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**Assessment of scale dependent function in
reef fish, and application to the evaluation of
coral reef resilience**

Thesis submitted by

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James Cook University

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Abstract

In response to the anthropogenic pressures affecting ecosystems, and the resultant habitat and community changes these impacts cause, there has been increasing interest in using resilience approaches to study ecosystems. The resilience of a system its capacity to adapt to changing conditions whilst maintaining core processes, and resisting shifts to different regimes. Thus, the resilience concept allows the state of a system to be thought about within a dynamic, ecosystem-based framework. Despite this interest in resilience approaches, quantitative indicators of ecosystem resilience are rarely tested. Understanding and quantifying the functional roles played by species, and thus their importance in driving key ecosystem processes, has been suggested as one approach for quantifying resilience. In the context of coral reefs, herbivory by reef fishes has been identified as an important process controlling algae and supporting coral dominance. As a result, there is an extensive literature characterising how herbivorous species provide their function. However, there has been little evaluation of the spatial scales over which fish perform their functional roles. Knowledge of the scales over which fishes provide their function may be used to develop a broader indicator of resilience: cross-scale redundancy. The cross-scale resilience model, first proposed by Peterson et al. in 1998, suggests that the scale at which an individual provides its function will influence its response to scale-specific disturbances. Thus, the presence of species operating at different scales within a community (cross-scale redundancy), should be a useful indicator of resilience. Implementation and testing of cross-scale redundancy on coral reefs would go some way to addressing the need for empirical testing of resilience indicators.

To test these indicators, this thesis is split into two parts: in **Part 1** (Chapter 2-5) I evaluate the spatial scales at which fish interact with the reef and provide their function; in **Part 2** (Chapter 6-8) I investigate the application of the cross-scale resilience model in the context of coral reefs. The knowledge developed in Part 1 is essential for assessing the appropriateness of implementing the cross-scale resilience model for reef fish because these chapters test the underlying assumptions of the model used in Part 2.

The relationship between body size and home range provides a useful way of summarising the spatial scales at which communities of fish operate. In **Chapter 2** I performed a quantitative review of studies examining home range in reef fishes, and assessed the interspecific relationship between body mass and home range area. Body mass and home range were positively related. Fishes appeared to occupy a smaller area per unit mass than terrestrial

vertebrates. When the small home ranges of reef fish are considered in concert with their apparent reluctance to cross open areas, it suggests that reserves aimed at protecting fish biodiversity may be more effective if located across whole reefs as home ranges are less likely to cross reserve boundaries.

Home ranges may include areas that are used for activities such as sleeping, rather than focusing on those locations where the organism is providing the core functions of interest, such as grazing. Therefore, in **Chapter 3** I assessed the allometric relationship between small-scale foraging movements and body size for herbivorous reef fishes within the functional groups: browsers, farmers, grazer/detritivores, and scraper/excavators. The relationship between vulnerability of species to fishing and their scale of foraging was also examined. I found evidence of a strong, positive, log linear relationship between scale of foraging movement and fish length. Some functional groups, such as scrapers/excavators, performed their role over a wide range of scales, whereas browsers were represented by few species and operated over a much narrower range of scales. Overfishing is likely to not only remove species operating at large scales, but also the browser group as a whole.

The spatial scales at which fish operate are not only affected by life history traits such as body size, they are also shaped by the habitats available to the individual. In **Chapter 4**, I assessed the influence of among-site variation in habitat condition on the short-term foraging range of two species of parrotfish. The primary predictor of these foraging movements was coral cover. The study suggests that future changes in coral cover are likely to alter the way reef herbivores forage. Habitat condition may also drive the underlying body size distribution of fish communities. In **Chapter 5** I characterized patterns of cross-scale habitat complexity, and examined how this related to body-depth abundance distributions of associated fish assemblages over corresponding spatial scales. I found that reefs formed from different underlying substrata exhibit distinct patterns of cross-scale habitat complexity and this is reflected in the fish body depth distributions.

The second part of the thesis used knowledge generated in Part 1 to test the applicability of Peterson et al.'s cross-scale resilience model on coral reefs. This model was developed from the discontinuity hypothesis, which explores inherent scales of structure within ecosystems. In **Chapter 6** I reviewed the conceptual framework underlying discontinuities. The chapter explored the utility of discontinuities for understanding cross-scale patterns by describing recent advances in examining non-linear responses to disturbance, and phenomena such as invasions, and resilience. I detailed outstanding knowledge gaps, in particular pertaining to the implementation of the cross-scale resilience model for taxa with indeterminate growth such as reef fishes.

To address the issue of applying the cross-scale resilience model to species with indeterminate growth, in **Chapter 7** I performed a comparison of bird (determinate growth) and fish (indeterminate growth) body mass distributions, assessing the respective suitability of distinct analytical approaches for understanding habitat-size relationships in different ecosystems. I evaluated three size distribution indices: species size relationships, species size-density relationships and individual size-density relationships, and two types of analysis: looking for either discontinuities or abundance modes in the distributions. All the indices and analyses were useful for examining the relationship between habitat structure and size for species with determinate growth. In contrast, for species with indeterminate growth, such as fishes, individual size-density relationships were more useful.

Finally, in **Chapter 8** I applied the cross-scale resilience model on coral reefs. I assessed the effectiveness of cross-scale redundancy in herbivores as an indicator of response diversity and benthic recovery on reefs monitored through a coral bleaching event. The distribution (redundancy) of herbivores operating across a broader range of spatial scales prior to the bleaching corresponded with increased reef recovery post-disturbance, as proposed by the cross-scale resilience model. Analysis of the change in biomass across size classes indicated that response diversity, with declines in small herbivores and increases in large herbivores, enhanced the overall herbivore biomass at recovering sites.

My research characterized the spatial ecology of reef fish communities, and herbivores in particular. This knowledge was used to underpin the testing of a potential resilience indicator: the cross-scale resilience model; a model that proved to be effective in the context of coral reefs. Critically, my research provides fundamental knowledge regarding the function provided by coral reef fishes, highlighting the spatial scales over which management is needed to support their critical functions. These results will help managers to predict the relative likelihood of different reefs declining or recovering following severe disturbances. Understanding the spatial ecology of fishes may hold the key to the management of coral reef recovery in the future.

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Chapter 1: General Introduction

In light of existing reef degradation (e.g. Gardner *et al.* 2003) and projected future losses of coral through increasing anthropogenic pressures (Veron *et al.* 2009), there is a clear need to manage reefs in a manner that supports their health and resilience. There is an increasing awareness that taking a functional approach to management may help maintain systems within a desired state, by supporting critical ecosystem processes in the face of future uncertainty (Christensen *et al.* 1996; Bellwood *et al.* 2004; Pikitch *et al.* 2004). In response, there have been calls for new ways to evaluate the delivery of function, to provide the knowledge needed by managers to effectively implement appropriate mitigation strategies (Hughes *et al.* 2010). Fish are key members of coral reef communities, driving critical processes that underlie the transfer of energy and material through the ecosystem (Bellwood & Wainwright 2002), and dominating essential functions, such as herbivory that promote coral dominance (Hughes 1994). Thus, studying fish communities, their function and their resilience provides a logical approach for assessing resilience of coral reefs (Bellwood *et al.* 2004).

1.1 THE IMPORTANCE OF FUNCTIONAL DIVERSITY

Species play a range of roles or ‘functions’ within ecosystems, for example seed dispersal, pollination, grazing and modification of water flows (Folke *et al.* 2004). As a result, there has been extensive research looking at the importance of functional groups and functional diversity for driving key ecosystem processes (Hooper *et al.* 2005). In the context of coral reefs, a major focus has been the ability of herbivores to mediate competition between coral and macroalgae, helping maintain reefs within a coral dominated state (Bellwood *et al.* 2004). However, terrestrial and marine research to date suggests that simple measures of functional diversity incorporating species richness and evenness are unlikely to be effective indicators of ecosystem function (e.g. Hooper *et al.* 2005), due to variations in function both among and within species (Rudolf *et al.* 2014). For example, herbivorous reef fish species may be more narrowly defined as grazers or browsers (Green & Bellwood 2009), and may exhibit ontogenetic changes in diet and functional impact (Bonaldo & Bellwood 2008; Lokrantz *et al.* 2008).

One area that has seen little study to date is the evaluation of the spatial scales over which fish interact with the reef and perform their functional roles, and how this may vary among species. Such information is critical, as the range of spatial scales over which species

interact with their environment influences their response to disturbances acting at certain scales (Elmqvist *et al.* 2003), and their specific role within the ecosystem (Fox *et al.* 2009). Furthermore, the arrangement and connectivity of interacting functional components impacts on ecosystem behaviour (Cumming *et al.* 2005; Page 2011). Therefore, there is a need to consider the functional role of species within the spatial patchiness of the landscape.

1.2 BODY SIZE AS A PROXY FOR SPATIAL SCALE

Although it is possible to evaluate the scale at which individual species are operating and providing their function, such a piecemeal approach does not lend itself to looking at function across communities. Thus, a process for making generalisations about the fish community as a whole is needed. Research, primarily in the terrestrial literature, suggests that organisms interact with their environment and perceive the availability of resources as a result of their body size (Woodward *et al.* 2005; Szabó & Mészéna 2006). As a consequence, allometric relationships between body size and variables such as home range area or stride length provide useful summaries of the scale at which whole communities or taxa operate (Holling 1992). And thus, body size provides an effective proxy for the scale at which individuals or species are operating (Calder 1984). In turn, body size distributions, where abundance or biomass is plotted against some measure of body size or mass, may provide indications of the concentration of individuals operating at different scales (Peterson, Allen & Holling 1998). Therefore, an exploration of the relationship between body size and scale of operation for fishes would be of benefit in understanding the delivery of function across scales on coral reefs.

