land area (km²)</th>
<th>Population 1988</th>
<th>Population 2011</th>
<th>Human pressure (ind./reef area (km²))</th>
<th>Fishing pressure and activity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rongelap</td>
<td>121</td>
<td>21.0</td>
<td>0</td>
<td>79</td>
<td>0.7*</td>
<td>Very low intensity and sporadic fishing of reef species (Pinca <em>et al.</em>, 2004; EPPSO, 2011).</td>
</tr>
<tr>
<td>Ailuk</td>
<td>56</td>
<td>5.4</td>
<td>488</td>
<td>339</td>
<td>6.1</td>
<td>Subsistence fishing of reef species using low technology gear (e.g. outrigger canoes, throw nets, gill nets and handlines) to provide food for residents (Pinca, 2006; EPPSO, 2011). Mole (siganids) and other small herbivores are the preferred food fish on this atoll.</td>
</tr>
<tr>
<td>Majuro</td>
<td>64.2</td>
<td>9.7</td>
<td>19664</td>
<td>27797</td>
<td>433</td>
<td>Intense subsistence and commercial fishing of reef species using modern means (e.g. power craft) to provide food for nearly 30,000 locals and supply international export trade (Pinca, 2005; EPPSO, 2011).</td>
</tr>
</tbody>
</table>

* Rongelap Atoll only recently re-populated. Predominately uninhabited from 1954-2002 except for minor resettlement in 1957 and then re-evacuation in 1984. A small group of construction workers have been present since 2002; however, these crews rely primarily on imported food.
Data analyses

We modelled variation in fish biomass (separately for trophic groups and all species combined) and included variables that relate to habitat attributes and putative human stressors. Habitat attributes used in models were: hard coral cover (%); reef complexity and depth (3 and 10 m). Other variables included in the models were atoll and distance to market/access point for each site. Distance to market was used on Majuro atoll (where commercial fishing occurs), whereas distance to access point was used on Ailuk and Rongelap where no fish markets were present, but locals all accessed the water from the same starting location. Generalised additive mixed models (GAMMs) were used to identify predictors of fish biomass (Wood, 2006). GAMMs were chosen to allow for potentially non-linear relationships, and to account for both fixed and random effects.

Site was included in all models as a random effect, to represent spatial variability within atolls that was not captured by our chosen predictor variables, and to also account for the potential autocorrelation of sites from the same atoll. Model overfitting was reduced by running all possible combinations of ≤ 4 factors and by restricting the number of spline knots (individual polynomial functions that combine to form the GAMM smooth) to four or less (k = 4) (Burnham and Anderson, 2002). Models were compared using the corrected Akaike information criterion (AICc) for small sample sizes (Burnham and Anderson, 2002). The relative importance of all variables included in each model set was calculated by summing weighted AICc values from each model containing the variable, where a higher value indicates a greater contribution (maximum of 1) (Gilby et al., 2015). Variables included in fixed effects components of the ‘best-fit’ model were also tested for significance (P <0.05). To increase confidence in each best-fit model, they were compared to ‘null’ models and the number of models within two AICc units of each best-fit model is also reported. Models were implemented using the mgcv and the MuMln packages in R (Barton, 2015; Wood, 2015).

To determine if the species composition of trophic group assemblages varied among atolls, and identify species responsible for any differences, species-level biomass data were examined using permutational multivariate analysis of variance (PERMANOVA) (Anderson et
Multivariate data on benthic assemblages (combined metric of coral cover, coral diversity and algal cover) were also compared between atolls using PERMANOVA. Pairwise tests on differences between fish assemblages for individual atolls were performed following PERMANOVA (Martin et al., 2015). Canonical analysis of principal coordinates (CAP) was used to visualise differences in assemblages among atolls (Anderson and Willis, 2003). All multivariate analyses were based on modified Gower (log base 2) similarity measures, which, by allocating equal weights to compositional changes in species and doubling weight to changes in abundances, emphasise changes in species abundance and cope well with multivariate heterogeneity of variance (Anderson et al., 2011). To meet normality assumptions all biomass data were transformed using an Ln (x + 1) transformation.

**Results**

Fish biomass varied among atolls for all trophic groups (Figure 2.2, Table 2.3). Overall fish biomass was highest (126 kg 1,000 m$^{-2}$) at the commercially-fished Majuro Atoll, intermediate (91 kg 1,000 m$^{-2}$) at near-pristine Rongelap, and lowest (67 kg 1,000 m$^{-2}$) at Ailuk, where subsistence fishing using traditional techniques is practised by approximately 350 locals (Figure 2.2).
Table 2.3: Best-fit models for fish biomass across all atolls (site included as a random variable across all models). Relative variable importance (RVI), calculated by summing Akaike variable weights for all possible GAMM models containing that variable, is given in parentheses. Larger RVI values indicate greater correlations between variable and fish biomass (maximum of 1). All models had 10 degrees of freedom. All trophic groups had zero secondary models within two ΔAICc units of the best-fit model. In addition, null models for each trophic group were compared to the final best-fit model. In each case, null models showed vastly decreased explanatory power (>80 ΔAICc units) for each trophic group.

<table>
<thead>
<tr>
<th>Trophic group</th>
<th>Variables included in “best fit” model and their relative importance across all possible GAMM models (RVI)</th>
<th>$R^2$</th>
<th>AIC</th>
<th>Significant variables in “best fit” model (P &lt; 0.05)</th>
</tr>
</thead>
<tbody>
<tr>
<td>All fish</td>
<td>Atoll (1.00), complexity (1.00), hard coral cover (1.00), distance to market/access point (1.00)</td>
<td>0.26</td>
<td>2146</td>
<td>Atoll, distance to market/access point</td>
</tr>
<tr>
<td>Herbivores</td>
<td>Atoll (1.00), complexity (1.00), hard coral cover (1.00), distance to market/access point (1.00)</td>
<td>0.25</td>
<td>2037</td>
<td>Atoll</td>
</tr>
<tr>
<td>Mesopredators</td>
<td>Atoll (1.00), complexity (1.00), hard coral cover (1.00), distance to market/access point (1.00)</td>
<td>0.21</td>
<td>2049</td>
<td>Atoll, distance to market/access point</td>
</tr>
<tr>
<td>Top predators</td>
<td>Atoll (1.00), complexity (1.00), hard coral cover (1.00), distance to market/access point (1.00)</td>
<td>0.13</td>
<td>1653</td>
<td>Atoll</td>
</tr>
</tbody>
</table>
The composition and biomass of each trophic group also differed among atolls (Figure 2.3). Top predators, such as grey reef sharks (*Carcharhinus amblyrhynchus*), were a dominant component of the fish community at Rongelap and Ailuk, where they comprised 34% and 35% of total fish biomass (Figure 2.2 & Figure 2.3). By contrast, sharks and other top predators were rare at the commercially-fished Majuro Atoll, where they made up only 5% of total fish biomass (Figure 2.2). Very low numbers of top predators on reefs at Majuro were juxtaposed by a significantly greater biomass of herbivorous fish. Herbivorous fish dominated the fish community at the commercially-fished Majuro Atoll, where they comprised 73% of total fish biomass; a substantial difference compared with the near-pristine Rongelap (49%), and subsistence-fished Ailuk (36%) atolls (Figure 2.2). Differences in herbivore assemblages among atolls were mainly due to a greater biomass of surgeonfish (Acanthuridae) at Majuro Atoll (Figure 2.3).
Figure 2.3: Trophic group biomass, assemblage composition, and size on each of the three atolls. Fishing levels at each atoll: Ailuk, subsistence; Majuro, commercial; Rongelap, negligible. **Left:** Biomass plots represent total biomass of each trophic group vs. human population density for each atoll. Note x-axis and y-axis scales vary among panels. **Middle:** Constrained canonical Analysis of Principal Co-ordinates (CAP) ordinations illustrating differences in trophic group composition among atolls. Species correlations with canonical axes are represented as vectors for species with Pearson R > 0.7; e.g. *Acanthurus nigricans* and *Ctenochaetus striatus* (herbivores) are positively correlated with Majuro Atoll. **Right:** Size plots represent average body sizes of fish plotted as differences from pristine (Rongelap). Letters above and beside data points illustrate significant differences between atolls.

Coral cover, complexity and depth did not significantly affect fish biomass for any trophic groups (Table 2.1). Distance to market/access point significantly affected all fish and mesopredator biomass (Table 2.3), where sites far from markets/access points had increased mesopredator and overall fish biomass (Appendix A). Benthic reef assemblages differed between Majuro and Rongelap (p = 0.01) and Majuro and Ailuk (p = 0.04), but not for Ailuk and Rongelap (p = 0.08) (Figure 2.4).
Discussion

This study identified fundamental differences in how commercial and subsistence harvesting affects coral reef fish on Pacific atolls in the Marshall Islands. We show that subsistence fishing by a small community using traditional gear does not dramatically alter the biomass or trophic composition of reef fish assemblages from a near-pristine state, or result in cascading ecosystem-level effects that are routinely associated with commercial harvesting of top predators. Counter-intuitively, we discover that although overall biomass was highest in the highly fished atoll of Majuro, its community was dominated by herbivores, suggesting that high overall biomass can sometimes be misleading indicator of fishing impact level. Our results suggest that impacts of fishing on reefs can depend on the style and intensity of fishing practised and the type of organisms targeted at each atoll.

Fish assemblages at Ailuk Atoll were dominated by small herbivorous fish, which are locally preferred food fishes (Petrosian-Husa, 2004). Small herbivorous fishes (i.e. rabbitfish, surgeonfish and parrotfish) typically have rapid population doubling times (between 1.5 – 4 years), which means they are less vulnerable to over-fishing than larger-bodied predators (i.e. groupers, snappers and sharks) that grow more slowly and are longer-lived (Froese and
There are, however, two issues with harvesting fish from lower trophic levels: (1) prey limitation of predatory fishes; and (2) loss of the ecological functions these fishes perform. Higher-order predators rely on smaller fish species for food; fisheries that remove ‘prey’ fish can, therefore, indirectly affect populations of their predators (Smith et al., 2010). Top predators were abundant under both low-pressure subsistence fishing and negligible fishing, suggesting that low levels of subsistence fishing has not reduced top-predator populations. Herbivorous fishes also maintain coral reef health by consuming algae that could otherwise overgrow corals; fisheries that remove herbivores can therefore alter reef functioning (Edwards et al., 2014). Despite different herbivore assemblages between Ailuk and Rongelap (Figure 2.3), there was no difference between the benthic reef assemblages of Ailuk and Rongelap atolls (Figure 2.4). This indicates that at present, there is no compensatory effect between atolls due to different benthos. However, care must be taken when interpreting these results, as differences in the functional capacity of herbivores and any flow on effects to the benthos may be hidden until after a major disturbance (Nash et al. 2016). Given low-pressure subsistence fishing practices, and isolation from commercial markets we suggest that Ailuk Atoll’s fish assemblages and reefs have not yet been strongly and persistently altered by humans. This finding suggests that in some cases, Pacific atolls may be able to support subsistence fishing by small communities while still retaining healthy reef and fish assemblages. However, the exact thresholds in the amount of fishing that can be sustained will vary according to environmental characteristics and population sizes of atolls and will require larger sampling sizes to elucidate.

Despite having the highest fishing pressure, Majuro Atoll supported the greatest biomass of fish (39-89% higher than other atolls), a result that has not been reported on other heavily fished Pacific atolls (Friedlander and DeMartini, 2002; Stevenson et al., 2007; Sandin et al., 2008; Pinca et al., 2012; Williams et al., 2015;). Reef fish assemblages at Majuro were, however, dominated by herbivores and contained far fewer top predators (70% less) than either the unfished or low-pressure subsistence-fished atolls. This novel result challenges the perception that fished reefs support less biomass than unfished reefs (MacNeil et al., 2015), therefore suggesting that studies which focus solely on total biomass changes may present a misleading picture of how fishing impacts food webs. Cascading trophic impacts from commercial fishing, such as this, are common on coral reefs and are often cited as the
mechanism behind both increases in the abundance of fish from lower trophic levels (i.e. mesopredators or herbivores), and declines in the health of heavily fished reefs (Friedlander and Demartini, 2002; DeMartini and Smith, 2015). Nevertheless, our findings suggest that fishers on Majuro Atoll have not yet started to “fish down the food web” (Pauly et al., 1998). If local fishers increase their catch rates of small herbivorous fish, while continuing to remove top predators, overall fish biomass is likely to decline and some ecosystem functioning of Majuro’s reefs may be compromised in the future (Edwards et al., 2014).

The removal of top predators from reefs at Majuro Atoll may have released herbivores, like the white-cheek surgeonfish (*Acanthurus nigricans*), from top-down regulation of their abundance and biomass (Houk and Musburger, 2013). Compounding this, despite negligible sediment runoff throughout the entire RMI (due to small land area and lack of agriculture, rivers and creeks), are strong impacts of sewage and leachates from solid waste in Majuro, which has a considerable waste management problem (Richards and Beger, 2011). Herbivores at Majuro are, therefore, also likely benefiting from an over-abundance of algae. This is supported by findings that reefs at Majuro have different benthic assemblages than those at Rongelap and Ailuk (Figure 2.4), which may mean that unlike at Rongelap and Ailuk, herbivore populations at Majuro are unlikely to be limited by bottom-up processes (Smith et al., 2010). White-cheek surgeonfish are the dominant herbivore on reefs at Majuro; they browse on red thallate and filamentous algae (Choat et al., 2002) and may, therefore, thrive on disturbed reefs that are characterised by long filamentous algae and sediment (Goatley & Bellwood 2013). This has been documented on other Pacific reefs, where surgeonfish are hyper-abundant and dominate fish biomass near large human settlements (Pinca et al., 2012; Houk and Musburger, 2013). The high biomass of browsing herbivorous fish at Majuro Atoll is therefore likely a joint response to the removal of their predators by humans and the positive effects of nutrients and sediments on the abundance of their food.