1.3 ALLOMETRY OF HOME RANGE

There are a range of movement or scale metrics that might be used to determine the scale at which species are operating and providing their function, but one of the simplest approaches is to use home range (Burt 1943; McNab 1963). A single review of home range allometry has been published for reef fishes, presenting a strong positive relationship between body length and home range length, suggesting that body size is a useful proxy for the scale at which fish are operating (Kramer & Chapman 1999). However, this result needs to be considered in light of a range of issues: 1) Before the late 1990's, studies were largely restricted to visual observations, indeed all of the research incorporated in the review with the exception of one study, used visual methods to track fish and estimate home range. The application and refinement of acoustic telemetry in the last few decades has made it possible to accurately monitor the movement of marine species and to estimate the home range of a wider number of

taxa (Bolden 2001); 2) The metric used by Kramer and Chapman (1999) was home range length. Home ranges of reef fish are not circular (Holland, Lowe & Wetherbee 1996), and therefore home range length may not accurately represent differences in home range among species; and 3) The study did not evaluate the effect of functional group on the allometry of home range, and thus it is not known whether herbivorous fishes show similar relationships to fishes as a whole, or to predatory species. These considerations suggest that there is a need to update home range body size scaling in reef fishes with new research and with different home range metrics.

1.4 ALLOMETRY OF FUNCTIONAL MOVEMENTS

Simply quantifying home range to determine the scale at which an individual provides its ecosystem function may present an oversimplification, by potentially masking a significant level of detail on the scale at which species are performing their role. Home range was defined by Burt (1943) as:

“that area traversed by the individual in its normal activities of food gathering, mating and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as part of the home range.”

And as such, the home range incorporates a number of activities that may not be directly relevant to the ecosystem function of interest (Lazenby-Cohen & Cockburn 1991). Work by Welsh and Bellwood (2012b) quantified the home range of *Chlorurus microrhinos* individuals along a reef crest on the Great Barrier Reef. They simultaneously recorded where in this range fish performed most of their excavating function. Foraging activities were found to occur predominantly within a small area towards the centre of the home range, and thus the home range area was not reflective of the foraging range. The functional role of an individual may be defined in a number of ways, dependent on the ecosystem processes under investigation, e.g. herbivory in the context of reef fish. As a result, the functional range may be defined as that area covered by an individual over the course of those activities relevant to providing its function and supporting the ecosystem process of interest. Thus, quantifying functional movements are an important, additional aspect of the spatial ecology of fishes that needs to be considered.

1.5 MOVEMENT AND HABITAT EFFECTS

Aside from functional impact, the influence of habitat on fish movement is a second detail that may be lost if we simply look at the relationship between body size and home range.

Foraging behaviour is not a static characteristic of individuals, rather, it may be influenced by environmental factors. Variation in foraging behaviour in response to habitat condition has been demonstrated in a wide array of mobile organisms, including seabirds (McLeay *et al.* 2010), marine mammals (Auge *et al.* 2011), and fish (Hoey & Bellwood 2011). Furthermore, habitat condition may alter the effect of foraging behaviour, for example the capacity of a herbivore assemblage to control algal growth may be reduced at sites with low coral cover, as grazing effort is diluted over a larger area of algal-covered reef (Williams, Polunin & Hendrick 2001). In light of existing degradation of reefs (e.g. Gardner *et al.* 2003), and projected future loss of coral through increasing anthropogenic pressures (Gardner *et al.* 2003; Alvarez-Filip *et al.* 2009), understanding the effect of habitat on foraging movements is critical to understand the delivery of function by herbivores.

1.6 BODY SIZE DISTRIBUTIONS AND HABITAT EFFECTS

Habitat may not only influence the scale of movements by individuals, but may also affect the underlying body size distribution of a community. The structural complexity of the reef provides refuge to fish (Luckhurst & Luckhurst 1978), and whilst the literature identifies a prevailing positive relationship between reef structural complexity, and fish biomass and abundance, the strength of this relationship is variable and some studies identify mixed effects (Graham & Nash 2013). A key reason for this discrepancy may be that the majority of studies tend to assess complexity at a single scale, presumably due to the implicit assumption that complexity is homogenous across scales, which may not be the case (Bradbury, Reichelt & Green 1984; Martin-Garin *et al.* 2007). Quantifying variations in complexity across spatial scales is important because fish perceive and use reef structure as a function of their size. The availability of shelter of different sizes has the potential to control the abundance of fish of differing body sizes: only fish that can fit within openings in the reef will be able to utilise the structure for shelter to help mediate predation risk (Hixon & Beets 1993). Therefore, it is predicted that body depth distributions of reef fish communities will reflect how habitat complexity varies across scales.

1.7 ASSESSMENT OF CORAL REEF RESILIENCE

Quantifying the spatial ecology of reef fishes provides useful information on the function of individual species and the fish community as a whole. System resilience is not readily measured, and yet operationalising resilience is critical for managers to anticipate and adapt to change before shifts occur (Nyström *et al.* 2008). The high diversity of coral reef systems and their interaction with increasing and often interconnected impacts provides a

particularly complex arena for scientists and managers aiming to quantify resilience. The predominance of studies using coral cover to indicate reef health, a coarse and ambiguous measure of condition, only enhances these difficulties (Hughes *et al.* 2010). To date there has been much discussion regarding drivers of resilience on reefs (Walker *et al.* 2006), presenting an array of potentially measurable indicators; however, empirical assessments are lacking (Carpenter, Westley & Turner 2005; Nyström *et al.* 2008).

The cross-scale resilience model, which incorporates information on body size distributions and the spatial scales at which species interact with their environment and provide their function, has been suggested as one potential indicator of resilience (Peterson, Allen & Holling 1998; Allen, Gunderson & Johnson 2005). Overlap of function among species provides redundancy, if reduction or removal of a species that dominates a particular role results in an increased contribution by other species (Walker, Kinzig & Langridge 1999; McClanahan, Polunin & Done 2002). However, this redundancy is only valuable if members of a functional group respond differently to a disturbance; if they all respond in a similar manner the anticipated insurance value is lost (Elmqvist *et al.* 2003). The cross-scale resilience model proposes that where members of a functional group operate at different spatial scales, they will respond differently to a scale-specific disturbance, providing cross-scale redundancy (Peterson, Allen & Holling 1998). Thus, in quantifying how function is distributed across scales, the model provides a measure of resilience.

To date the examination of functional distribution across scales and its implications for system resilience has been tested with respect to bird and invertebrate communities (e.g. Fischer *et al.* 2007; Angeler, Allen & Johnson 2013). However, this approach has not been applied in the context of coral reefs (Nyström *et al.* 2008). On reefs, the distribution of herbivore function across scales would provide an indication of the resilience of the process of herbivory, which could then be combined with other indicators such as the presence of a diverse and resistant coral assemblage (McClanahan *et al.* 2012), and connectivity among reefs (Nyström *et al.* 2008), to provide an overarching picture of the resilience of coral reefs. Application of the cross-scale resilience model on reefs now needs to be assessed to evaluate the usefulness of this approach.

Implementation of the cross-scale resilience model is reliant on knowledge regarding the functional role of species, and is based on two main assumptions: (1) That body size is a useful proxy for the spatial scales over which species are delivering their ecosystem function. Therefore, the range of body sizes within a functional group indicates the range of scales over which a particular function is being provided; and (2) That habitat and resource availability at different spatial scales will influence the underlying body size distribution of associated animal

communities. Thus, to implement and evaluate the usefulness of the cross-scale resilience model on coral reefs, an essential first step is quantifying the spatial scales at which fish interact with the reef (Fig. 1-1).

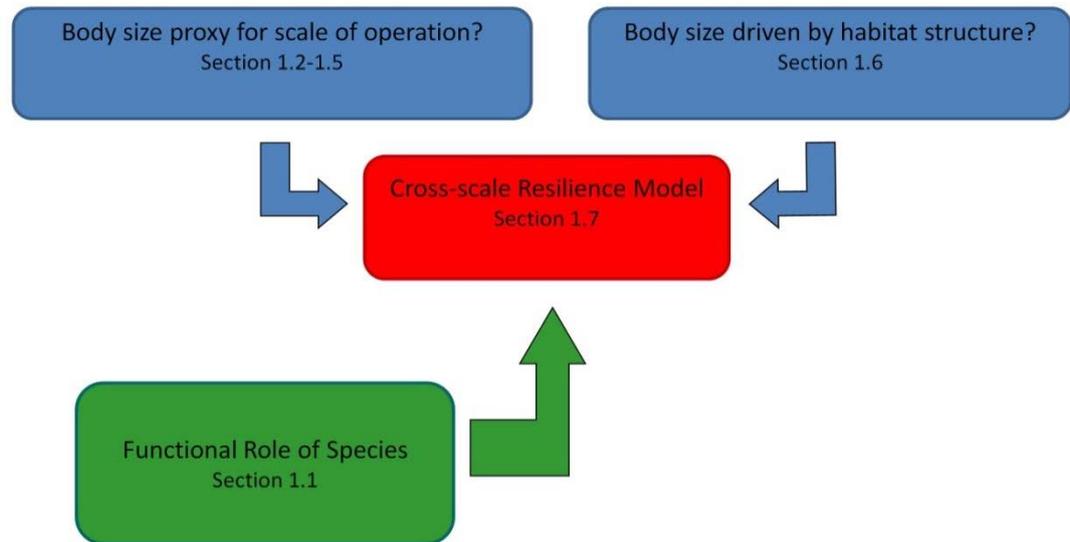


Figure 1-1: Relationship between the cross-scale resilience model (red), required knowledge on the functional role of species (green), and the underlying assumptions of the model relating to the spatial ecology of reef fishes (blue).

1.8 AIMS AND THESIS OUTLINE

This study has two main aims, corresponding to the two parts of the thesis: Part 1 aims to evaluate the spatial scales at which fish interact with the reef and provide their function; and Part 2 evaluates the application of the cross-scale resilience model in the context of coral reefs. These aims are addressed in seven separate studies focusing on distinct research questions:

Part 1: Evaluate the spatial scales at which fish interact with coral reefs

- Chapter 2. Is body size related to home range area in reef fish?
- Chapter 3. Is body size related to foraging movements in reef fish?
- Chapter 4. How are foraging movements influenced by habitat condition?
- Chapter 5. Do cross-scale distributions in habitat complexity drive fish body size distributions?

Part 2: Implement the cross-scale resilience model for coral reef fish

- Chapter 6. What is the current state of knowledge regarding the cross-scale resilience model and its underlying conceptual framework, the discontinuity hypothesis?

- Chapter 7. What body size distribution metrics are appropriate for evaluating the effect of habitat on coral reef fishes?
- Chapter 8. What is the relationship between cross-scale herbivore functional redundancy and reef benthic condition across and following a disturbance event?

The research questions are addressed in the seven studies outlined below, which correspond to the publications derived from this thesis. **Part 1** of the thesis tests the assumptions underlying the cross-scale resilience model and is composed of four chapters: **Chapter 2** is a quantitative review describing the allometric relationship between body length and home range area in reef fish, and exploring the effect of functional group and tracking method on this relationship. The review tests the premise that a species' body size is indicative of the scale at which it operates. **Chapter 3** investigates the allometry of foraging movements for herbivorous reef fish. Furthermore it assesses the range of scales over which different herbivore functional groups provide their role, and the potential effect of fishing on these patterns. Thus, this chapter provides an understanding of the spatial component of reef fish function. **Chapter 4** explores the association between reef condition and foraging behaviour, exploring changes in foraging distances and areas on reefs with different disturbance and recovery histories. This chapter provides an understanding of the dynamics of foraging behaviour in response to habitat modifications. **Chapter 5** quantifies patterns of cross-scale habitat complexity on reefs of different habitat types, and compares these patterns to body depth distributions of the associated fish community. This investigation indicates the potential influence of cross-scale habitat availability on the size distributions of allied taxa. **Part 2** of the thesis is composed of three chapters: **Chapter 6** is a literature review outlining the conceptual framework of the discontinuity hypothesis, which underpins the cross-scale resilience model. The review also explores applications of the discontinuity approach, including characterisation of scales within systems, identification of non-linear dynamics, and the cross-scale resilience model. Finally the review presents research gaps, highlighting the potential problems of using this approach in aquatic systems and for fish taxa. **Chapter 7** builds on a key gap identified in Chapter 6, specifically it explores appropriate body size distribution metrics to use when evaluating the effect of habitat on associated taxa with either determinate or indeterminate growth. The results of this study inform the development of the analysis in Chapter 8. **Chapter 8** draws together all the information from the earlier chapters, implementing the cross-scale resilience model in the context of coral reefs. Specifically it assesses the relationships between changing benthic condition and cross-scale redundancy within the associated herbivorous fish community. Thus, it provides an indication of the utility of the model as an indicator of reef resilience.

In characterising scale dependent function in reef fish, this thesis will provide a fundamental understanding of the spatial scales at which fish interact with their environment and perform functions critical to coral reef resilience. From a management perspective, this research will: 1) Identify the scales at which action is needed to support resilience; 2) Highlight areas that need protection to support existing resilience or counteract its erosion (Cumming *et al.* 2005); and 3) inform appropriate targeted actions such as gear-based management to allow recovery of certain body sizes and thus support key functional groups operating at certain spatial scales.

Chapter 2: Home range allometry in coral reef fishes: comparison to other vertebrates, methodological issues and management applications¹

2.1 ABSTRACT

Body size has been identified as a key driver of home range area. Despite considerable research into home range allometry, the mechanisms driving this relationship are still under debate. This uncertainty stems from a primary focus on terrestrial taxa, and the relatively high variability in the relationship among taxa. Coral reef fishes in particular, have received little attention. I quantitatively reviewed studies examining home range in reef fishes, and assessed the interspecific relationship between body mass and home range area. Body mass and home range are positively related in reef fish (slope of 1.15 to 1.72), with predators having larger home ranges than herbivorous species. This may be attributed to the mobility and lower abundance of predators' food items. Coral reef fishes, and fish in general, appear to occupy a smaller area per unit mass than terrestrial vertebrates (intercepts of -0.92 to 0.07 versus ≥ 1.14). This is likely linked to the relative metabolic costs of ectothermy versus endothermy and aquatic versus terrestrial habitats. When the small home ranges of reef fish are considered in concert with their apparent reluctance to cross open areas, it suggests that reserves aimed at protecting fish species may be more effective if located across whole reefs, rather than covering subsections of contiguous reef, as home ranges in the former are less likely to cross reserve boundaries.

2.2 INTRODUCTION

Home range is an intrinsic component of animal ecology (Burt 1943; Harris *et al.* 1990), with significant consequences for population distributions and densities (McNab 1963; Makarieva, Gorshkov & Li 2005), predator-prey interactions (Harestad & Bunnell 1979) and community structure (Buchmann *et al.* 2011). An extensive body of literature has endeavoured to quantify the spatial biology of taxa, and the physical and biological drivers that influence movements (Börger, Dalziel & Fryxell 2008). These drivers include physical elements of an

¹ Currently in press: Nash KL, Welsh JQ, Bellwood DR, Graham NAJ. *In press*. Home range allometry in coral reef fishes: comparison to other vertebrates, methodological issues and management applications. *Oecologia*.

individual's environment, such as the distribution of food (Owen-Smith, Fryxell & Merrill 2010), water (Scholz & Kappeler 2004), and shelter (Saïd & Servanty 2005; Avgar *et al.* 2013), as well as biological factors such as morphology (Calder 1984), conspecific densities (Johnson, Parker & Heard 2001), territorial behaviours (Civantos 2000) and bioenergetics (Gillingham, Parker & Hanley 1997). Body size, in particular, has received substantial attention (Seton 1909; Hendriks *et al.* 2009), potentially due to its ease of measurement, and 'taxon-free' nature (White *et al.* 2007).

The body size of a species has been shown to be a significant predictor of home range area (e.g. Harestad & Bunnell 1979; Lindstedt, Miller & Buskirk 1986). However, confusion remains regarding the relative importance of mechanisms underpinning this size-home range relationship (Haskell, Ritchie & Olf 2002; Makarieva, Gorshkov & Li 2005). Some of this uncertainty stems from variability in the rate of home range increase with body size among taxa, particularly when compared with allometry of other factors such as metabolic rate (Hendriks 2007). This variability in home range allometry among taxa is important as it affects the relative applicability of purely metabolic explanations for home range behaviour (McNab 1963), versus explanations incorporating factors such as food availability (Schoener 1968) or conspecific density (Jetz *et al.* 2004). Furthermore, the steepness of these relationships will affect the spatial distribution of community interactions (Basset 1995; Jetz *et al.* 2004) and the response of communities to habitat change, for example, the likely impact of habitat fragmentation among body sizes within a taxon (Haskell, Ritchie & Olf 2002); critically, the steeper the allometric slope the more such factors will change among different sized species. Similarly, variation in the intercepts of home range allometric relationships indicates differences in the absolute home range area among taxa, for example lake fishes tend to have smaller home ranges than similarly sized river fishes (Minns 1995). This has consequences for the appropriate size of protected areas established to support specific taxa (Moffitt *et al.* 2009; Barnett *et al.* 2012).

Despite the important implications of variability within home range-body size relationships, the majority of home range allometric studies have focused on more charismatic taxonomic groups, such as mammals, leaving these relationships largely unevaluated within fishes and invertebrates (Hendriks *et al.* 2009). Quantifying relationships for understudied taxa that inhabit specific environments and comparing findings with existing work has the potential to clear up some of the remaining confusion regarding the relative importance of mechanisms underpinning the size-home range relationship (Haskell, Ritchie & Olf 2002; Börger, Dalziel & Fryxell 2008). To date, only two studies have looked at interspecific allometry of home range size in fishes, one in freshwater (Minns 1995) and one on coral reefs (Kramer & Chapman

1999). Considering the importance of fish communities within different aquatic systems, such little emphasis on generating a broad scale understanding of home range in fishes, is surprising. The single study that investigated the allometry of home range in coral reef fishes used body length and range length to examine the relationship (Kramer & Chapman 1999). This design has an important limitation: due to the often non-circular nature of many fish home ranges (Holland, Lowe & Wetherbee 1996) and the reliance on length rather than mass data, direct comparisons with allometric relationships derived for other taxa are not possible. In light of current interest in the veracity of traditionally-recognised terrestrial-aquatic differences in structure and processes (Raffaelli, Solan & Webb 2005), such comparisons are essential to tease apart ecosystem differences and similarities (Webb 2012).

Comparisons among taxa and studies are further complicated by methodological differences. The techniques used to quantify movement have transitioned over time from visual observations and mapping, to radio telemetry (Harris *et al.* 1990; Laver & Kelly 2008) and satellite tagging (Jouventin & Weimerskirch 1990). In the case of marine species, especially fishes, before the late 90's studies were largely restricted to visual observations (Kramer & Chapman 1999), due to the logistics of working in the marine environment (but see Holland, Lowe & Wetherbee 1996). However, the application and refinement of acoustic telemetry in the last few decades has made it possible to accurately monitor the movement of marine species and to estimate the home range of a wider number of taxa (Bolden 2001). The method used to track animals may impact home range estimates (e.g. Lira & Fernandez 2009), thus this evolution of tracking methods over time means that where data are incorporated from multiple studies into a quantitative review, it is important to account for the effect of these methodological changes on estimates of home range.

The aim of this study is therefore, to provide a quantitative analysis of movement in coral reef fishes in order to: (1) explore the change in home range methods used in coral reef systems over time; (2) determine the interspecific relationship between body size and home range, exploring the influence of trophic status and tracking method on this relationship; and (3) compare home range allometry in reef fishes with those of other vertebrate taxa.