Human communities on coral islands rely on reef fish for their protein and income. To manage their reef fisheries effectively, it is critical that we understand how variation in the style and intensity of fishing practised and the type of organisms targeted regulate the biomass and trophic structure of fish assemblages. We show that in the Marshall Islands, commercial fishing can remove large predators, promoting populations of herbivorous ‘prey’ fishes and thereby enhancing total fish biomass in the system. Studies that seek to
quantify fishing impacts in marine ecosystems should, therefore, test for changes in the trophic composition of assemblages rather than focusing solely on variation in fish biomass. Although exact thresholds in fishing pressure would vary between atolls, our findings suggest that isolated coral atolls may be able to support subsistence fishing by small human communities while still retaining healthy reef and fish assemblages.

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Chapter 3 Habitat connectivity exerts opposing effects on key ecological functions

Herbivory by rabbitfish on macroalgae assays (Image: Tyson Martin)

This chapter is a co-authored paper currently under review in Landscape Ecology. My contribution involved: designing the study, conducting the fieldwork, data analysis, interpretation of results, writing the manuscript and submission to the journal. The bibliographic details of the paper, including all authors, are:

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(Signed) Tyson Martin (corresponding author)  (Countersigned)  Rod Connolly (supervisor)
Abstract

Context: Connectivity is an important property of landscapes that shapes populations and ecosystem functioning. We do not know, however, whether and how different types of spatial linkages combine to influence ecological functions, and this hampers the integration of connectivity into conservation plans.

Objectives: We used coral reef seascapes in eastern Australia as a model system to test whether habitat connections (between reefs) and seascape connections (among reefs and other habitats) exert similar effects on two key ecological functions (herbivory and piscivory).

Methods: We measured rates of herbivory (on fleshy macroalgae) and piscivory (on prey fish) on reefs that differed in their level of connectivity to both other reefs and nearby mangroves and seagrass.

Results: The extent of habitat connectivity between reefs significantly influenced both ecological functions, but in different ways: isolated reefs supported high herbivory but low piscivory, whilst, conversely, reefs that were closer to other reefs supported high piscivory but low herbivory. This was not caused by herbivores avoiding their predators, as the dominant piscivores (small predatory snappers) were too small to consume the dominant herbivores (large rabbitfishes). Seascape connections (e.g. distance to mangroves or seagrass) were less important in shaping ecological functions on reefs in this system.

Conclusions: We suggest that the effects of connectivity on ecological functions depend on the types of spatial linkages, and the ecological functions in question. To better integrate connectivity into conservation, we must develop a deeper understanding of how different spatial linkages combine to shape ecosystem functioning across landscapes.
Introduction

When animals move among habitats they link populations, food webs and ecological functions across landscapes (Lundberg et al. 2008; Massol et al. 2011). The significance of these spatial linkages is widely appreciated because many animals rely on multiple habitats throughout their lives (Kool et al. 2013; Nagelkerken et al. 2015). Consequently, connectivity has become an increasingly important consideration in spatial conservation planning (Tscharntke et al. 2012; Magris et al. 2016). High connectivity can improve conservation outcomes by: increasing the abundance and diversity of species inside reserves (Bennett 1999; Olds et al. 2012a); promoting the export of harvested species from reserves (i.e. spillover) to areas where they can be captured (Brudvig et al. 2009; Harrison et al. 2012); and linking populations among different reserves in conservation networks (Tewksbury et al. 2002; Beger et al. 2010). The effects of connectivity can also modify the spatial distribution of ecological functions (e.g. propagule dispersal, pollination, herbivory, predation, carbon processing) across terrestrial, freshwater and marine landscapes (e.g. Nystrom and Folke 2001; Bernhardt and Leslie 2013; Bregman et al. 2016). Understanding how connectivity shapes ecosystem functioning and ecological resilience is a central goal of landscape ecology (Lundberg and Moberg 2003; Cumming 2011), but the functional effects of connectivity are rarely tested with empirical data, and most studies use patterns in species richness and abundance as surrogates for ecological functions (e.g. Staddon et al. 2010; Pagès et al. 2014; Yabsley et al. 2016).

Animals that move among ecosystems usually link multiple ecological functions across landscapes (Crooks and Sanjayan 2006; Cumming 2011; Olds et al. 2016). For example, birds move between nesting sites and feeding areas, modifying pollination rates, seed dispersal and predation across terrestrial landscapes (Mueller et al. 2014; Pérez-Hernández et al. 2015; Kleyheeg et al. 2017). The migration of fish between marine and freshwater systems, and among tropical marine habitats, also alters herbivory, predation, carbon processing and primary production in coastal seascapes (Bostrom et al. 2011; Nagelkerken et al. 2015; Olds et al. 2017). These effects of connectivity on ecological functions are shaped by the dispersal capability of organisms, the spatial patterning of habitats in landscapes, and by biological interactions between species (e.g. predators, prey, competitors) (Lundberg and Moberg 2003; Sheaves 2009; Cumming 2011). However, because the functional effects of
connectivity are rarely tested with empirical data, we do not know to what degree, and how consistently, ecological functions are affected by connectivity (Pagès et al. 2014; Olds et al. 2016). The effects of connectivity might differ between individual ecological functions, occurring at different spatial scales or in response to different spatial linkages, and landscape features that benefit one ecological function might adversely affect others (Beger et al. 2010; Yabsley et al. 2016). To better integrate connectivity into spatial conservation planning, we therefore require empirical data on how connectivity shapes multiple ecosystem functions across landscapes (Olds et al. 2016).

In coastal seascapes, fish move among habitats to feed and reproduce (Nagelkerken 2009; Sheaves 2009; Pittman and Olds 2015). Spatial linkages among habitat patches of the same type (i.e. habitat connectivity), and between different habitats (i.e. seascape connectivity), structure the abundance, diversity and composition of fish assemblages in seagrass meadows, mangrove forests, and on coral reefs (reviewed by Bostrom et al. 2011; Berkhrom et al. 2012; Igulu et al. 2014; Nagelkerken et al. 2015). Connectivity can also modify the distribution of key ecological functions performed by fishes, with higher rates of both herbivory and predation often reported from seagrass, mangroves and reefs that are closer together (i.e. within 1 km of each other) (Valentine et al. 2008; Hammerschlag et al. 2010; Olds et al. 2012c; Downie et al. 2013; Peterson et al. 2013). It is not clear, however, whether the effects of connectivity on herbivory and predation occur over different scales, or how they are affected by different types of spatial linkages (e.g. habitat connectivity or landscape connectivity).

We used inshore coral reef seascapes in Hervey Bay, eastern Australia, as a model system to examine how connectivity shapes multiple ecosystem functions across landscapes, and test whether patterns in these ecosystem functions align with the distribution of the fish that provide them. In Hervey Bay, fish can migrate tidally between coral reefs, mangroves and seagrass meadows (Zann 2012), and the spatial configuration of these habitats affects the diversity and abundance of both herbivorous and predatory fishes (Martin et al. 2015). Here we test whether, and how, habitat and seascape connections combine to shape two key ecological functions on coral reefs: herbivory (consumption of fleshy macroalgae) and piscivory (predation on live fish).
Methods

Study seascape

To measure the effects of habitat and seascape connectivity on fish assemblages and ecological functions, we performed underwater visual censuses (UVC) and deployed fleshy macroalgae (herbivory) and live fish (piscivory) assays on ten coral reefs in Hervey Bay, eastern Australia (Figure 3.1). Hervey Bay is a subtropical embayment that supports inshore coral reefs, mangroves and seagrass beds (Zann 2012; Martin et al. 2015), making it an ideal seascape to test for effects of habitat and seascape connectivity on ecological functions. Reef sites were separated by a minimum of 1 km and each was surrounded by seascapes of varying configuration. Sites spanned a gradient from low to high levels of seascape and habitat connectivity. For example, some sites only contained focal reef (i.e. the reef the site was located on), whereas others were nearby to mangroves forests, seagrass beds, and other reefs (Figure 3.1). In addition, although the overall mapping scale can make it difficult to see fine detail, we point out that in the western bay, sites varied according to the size of the focal reef, as well as the area, and distance to other reef and mangrove habitats (Figure 3.1). To summarise, the seascape configuration surrounding each site is very different and we are not at high risk of spatial autocorrelation.
Calculating connectivity metrics and reef characteristics

We calculated habitat and seascape connectivity metrics, quantified within-reef characteristics and measured the distance from each reef to anthropogenic influences using existing benthic habitat maps, ArcGIS and Google Earth Pro (sources: Queensland Department of Science; Information Technology and Innovation; Campbell and McKenzie 2004; Martin et al. 2015; Zann et al. 2017). As seascape studies need to be scaled to the species and ecological functions of interest (Grober-Dunsmore et al. 2009), we adopted a multi-scale approach, capturing habitat-use patterns of species that respond to seascape structure at differing scales (Pittman and Brown 2011; Olds et al. 2012b; Berkstrom et al. 2013). Habitat and seascape connectivity were quantified at each site by calculating: (1) the proximity of nearby reefs (habitat connectivity) (Engelhard et al. 2017); (2) the proximity of adjacent mangrove and seagrass habitats (seascape connectivity) (Olds et al. 2012b); (3) the number of reef, seagrass or mangrove patches (habitat richness); (4) the diversity of
habitats (habitat diversity); and (5) the area of focal reef habitat (the reef that the piscivory
and browsing assays were located on) within 250, 500, 750 and 1000 m (radii) circular
buffers centred on reef sites (Table 3.1). We used these buffer sizes because fish in the
region have previously been shown to respond to seascape structure at distances of 500–
1000 m (Martin et al. 2015). The use of Euclidean distance approaches to measure
connectivity has previously been criticised for being overly simplistic (Moilanen and
Nieminen 2002; Saura and Pascual-Hortal 2007), however its inherent simplicity gives it
great appeal to conservation planning (Calabrese and Fagan 2004). Given that we lack
quantitative information about vectors likely to impact connectivity between habitats in this
area, such as the direction and speed of water movement, we therefore cannot speculate
about the strength of these connections. Thus, we used straight-line distances (Euclidean) to
quantify these connectivity metrics (as used previously by Olds et al. 2012 a, b; Martin et al.
2015). To check that the effects of connectivity were not modified by within-reef
characteristics or anthropogenic impacts, for each site we also quantified the amount (%) of
hard substrate (coral and bedrock), live coral, and algal cover (within-reef characteristics)
using benthic photo transects (Butler et al. 2013), and calculated distance to the nearest no-
take marine reserve and distance to the nearest boat ramp (a proxy for anthropogenic
influences such as fishing pressure (Stuart-Smith et al. 2008)) (Table 3.1). Values for each of
these variables remained the same regardless of buffer size. No reef sites were located
inside reserves.
Table 3.1: List of connectivity variables, within-reef characteristics and anthropogenic influences included in analyses. Proximity is the distance to nearby coral reef, mangrove and seagrass habitats within each buffer, divided by the area of that habitat enclosed by the buffer. Focal reef area is the area of the focal reef inside each buffer. Habitat richness is the number of reef, seagrass or mangrove patches inside each buffer. Habitat diversity is the number of different habitats inside each buffer.

<table>
<thead>
<tr>
<th>Variable type</th>
<th>Variable name</th>
<th>Buffer scale</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Seascape scale</strong></td>
<td><strong>Habitat connections</strong></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Coral reef proximity (distance/area)</td>
<td>250, 500, 750, 1000 m</td>
</tr>
<tr>
<td></td>
<td>Mangrove proximity (distance/area)</td>
<td>250, 500, 750, 1000 m</td>
</tr>
<tr>
<td></td>
<td>Seagrass proximity (distance/area)</td>
<td>250, 500, 750, 1000 m</td>
</tr>
<tr>
<td></td>
<td>Habitat richness</td>
<td>250, 500, 750, 1000 m</td>
</tr>
<tr>
<td></td>
<td>Habitat diversity</td>
<td>250, 500, 750, 1000 m</td>
</tr>
<tr>
<td></td>
<td>Focal reef area</td>
<td>250, 500, 750, 1000 m</td>
</tr>
<tr>
<td><strong>Within-reef characteristics</strong></td>
<td>Total hard substrate*</td>
<td>Same for all scales- measured at site level (%)</td>
</tr>
<tr>
<td></td>
<td>Macroalgae cover</td>
<td>Same for all scales- measured at site level (%)</td>
</tr>
<tr>
<td></td>
<td>Hard coral cover*</td>
<td>Same for all scales- measured at site level (%)</td>
</tr>
<tr>
<td><strong>Anthropogenic influences</strong></td>
<td>Distance to nearest boat ramp</td>
<td>Same for all scales- absolute distance (m)</td>
</tr>
<tr>
<td></td>
<td>Distance to nearest marine reserve</td>
<td>Same for all scales- absolute distance (m)</td>
</tr>
</tbody>
</table>

* Total hard substrate encompasses the cover of solid seafloor formed by both rocks and corals, but the cover of hard corals was not correlated with the cover of total hard seafloor (Appendix B).
Herbivory experiments

We quantified spatial variation in browsing herbivory by measuring the rate of consumption of brown algae (*Sargassum flavicans*), a genus widely used in browsing studies throughout the Indo-Pacific (e.g. Hoey and Bellwood 2010; Bennett and Bellwood 2011; Michael et al. 2013; Yabsley et al. 2016). *Sargassum* occurs seasonally in Hervey Bay and is consumed by most browsing herbivores in the region (Yabsley et al. 2016). We collected *Sargassum* from other nearby (<200 km) rocky areas because, at the time of the experiment, the cover of *Sargassum* was low across all reef sites. This consistently low cover of *Sargassum* on reef sites, was therefore unlikely to affect herbivory on deployed assays, and fish that detected assays usually consumed all of the deployed algae (Table 3.2). Natural algal cover in the region was dominated by *Lobophora variegata* and *Asparagopsis taxiformis*, both of which are not preferred food for rabbitfish (Siganidae) (Paul et al. 1992; Pillans et al. 2004), the dominant herbivore in the region (Martin et al. 2015). In summary, as there was no *Sargassum* in the area, and other common algae are not fed on by rabbitfish, the cover of each is unlikely to have affected herbivory rates. *Sargassum* assays were deployed for 24 hrs, which was shown in a pilot study to result in a relatively even spread of assays that had either been consumed, or left untouched. We deployed 11 algal assays (ten experimental, one procedural control) composed of 2-3 *Sargassum* thalli at each site, with algal weights recorded before and after deployment (e.g. Mantyka and Bellwood 2007; Yabsley et al. 2016). Deployments were 10-15 g in weight and 25-30 cm long. Minimum separation distance between assays was 6 m (visibility was ≤5 m). One replicate per site served as a procedural control and was covered by a fish exclusion cage (0.7 x 0.7 x 0.7 m, 10 mm monofilament mesh) to prevent herbivores from consuming the algae. Algal loss in procedural controls was minimal (<1%). To identify browsing species that consumed *Sargassum*, we recorded three assays at each site for 4 hrs (using high-definition GoPro cameras).