2.3 MATERIALS AND METHODS

I conducted a comprehensive search of the ISI Web of Science database and Google Scholar for primary research using the following keywords: coral reef AND fish AND home range OR move* OR spatial. I thoroughly checked the returned literature and only papers specifically related to measuring the spatial movement of coral reef fishes were retained, resulting in a database of 154 publications. Details of the field methods and the movement

analyses used to quantify home range were extracted from each paper. Where more than one technique was used to track individuals and quantify movement, I classified the publication as using a mixed-method approach.

Of the studies considered, I incorporated 31 into a quantitative analysis examining the relationship between body size and home range of different trophic groups on coral reefs (Appendix A Table S1). These data quantified home range in 40 species. I chose publications if they fulfilled the following criteria: (i) Research was undertaken on coral reefs and studied reef-associated teleost fish species; (ii) Mean or individual home range area data were presented; (iii) Home range was estimated using Minimum Convex Polygons (MCP; although not all papers used the term MCP, all estimates that delineate the outer boundaries of a fish's movement within its area of habitation were included). There has been some discussion regarding a preference for Kernel Density Estimation (KDE) rather than MCP derived estimates of home range due to unpredictable biases inherent in the latter (Börger, Dalziel & Fryxell 2008). There were insufficient studies using KDE to allow incorporation of these data. However, work by Nilsen et al. (2008) suggest that despite inherent biases in MCP data, such an approach is appropriate where comparisons are made among species (as in my study) rather than within species where the magnitude of the methodological biases may exceed biological differences; (iv) Home range estimates were for adult individuals, as fish species may exhibit ontogenetic shifts in behavior (Welsh, Goatley & Bellwood 2013); (v) Home range estimates did not include spawning aggregations or movements related to reproduction; (vi) Where fish were tagged in short term studies, fish were assessed to ensure their behaviour was not modified by the tag; (vii) Where fish were tracked using passive acoustic telemetry, the detection range of the sonic receivers was investigated.

I extracted data on the fish home range (standardised to m²), fish body length (cm) or body mass (g), life stage (adult or juvenile), and the method of tracking (visual or telemetry) from each study. Information on the trophic group of species was sourced from the literature (Green & Bellwood 2009) and from FishBase (Froese & Pauly 2012). I classified species into the two broad trophic groups 'Herbivore' and 'Predator' (herbivore incorporates detritivorous species feeding on the epilithic algal matrix and predator incorporates invertivore species), as this corresponded to the classifications used in comparable terrestrial studies (e.g. Hendriks *et al.* 2009). Body masses of fishes were calculated from the size data using length:body mass conversions available from FishBase (Froese & Pauly 2012).

I assessed the interspecific relationship between mean body mass and mean home range by modelling 'log₁₀ home range', as a function of the factors 'trophic group' (predator versus herbivore) and 'tracking method' (visual versus telemetry), and the continuous variable 'log₁₀

body size' (n=40). Phylogenetic relationships may confound interspecific relationships due to non-independence of data points. To control for this, I included family as a random factor (following Kelt & Vuren 2001). Incorporating this variable as a random factor prevents pseudoreplication by accounting for having multiple species within a family (Bolker *et al.* 2009). I fitted multi-level linear models with identity link functions and normal errors to the data (glmmADMB package in R; R Development Core Team 2011). To select the best-fit random structure (varying intercepts or varying intercepts and slopes among families) I fitted both models and compared Akaike Information Criteria (AIC) values. I assessed the importance of the random variables before testing the fixed variables (Zuur *et al.* 2009). To choose the best-fit fixed model I fitted multiple models using the explanatory variables and compared AIC values corrected for small sample sizes (AICc, MuMIn package in R; Barton 2013), where the set of candidate models were all possible combination of models within the global model (\log_{10} home range $\sim \log_{10}$ body mass + trophic group + tracking method). I fitted the models with differing fixed effect structures using maximum likelihood (ML) estimation, to allow comparison of the nested models (Zuur *et al.* 2009). AICc values are provided for all models, with details of the change in AICc with respect to the top ranked model (Δ AICc), and AICc weights (w AICc). Model parameters with Highest Posterior Density (HPD) credible intervals are presented for the models within 2 AICc units of the best-fit model (Burnham & Anderson 2002). To understand the variation in home range, explained by the best-fit model, I calculated the marginal (fixed effect) and conditional (whole model) coefficients of determination (R^2) according to Nakagaw & Schielzeth (2013). The assumptions of normality and homogeneity of variances were checked by visual inspection of residual plots; the assumptions were met. Body size was confounded by tracking method, with all small species observed using visual methods, and large species tracked via telemetry, therefore I reran the analysis without tracking method as a fixed factor to evaluate the change in model coefficients and performance. To allow comparison of reef fish home range allometry with other taxa, I sourced ranges for slopes and rescaled intercepts for vertebrate groups from Hendriks *et al.* (2009). I plotted example relationships for mammals (Kelt & Vuren 2001), birds (Schoener 1968), lizards (Turner, Jennrich & Weintraub 1969) and freshwater fishes (Minns 1995) alongside the coral reef fish data, to allow visual comparison with home range body size scaling in reef fishes.

2.4 RESULTS

There has been a steady increase in the number of studies evaluating movement and space use by fishes over the last 60 years (Fig. 2-1). In this time period there has been a shift from studies primarily using visual tracking methods to research incorporating acoustic

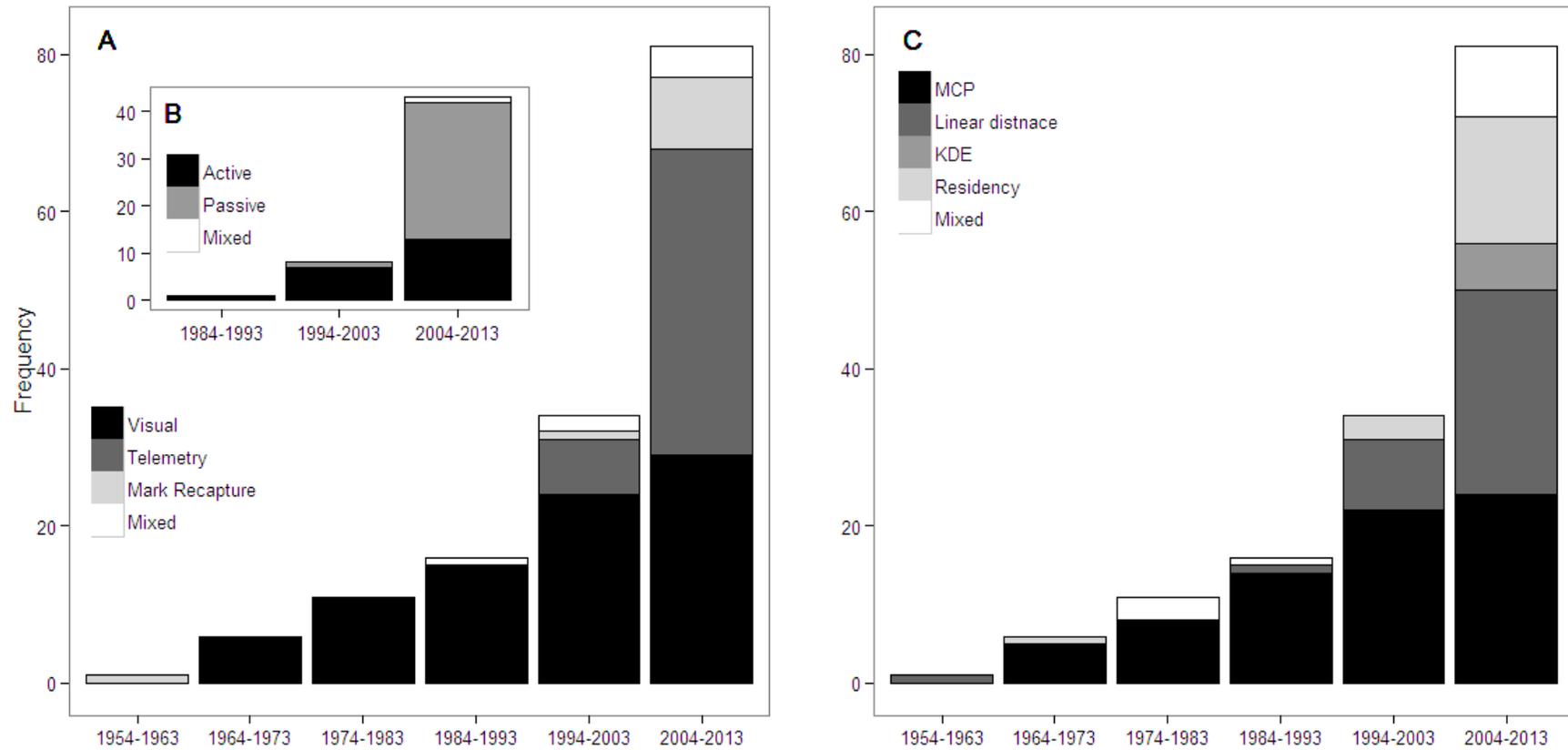


Figure 2-1: Number of publications documenting home range in coral reef fishes, categorised according to year of publication and A) Tracking method used, B) Detection method of telemetry studies, and C) Analytical method undertaken.

telemetry (Fig. 2-1A). Of these telemetry studies, the dominance of active methods used to track and detect individuals has shifted to a greater prevalence of studies using passive approaches and fixed receiver arrays (Fig. 2-1B). In concert with the increase in movement-related studies, there has been a shift in analytical approaches from predominantly quantifying the areas used by fishes with minimum convex polygons, to a broader variety of approaches. These include linear estimation of distances moved, areas occupied using KDE, and studies of site fidelity and residency (Fig. 2-1C).

Table 2-1: Comparison of random effect structures for models that either A) included tracking method or B) did not include tracking method in the analysis.

Model	AIC
A Log home range ~ Log body mass + trophic grp. + method + (1 family) – slopes and intercepts varying	96.71
Log home range ~ Log body mass + trophic grp. + method + (1+log10mass family) – intercepts varying	98.34
B Log home range ~ Log body mass + trophic grp. + (1 family) – slopes and intercepts varying	117.3
Log home range ~ Log body mass + trophic grp. + (1+log10mass family) – intercepts varying	118.7

The random model structure incorporating varying intercepts for family was better supported than the model incorporating varying intercepts and slopes for the interspecific analyses including tracking method (Table 2-1A). The best-fit fixed model for this analysis incorporated log body mass and varying intercepts among trophic groups and tracking methods (Table 2-2A). This model was more than 2 AICc units lower than the next best model (AICc 96.90 and 102.0 respectively). Log home range size was strongly and positively related to log body mass (slope of 1.12; Fig. 2-2; Table 2-3A). Predatory species had greater home range areas than herbivores of similar sizes, similarly home ranges estimated using telemetry were larger than those estimated using visual observations when controlling for body size. The fixed effects explained 84% of the variance (marginal R^2) in log home range, whereas the whole model (incorporating the random variable family) explained 87% of the variance (conditional R^2) in log home range.

In the analysis that did not incorporate tracking method, once again the random model structure with varying intercepts for the random factor ‘family’ was better supported than the model incorporating varying intercepts and slopes (Table 2-1B). The best-fit fixed model incorporated log body mass, but did not include the factor ‘trophic group’ (Table 2-2B).

However, this model had only a slightly lower AICc value than the model incorporating trophic group (Table 2-2B; AICc of 117.3 and 117.7 respectively). Log home range size was strongly and positively related to log body mass (slope of 1.71; Fig. 2-2; Table 2-3B). Once again, in the model including trophic group, predatory species covered greater home range areas than herbivores of similar sizes. The fixed effects explained 74% of the variance (marginal R^2) in log home range, whereas the whole model (incorporating the random variable family) explained 80% of the variance (conditional R^2) in log home range.

Table 2-2: Set of candidate models compared using AICc values to determine the best-fit fixed structure, for models that either A) included tracking method or B) did not include tracking method in the analysis.

Model	AICc	Δ AICc	Weight
A Log home range ~ Log body mass + trophic grp. + method + (1 family)	96.90	0.00	0.928
Log home range ~ Log body mass + method + (1 family)	102.0	5.13	0.072
Log home range ~ Log body mass + (1 family)	117.3	40.43	0.000
Log home range ~ Log body mass + trophic grp. + (1 family)	117.7	20.82	0.000
Log home range ~ trophic grp. + method + (1 family)	129.1	32.27	0.000
Log home range ~ method + (1 family)	131.9	35.02	0.000
Log home range ~ 1 + (1 family)	167.8	70.88	0.000
Log home range ~ trophic grp. + (1 family)	169.7	72.85	0.000
B Log home range ~ Log body mass + (1 family)	117.3	0.00	0.548
Log home range ~ Log body mass + trophic grp. + (1 family)	117.7	0.39	0.452
Log home range ~ 1 + (1 family)	167.8	50.45	0.000
Log home range ~ trophic grp. + (1 family)	169.7	52.42	0.000

Coral reef fish exhibit steeper body size-home range relationships than freshwater fish (slope of 0.58), regardless of model used (1.12 and 1.71 for the coral reef model incorporating and excluding tracking method, respectively; Fig. 2-3A&B). Reported slopes of lizard, mammals and birds were generally higher than those of freshwater fishes, but were similar to those of coral reef fishes when tracking method was incorporated into the allometric model (Fig. 2-3A). However, they were generally lower than that of coral reef fishes when tracking method was excluded from the model (Fig. 2-3B). The reported slope for lizards range from 0.42 to 1.09, for birds from 0.64 to 1.39, and for mammals vary from 0.47 to 1.56 (examples provided in Fig. 2-3).

The intercept for reef fish body-size home range relationships overlapped with or were lower than those for freshwater taxa, depending on the model used. Whereas, the intercept was predominantly lower for the reef fish relationships compared with terrestrial taxa. Specifically, when tracking method was incorporated into the allometric model of home range for reef fishes

Table 2-3: Coefficients of the best-fit fixed models exploring the relationship between log home range and log body size for models that either A) included tracking method or B) did not include tracking method in the analysis. Only those models within 2AICc value of the optimal model are presented.

Model	Intercept	Slope	R ² (Marginal)	R ² (Conditional)
A Log home range ~ Log body mass + trophic grp. + method + (1 family)	Intercept: 0.98 (-0.08,2.11) Predator: 0.74 (0.19,1.32) Visual: -1.69 (-2.40,-1.05)	1.12 (0.79,1.46)	0.84	0.87
B Log home range ~ Log body mass + (1 family)	-0.92 (-1.85 ,-0.05)	1.71 (1.33,2.11)	0.74	0.80
Log home range ~ Log body mass + trophic grp. + (1 family)	Intercept: -1.20 (-2.22, -0.22) Predator: 0.48 (-0.39,1.32)	1.70 (1.36,2.06)	0.74	0.80

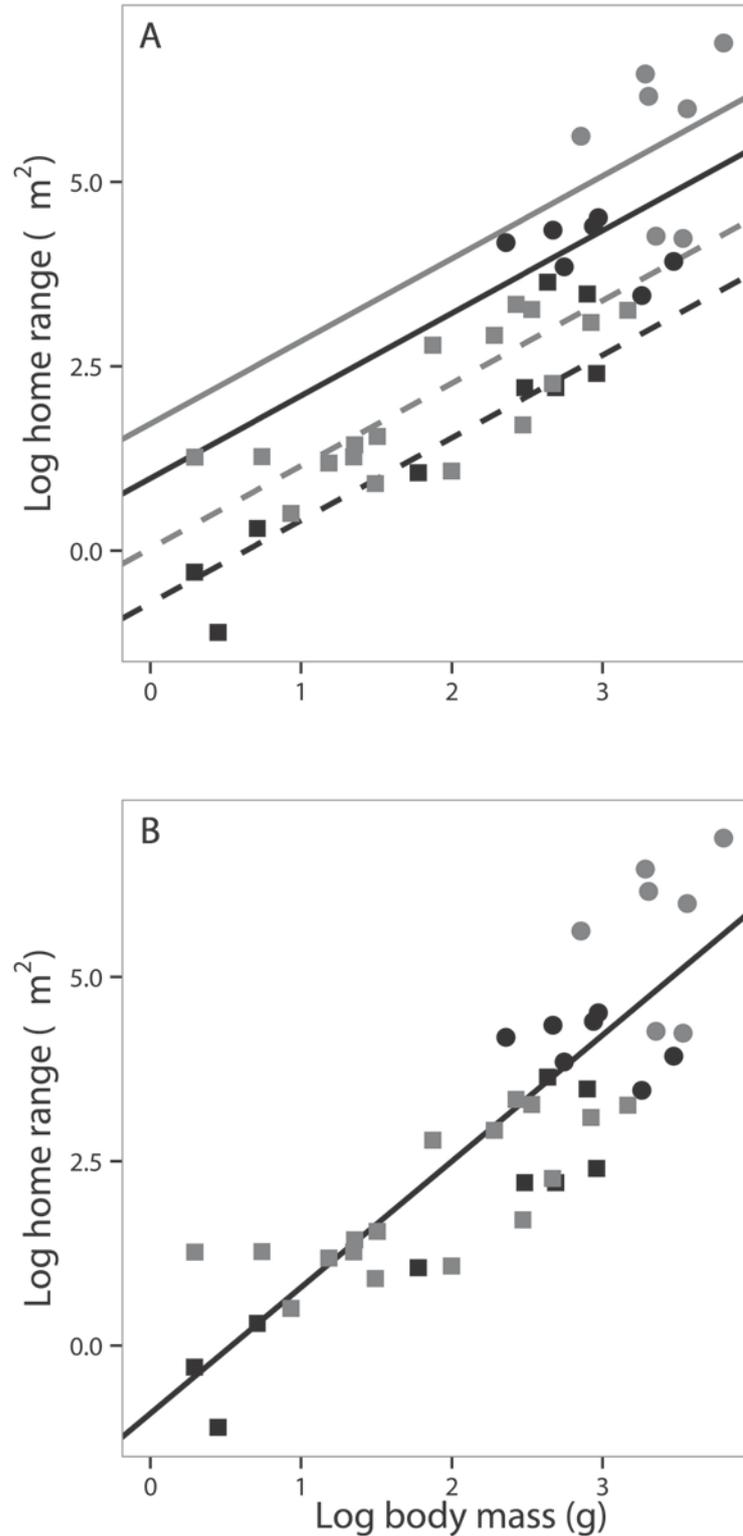


Figure 2-2: Interspecific relationship between log body mass (g) and log home range (m²) for coral reef fishes from studies estimating home ranges using Minimum Convex Polygons (MCPs), for models that A) included tracking method with different intercepts among the two tracking methods and trophic groups, and B) did not include tracking method in the analysis. Symbols: squares & dotted lines – visual tracking; circles & solid lines – telemetry tracking; grey – predators, black – herbivores.

(Fig. 2-2A), the intercept of predatory reef fish taxa was higher for telemetry studies (1.72) but lower for visual studies (0.03) than those of river fishes (0.52) and lake fishes (0.80) (Fig. 2-3). A similar pattern was seen for herbivorous reef fishes (Intercepts for Telemetry: 0.98 and Visual: -0.71). When tracking method was excluded from the model for reef fishes, the intercept was lower (-0.92) than either river or lake fishes (Fig. 2-2B; Fig. 2-3). Regardless of the model used, the intercept for reef fish was lower than reported intercepts for terrestrial taxa with the exception of predatory fish followed using telemetry (1.72). The intercepts of terrestrial species were in the order of 2.23 for lizards, 1.14 to 3.04 for mammals, and ranged from 2.11 to 5.21 for birds (examples provided in Fig. 2-3).