Piscivory experiments

Experiments that tether live prey are commonly used to measure relative predation rates in aquatic ecosystems (e.g. Baker and Sheaves 2007; Dorenbosch et al. 2009; Hammerschlag et
We conducted tethering experiments using common hardyheads (*Atherinomorus vaigiensis*; Atherinidae) as prey species. This species suited the study as it is abundant in all focal coastal habitats (reefs, seagrasses and mangroves), and is preyed upon by most mesopredators on the inshore coral reefs in this region (Olds et al. 2012a; Martin et al. 2015). Tethered hardyheads were deployed for 1 hr, which was shown in a pilot study to result in a relatively even spread of fish that had either been consumed, or left untouched.

We deployed 25 prey fish at each site, with a minimum separation distance of 6 m (visibility ≤5 m). Fish were tethered to coral by a thin monofilament fishing line (6 lb breaking strain, 50-80 cm long), which passed through the lower jaw and allowed fish to move as naturally as possible. Piscivory events were recorded when fish were absent from their tethers or showed clear marks of an attack by a predator. At the end of the deployment, remaining fish were untied and released. To identify predator species that preyed on hardyheads, and confirm that uneaten fish remained attached to their tethers, we recorded ten fish deployments at each site for 1 hr (using high-definition GoPro cameras). Video footage confirmed that no fish were able to break the tether and escape.

**Fish surveys**

We conducted five replicate underwater visual censuses (UVC) at each site to characterise fish communities (following Olds et al. 2012a; Martin et al. 2015; Yabsley et al. 2016). Each replicate consisted of a 50 x 4 m belt transect with at least 50 m between transects (Olds et al. 2012b). Despite the relatively poor visibility in the study region (≤5 m), these transects are an accurate method of counting fish as the observer can still clearly see 2 m either side of the transect (Olds et al. 2012a; Martin et al. 2015). Fish counts were performed at the same time of day as predation experiments, between 0900 and 1600. The same diver carried out all surveys, within three hours of low tide, recording the abundance and total length of all fish greater than 5 cm. We converted these data into biomass values using published length-weight relationships (Kulbicki et al. 2005). We classified fish as either browsing herbivores or piscivores (Appendix B). UVC was performed at the completion of the piscivory and herbivory assays and all fieldwork was completed within a three week
period (late March/early April, 2016) without breaks. Prior to the UVC surveys, the surveyor trained by estimating fish size on templates.

Data Analysis

The effects of habitat and seascape connectivity on fish biomass, herbivory and piscivory were analysed using Boosted Regression Tree analysis (BRT) (Elith et al. 2008). BRTs combine the benefits of regression trees, models that relate dependent variables to predictors by iteratively partitioning the data into increasingly smaller groups, and boosting, a forward, stage-wise process that uses training data to compare residuals of simple models and combines these to improve model performance (Elith et al. 2008). BRTs can fit non-linear relationships, cope with collinearity among predictors and are ideal for situations where there are many predictor variables over multiple spatial scales (Olds et al. 2012b). They have been used successfully to assess the importance of seascape characteristics to fish (e.g. Pittman and Brown 2011; Olds et al. 2012b). BRT models were fitted using a Bernoulli distribution for presence/absence data, and a Poisson distribution for fish count data (Table 3.2). Predictor variables used in BRT models included habitat (i.e. reef proximity) and seascape connectivity (i.e. proximity of reefs, mangroves and seagrass habitats; habitat richness and diversity) variables; and, area of focal reef habitat in 250, 500, 750 and 1000 m buffers (Table 3.1). BRT models also included within-reef characteristics and anthropogenic influences (Table 3.1). In BRTs, the learning rate controls the contribution of each tree to the model, while tree complexity determines the number of interactions that can be present in the model (Elith et al. 2008). We optimized model performance by comparing combinations of slow learning rates (0.0001 - 0.001) and low tree complexities (2 - 4) using the area under the receiver operating characteristic curve cross-validation (AUC CV) and total cross-validation (Total CV) statistics (Pittman and Brown 2011).
Table 3.2: Overview of all dependent variables measured. For lists of species categorised into browsing herbivore and piscivore groups, see Table S5 in Appendix B.

<table>
<thead>
<tr>
<th>Variable name</th>
<th>Units</th>
<th>Attributes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Herbivory</td>
<td>(%) / 0, 1 (uneaten, consumed)</td>
<td>Binary*</td>
</tr>
<tr>
<td>Herbivore biomass</td>
<td>g/200 m²</td>
<td>Herbivores known (Froese and Pauly 2000), or observed, to consume Sargassum.</td>
</tr>
<tr>
<td>Piscivory</td>
<td>0, 1 (uneaten, consumed)</td>
<td>Binary</td>
</tr>
<tr>
<td>Piscivore biomass</td>
<td>g/200 m²</td>
<td>Piscivores known (Froese and Pauly 2000), or observed, by us to consume live small prey fish</td>
</tr>
</tbody>
</table>

* BRT analyses need data of either a Poisson or Bernoulli distribution. Herbivory rates had a bi-modal distribution and video footage showed that roving schools of rabbitfish either did not find algae, or found and consumed the whole algal sprig. For BRT analyses, herbivory was therefore converted to presence/absence (binary) data. If herbivory was <30% it was given a value of 0 (not consumed); if it was >70% it was given a value of 1 (consumed). Any herbivory rates between 30-70% were excluded from the analysis (88/100 replicates remaining).

For each type of seascape scale variable (see Table 3.1), we performed individual BRTs to identify the scale at which connectivity effects were most strongly correlated with fish biomass and ecological functions. The 'best' scale for each type of connectivity was then included in a BRT, which tested for effects of connectivity relative to variation in other seascape variables (see Table 3.1). Variables which showed an importance value of >10% were then included in a final BRT, which tested for effects of connectivity variables relative to variation in within-reef characteristics and anthropogenic influences. For example, coral reef proximity was most strongly correlated with herbivory at the 750 m scale; consequently, all subsequent analyses for herbivory used coral reef data at that scale. This process optimised selection of connectivity and seascape variables at scales relevant to the fish functional groups and ecological functions in question. It also allowed us to contrast the influence of connectivity with possible confounding effects of variation in within-reef characteristics and anthropogenic variables in final BRT models. The fit of BRT models ranged from acceptable (AUC CV or Total CV >0.7), to outstanding (>0.9) (Hosmer and Lemeshow 2000), suggesting that our final models were able to accurately interpret the
effects of connectivity, within-reef characteristics and anthropogenic variables on fish biomass and ecological functions.

Results

Variability in herbivory and piscivory among reefs was strongly correlated with habitat connectivity (i.e. the proximity of reefs to other coral reefs within 500 and 750 m) (Table 3.3). These effects of habitat connectivity differed, however, between the two ecological functions. Herbivory was high on reefs that were isolated from other reefs and low on reefs that were closer to other reefs, whilst piscivory was lowest on isolated reefs (Figure 3.2 & Table 3.4). By contrast, neither distance to mangroves or to seagrass were important predictors of either ecological function on coral reefs. Habitat connectivity (i.e. links between focal reefs and other nearby reefs) was, therefore, a better predictor than seascape connectivity (i.e. links between focal reefs and other habitats) of ecological functions on coral reefs.
Table 3.3: Boosted regression tree (BRT) results for each ecological function and fish functional group. Pie charts for herbivory and piscivory represent the proportion of total herbivory and piscivory instances performed by each fish family captured on video (also includes a small number of non-fish occurrences; turtles (Cheloniidae), cephalopods, crustaceans). Pie charts for herbivore and piscivore fish biomass represent the composition of fish assemblages on each reef. Variable importance (%) represents the percentage contribution of the variable to the final model. Variable types: habitat connection; seascape connection; within-reef, anthropogenic. AUC CV or Total CV measures the fit of BRT models (acceptable: >0.7; outstanding: >0.9).

<table>
<thead>
<tr>
<th>Function/functional group</th>
<th>Video/assemblage data</th>
<th>Variables with &gt;10% importance to BRT</th>
<th>Variable type: AUC CV/ Tot. CV</th>
</tr>
</thead>
<tbody>
<tr>
<td>Herbivory</td>
<td></td>
<td>Coral reef prox&lt;sub&gt;750&lt;/sub&gt; (68.3)</td>
<td>Habitat connection: 0.91&lt;sup&gt;†&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Hard coral cover (21.7)</td>
<td></td>
</tr>
<tr>
<td>Herbivore biomass</td>
<td></td>
<td>Distance to reserve (49.3)</td>
<td>Anthropogenic: 0.74&lt;sup&gt;‡&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Hard coral cover (28.1)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Hard substrate (10.3)</td>
<td></td>
</tr>
<tr>
<td>Piscivory</td>
<td></td>
<td>Coral reef prox&lt;sub&gt;500&lt;/sub&gt; (43.1)</td>
<td>Habitat connection: 0.74&lt;sup&gt;†&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Distance to ramp (37.7)</td>
<td>Anthropogenic</td>
</tr>
<tr>
<td>Piscivore biomass</td>
<td></td>
<td>Hard substrate (69)</td>
<td>Within-reef: 0.73&lt;sup&gt;‡&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Habitat richness (22.2)</td>
<td>Seascape connection</td>
</tr>
</tbody>
</table>

<sup>†</sup> AUC CV used for BRT’s fitted with a Bernoulli distribution (binary data: herbivory and piscivory). <sup>‡</sup> Total CV used for BRT’s fitted with a Poisson distribution (normally distributed biomass data).
Table 3.4: Functions fitted in boosted regression tree (BRT) models relating to the distribution of herbivory, herbivore biomass, piscivory and piscivore biomass, to the most important habitat, seascape, within-reef and anthropogenic variables. The relative importance for each of the top three variables for each ecological function and fish functional group is shown in the top right corner of each plot.

<table>
<thead>
<tr>
<th>Ecological function / functional group</th>
<th>Important variables in final BRT model (top 3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Herbivory</td>
<td>Fitted function</td>
</tr>
<tr>
<td></td>
<td>Coral reef proximity&lt;sub&gt;750&lt;/sub&gt;</td>
</tr>
<tr>
<td></td>
<td>Hard coral cover (%)</td>
</tr>
<tr>
<td>Herbivore biomass</td>
<td>Fitted function</td>
</tr>
<tr>
<td></td>
<td>Distance to reserve (m)</td>
</tr>
<tr>
<td></td>
<td>Hard coral cover (%)</td>
</tr>
<tr>
<td>Piscivory</td>
<td>Fitted function</td>
</tr>
<tr>
<td></td>
<td>Coral reef proximity&lt;sub&gt;500&lt;/sub&gt;</td>
</tr>
<tr>
<td></td>
<td>Distance to ramp (m)</td>
</tr>
<tr>
<td>Piscivore biomass</td>
<td>Fitted function</td>
</tr>
<tr>
<td></td>
<td>Total hard substrate (%)</td>
</tr>
<tr>
<td></td>
<td>Habitat richness (750)</td>
</tr>
</tbody>
</table>
Figure 3.2: Habitat connectivity was associated with both herbivory and piscivory, but in opposing ways. Herbivory was negatively correlated with habitat connectivity (i.e. highest on reefs that were isolated from other reefs), whereas piscivory was positively correlated with habitat connectivity (i.e. highest on reefs that were close to other reefs).

Fish biomass was most strongly correlated with anthropogenic and within-reef variables. Herbivore biomass was highest on reefs close to reserves, and with low coral cover, whereas piscivore biomass peaked on reefs with high coverage of total hard substrate (Tables 3.3 & 3.4). Herbivore assemblages were dominated by rabbitfish (Siganidae), which performed the majority (75%) of browsing that was captured on video (Table 3.3). Piscivore assemblages were dominated by snappers (Lutjanidae), trevally (Carangidae) and groupers (Serranidae); and snappers were the most common predator of hardyheads (37%) on video footage (Table 3.3).

Patterns in herbivory and piscivory did not correlate with the biomass of fish species that fulfil these ecological functions. Herbivory was negatively correlated with habitat connectivity (i.e. highest on reefs that were isolated from other reefs), whereas the biomass of herbivorous fishes was highest on reefs near to reserves (Tables 3.3 & 3.4). Piscivory was positively correlated with habitat connectivity (i.e. highest on reefs that were close to other reefs), whereas the biomass of piscivorous fishes was highest on reefs with high coverage of total hard substrate (Tables 3.3 & 3.4).
Discussion

This study is the first to contrast the effects of habitat and seascape connectivity on multiple ecological functions. Our results show that habitat connectivity has opposing effects on ecological functions on inshore coral reefs, and demonstrate that habitat linkages might be more important than seascape connectivity for ecosystem functioning in this system. Connectivity is an important consideration in spatial conservation planning, but it is not clear how ecological functions are shaped by combined effects of multiple landscape linkages (Beger et al. 2010; Pagès et al. 2014; Olds et al. 2016). The apparent asymmetrical effects of connectivity revealed here suggest that a more nuanced approach might be needed when prioritising habitat connectivity in spatial conservation planning. Because habitat connectivity can exert opposing effects on ecological functions, and some functions respond negatively to landscape linkages, we need explicit data on the functional effects of connectivity to improve spatial conservation planning.

Contrasting responses of ecological functions to particular habitat connections have been reported elsewhere (e.g. Ferreras 2001; Bélisle 2005; Vuilleumier and Possingham 2006; Beger et al. 2010). These opposing effects of connectivity on ecological functions could be rather common and might result from differences in species dispersal capabilities, or biological interactions between species from different functional groups (e.g. predators, competitors) (Lundberg and Moberg 2003; Yabsley et al. 2016). For example, herbivores might prefer to feed in safe locations where the risk of encountering their predators is low (White et al. 2003; Madin et al. 2011; Burkholder et al. 2013). Spatial separation of herbivory and predation might, therefore, be a common feature in some landscapes (Heithaus et al. 2012; Christianen et al. 2014; Madin et al. 2016). This is, however, not likely to be the reason for the opposing effects of connectivity we report, because most tethered fish were consumed by predatory snappers (i.e. mesopredators), which were too small to consume the large rabbitfishes that dominated herbivory on the reefs we studied.

In this study, both ecological functions were dominated by fish from a single family: rabbitfishes dominated herbivory (eating 75% of algae consumed), and snappers dominated piscivory (eating 37% of fish consumed). This finding suggests that coral reefs in the subtropical waters of Hervey Bay might support low functional redundancy (i.e. few species
that perform similar ecological functions), with rates of herbivory and piscivory being lower than reefs in tropical waters (sensu Vergés et al. 2014). It has been suggested that low diversity and functional redundancy might be common for herbivorous fish assemblages on subtropical reefs (Yabsley et al. 2016; Gilby et al. 2017); our findings corroborate this assertion, and suggest that limited functional redundancy might also be a feature of piscivorous fish assemblages on subtropical reefs that experience high fishing pressure (Olds et al. 2012a; Martin et al. 2015).

Black rabbitfish (*Siganus fuscescens*) were the dominant herbivore in this study. They are browsing herbivores that consume brown and red macroalgae (Pillans et al. 2004), and rove widely across coral reefs and migrate tidally from reefs to feed in other habitats (e.g. mangroves and seagrass) (Olds et al. 2012c; Davis et al. 2014; Yabsley et al. 2016; Gilby et al. 2017). Because black rabbitfish rove hundreds of metres between reefs and adjacent habitats (Olds et al. 2012c; Davis et al. 2014; Yabsley et al. 2016; Gilby et al. 2017), the rates at which they encountered our algae deployments might have been low. This is supported by our video data, which shows that algae assays often went undetected, but that once located they were consumed entirely. Spatial patterns of herbivory might also have been modified by the cover of natural macroalgae on reefs and the effects of nearby marine reserves, which are known to affect rates of herbivory on coral reefs elsewhere (Hoey and Bellwood 2011; Olds et al. 2012c). Isolated reefs supported a higher cover of natural macroalgae than reefs that were closer together, and were also closer to marine reserves (Appendix B). Reefs in marine reserves in Hervey Bay support more rabbitfish than those that are open to fishing (Martin et al. 2015); our findings show that the biomass of herbivores on fished reefs also increases with proximity to marine reserves. Herbivory might, therefore, have been greater on isolated reefs because these areas support slightly more rabbitfish (i.e. they are closer to reserves), and more food for rabbitfish (i.e. natural macroalgae), than reefs that were closer together. Snappers (*Lutjanus carponotatus, L. fulviflamma, L. russelli*) were the dominant piscivores in this study. These are mesopredators of fish and crustaceans, which migrate among coral reefs and from reefs to other habitats (e.g. mangroves and seagrass) to feed and reproduce (Grober-Dunsmore et al. 2007; Sheaves 2009). The abundance of snappers on subtropical coral reefs is often correlated with the proximity of reefs to both other reefs, and adjacent mangroves (Olds et
Higher rates of piscivory on coral reefs with high connectivity to other reefs might, therefore, reflect the importance of these areas as staging points, or stepping stones, for snapper migrations.

The presence of large numbers of herbivorous and piscivorous fishes did not necessarily always correlate with higher rates of herbivory and piscivory on coral reefs. Herbivory was negatively correlated with habitat connectivity (i.e. reef proximity), whereas piscivory was positively correlated with connectivity. By contrast, the biomass of herbivorous fishes was highest on reefs near to reserves, whereas piscivore biomass was highest on reefs with lots of hard substrate. These findings suggest that ecological functions do not always align with the diversity, abundance or perceived functional niches of particular fishes (Fox and Bellwood 2008). The discrepancies we report between ecological functions and consumer biomass might reflect diel or tidal changes in the movement biology and foraging behaviour of functionally important fishes (sensu Sheaves 2009; Nagelkerken et al. 2015; Pittman and Olds 2015). Both rabbitfishes and snappers form large schools that migrate among reefs, and between reefs and other habitats, to feed, with changes in tidal state and diel period (Grober-Dunsmore et al. 2007; Igulu et al. 2014; Olds et al. 2016). For example, black rabbitfish migrate from coral reefs with the rising tide to feed in adjacent mangrove forests (Olds et al. 2012a; Davis et al. 2014), whilst snappers often feed during crepuscular periods or at particular stages of the tide (Krumme 2009; Sheaves 2009; Hammerschlag et al. 2010). Our fish surveys might not, therefore, have always recorded fish abundance at times when functionally important species were feeding. Nevertheless, data from our video deployments confirm that rabbitfishes and tropical snappers dominated herbivory and piscivory on coral reefs in the study area.

Greater connectivity might improve conservation outcomes by enhancing the capacity of reserves to promote ecosystem functioning, but we do not know whether, and how, different ecological functions are shaped by the combined effects of multiple landscape linkages. We show that habitat connectivity exerts opposing effects on two key ecological functions (i.e. herbivory and piscivory), and demonstrate that habitat linkages might be more important than seascape connectivity for ecosystem functions on inshore coral reefs. This finding has broad implications for conservation planning in the sea and on land. If different ecological functions have divergent responses to connectivity, prioritisation of
connectivity for conservation cannot be treated as “one size fits all”. Instead, conservation planners will need to tailor management solutions to prioritise the landscape connections that most strongly influence the ecosystem functions of interest in their area. Additionally, given the paucity of information on how connectivity affects ecosystem functions, we suggest that landscape conservation will benefit from developing a deeper understanding of how different spatial linkages combine to shape ecosystem functioning.

**Acknowledgements**

We thank A. Delaforce, A. Martin, K. Martin, C. Mapstone, R. Murphy and I. Pollard-Palmer for field assistance, and S. Engelhard, K. Gleeson and C. Henderson for helpful discussion of the manuscript. This study was funded by an Australian Postgraduate Award (TM). This research was carried out in accordance with Griffith University ethics guidelines under ethics approval ENV/02/16/AEC and conducted in accordance with Great Sandy Strait Marine Park research permit QS2016/GS065.
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Chapter 4 Tidal regime shapes the configuration of coral reef seascapes and the effects of mangroves on reef fish

Mangrove Jack (Lutjanus argentimaculatus) perform ontogenetic habitat shifts between mangroves and coral reefs (Image: Tyson Martin)

This chapter is a co-authored paper formatted for review in Global Ecology and Biogeography. My contribution involved: designing the study, conducting the fieldwork, data analysis, interpretation of results, writing the manuscript and submission to the journal. The bibliographic details of the paper, including all authors, are:


(Signed)  
Tyson Martin (corresponding author)  
(Countersigned)  
Rod Connolly (supervisor)
Abstract

How animals use connected habitats depends on their spatial configuration, the movement capabilities and biology of the animal, as well as vectors which may facilitate or hinder connectivity. Connections between coral reefs and mangroves are crucial for fish, and tide is likely to modify the spatial configuration of reefs and mangroves, as well as determine whether fish have permanent, or only temporary tidal access to mangroves. We performed a global meta-analysis to measure the spatial characteristics of coastal seascapes containing coral reefs and nearby mangroves, and collected data on the abundance of crucial functional groups of fish across three marine realms with varying tidal regimes (tropical Atlantic Ocean: predominantly micro-tidal; western Pacific Ocean: variable tides; western Indian Ocean: generally large tides). We predicted that due to differences in tidal range, the configuration of mangrove-coral reef seascapes would vary between marine realms. We show that the configuration of coastal mangrove and coral reef seascapes is correlated with tidal range, with reefs generally located farther offshore from mangroves in the western Indian Ocean compared to the western Pacific and tropical Atlantic. The effects of mangroves on coral reef fish declined gradually in the micro-tidal tropical Atlantic, and rapidly in the western Pacific where tides are intermediate. Despite these differences in configuration, reefs close to mangroves generally had high abundance of herbivores, invertivores, omnivores and piscivores. We suggest that tidal regime is a major driver of fish, coral and mangrove distribution across coastal seascapes and could be used as a surrogate to represent spatial variation in the effects of mangrove-reef connectivity.
Introduction

Spatial linkages among ecosystems modify the distribution, abundance and diversity of animals across landscapes (Saura & Rubio, 2010; Kool et al., 2013). This connectivity can also affect the ecological functions that animals provide in terrestrial (Mueller et al., 2014), marine (Yabsley et al., 2016), and freshwater (Hughes, 2007) ecosystems. The effects of connectivity are likely to depend on the spatial configuration of ecosystems (e.g. their spatial proximity) (Ferreras, 2001; Olds et al., 2013), the movement capability of animals (e.g. their daily movements or ontogenetic migrations) (Pittman & Brown, 2011), the reason they use adjoining ecosystems as habitat (e.g. feeding zones, sheltering sites, breeding areas) (Pittman & Olds, 2015; Kleyheeg et al., 2017), and any vectors that facilitate connectivity (e.g. wind, water movement) (Soons et al., 2004; Krumme, 2009).

Mangroves and coral reefs are ubiquitous in tropical and subtropical seascapes, where they can occur in close proximity, and frequently exchange nutrients, matter, energy and organisms (Sheaves, 2009; Hyndes et al., 2014; Nagelkerken et al., 2015; Olds et al., 2017). Spatial connections between mangroves and coral reefs play an important role in structuring fish assemblages (Mumby et al., 2004; Dorenbosch et al., 2005; Nagelkerken, 2007; Martin et al., 2015), and the ecological functions that fish perform in both ecosystems (Yabsley et al., 2016), globally. Differences in the spatial arrangement of mangroves and coral reefs in coastal seascapes, can affect the scale of connectivity effects and modify the degree to which these habitats are functionally linked (e.g. Martin et al., 2015; Olds et al., 2017). The configuration of ecosystems in coastal seascapes differs among marine realms (e.g. Atlantic, Indian and Pacific oceans) (Spalding et al., 2007), but is also likely determined by variation in local topography and tidal regimes (Igulu et al., 2014; Castellanos-Galindo & Krumme, 2015). No research has yet quantified whether there are differences in the spatial configuration of mangrove and coral reef ecosystems globally, or tested for effects of this variation on fish in coastal seascapes (Igulu et al., 2014; Olds et al., 2016). Spatial linkages between mangroves and coral reefs are now widely integrated into conservation (Weeks, 2017), but it is not clear whether the scale, and functional effects, of this connectivity vary across seascapes with different configurations (e.g. Martin et al., 2015) and tidal regimes (Krumme, 2009; Igulu et al., 2014).
Coral reef fish use mangroves as juvenile nursery habitats and feeding areas (Mumby et al., 2004; Nagelkerken, 2009; Olds et al., 2016). Juvenile reef fish feed, shelter and live in mangroves before moving offshore to coral reefs as they grow and age (e.g. Nagelkerken, 2009; Berkstrom et al., 2013a; Kimirei et al., 2013; Olds et al., 2014). Numerous fish species also live on inshore coral reefs and swim into mangroves at high tide to feed, before returning to reef habitat with the receding tide (Barnes et al., 2012; Olds et al., 2012a). There are also many fish species that live on inshore coral reefs and never venture into adjacent mangroves, but which benefit from organic matter that is transported from mangroves to reefs with tidal currents (Bouillon & Connolly, 2009; Sheaves, 2009). Thus, the value of mangroves as habitat for reef fish is likely moderated by tide, which shapes how accessible mangroves are for fish, and provides a vector to transport both fish and organic matter among habitats (Krumme, 2009; Igulu et al., 2014). Tidal regime dictates how reef fish use mangroves as habitat, globally (Igulu et al., 2014). It might also modify the spatial configuration of coral reefs and mangroves in coastal seascapes by determining where mangroves and coral reefs establish, through effects on water depth and clarity (Castellanos-Galindo & Krumme, 2015). Similarly, coral reefs might not occur close to mangroves in areas where the tidal range is large because they cannot cope with prolonged exposure to the air (i.e. at low tide), or with high turbidity (i.e. higher sediment resuspension in areas where tides are larger) (Wright et al., 1999). Large tides also restrict the accessibility of mangroves to fish, which can only use these forests when they are inundated, and this potentially limits the value of mangroves as juvenile nurseries (i.e. fish must also use other habitats as nurseries when mangroves are not inundated) (Barnes et al., 2012; Igulu et al., 2014).

The proximity of coral reefs to mangrove forests can increase the abundance, biomass and diversity of fish on tropical and sub-tropical reefs in the tropical Atlantic (e.g. Mumby et al., 2004; Huijbers et al., 2008; Jaxion-Harm et al., 2012; Nagelkerken et al., 2012), western Pacific (e.g. Honda et al., 2013; Olds et al., 2013; Martin et al., 2015), and western Indian (e.g. Dorenbosch et al., 2005; Kimirei et al., 2011; Berkstrom et al., 2013b) Oceans. We do not know, however, if the spatial configuration of mangroves and coral reefs varies between each of these marine realms, or if the effects of mangrove-reef connectivity on coral reef fish operate over similar spatial scales (Martin et al., 2015; Olds et al., 2016). We measured
the spatial characteristics of coastal seascapes containing coral reefs and nearby mangroves, and used a global meta-analysis to test how changes in seascape configuration between the tropical Atlantic, western Pacific and western Indian Oceans modified fish abundance on coral reefs. We predicted that the spatial configuration of coastal seascapes would vary between the tropical Atlantic (micro-tidal), western Pacific (meso-tidal) and western Indian (macro-tidal) Oceans, due to differences in tidal regime (sensu Igulu et al., 2014). Differences in the spatial configuration of mangroves and coral reefs can alter the functional composition of fish assemblages on coral reefs (Olds et al., 2016). We, therefore, expected that fish (particularly piscivores, herbivores and invertivores) would be most abundant on reefs close to mangroves (Grober-Dunsmore et al., 2009; Berkstrom et al., 2012). The scale over which fish abundance declined with increasing distance from mangroves was, however, predicted to vary between realms, as a function of changes in tidal regime (sensu Martin et al., 2015). In the micro-tidal tropical Atlantic Ocean, fish can reside in mangroves at all stages of the tide, whereas in the meso-tidal western Pacific Ocean and macro-tidal western Indian Ocean, fish must migrate tidally between mangroves and coral reefs to avoid being stranded (Barnes et al., 2012; Igulu et al., 2014). The abundance of fish on coral reefs was, therefore, expected to decline gradually with increasing distance from adjacent mangroves in the tropical Atlantic, where fish make ontogenetic migrations from mangroves to coral reefs. By contrast, reef fish abundance was expected to decline rapidly with increasing distance from adjacent mangroves in the western Pacific and western Indian Oceans, where fish move tidally between mangroves and coral reefs to feed and aggregate on reefs near mangroves to minimise the energetic cost of tidal migration.