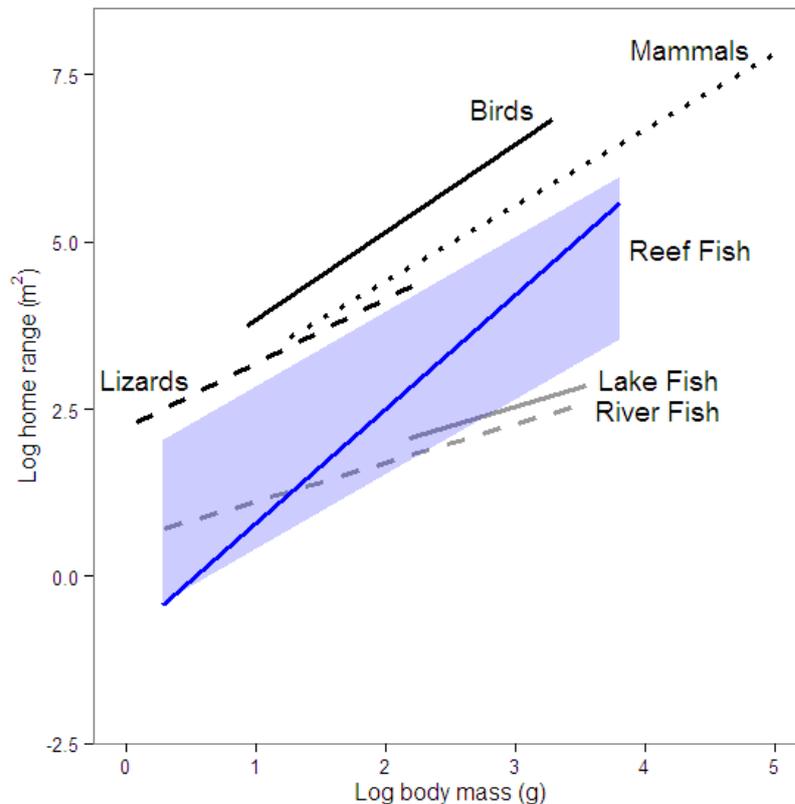


Figure 2-3: Comparison of interspecific relationship between log body mass (g) and log home range (m^2) among vertebrate taxa. Blue shaded area represents range of intercepts provided by model for reef fish incorporating tracking method; solid blue line – reef fish for model not incorporating tracking method; solid grey line – lake fish (Minns 1995); dashed grey line – river fish (Minns 1995); solid black line – birds (Schoener 1968 recalculated in Harestad & Bunnell 1979); dashed black line – lizards (Turner et al. 1969); dotted black line – mammals (Kelt and Vuren 2001).

2.5 DISCUSSION

The home range area of coral reef fishes is positively related to body size, and is smaller in herbivorous species than predators of a similar body size. Fishes generally occupy a smaller area per unit of body mass than terrestrial vertebrate species. This has important consequences for the effective management of coral reef fishes and the ecosystem they inhabit. The change in methodology used in studies over time, and the effect of tracking method on home range estimates introduce uncertainty that requires careful consideration and highlights the need for more, methodologically rigorous, home range research.

2.5.1 *Evolution in home range methods*

Coral reef studies have lagged behind terrestrial research with only recent adoption of telemetry approaches that have been more common in the terrestrial literature. Visual tracking and mark recapture studies have been the mainstays of coral reef research up until the last 10 years, when a shift to acoustic telemetry has been observed. Following the rise in telemetry based studies, there has been a shift from primarily active monitoring to passive acoustic tracking. This shift has been driven by the need for less intensive field time and longer monitoring periods made possible by passive tracking (Heupel, Semmens & Hobday 2006). Analysis approaches to home range data from coral reefs has also trailed terrestrial ecology. KDE methods came to the fore in terrestrial studies in the late 1980s (Worton 1989), and yet this analysis method has only recently become popular in the coral reef literature, with just 14 studies in my review incorporating KDE or a mix of KDE with other techniques; all published since 2003. The coral reef literature has traditionally relied on MCPs for home range estimation.

The relatively slow uptake of new methods (telemetry and KDE analyses) in coral reef-home range studies affected my ability to compare among species and studies. For example, the change in tracking method from predominantly visual to telemetry has not been evenly applied across body sizes, such that size and tracking method co-vary, with the home range of larger species predominantly estimated using telemetry. This has consequences for estimating the home range allometric relationship of reef fish, as discussed in the following section. Similarly, variation in the methods used affects the type of research questions that can be asked using home range estimates (Börger, Dalziel & Fryxell 2008; Laver & Kelly 2008). For example, KDE estimates of home range may be useful for looking at activity centres and the intensity of use, but may miss less used but important areas of home range such as sites of territorial display or migrations to sleeping sites that would be included in MCP estimates (van Rooij, Kroon & Videler 1996; Kie *et al.* 2010; Welsh & Bellwood 2012b).

2.5.2 *Home range allometry in reef fishes and effects of tracking method*

Home range area is positively related to body size in coral reef fishes. This relationship can be explained by the greater energy requirements of large versus small species (McNab 1963). However, providing a robust estimate of the slope of this relationship is currently problematic. The method of tracking an organism influences the home range estimate (Laver & Kelly 2008). This is not surprising considering the different strengths and trade-offs of the methods. However, due to the lack of overlap in body size among species studied using telemetry versus visual methods, a more detailed understanding of the effects of tracking method on home range estimates is currently lacking, and thus uncertainty remains regarding the slope of the allometric home range relationship in coral reef fish.

It is also not clear from the analyses whether tracking method per se or the sampling period over which these methods are applied is of more importance. Large telemetry datasets provide ways of characterising home range behaviour over longer time periods and more comprehensively than visual observations (Bolden 2001). This difference may be accounted for in comparisons among studies *if* sampling period is incorporated into an explicit description of the home range estimation, e.g. differentiating between a daily range versus a monthly or seasonal range (e.g. Savitz *et al.* 1993). However, few of the coral reef studies (4 out of 40) made overt mention of time within their home range description, merely presenting a ‘home range’ estimate. Furthermore, description of the methods were often inadequate and made it difficult to standardise time across studies. Therefore, although ‘tracking method’ appears to influence home range estimates among studies, it may be that telemetry approaches are merely representative of longer-term home range estimates, compared with visually observed ranges, which are likely to represent shorter-term periods of site attachment. Clearly there is a need for more, methodologically robust estimates of home range in reef fish, which are explicitly assigned to a temporal period such as weekly or seasonal home range.

Regardless of the effect of tracking method on the slope of the relationship between home range and body size, trophic group appears to influence home range area. Trophic group was found within the best-fit model for the analysis incorporating tracking method, and in the second best model (change in AICc of 0.39 from the best-fit model) for the analysis not including tracking method. Thus predatory reef fish appear to have larger home ranges than similarly sized herbivorous species. Larger home ranges in predators are attributed to their food sources being more mobile and less abundant than herbivores, causing individuals to travel further to meet energy requirements (Schoener 1968). Similar patterns have been seen across a range of taxa, although this information is currently lacking from freshwater species where only predators have been studied (Minns 1995; Hendriks *et al.* 2009).

2.5.3 Comparisons in home range allometry across taxa

In all the analyses the intercepts of the relationship between body size and home range were lower for ectotherms (fish and lizards) compared with the endothermic taxa (birds and mammals), indicating that ectotherms generally occupy a much smaller area per unit of body mass than endothermic vertebrates. Thus, the lower metabolic requirements of ectotherms may be achieved within smaller home range areas (Hendriks *et al.* 2009). In addition, the aquatic ectotherms (fishes) appear to have smaller home ranges than their terrestrial counterparts (lizards), which may be indicative of the relatively lower metabolic costs of living in water versus air (White *et al.* 2007).

Despite the underlying importance of metabolism in influencing space use by vertebrates (McNab 1963), a slope of greater than 0.75 across most vertebrate groups implies that metabolism cannot be the sole driver in body size-home range scaling and that other factors play a part (Kelt & Vuren 2001). Home range may be constrained by body size (McNab 1963) and the costs associated with travel (Kelt & Vuren 2001). The presence of both fishes and whales in the aquatic environment that are larger than coral reef fishes, suggests that upper limits in reef fish home range area are unlikely to be the result of structural constraints on size. Instead, there is considerable evidence that open patches act as barriers to fish movement, with fishes either unable to cross open areas (Turgeon *et al.* 2010), or showing significant reluctance even when physically capable. This may be due to perceived predation risk and thus the high cost of travel among reefs (Chapman & Kramer 2000; Kelt & Vuren 2001; Welsh & Bellwood 2012a). Similarly, the home ranges of freshwater fishes are limited by the size of the body of water in which they live (Woolnough, Downing & Newton 2009). Thus, the relatively small home ranges of fishes are likely due to access to sufficient food resources within a small area, and the fragmented or constrained nature of their habitat. Similar adaptation to constrained landscape areas can be seen in some lizards, where species of *Anolis* lizards found on islands have smaller home ranges than continental species, even when differing body sizes have been accounted for (Schoener & Schoener 1982).

In addition to considering the relative magnitude of home ranges among similarly-sized species in different taxa (different intercepts), variations in the slope of the home range-body size relationship among taxa, is also of importance. The slope for coral reef fish appears to be somewhat higher than for freshwater fishes regardless of the model used (i.e. incorporating versus excluding tracking method). Minns (1995) proposed that the interaction of indeterminate growth and energy consumption drives the shallow slope in freshwater fishes, however, the apparently steeper relationship in coral reef fishes indicates that indeterminate growth is unlikely to be a factor in the freshwater home range allometry. It may be that the constraints of

water body size on the home range of freshwater species, discussed previously, has a greater effect on large freshwater species than reef fragmentation has on large reef species, driving a lower slope in the body size-home range scaling of freshwater fishes.