**Methods**

**Testing differences in mangrove-coral reef configuration among seascapes**

To test for global and regional differences in the spatial configuration of mangroves and coral reefs in coastal seascapes, and to examine possible connectivity effects on fish, we compiled a database of all peer-reviewed studies that reported effects of mangroves on coral reef fish assemblages, or the ecological functions fish perform. We searched the ISI Web of Knowledge database using all combinations of the following keywords: mangrove*,
coral reef*, fish*, connect*, and seascape*. From these papers, we included only those that contained maps of both mangrove and coral reef ecosystems. Duplicate studies within each unique location were excluded. This search yielded 25 suitable studies and locations for detailed spatial analysis (Appendix C), which were distributed among three marine realms (i.e. tropical Atlantic, western Pacific and western Indian Oceans) where studies have reported effects of mangroves on coral reef fish (Spalding et al., 2007) (Figure 4.1). At each of these locations, we used Google Earth Pro to measure a suite of seascape metrics that were likely to be important for fish that rely on mangrove-coral reef connectivity (Wedding et al., 2011; Olds et al., 2012b)(Table 4.1). At each location, if there were ≤10 individual reefs, all reefs and their nearest mangrove forests were measured. If there were ≥10 reefs at a location, then 10 reefs were randomly selected and measured (see Appendix D for further details). We performed correlations on all combinations of the seascape metrics. If two metrics were strongly correlated (Pearson's r: >0.6), the least ecologically important of the pair was omitted from further analyses (Alonso Aller et al., 2014) (Table 4.1). For example, coral reef area and coral reef perimeter were correlated (r = 0.93), so coral reef area was retained, and coral reef perimeter was omitted (Table 4.1). All remaining metrics were correlated by <0.6 (Appendix E). Tidal range was also calculated for each location (www.tide-forecast.com) (Igulu et al., 2014).

Figure 4.1: The 25 focal seascapes for which seascape metrics were measured to describe variation in the configuration of mangrove and coral reefs (tropical Atlantic Ocean: 13; western Pacific Ocean: 7; western Indian Ocean: 5). Fish data was also available from published studies in 12 seascapes (tropical Atlantic Ocean: 6; western Pacific Ocean: 5; western Indian Ocean: 1).
Table 4.1: Seascape metrics calculated for each coral reef and corresponding nearest mangrove forest using Google Earth Pro. For more detail and a full explanation on how each of these metrics was measured, please refer to Appendix D. We performed correlation tests between all combinations of metrics, if two metrics were strongly correlated (Pearson’s r: >0.6), one of the pair was omitted from further analyses. For correlation values between retained metrics, please refer to Appendix E.

<table>
<thead>
<tr>
<th>Metric</th>
<th>Abbreviation</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reef area</td>
<td>CR area</td>
<td>Area of focal reef (m²) (Olds et al., 2012b)</td>
</tr>
<tr>
<td>Mangrove area</td>
<td>MG area</td>
<td>Area of mangrove forest nearest to focal reef (m²) (Olds et al., 2012b)</td>
</tr>
<tr>
<td>Nearest reef edge to mangroves via shallow water</td>
<td>Near RE to MG (SW)</td>
<td>Distance from reef edge to nearest mangrove forest via reef and shallow water (fish may preferentially swim along reefs and shallow habitat to decrease predation risk) (m)</td>
</tr>
<tr>
<td>Farthest reef edge to mangroves via shallow water</td>
<td>Far RE to MG (SW)</td>
<td>Distance from reef edge farthest from mangroves to nearest mangrove forest via reef and shallow water (fish may preferentially swim along reefs and shallow habitat to decrease predation risk) (m)</td>
</tr>
<tr>
<td>Distance along reef</td>
<td>Dist. along reef</td>
<td>Distance along reef from edge closest to nearest mangrove forest to reef edge farthest from nearest mangrove forest (m)</td>
</tr>
<tr>
<td>Isolation distance</td>
<td>Isolation</td>
<td>Distance across deep water for reefs that are located offshore (m) (Olds et al., 2012b)</td>
</tr>
<tr>
<td>Reef perimeter</td>
<td>CR peri</td>
<td>Perimeter of focal reef (m)</td>
</tr>
<tr>
<td>Mangrove perimeter</td>
<td>MG peri</td>
<td>Perimeter of mangrove forest nearest to focal reef (m)</td>
</tr>
<tr>
<td>Nearest reef edge to mangroves</td>
<td>Near RE to MG</td>
<td>Shortest possible distance between reef edge and nearest mangrove forest via water (m)</td>
</tr>
<tr>
<td>Farthest reef edge to mangroves</td>
<td>Far RE to MG</td>
<td>Shortest possible distance between reef edge farthest from mangroves to nearest mangrove forest via water (m)</td>
</tr>
</tbody>
</table>

Permutational multivariate analysis of variance (PERMANOVA) was used to test whether the multivariate spatial attributes of coral reef and mangroves seascapes (i.e. the seascape metrics that we measured and retained in our analyses, see Table 4.1) varied between marine realms or locations (Anderson, 2005). Marine realm was a fixed factor and location
was nested within realm. Following PERMANOVA, pairwise tests were applied to significant factors, and canonical analysis of principal coordinates (CAP) was used to visualise results (Anderson & Willis, 2003). Multivariate analysis of seascape metrics was based on Euclidean distance, which is appropriate for spatial environmental variables (Goslee & Urban, 2007). All data were logged and normalised to reduce the influence of outliers, and to standardise between variables with different orders of magnitude. A SIMPER analysis was used to determine which seascape properties differed most between marine realms. Statistical significance was set at $\alpha < 0.05$.

Quantifying relationships between mangrove-coral reef configuration and fish abundance

To investigate the relationship between mangrove-coral reef seascape configuration and fish, we collected fish abundance data for 12 (tropical Atlantic Ocean: 6; western Pacific Ocean: 5; western Indian Ocean: 1) of the original 25 locations (Figure 4.1). There are published studies that describe reef fish assemblages from the remaining 13 locations, but we could not obtain data to describe spatial patterns in fish abundance at the scale of individual reefs at these locations. Fish counts were performed using underwater visual transects (UVC) (e.g. Olds et al., 2013; Martin et al., 2015) and stationary point counts (e.g. Berkstrom et al., 2012; Nagelkerken et al., 2012). Differences in the approach taken to survey fish will not have biased our results because our analyses only tested for differences in fish abundance with changes in seascape configuration at individual locations (i.e. that were surveyed using the same method), and we did not contrast fish abundance between locations (i.e. that were surveyed using different methods). Changes in seascape configuration may affect fish from functional groups in different ways (sensu Olds et al., 2013), so our analyses focussed on changes at the functional group level and we allocated fish to the following groups: all fish, herbivores, invertivores, omnivores and piscivores (Paddack et al., 2009). The abundance of fish on inshore coral reefs is modified by both the distance of the reef from adjacent mangroves (i.e. reef edge to mangroves), and the distance of their position on the reef to adjacent mangroves (i.e. reef site to mangroves) (Olds et al., 2012a; Olds et al., 2013; Martin et al., 2015). Therefore, for each location and functional group, we performed correlations between fish abundance and both: (1) the distance of the near reef edge to mangroves; and (2) the distance of the reef site to
mangroves (both measured via shallow water) (Olds et al., 2013). Preliminary testing confirmed that these two variables had the strongest relationship with the abundance of fish on coral reefs (Appendix F).

Regression models were used to test for possible linear, exponential, logarithmic and logistic effects of both mangrove distance variables (i.e. distance of the near reef edge to mangroves and distance of the reef site to mangroves) on the abundance of fish on coral reefs (nls package in R) (Baty & Delignette-Muller, 2015) (Appendix F). By fitting this variety of curves, we established what relationship best fitted the relationship between fish abundance and both mangrove distance variables. Exponential and logarithmic decay showed the best fit, with the highest proportions of significant negative relationships (Appendix F). We chose to use exponential decay functions for all further analyses because logarithmic curves have poor logical alignment with our hypotheses, because of a theoretically infinite abundance approaching the ordinate axis. At $\alpha = 0.05$, few significant relationships were found because of modest numbers of reef sites at some locations, and we therefore loosened the significance criterion to $\alpha = 0.1$. To test how the effects of mangrove-reef connectivity on fish abundance declined with increasing distance from mangroves, and to contrast these connectivity effects among realms, we plotted relationships between tide and the slope value (i.e. “$m$” in $y = e^{(mx+c)}$) from site to mangrove distance variables for each location. This was done for all functional groups for which fish abundance was negatively correlated (i.e. a negative slope value) with the distance of reef sites from adjacent mangroves.

Results

Testing for differences in mangrove-coral reef configuration among seascapes

The spatial configuration of mangroves and coral reefs varied between marine realms ($p = 0.011$) (Figure 4.2). The western Indian Ocean has a different mangrove-coral reef seascape configuration than both the western Pacific ($p = 0.024$), and the tropical Atlantic ($p = 0.024$) Oceans. By contrast, the tropical Atlantic and western Pacific Oceans did not differ ($p = 0.080$). Differences in seascape composition were primarily a result of degrees of
isolation; reefs in the western Indian Ocean are more isolated from mangroves (separated by deep water) than those in the tropical Atlantic and western Pacific Oceans (Figure 4.2).

![Figure 4.2: Constrained canonical analysis of principle coordinates (CAP) showing differences and similarities between marine realms. Centroids are plotted for each location (25 locations in total). These patterns are primarily driven by isolation (separation of reef and mangroves by deep water), and the distance between the far and near edge of reefs to mangroves. $\delta^2$ (canonical correlation value) = 0.96, LoA (level of accuracy for correct allocations to groups) = 55%, $m$ (no. of axes) = 5. Vectors represent variables that correlate with the canonical axis with Pearson R-values $>0.7$. Differences in the configuration of mangroves and coral reefs were correlated with tidal range. Tidal range correlated with “CAP Axis 1” ($r^2 = 0.32$, $p = 0.002$) (Figure 4.3A) and isolation ($r^2 = 0.29$, $p = 0.007$) (Figure 4.3B). Therefore, seascapes where mangroves and coral reefs are separated by large distances, and deep water, generally also have large tidal ranges (Figure 4.3B).
Figure 4.3: A: Tidal range plotted against CAP Axis 1 (linear regression: tidal range vs. CAP Axis 1, $r^2 = 0.32$, $p = 0.002$). B: Isolation plotted against tidal range (linear regression: isolation vs. tidal range, $r^2 = 0.29$, $p = 0.007$). Tides ranged from: 0.21 m in Al Lith Bay, Saudi Arabia (western Indian Ocean) to 4.64 m at Zanzibar Island, Tanzania (western Indian Ocean).

Quantifying relationships between mangrove-coral reef configuration and fish abundance

Fish from all four functional groups (i.e. herbivores, invertivores, omnivores and piscivores) were more abundant on reefs, and at reef sites, that were close to mangroves, and
abundance declined exponentially with increasing distance from mangroves (Table 4.2, Appendix F). The effects of mangrove-coral reef connectivity on fish (i.e. the slopes of negative relationships between fish abundance and the distance of reef sites to mangroves) differed among realms, and with variation in tidal range (Figure 4.4). The effects of connectivity on herbivores and piscivores declined gradually in both the tropical Atlantic and western Indian Oceans (Figure 4.4). Zanzibar was, however, the only location in the western Indian Ocean for which we could include fish data, and it experiences the largest tides. By contrast, the effects of connectivity declined rapidly in the western Pacific Ocean (Figure 4.4). Gradual declines (i.e. low slopes) in the effects of connectivity on reef fish occurred at locations with both very small and very large tidal ranges (i.e. micro- and macro-tidal seascapes), whereas rapid declines (i.e. higher slopes) occurred at locations with intermediate tides (i.e. meso-tidal seascapes) (Figures 4.2 & 4.3). The effects of connectivity on invertivores and omnivores were more varied, with no clear pattern of differences among marine realms.

Table 4.2: Summary of the effects of mangrove-reef connectivity on coral reef fish. Figures show the percentage of negative and positive slopes for relationships between fish functional groups and the size of seascapes (indexed by CAP Axis 1) at each location. All relationships were fitted with the exponential decay function \( y = e^{(mx+c)} \).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Functional group</th>
<th>Locations with negative trend (%)</th>
<th>Locations with positive trend (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Total</td>
<td>Significant (p &lt; 0.1)</td>
</tr>
<tr>
<td>Near reef edge to mangroves (via shallow water)</td>
<td>All fish</td>
<td>83</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>Herbivores</td>
<td>58</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>Invertivores</td>
<td>67</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>Omnivores</td>
<td>67</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>Piscivores</td>
<td>67</td>
<td>8</td>
</tr>
<tr>
<td>Site to mangroves</td>
<td>All fish</td>
<td>67</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>Herbivores</td>
<td>58</td>
<td>17</td>
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<td></td>
<td>Invertivores</td>
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<td></td>
<td>Omnivores</td>
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</tr>
<tr>
<td></td>
<td>Piscivores</td>
<td>58</td>
<td>25</td>
</tr>
</tbody>
</table>
Figure 4.4: Relationships between the effects of mangrove-coral reef connectivity and tidal range. Connectivity effects are indexed as the slope of exponential decay equations ($y = e^{mx+c}$) that describe correlations between fish abundance and the distance of reef sites from mangroves (Table 4). Data is displayed for locations where fish abundance declined with increasing distance from mangroves, these effects are significant ($p < 0.1$) at locations shown in bold.
Discussion

Understanding how the spatial configuration of ecosystems modifies the effects of connectivity on animals is a key consideration in modern spatial conservation (Bélisle, 2005; Wedding et al., 2011; Pittman & Olds, 2015; Magris et al., 2016). Our study is the first to test for global differences in the configuration of two critical fish habitats (i.e. coral reefs and mangroves), and to examine how these differences affect fish. We show that the configuration of mangrove and coral reef ecosystems in coastal seascapes is correlated with tidal range. Moreover, our results demonstrate that the effects of mangroves on coral reef fish are also related to tidal range. The abundance of piscivorous, herbivorous and invertivorous fishes on coral reefs declines gradually with increasing isolation from mangroves in the micro-tidal tropical Atlantic Ocean and macro-tidal western Indian Ocean, but this decline in fish abundance occurs rapidly in the meso-tidal western Pacific Ocean. The role of tide in determining how fish assemblages are distributed across mangrove-coral reef seascapes outlines the importance of including hydrodynamic vectors into marine spatial planning (Krumme, 2009; Igulu et al., 2014).

The configuration of mangroves and coral reefs varied between marine realms. Coral reefs were located farther offshore from mangroves in the western Indian Ocean than in the western Pacific and tropical Atlantic Oceans. These differences were correlated with tidal range, with seascapes in the western Indian Ocean generally having large tidal ranges compared to the small tides of the tropical Atlantic and intermediate tides of the western Pacific (Igulu et al., 2014). It is likely that tidal range and mangrove-coral reef configuration are linked through two mechanisms: turbidity and water depth. The increased water movement caused by large tides results in increased resuspensions of sediments and reduces water clarity (Wright et al., 1999). As corals require clear water for photosynthesis, this likely restricts areas that are suitable for reef accretion to clearer offshore waters. Intertidal zones are also frequently wider in areas where tides are larger (Bird et al., 2013). As corals need water to grow, this likely restricts reefs to subtidal areas that are farther offshore.

Tidal conditions modify patterns in fish abundance across tropical seascapes (Igulu et al., 2014). Our results show that tide determines the spatial configuration of mangrove and coral reef ecosystems in coastal seascapes, and shapes how fish use these ecosystems as
habitat. The importance of tidal range likely reflects its effects on two of the most important functions that mangroves provide for coral reef fish: (1) juvenile nursery habitats (e.g. Nagelkerken, 2009), and (2) feeding areas (e.g. Sheaves, 2009). In areas with small tidal ranges (e.g. the tropical Atlantic Ocean), mangroves are always submerged and are used by fish as nursery areas, before they migrate offshore to coral reefs as they grow and age (Nagelkerken, 2009). Species of juvenile reef fish that use mangroves as nursery habitats, are thus most abundant in mangroves, and their abundance declines gradually on reefs with increasing distance offshore. By contrast, in areas with intermediate tidal ranges (e.g. the western Pacific Ocean), mangroves dry at low tide and can only be accessed by fish for a limited period each day (Barnes et al., 2012). Fish must, therefore, use other habitats as nurseries at low tide, and make feeding forays into mangroves when they are inundated. Reef fish, which use mangroves as feeding habitats, are thus most abundant on reefs that are as close to mangroves as the configuration of the seascape allows because this limits the energetic cost of tidal movements between habitats (Martin et al., 2015). In areas with large tidal ranges (e.g. the western Indian Ocean), many reefs might simply be so far from mangroves that the energetic costs of moving between habitats outweigh any biological benefits. In these areas, reef fish might not move into mangroves at all, but they could still derive indirect benefits from the outwelling of carbon from mangroves to adjacent coral reefs (i.e. reefs within 3 km of mangroves) (Hemminga et al., 1994; Bouillon & Connolly, 2009). This is a promising avenue for future research because there is little data to substantiate the scale over which the outwelling of carbon from mangroves affects fish assemblages on adjacent coral reefs (sensu Davis et al., 2014, but see Hemminga et al., 1994).

Our results show, for the first time, that tidal range determines the configuration of mangrove and coral reef ecosystems in coastal seascapes, and shapes how these ecosystems are used as habitat by fish. Mangroves promoted the abundance of crucial functional groups (i.e. herbivores, piscivores, omnivores and invertivores) on most coral reefs, and the abundance of these fishes on reefs declined with increasing distance from mangroves. In micro-tidal areas, the effects of mangroves on coral reef fish declined gradually, whereas in meso-tidal areas these connectivity effects declined rapidly. These findings emphasise the importance of mangrove-reef connectivity for reef fish, but suggest...
that we cannot generalise across realms about the scale over which mangrove connections modify fish assemblages on coral reefs (Grober-Dunsmore et al., 2009; Berkstrom et al., 2012). Furthermore, we propose that tide should be considered a major driver of how mangroves, coral reefs and fish are distributed across coastal seascapes (Krumme, 2009; Igulu et al., 2014; Olds et al., 2016) and that future conservation planning decisions could seek to use tidal range as a possible surrogate to represent spatial variation in the effects of mangrove-reef connectivity.

Acknowledgements

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Chapter 5 General discussion: next steps in the conservation of coral reef fish

Overview of key findings

Reef fish provide essential protein and income for many people (Moberg & Folke 1999), but the way fish communities respond to low levels of subsistence fishing using traditional techniques (fishing for food, few fishers) is not widely known (but see Jennings & Polunin 1996a, 1996b, 1997, Graham et al. 2005 for exceptions). To address this knowledge gap, Chapter 2 of this thesis presented a field study used to investigate how changes in fishing pressure affected the fish assemblages of remote coral atolls. A pristine reef which has not been inhabited or fished for over 60 years was compared to those that had either been fished using traditional gear to feed approximately 350 locals, or fished using modern technology for food and commercial export. Fish assemblages hardly differed between the pristine and subsistence-fished reefs, suggesting that some reefs can support subsistence fishing by small communities and retain intact fish assemblages. Growing human populations on Pacific islands place increased fishing pressure on reefs (Graham et al. 2005) and in addition, these nations are often approached to increase commercial fish exports, or sell or trade the rights to fish their waters in exchange for money or foreign aid (Havice 2010). My findings imply that by encouraging small Pacific Island communities to continue using traditional fishing methods to fish to feed the local community, rather than selling their fishing rights or increasing commercial export, their reefs and fish assemblages may remain healthy and productive.

The way connectivity affects ecosystem functioning in coastal seascapes is still poorly understood (Olds et al. 2016). Studies often assume that ecosystem functions will be high where the animals that provide them are numerous (e.g. Staddon et al. 2010, Pagès et al. 2014, Yabsley et al. 2016). However, for highly mobile animals that move between different habitats to feed, it is likely that the ecosystem functions they provide will be spread throughout the seascape. Using a field experiment in a seascape where coral reef, mangrove and seagrass habitats are all linked by fish and water movement, Chapter 3 examined how different types of connectivity affected ecosystem functions, and whether patterns in these
ecosystem functions aligned with fish biomass. High degrees of habitat connectivity affected
the ecosystem functions differently, with isolated reefs supporting high herbivory but low
piscivory, whilst, conversely, reefs that were closer to other reefs supported high piscivory
but low herbivory. In addition, patterns in ecosystem function did not align with the biomass
of the animals that provide those functions. This finding represents a critical step in
understanding how ecosystem functions are affected by connectivity in coastal seascapes. It
suggests that prioritising connectivity can affect ecosystem functions differently, and that
proxies of ecosystem functions, such as animal abundance and biomass, may not always
provide an accurate measure of how the function is distributed throughout a seascape.

The configuration of coral reef and mangrove seascapes affects how fish use them (Pittman
& Olds 2015). Tide is likely to determine where coral reefs and mangroves are able to
establish, and whether fish have permanent, or only temporary tidal access to the
mangroves. Using a global meta-analysis, Chapter 4 revealed that the configuration of
coastal mangrove and coral reef seascapes is correlated with tidal range, with reefs
generally located farther offshore from mangroves in the western Pacific compared to the
western Indian and tropical Atlantic Oceans. Chapter 4 also showed that the influence of
mangroves on coral reef fish declined gradually in the tropical Atlantic where tides were
small, and rapidly in the western Pacific where tidal variation is larger. These findings add
weight to the importance of coral reef-mangrove connectivity for fish abundance, and
suggest that tide largely determines how those seascapes are used by fish.

Synthesis and avenues for future research

Subsistence fishing

Reef fish are the primary source of protein for millions of people and harvesting them
sustainably is a crucial goal of people that live on tropical islands (Jennings & Polunin 1996).
Traditional fishing practices are still used in many locations, and these techniques are often
accompanied by a strong sense of stewardship and sustainable use of marine resources,
where fishers catch only enough to supply their immediate needs (Berkes 1988). Many
island nations, however, are approached to sell the rights to fish their waters (mainly for pelagic species), or increase catch rates of reef-associated species to commercial levels, exporting fish to increase income (Petersen 2002, Havice 2010). Previous research has shown that the effects of fishing on Pacific coral reefs depends on a myriad of factors including gear used and species targeted (e.g. DeMartini et al. 2008, Friedlander et al. 2010, Albert et al. 2015), local human population size (e.g. Jennings & Polunin 1996a, 1996b, Friedlander & DeMartini 2002) and island or reef biogeography (Pinca et al. 2012, Guillemot et al. 2014, Williams et al. 2015), thus presenting a complex picture to local managers who may wish to manage fishing on their own reef and island systems. The results presented in Chapter 2 suggest that traditional fishing to feed a small number of people hardly alters reef fish assemblages from a pristine condition. Although these results are limited spatially (comparing three atolls in the Marshall Islands) and temporally (surveys only conducted once), it provides a clear example of how coral reef fish can be harvested sustainably. In addition, these results are an important case-study for other island nations which may be facing similar issues, such as choosing between continuing low-level subsistence fishing to feed local communities, or selling fishing rights to other nations/increasing fishing for export and increased revenue (Petersen 2002, Havice 2010). What is now needed is a review, or meta-analysis, of this work, to elucidate more general subsistence fishing thresholds (sensu McClanahan et al. 2011). This will allow other nations (some of which may not be able to afford their own location-specific research) to make informed decisions on fishing practices and limits.

**Seascape ecology**

A recent aim of seascape ecology has been to integrate ecosystem functions into marine spatial planning (Pittman & Olds 2015, Olds et al. 2016). Attempts to quantify ecosystem functioning on coastal coral reefs with various levels of seascape connectivity have recently been made (e.g. Olds et al. 2012c, Yabsley et al. 2016), but these did not use cameras to provide evidence of what species are performing each function. Chapter 3 addressed this problem, by counting fish and deploying and filming herbivory and piscivory assays on reefs with various levels of connectivity to mangroves, seagrasses and other reefs. Although the
deployments were not filmed for their entire duration, the results still provide a clear indication that ecosystem functions can be misaligned with the ‘snapshot’ counts of animal abundance from underwater visual censuses. This misalignment of ecosystem function and animal abundance is not particularly surprising, particularly on coastal coral reefs where many species of fish perform either ontogenetic or tidal movements to other reef, mangrove and seagrass habitats (e.g. Mumby et al. 2004, Dorenbosch et al. 2005, Nagelkerken 2007, 2009b, Olds et al. 2012a, Berkstrom et al. 2013, Kimirei et al. 2013). This is an obvious avenue for further research and future studies should focus on quantifying rates of ecosystem functions (with video footage to determine important species), rather than relying on ‘snapshot’ counts of highly mobile animals to infer function.

Terrestrial animals that move between habitats are known to exploit resources along ecotones (Lidicker 1999, Hilty et al. 2012). The same is likely true for fish that move between coral reefs and mangroves, where fish are likely to spend more time on the reef edge that is closest to mangroves, however few studies have acoustically tracked fish movement over daily tidal cycles in coastal seascapes (but see Luo et al. 2009, Meyer et al. 2010, Farmer & Ault 2011, Fox & Bellwood 2011, Farmer et al. 2013, Huijbers et al. 2015 for exceptions). Consequently, little is known about how fish swim between these habitats. Do they position themselves to be on the reef edge closest to mangroves, and then move to mangroves via other shallow, structured habitats such as seagrasses? Or do they simply swim the shortest possible distance, even if it is over barren, deep water? Future research should manually track tagged fish, providing detailed information on how fish use coastal seascapes. This will help to fill important knowledge gaps about fish distributions within coastal seascapes. For example, it is largely unknown whether fish distribute themselves homogeneously along reefs, or if they instead preferentially use the reef edges that are closest to mangroves (Figure 5.1). The distance of a site to mangroves has already been shown to affect fish (Olds et al. 2012a, Olds et al. 2013, Martin et al. 2015), however, it is likely that if a reef has an edge located close to mangroves, this will also affect fish as they can move to mangroves using the reef as cover from predators. Therefore, future research should focus on distinguishing whether it is the distance of a site on a reef to mangroves, or the distance of the reef edge itself that is more important for fish (Figure 5.2). Results from Chapter 4 suggested that both the distance of a site to mangroves, as well as the distance of the
nearest reef edge to mangroves affect fish, however, future studies should be tailored to specifically address this question. This could be done by firstly tracking fish in their daily movements through reef and mangrove seascapes, and secondly by quantifying fish abundance at sites located at increasing distances from mangroves along the same reef (Figure 5.1).

Figure 5.1: Theoretical representation of potential relationship between fish abundance and the position of the site along a reef. An important area of future research will be to test if the abundance of fish that use both mangroves and coral reef habitats is higher on sections of reef that are closest to mangroves.

Figure 5.2: Differences in site to mangrove distance and reef edge distance. (A) Depicts a seascape where the reef’s edge is located close to mangroves, but the site itself is distant from mangroves. (B) Contrasting seascape where the reef’s edge is located farther from mangroves, but the site itself is closer to mangroves. Future research should quantify which is more important and how they interact to promote fish abundance on reefs near to mangroves.
Implications for marine conservation

A primary aim of marine conservation is to ensure the sustainable use of the marine environment by developing and improving strategies that prevent the overharvesting of fish (Allison et al. 1998, Gladstone 2009). These conservation strategies either indirectly control the amount of fish caught through restrictions on fishing effort, techniques, and areas, or they directly limit catch using quotas (total allowable catch limits) for each fishery (Allison et al. 1998). This thesis provides crucial information on how to improve the conservation of fish on coral reefs. It demonstrates that for isolated reefs where connectivity with other habitats and reefs is low, indirectly managing the amount of fish removed from a reef by using traditional fishing techniques and limiting the number of fishers (i.e. subsistence fishing), may be an effective way of maintaining pristine reef fish assemblages (Chapter 2) (Figure 5.3). Future marine conservation initiatives should, therefore, aim to promote traditional subsistence fishing on tropical islands.