Comparison of the slope between reef fish and terrestrial taxa is more problematic. The study incorporating tracking method suggests that home range allometry of reef fishes have a similar slope to that of terrestrial vertebrates, whereas the study excluding tracking method indicates a steeper slope for reef fishes compared with terrestrial taxa. The most parsimonious explanation would appear to be that the slope in coral reef fishes is similar to those of other vertebrates (as in the model incorporating tracking method). However, uncertainty remains and there is the potential that reef fishes exhibit home range allometric slopes at the upper end of the range found in vertebrate taxa.

2.5.4 Management and ecological implications

Traditionally, the study of animal home ranges in the terrestrial environment has been used to identify key components of a species' habitat such as important foraging and shelter areas, as well as migration paths (Baker 1978; Börger, Dalziel & Fryxell 2008). In the marine environment, the quantification of animal movements has been applied to conservation objectives, and considerable interest in the home range of reef fishes has stemmed from the desire to optimise marine reserve design in relation to fish movements (Kramer & Chapman 1999; Moffitt *et al.* 2009; Meyer, Papastamatiou & Clark 2010). The relatively small home ranges of reef fishes compared to terrestrial taxa, appears to suggest that where the aim of a marine protected area (MPA) is to support particular fish species, reserve size may be smaller than that needed in terrestrial protected areas with similar objectives. However, caution needs to be exercised when designing reserves based on individual home ranges as the space needs of individuals or individual species may not scale up to reflect community needs (Basset 1995) or ensure the maintenance of minimum viable populations (Shaffer 1981). Furthermore, I only included studies where space use was non-reproductive in nature, and although such research made up the majority of the available literature, larger-scale migrations to spawning aggregations are common within reef fishes (Claydon, McCormick & Jones 2012). These migrations drive movements outside the normal home range, causing fish to cover greater areas and thus potentially move outside protected sections of reef (Afonso *et al.* 2008; Welsh & Bellwood 2014). Recent research is exploring the importance of overlapping marine reserve placement with spawning locations (e.g. Hamilton, Potuku & Montambault 2011), however, as noted above, caution needs to be exercised when basing reserve design decisions on published home range data for specific species.

The unresolved relationship between home range and body size in reef fishes is of concern because considerable research into the effectiveness and design of marine reserves (e.g. Palumbi 2004; Sale *et al.* 2005) has relied on an existing estimate of the relationship between home range and body size in reef fishes (Kramer & Chapman 1999). Kramer & Chapman's (1999) study was based almost exclusively on visual home range estimates. My review suggests different home range allometric relationships may be derived when either separating out different tracking methods or combining all data, therefore it is currently not possible to ascertain the most accurate coefficients for this relationship. However, the relatively small home ranges and apparent reluctance of fish to cross open areas between reefs provides an avenue for managers to effectively design marine reserves, even as more data are being collected to parameterise models of home range allometry in reef fishes. Specifically, these findings suggest that reserves which encompass whole reefs or sections of reef separated from neighbouring sectors by open water are likely to be more effective at protecting fish populations across the full range of species' body sizes, compared with MPAs that only cover a segment of a reef. Such an approach was undertaken during the rezoning of the Great Barrier Reef Marine Park in 2003, where green zones (no-take areas) were primarily designated to cover whole reefs (GBRMPA 2002).

Home range has significant implications for ecosystem health and functioning (Freiwald 2012). Organisms interact with their environment in a manner that facilitates vital ecological processes, such as nutrient cycling (Vanni 2002) and herbivory (Nash, Graham & Bellwood 2013). The interactions between an individual and its environment are, however, bound within the individual's home range. Thus, the spatial scale of ecological functioning and the connectivity of ecosystems are closely associated with home range (Nystrom & Folke 2001; Fagan, Lutscher & Schneider 2007; Fox & Bellwood 2011). The relatively small areas used by reef fishes suggest that the scale of function provided by populations are somewhat constrained, although once again the unresolved nature of the slope between size and home range means that the scale of function and connectivity provided across species of different body sizes is as yet unclear. Nevertheless, supporting healthy populations of larger reef fish species is likely to be critical to the maintenance of key ecosystem function and processes, and may facilitate the recolonization and rehabilitation of degraded ecosystems (Nash, Graham & Bellwood 2013).

2.5.5 Conclusions and future directions

In this study I extend the scope of home range allometric studies by quantifying home range-body size scaling in coral reef fishes. I show that body size and home range are positively related in coral reef fishes, and that fish, in general, have relatively small home

ranges compared with terrestrial taxa of similar body size. Furthermore, predatory fish species appear to have larger home ranges than herbivores per unit mass. My study highlights a number of important avenues for future home range work on coral reef fishes, including: i) a need for mixed-method (visual vs. telemetry) empirical studies to help quantify differences in estimates among tracking methods, understand the effect of sampling period, and resolve the steepness of the relationship between body size and home range; and ii) a need for more coral reef studies using KDE approaches.

Chapter 3: Fish foraging patterns, vulnerability to fishing and implications for the management of ecosystem function across scales²

3.1 ABSTRACT

The function of species has been recognized as critical for the maintenance of ecosystems within desired states. However, there are still considerable gaps in our knowledge of inter-specific differences in the functional roles of organisms, particularly with regards to the spatial scales over which functional impact is exerted. This has implications for the delivery of function and the maintenance of ecosystem processes. In this study I assessed the allometric relationship between foraging movements and fish body length at 3 sites, for 20 species of herbivorous reef fishes within four different functional groups: browsers, farmers, grazer/detritivores, and scraper/excavators. The relationship between vulnerability of species to fishing and their scale of foraging was also examined. I present empirical evidence of the strong, positive, log linear relationship between scale of foraging movement and fish body length. This relationship was consistent among sites and between the two different movement metrics used. Phylogeny did not affect these results. Functional groups foraged over contrasting ranges of spatial scales, for example scraper/excavators performed their role over a wide range of scales, whereas browsers were represented by few species and operated over a narrow range of scales. Overfishing is likely to not only remove species operating at large scales, but also the browser group as a whole. Large fishes typically have a significant role in removing algae on reefs, and browsers are key to controlling macroalgae and reversing shifts to macroalgal dominated states, this vulnerability to exploitation has serious consequences for the ability of fish assemblages to deliver their functional role in the face of anthropogenic impacts. However, identification of the scales at which herbivorous fish assemblages are susceptible to fishing, provides managers with critical knowledge to design management strategies to support coral-dominated reefs, by maintaining function at the spatial scales at which vulnerable species operate.

² Published as: Nash KL, Graham NAJ, Bellwood DR. 2013. Fish foraging patterns, vulnerability to fishing and implications for the management of ecosystem function across scales. *Ecological Applications* 23: 1632-1644.

3.2 INTRODUCTION

Species of different body sizes perceive and interact with their environment over different spatial and temporal scales (Holling 1992). These relationships have been explored thoroughly in many terrestrial systems, particularly for birds and mammals, with respect to length of stride (Calder 1984), home range area (Harestad & Bunnell 1979; Peters 1983), and aggregation of resources (Laca *et al.* 2010). In contrast, such relationships have not been adequately investigated in aquatic systems with many studies of movement limited to one or a few species (e.g. Nanami & Yamada 2008; Freiwald 2012), and few reviews aimed at consolidating this information with respect to body size (but see Kramer & Chapman 1999). Aquatic organisms are subject to different processes and constraints than terrestrial species (White *et al.* 2007), and as such may show contrasting allometric patterns, driving a need for further studies in this area.

The role or function organisms play within a particular environment, such as pollination, grazing and nitrogen fixation has attracted considerable attention in recent years (Folke *et al.* 2004). There is an increasing awareness that management may support a system within a desired state by maintaining the core ecosystem processes provided by different functional groups (e.g. Christensen *et al.* 1996; Bellwood *et al.* 2004; Pikitch *et al.* 2004). In response, there have been calls for new ways to evaluate the delivery of function, to provide the knowledge needed by managers to effectively implement appropriate mitigation strategies to support important ecosystem processes (Hughes *et al.* 2010). One avenue of research has examined the significance of multiple species performing a similar role within an ecosystem, providing redundancy or a degree of ‘insurance’ in the face of anthropogenic pressures that drive species declines and in turn may reduce functional impact (Walker, Kinzig & Langridge 1999; Elmqvist *et al.* 2003; Cheal *et al.* 2010). The benefits of this redundancy are reliant on the members of a functional group responding to a disturbance differently, with some species maintaining or increasing their functional impact to compensate for the loss or decline of other members of their functional group (Walker, Kinzig & Langridge 1999; Elmqvist *et al.* 2003). Species performing similar functions at different spatial and/or temporal scales are likely to exhibit a range of responses to disturbances impacting at specific scales, thus providing effective redundancy (Peterson, Allen & Holling 1998; Elmqvist *et al.* 2003). As a result, characterizing the scales at which species within a functional group operate and provide their role is fundamental knowledge needed to inform management actions aimed at supporting: (i) redundancy of function across scales (termed cross-scale redundancy), and (ii) delivery of function at specific scales.