<table>
<thead>
<tr>
<th>Protection strategies for coral reef fish</th>
</tr>
</thead>
<tbody>
<tr>
<td>Is the reef severely isolated from other reefs or other habitats (1 - 1000's kilometres)?</td>
</tr>
<tr>
<td>Yes</td>
</tr>
<tr>
<td>Is it heavily fished using modern techniques?</td>
</tr>
<tr>
<td>No</td>
</tr>
<tr>
<td>Does the reef have other habitats such as mangroves and seagrass nearby (10 - 100's metres)?</td>
</tr>
<tr>
<td>Yes</td>
</tr>
<tr>
<td>Are the other habitats permanently submerged and available at all stages of the tide?</td>
</tr>
<tr>
<td>No</td>
</tr>
<tr>
<td>Fish will likely position themselves on reefs close to other habitats (i.e. mangroves) to perform tidal feeding migrations</td>
</tr>
<tr>
<td>Continue promoting traditional fishing and sense of stewardship of marine resources (Chapter 2)</td>
</tr>
<tr>
<td>Fish will likely use reefs close to other habitats as ontogenetic stepping stones</td>
</tr>
</tbody>
</table>

Figure 5.3: Summarising the conservation techniques for coral reef fish proposed by this thesis.

For coastal coral reefs, connectivity with other nearby habitats such as mangroves and seagrass beds is important for fish (Dorenbosch et al. 2005, Nagelkerken 2009a, Olds et al. 2012a, 2012b, Berkstrom et al. 2013). This seascape connectivity, however, is likely to be a function of the spatial configuration of the habitats (Olds et al. 2016), and can be modified by abiotic and biotic vectors such as tidal flow and fish movements (Igulu et al. 2014).
findings of this thesis imply that ecosystem functions may be affected differently by various types of seascape connectivity, and that patterns in ecosystem functions may not always align with the distribution of the animals that provide them (Chapter 3). I therefore suggest that if marine spatial plans aim to incorporate ecosystem functions into their framework, they need to explicitly measure ecosystem function, rather than using proxies such as fish abundance (Figure 5.3). This thesis demonstrates that the configuration of mangrove-coral reef seascapes and how fish use them is correlated with tidal range (Chapter 4). In addition, mangrove-coral reef connectivity generally increased the abundance of crucial functional groups of fish on reefs near to mangroves (Chapter 4). Future marine conservation initiatives should recognise the global importance of tidal regime and mangrove-coral reef connectivity for fish by protecting reefs as close as possible to mangroves (Figure 5.3).

Conclusion

This thesis has addressed crucial knowledge gaps for improving the conservation of coral reef fish. It provides specific information on how subsistence fishing and seascape connectivity affect populations of reef fish and the ecosystem services they provide. It also makes direct recommendations on how to improve the conservation of coral reefs in the face of increasing human disturbance. By promoting subsistence fishing and improving our understanding of how fish use coastal seascapes, we can expect to improve conservation strategies for coral reef fish, making them as practical and effective as possible.
References

Graham NAJ, Dulvy NK, Jennings S, Polunin NVC (2005) Size-spectra as indicators of the effects of fishing on coral reef fish assemblages. Coral Reefs 24:118-124
Jennings S, Polunin NVC (1996b) Impacts of fishing on tropical reef ecosystems. Ambio 25:44-49


Appendices

Note: Each appendix is formatted for its relevant chapter.

Appendix A: Subsistence harvesting by a small community does not substantially compromise reef fish assemblages (Chapter 2)

1. Trophic groups

Table S1: Species included in each trophic group (Froese and Pauly, 2000; Palomares, 2000; Choat et al., 2002; Stevenson et al., 2007; Sandin et al., 2008).

<table>
<thead>
<tr>
<th>Group name and species included</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Herbivores</strong></td>
<td></td>
</tr>
<tr>
<td><strong>Mesopredators</strong></td>
<td></td>
</tr>
<tr>
<td><strong>Top predators</strong></td>
<td></td>
</tr>
<tr>
<td>Aprion virescens, Caranx ignobilis, Caranx melampygus, Carcharhinus amylorrhynchos, Carcharhinus melanopterus, Epinephelus fuscoguttatus, Gymnosarda unicor, Lutjanus bohar, Nebrius ferrugineus, Plectropomus aerolatus, Plectropomus laevis, Plectropomus leopardus, Plectropomus olsiganthus, Sphyraena barracuda, Triacodon obesus (Stevenson et al., 2007; Sandin et al., 2008)</td>
<td></td>
</tr>
</tbody>
</table>
2. Effects of distance to market/access point

Effects of distance to market/access point on all fish and mesopredator biomass from GAMM modelling. All fish and mesopredators were significantly affected by distance to market/access point. More impacted sites (higher distance to market/access point values) held less mesopredators and overall fish biomass (Figure S1).

Figure S1: Effects of distance to market/access point on all fish and mesopredator biomass from GAMM modelling. Partial plots of fitted GAMM model trend lines (± 95% CI’s) of residuals vs. distance to market/access point for the biomass of: all fish (top); and mesopredators (bottom).
References:


Appendix B: Habitat connectivity exerts opposing effects on key ecological functions (Chapter 3)

Table S2. Correlations between the anthropogenic and within-reef predictor variables used in the DistLM analyses.

<table>
<thead>
<tr>
<th></th>
<th>Distance to reserve</th>
<th>Distance to ramp</th>
<th>Hard coral cover</th>
<th>Total hard substrate</th>
<th>Macroalgae cover</th>
<th>Focal reef area (250)</th>
<th>Focal reef area (750)</th>
<th>Habitat richness (750)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance to ramp</td>
<td>-0.71</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hard coral cover</td>
<td>0.41</td>
<td>-0.63</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total hard substrate</td>
<td>-0.07</td>
<td>-0.27</td>
<td>0.63</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Macroalgae cover</td>
<td>0.41</td>
<td>-0.2</td>
<td>-0.39</td>
<td>-0.73</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Focal reef area (250)</td>
<td>0.21</td>
<td>-0.53</td>
<td>-0.04</td>
<td>-0.08</td>
<td>0.28</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Focal reef area (750)</td>
<td>0.14</td>
<td>-0.4</td>
<td>0.07</td>
<td>0.09</td>
<td>0.31</td>
<td>0.78</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Habitat richness (750)</td>
<td>0.08</td>
<td>0.4</td>
<td>0.09</td>
<td>0.02</td>
<td>-0.35</td>
<td>-0.73</td>
<td>-0.78</td>
<td></td>
</tr>
<tr>
<td>Coral reef prox. (750)</td>
<td>0.44</td>
<td>-0.34</td>
<td>0.60</td>
<td>0.27</td>
<td>-0.3</td>
<td>-0.17</td>
<td>-0.34</td>
<td>0.49</td>
</tr>
</tbody>
</table>
Table S3: Importance of each individual seascape variable across 250, 500, 750 and 1000 m scales (each row represents an individual BRT). The best scale for each variable is in bold. MG, mangroves; SG, seagrass; CR, coral reef.

<table>
<thead>
<tr>
<th>Ecosystem process/ functional group</th>
<th>Seascape variable</th>
<th>250 m (%)</th>
<th>500 m (%)</th>
<th>750 m (%)</th>
<th>1000 m (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Herbivory</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MG</td>
<td>1</td>
<td><strong>39</strong></td>
<td>23</td>
<td>37</td>
<td></td>
</tr>
<tr>
<td>SG</td>
<td><strong>100</strong></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>CR</td>
<td>0</td>
<td>8</td>
<td><strong>61</strong></td>
<td>31</td>
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</tr>
<tr>
<td>Focal reef area</td>
<td><strong>60</strong></td>
<td>19</td>
<td>21</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Habitat richness</td>
<td><strong>41</strong></td>
<td>14</td>
<td>40</td>
<td>4</td>
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<tr>
<td>Habitat diversity</td>
<td><strong>55</strong></td>
<td>5</td>
<td>11</td>
<td>28</td>
<td></td>
</tr>
<tr>
<td><strong>Herbivore biomass</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MG</td>
<td>0</td>
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<td>15</td>
<td><strong>70</strong></td>
<td></td>
</tr>
<tr>
<td>SG</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td></td>
</tr>
<tr>
<td>CR</td>
<td>0</td>
<td>7</td>
<td><strong>51</strong></td>
<td>42</td>
<td></td>
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<tr>
<td>Focal reef area</td>
<td><strong>42</strong></td>
<td>25</td>
<td>33</td>
<td>0</td>
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<tr>
<td>Habitat richness</td>
<td>8</td>
<td>6</td>
<td><strong>62</strong></td>
<td>24</td>
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<tr>
<td>Habitat diversity</td>
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<td>na</td>
<td>na</td>
<td>na</td>
<td></td>
</tr>
<tr>
<td><strong>Piscivory</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>MG</td>
<td>18</td>
<td><strong>56</strong></td>
<td>15</td>
<td>11</td>
<td></td>
</tr>
<tr>
<td>SG</td>
<td><strong>100</strong></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>CR</td>
<td>0</td>
<td><strong>52</strong></td>
<td>35</td>
<td>13</td>
<td></td>
</tr>
<tr>
<td>Focal reef area</td>
<td>42</td>
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<td>8</td>
<td>0</td>
<td></td>
</tr>
<tr>
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<td><strong>45</strong></td>
<td>37</td>
<td>6</td>
<td>3</td>
<td></td>
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<tr>
<td>Habitat diversity</td>
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<td>40</td>
<td>10</td>
<td>6.2</td>
<td></td>
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<tr>
<td><strong>Piscivore biomass</strong></td>
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<td></td>
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</tr>
<tr>
<td>MG</td>
<td>0</td>
<td>2</td>
<td>3</td>
<td><strong>95</strong></td>
<td></td>
</tr>
<tr>
<td>SG</td>
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<td></td>
</tr>
<tr>
<td>CR</td>
<td>0</td>
<td>3</td>
<td><strong>55</strong></td>
<td>42</td>
<td></td>
</tr>
<tr>
<td>Focal reef area</td>
<td>43</td>
<td>10</td>
<td><strong>47</strong></td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Habitat richness</td>
<td>0</td>
<td>3</td>
<td><strong>95</strong></td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Habitat diversity</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td><strong>98</strong></td>
<td></td>
</tr>
</tbody>
</table>
Table S4: Results from BRT’s run on each functional group containing only seascape variables.

<table>
<thead>
<tr>
<th>Ecosystem process/functional group</th>
<th>Seascape-scale/within-reef variables with &gt;10% importance to BRT (% importance)</th>
<th>AUC CV†/Total CV*</th>
<th>No. of trees</th>
</tr>
</thead>
<tbody>
<tr>
<td>Herbivory</td>
<td>Coral reef prox&lt;sub&gt;500&lt;/sub&gt; (88.5)</td>
<td>0.94†</td>
<td>3450</td>
</tr>
<tr>
<td>Herbivore biomass</td>
<td>Coral reef prox&lt;sub&gt;750&lt;/sub&gt; (59), Focal reef area (41.3)</td>
<td>0.72*</td>
<td>900</td>
</tr>
<tr>
<td>Piscivory</td>
<td>Coral reef prox&lt;sub&gt;500&lt;/sub&gt; (72.2), Focal reef area (19.6)</td>
<td>0.75†</td>
<td>3150</td>
</tr>
<tr>
<td>Piscivore biomass</td>
<td>Habitat richness&lt;sub&gt;750&lt;/sub&gt; (75.1), Focal reef area (15.7)</td>
<td>0.37*</td>
<td>2200</td>
</tr>
</tbody>
</table>

† AUC CV used for BRT’s fitted with a Bernoulli distribution (binary data). * Total CV used for BRT’s fitted with a Poisson distribution (normal data).

Table S5: Species included in piscivore and browsing herbivore groups. Note: these species are either known piscivores and browsers (Froese & Pauly 2000) or were seen to be consuming live hardyheads or sargassum on our video footage.

<table>
<thead>
<tr>
<th>Functional group</th>
<th>Species included</th>
</tr>
</thead>
<tbody>
<tr>
<td>Piscivores</td>
<td><em>Acanthopagrus australis, Cephalopholis argus, Dasyatidae spp, Epinephelus coioides, Epinephelus merra, Epinephelus quoyanus, Gnathanodon speciosus, Gymnothorax favagineus, Lethrinus laticaudis, Lutjanus carponotatus, Lutjanus fulviflamma, Lutjanus russelli, Platyccephalus fuscus, Plectropomus maculatus, Psammoperca waigiensis, Pseudolabrus guentheri, Sargocentron rubrum, Sphyraena obtusa</em></td>
</tr>
<tr>
<td>Browsing herbivores</td>
<td><em>Siganus fuscescens, Chaetodontoplus duboulayi, Kyphosus sydneyanus, Monacanthus chinensis</em></td>
</tr>
</tbody>
</table>
### Appendix C: Studies and locations where environmental and fish data were collected (Chapter 4)

Table S6: Studies and locations where environmental and fish data were collected.

<table>
<thead>
<tr>
<th>Data type</th>
<th>Realm</th>
<th>Study</th>
<th>Location</th>
<th>No. of individual reefs surveyed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seascape only</td>
<td>Tropical Atlantic</td>
<td>Anguilar-Perera &amp; Appeldoorn, 2007 Chittaro et al., 2005</td>
<td>South-west Puerto Rico Turneffe Atoll, Belize</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dorenbosch et al., 2007 Drew &amp; Eggleston, 2008</td>
<td>Aruba Southern Florida Keys</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Huntington et al., 2010</td>
<td>Grovers Atoll, Belize</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Layman et al., 2004</td>
<td>Andros Island, Bahamas</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Machemer et al., 2012</td>
<td>Biscayne Bay, Southern Florida Keys</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Honda et al., 2013</td>
<td>Phillipines</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pailon et al., 2014</td>
<td>New Caledonia</td>
<td>10</td>
</tr>
<tr>
<td>Pacific</td>
<td></td>
<td>Dorenbosch et al., 2005</td>
<td>Zanzibar</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dorenbosch et al., 2005</td>
<td>Pemba Island</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dorenbosch et al., 2005</td>
<td>Mafia Island</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dorenbosch et al., 2005</td>
<td>Mbuanya</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td></td>
<td>McMahon et al., 2011</td>
<td>Al Lith Bay, Saudi Arabia</td>
<td>10</td>
</tr>
<tr>
<td>Seascape &amp; fish</td>
<td>Tropical Atlantic</td>
<td>Alligeir et al., 2016</td>
<td>Abaco</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dorenbosch et al., 2004</td>
<td>Curacao</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Huijbers et al., 2008</td>
<td>Bermuda</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Jaxion-Harm et al., 2011</td>
<td>Utila</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Nagelkerken, Grol &amp; Mummy, 2012</td>
<td>Grand Cayman</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Nagelkerken et al., unpublished</td>
<td>Bimini</td>
<td>4</td>
</tr>
<tr>
<td>Pacific</td>
<td></td>
<td>Martin et al., 2015</td>
<td>Hervey Bay</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Martin et al., 2015</td>
<td>Bargara</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Olds et al., 2013</td>
<td>Palm Islands</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Olds et al., 2012</td>
<td>Moreton Bay</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Olds et al., 2013</td>
<td>Solomon Islands</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Berkstrom et al., 2013</td>
<td>Zanzibar</td>
<td>9</td>
</tr>
</tbody>
</table>

Indian Ocean
References:


Appendix D: Quantifying the spatial configuration of mangroves and coral reefs (Chapter 4)

For each study, the map of the survey location was compared to current Google Earth satellite imagery for the same location. Spatial characteristics of mangrove and coral reefs were used to establish a point of reference for identifying other mangrove and reef areas within the broader area of each study (Figure S2).

Figure S2: (a) Example study region showing line drawings of mangrove and reef areas from Kimirei et al. (2011). (b) Confirmation of mangrove and reef areas using current satellite imagery on Google Earth Pro (b).

Coral reef sites from each of the 25 studies were then plotted onto satellite imagery using Google Earth Pro. The centroid of each study location was determined by visual inspection. A variety of spatial pattern metrics (Table S6) were then quantified for all coral reef and mangrove ecosystems within a radius of 10 km from this centroid (Figure S3). The scale of 10 km was chosen because this is the maximum distance that fish commonly move from mangroves to coral reefs during ontogenetic development (Mumby, 2006).
Table S6: Seascape metrics calculated for each reef and corresponding nearest mangrove forest (MG) using Google Earth Pro.

<table>
<thead>
<tr>
<th>Metric</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reef area</td>
<td>Area of focal reef (m$^2$)</td>
</tr>
<tr>
<td>Reef perimeter</td>
<td>Perimeter of focal reef (m)</td>
</tr>
<tr>
<td>Mangrove area</td>
<td>Area of mangrove forest nearest to focal reef (m$^2$)</td>
</tr>
<tr>
<td>Mangrove perimeter</td>
<td>Perimeter of mangrove forest nearest to focal reef (m)</td>
</tr>
<tr>
<td>Nearest MG</td>
<td>Shortest possible distance between reef edge and nearest mangrove forest via water (m)</td>
</tr>
<tr>
<td>Farthest reef edge from MG</td>
<td>Shortest possible distance between reef edge farthest from mangroves to nearest mangrove forest via water (m)</td>
</tr>
<tr>
<td>Nearest MG via shallow water</td>
<td>Distance from reef edge to nearest mangrove forest via reef and shallow water (fish may preferentially swim along reefs and shallow habitat to decrease predation risk) (m)</td>
</tr>
<tr>
<td>Farthest reef edge MG via shallow water</td>
<td>Distance from reef edge farthest from mangroves to nearest mangrove forest via reef and shallow water (fish may preferentially swim along reefs and shallow habitat to decrease predation risk) (m)</td>
</tr>
<tr>
<td>Distance along reef</td>
<td>Distance along reef from edge closest to nearest mangrove forest to reef edge farthest from nearest mangrove forest (m)</td>
</tr>
<tr>
<td>Isolation distance</td>
<td>Distance across deep water for reefs that are located offshore (m)</td>
</tr>
<tr>
<td>Site to mangroves</td>
<td>Distance of the site to mangroves (via shallow water) where fish abundance/biomass data was measured (only used in Part 2 of analysis: Quantifying the effects of mangrove-coral reef configuration on fish)</td>
</tr>
</tbody>
</table>

Figure S3: Example study region (from Olds et al., 2013) showing survey sites (yellow placemarks), the centroid for the study area (pink placemark), and the seascape enclosed by a buffer radius of 10 km (green circle) around the centroid.
Several of the 25 published studies also reported additional mangroves and coral reefs in the vicinity of their study areas. To also incorporate these potentially important nearby ecosystems we then identified all mangroves and coral reefs within 10 km of the centroid using the previously established point of reference for each ecosystem type (Figure S4).

![Figure S4: Locating additional nearby mangrove (red) and coral reef (yellow) ecosystems (from Kimirei et al. 2011).](image)

To ensure that other benthic habitats, such as beds of macroalgae or ephemeral seagrass, were not incorrectly identified as coral reefs, we compared satellite images of the same area through different years to establish if the dark masses of suspected reefs changed shape over time. Where regions did not change dramatically they were deemed to be stable reef structure; regions that changed shape between the years were excluded from the analysis (Figure S5). Once the location of a reef was confirmed, an outline was marked around the reef and nearest stand of mangroves, and the area and perimeter of both ecosystems was recorded (Figure S6).
Figure S5: Comparing dark masses over years. The reef has not moved whereas the algae or seagrass that is nearby in 2014 was not present in 2006.

Figure S6: Reef area outlined in red and mangroves in yellow. The perimeter and area of both ecosystems were then recorded. Note: the reef is the same patch as shown in Figure S4.

The distance from the edge of each reef to the nearest edge of adjacent mangroves was then measured and recorded as the shortest possible route through water (Figure S7). The distance from the reef edge furthest from mangroves to adjacent mangroves was then measured via: (a) the shortest possible route through water (Figure S8); and (b), the shortest possible route through available reef and shallow water (to account for the
potential preferential selection of safer shallow water habitats by fish while migrating) (Figure S9).

Figure S7: Distance between near coral reef edge and adjacent mangroves via the shortest possible route through water (yellow line).
Figure S8: Distance between far coral reef edge and adjacent mangroves via the shortest possible route through water (yellow line).

Figure S9: Distance from far coral reef edge and adjacent mangroves via available reef and shallow complex habitat (yellow line).

The distance from the edge of each reef to the nearest edge of adjacent mangroves via shallow habitat was also measured (Figure S10), but this was only relevant for reefs that did
not directly border mangroves, and only included adjacent reefs that were within 45° of the primary direction of travel to mangroves (also see Figure S10, Table S7).

Figure S10: Distance between near coral reef edge and adjacent mangroves via the shortest possible route through shallow complex habitat (yellow line).

The distance between reefs and mangroves via deep water was also measured for reefs that are isolated from mangroves (Figure S11, Table S7).

Figure S11: Isolation distance by deep water between reefs (green) and between reefs and mangroves (blue).
Table S7: Assumptions, caveats and definitions needed to parameterise seascape analysis

<table>
<thead>
<tr>
<th>Name</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Minimum size of coral reef</td>
<td>For coral reefs to be included, they must be at least 100 m²</td>
</tr>
<tr>
<td>Minimum size of mangrove</td>
<td>For mangroves to be included, they must be at least 100 m²</td>
</tr>
<tr>
<td>forest</td>
<td></td>
</tr>
<tr>
<td>Minimum separation of reefs</td>
<td>Reefs must be separated by a minimum of 100 m, otherwise they are deemed to be the same reef as surveyed as one*</td>
</tr>
<tr>
<td>Distance via shallow habitat</td>
<td>To be included in this measurement, shallow habitat must be within 45° of the intended direction of travel to nearest mangroves* We selected 45° as the angle because in most cases, travelling to shallow habitat outside 45° of the intended direction meant that the distance to the desired location (i.e. the mangroves) is no longer reducing, hence increasing the overall energetic cost of migration for fish.</td>
</tr>
<tr>
<td>≤ 10 reefs inside 10 km of centroid</td>
<td>If ≤ 10 reefs within 10 km of centroid, all reefs (and corresponding nearest mangroves) are surveyed</td>
</tr>
<tr>
<td>&gt;10 reefs inside 10 km of centroid</td>
<td>If &gt;10 reefs within 10 km of centroid (Mumby 2006), a 10x10 grid is over laid onto seascape and 10 grid squares are picked at random. If they contain a reef this reef is then measured, if not, the process is repeated until 10 reefs are measured</td>
</tr>
<tr>
<td>Reef extends outside of study area</td>
<td>If the reef extends away from mangroves continuously to be farther than 10 km from centroid, we continued to measure the reef (i.e. in these cases the reef may be over 10 km long)</td>
</tr>
</tbody>
</table>

* Seascape analyses such as this have never been undertaken before. Assumptions and definitions such as these are necessary to parameterise the study.

References


### Table S8: Correlations and significance values for remaining seascape variables.

<table>
<thead>
<tr>
<th></th>
<th>CR Area</th>
<th>MG Area</th>
<th>Near RE to MG (SW)</th>
<th>Far RE to MG (SW)</th>
<th>Isolation</th>
</tr>
</thead>
<tbody>
<tr>
<td>CR Area</td>
<td>1</td>
<td>0.01, 0.84</td>
<td>0.09, 0.19</td>
<td>0.34, &lt;0.001</td>
<td>0.07, 0.33</td>
</tr>
<tr>
<td>MG Area</td>
<td></td>
<td>1</td>
<td>0.08, 0.24</td>
<td>0.23, 0.001</td>
<td>0.04, 0.52</td>
</tr>
<tr>
<td>Near RE to MG (SW)</td>
<td></td>
<td></td>
<td>1</td>
<td>0.59, &lt;0.001</td>
<td>0.59, &lt;0.001</td>
</tr>
<tr>
<td>Far RE to MG (SW)</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>0.39, &lt;0.001</td>
</tr>
<tr>
<td>Isolation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
</tr>
</tbody>
</table>
Appendix F: Shape of relationship between fish abundance and distance to mangroves (Chapter 4)

There were no distinct ‘thresholds’ in how quickly the effects of mangrove-coral reef connectivity on fish diminished, instead, the decline in mangrove-coral reef connectivity effects on fish was best modelled by exponential decay (Table S9). Using linear and non-linear regression (“nls” program in R), we fitted linear, exponential, logarithmic and logistic curves to plots of fish abundance (for each functional group) vs. “Near RE to MG” as well as “Site to MG” (Table S9). Exponential decay showed the highest proportion of significant negative relationships fitted (Table S9). Sites and reefs close to mangroves, therefore, had high abundance of important functional groups (e.g. particularly herbivores, invertivores, omnivores and piscivores), which then decreased exponentially as sites and reefs were located further from mangroves (Table S9). Negative relationships between fish abundance and increasing site and reef distance to mangroves outnumbered positive relationships by a factor of 9 or more (Near RE to MG: 24.4% and 2.6% respectively; Site to MG: 20.5% and 1.3% respectively).
Table S9: Summary of curves fitted to regressions of fish abundance vs. Near RE to MG and Site to MG for each location and functional group. Curve fitting deemed significant if p ≤ 0.10.

<table>
<thead>
<tr>
<th>Variable type</th>
<th>Curve fitted</th>
<th>General equation</th>
<th>Negative curves with p ≤ 0.10 / total curves attempted</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Near RE to MG</td>
<td>Linear</td>
<td>$y = mx + c$</td>
<td>9/78</td>
<td>11.5</td>
</tr>
<tr>
<td></td>
<td>Exponential</td>
<td>$y = e^{(mx+c)}$</td>
<td>12/78</td>
<td>15.4</td>
</tr>
<tr>
<td></td>
<td>Logarithmic</td>
<td>$y = m(\ln x) + c$</td>
<td>12/78</td>
<td>15.4</td>
</tr>
<tr>
<td></td>
<td>Logistic</td>
<td>$y = \frac{a}{(1 + be^{-kx})}$</td>
<td>9/78</td>
<td>11.5</td>
</tr>
<tr>
<td>Total</td>
<td>Linear</td>
<td>$y = mx + c$</td>
<td>11/78</td>
<td>14.1</td>
</tr>
<tr>
<td></td>
<td>Exponential</td>
<td>$y = e^{(mx+c)}$</td>
<td>13/78</td>
<td>16.7</td>
</tr>
<tr>
<td></td>
<td>Logarithmic</td>
<td>$y = m(\ln x) + c$</td>
<td>14/78</td>
<td>17.9</td>
</tr>
<tr>
<td></td>
<td>Logistic</td>
<td>$y = \frac{a}{(1 + be^{-kx})}$</td>
<td>11/78</td>
<td>14.1</td>
</tr>
<tr>
<td>Site to MG</td>
<td>Linear</td>
<td>$y = mx + c$</td>
<td>11/78</td>
<td>14.1</td>
</tr>
<tr>
<td></td>
<td>Exponential</td>
<td>$y = e^{(mx+c)}$</td>
<td>13/78</td>
<td>16.7</td>
</tr>
<tr>
<td></td>
<td>Logarithmic</td>
<td>$y = m(\ln x) + c$</td>
<td>14/78</td>
<td>17.9</td>
</tr>
<tr>
<td></td>
<td>Logistic</td>
<td>$y = \frac{a}{(1 + be^{-kx})}$</td>
<td>11/78</td>
<td>14.1</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td>16/78</td>
<td>20.5</td>
</tr>
</tbody>
</table>

Note: 2/78 (total) showed a significant (p ≤ 0.10) positive trend for Near RE to MG (2.6%), and 1/78 (total) showed a significant (p ≤ 0.10) positive trend for Site to MG (1.3%).