The temporal and spatial characteristics of movement may be assessed at a number of levels, from the large scales of dispersal, through mid-scales of home range use, down to small scales of patch and food selection (Holling 1992). Movements at these various scales have a range of implications for the ecology of communities and populations, and a species' impact on the ecosystems they inhabit. For example, dispersal will influence community assembly (Chase 2003), whereas more localized movements may affect the function of a species within a system (e.g. Vaughn & Hakenkamp 2001). Movement is often investigated at the scale of home range (Börger, Dalziel & Fryxell 2008). However, these types of studies may not effectively describe the spatial dimensions of a species' functional impact. Home range encompasses the area occupied by an organism whilst performing a range of activities such as feeding, sleeping and breeding (Samuel, Pierce & Garton 1985; Börger, Dalziel & Fryxell 2008). The location of these activities may not overlap (Lazenby-Cohen & Cockburn 1991); as a result the home range will incorporate areas in which an individual is exerting critical functional impact, and areas where this impact may not be as significant (Welsh & Bellwood 2012b). Furthermore, differences in home range size among species may not correlate with differences in functional range size among species, as distinct drivers influence decision making and movements at different scales (Senft *et al.* 1987). For example, decisions regarding reproductive opportunities within the broader home range will be driven by different factors than those regarding movements in relation to food choice (Senft *et al.* 1987). As a result, although there is evidence from a range of systems that species' body size is positively related to home range (e.g. Harestad & Bunnell 1979), it cannot be assumed that the relationship between body size and movement at the home range scale is representative of movements at other scales. To gain a comprehensive understanding of the functional impact of a species, there is a need to examine the allometry of movement at a scale relevant to the use of space whilst individuals are actively performing their functional role.

Herbivorous reef fishes drive a key ecosystem process on coral reefs by mediating competition between coral and algae, removing algae, and creating space for coral recruits (Hughes *et al.* 2007a). However, there is growing evidence that herbivorous fish functions on reefs are more complex than simple classifications such as 'herbivore' suggest, with important differences both within and among species. For example, ontogenetic changes and growth within species may influence diet (e.g. Buckle & Booth 2009), grazing rate and bite size, with larger individuals providing greater functional impact through higher rates of grazing and larger bite areas (Ferreira, Peret & Coutinho 1998; Paddock, Cowen & Sponaugle 2006; Lokrantz *et al.* 2008). Similarly, interspecific differences in foraging behaviour have been shown to influence finer scale functional classifications within broad diet groups. Herbivorous fish species may be split into farmers, grazer/detritivores, scraper/excavators, and browsers (Green

& Bellwood 2009). Farmers are site-attached species which actively tend and defend algal resources within their territory (Ceccarelli, Jones & McCook 2001). Grazer/detritivores feed on the epilithic algal matrix (EAM), which is composed of algal turf, detritus, microbes, sediment and invertebrates (Wilson & Bellwood 1997), whereas scraper/excavators remove both components of the EAM and underlying substrate and therefore are also important for the process of bioerosion (Green & Bellwood 2009). These groups help reduce colonization by macroalgae and so assist in maintaining reefs within a coral dominated state. In contrast, browsers feed on mature macroalgae and as such are critical for reversing shifts from coral to macroalgal dominance (Bellwood, Hughes & Hoey 2006). Despite this growing literature on the role of herbivores on reefs, very little work has examined the scale of foraging by fish species.

One of the greatest potential threats to herbivore redundancy on coral reefs is fishing. Fishing is exerting significant pressure on marine systems worldwide (Jackson *et al.* 2001), influencing the delivery of ecosystem processes (Hughes 1994). For example, in areas subject to heavy fishing pressure, 95% of parrotfish may be less than 25cm in length, with significant consequences for sediment removal and bioerosion (Bellwood, Hoey & Hughes 2012). Currently, however, we have no understanding of how fishing is likely to impact on the scale at which ecosystem functions are delivered. In light of the degree of overfishing in certain areas, there is potential for significant modifications to cross-scale patterns of redundancy within functional groups, with serious implications for the stability of ecosystem processes. For managers to be able to address these pressures effectively, detailed knowledge of the spatial scales of functional impact is needed.

In examining the scales over which herbivorous reef fishes forage, this study will evaluate interspecific patterns in functionally important space use by herbivorous species. The outcome will indicate the potential for cross-scale redundancy within reef ecosystems, and reveal the influence of fishing pressure on these patterns, neither of which has been assessed to date. The aims of this study, therefore, were to use assessments of foraging movements to: (1) determine the inter-specific relationship between body size and space use at scales pertinent to functional impact; (2) examine if the scales of operation of species within herbivorous functional groups are distributed across spatial scales (i.e. assess the potential for functional redundancy); and (3) determine the relationship between vulnerability to fishing and foraging scale. This will provide fundamental knowledge needed to understand patterns of cross-scale redundancy of function on reefs. Furthermore, it will indicate how fishing impacts may modify the delivery of ecosystem processes, and thus highlight the scales at which targeted mitigation measures are needed to support reefs within a coral-dominated state.

3.3 METHODS

3.3.1 *Study sites & species*

This study was undertaken in July and August 2012 on the sheltered, western side of Lizard Island (14°40'S, 145°28'E; Fig. 3-1) on the Great Barrier Reef, Australia. Observations of foraging behaviour were made at three sites (Mermaid, Turtle Beach and Big Vickies; Fig. 3-1) to determine whether foraging behaviour varied consistently with body size across sites. Mermaid and Turtle Beach are south-west facing fringing reefs with a narrow reef flat and shallow slope down to a maximum depth of about 10m. Big Vickies is a large patch reef and observations were made on the south-east side, where the reef structure meets the sand at a depth of 5-7m. All three sites are in a marine park, designated as a no-take area since 2003, and subject to fishing restrictions since 1983.

3.3.2 *Fish and benthic censuses*

Fish abundance of diurnally active non-cryptic herbivorous species were estimated at each site using instantaneous underwater visual census (UVC) along eight 50m transects; 4 transects were located on the reef slope and 4 on the reef crest. All species (≥ 5 cm) were recorded in a 5m swath as the transect was laid, with the exception of Pomacentrids, which were recorded on the return swim along the transect in a 2m swath. Replicates were haphazardly arranged along the reef, with a minimum of 15m separating neighbouring transects. The percent cover of different benthic types, such as coral genera and lifeform, algae, sponges etc, were calculated from observations taken every 50cm along each transect using the point intercept method. Structural complexity was estimated for each transect, using a six-point visual scale (Wilson et al. 2007).

3.3.3 *Study species*

Herbivorous species were chosen as the focus for this study for two reasons (1) they drive a critical ecosystem function on reefs (Bellwood *et al.* 2004), and (2) by feeding on the substrate, it is possible to clearly delineate and mark where feeding occurs and to observe multiple feeding events, thus ensuring high levels of replication. Twenty nominally herbivorous reef fish species (Appendix B Table S1) were selected for study at each site, including representatives from browser, farmer, grazer/detritivore, and scraper/excavator functional groups (Green & Bellwood 2009). The exact composition of species differed between sites due to localized relative abundance. The species ranged in length from 6 cm to 55 cm total length (TL), and at least a 36 cm body size range was maintained at all sites. The focus of the study

was interspecific differences in foraging and space use by adult herbivorous reef fishes. Fish species may exhibit ontogenetic shifts in diet (e.g. from herbivore as a juvenile to planktivore as an adult; Green & Bellwood 2009), and foraging behaviour (Lokrantz *et al.* 2008). Therefore, to remove the influence of ontogenetic changes within species (Bonaldo & Bellwood 2008), and allow comparability among species of different adult body sizes, a single 5-6cm size class was selected for each species up to 35cm, and a 5-10cm size class for the larger species (Appendix B Table S1). These size classes were based on the most abundant adult body lengths.

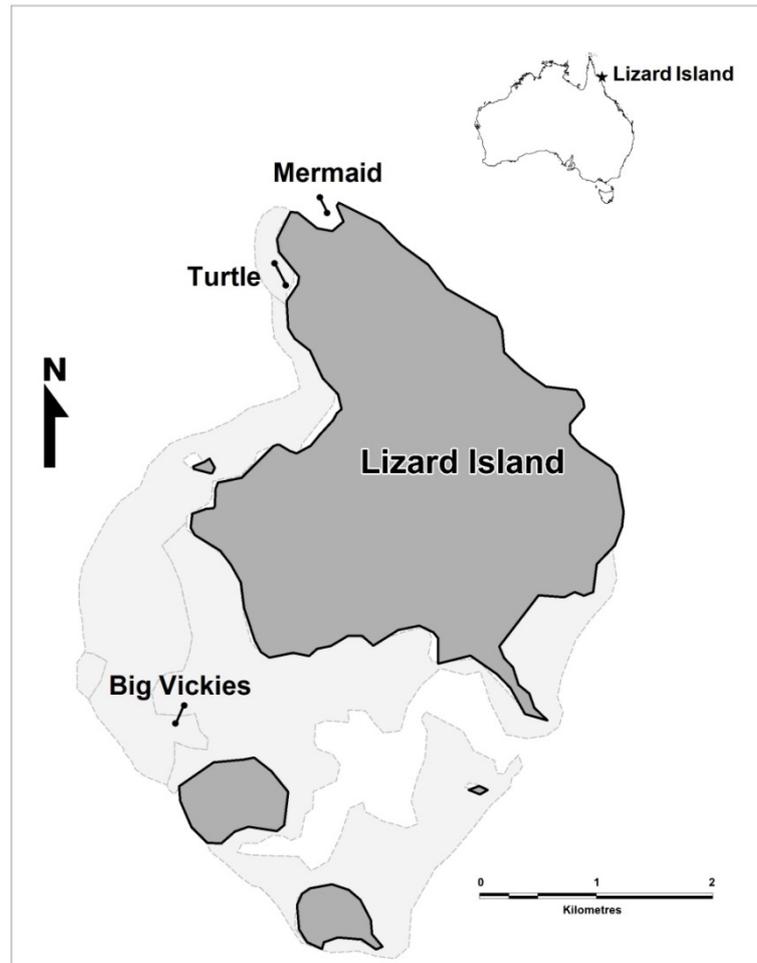


Figure 3-1: Map of study sites at Lizard Island. Prevailing winds are from the south east.

3.3.4 Behavioral studies

All behavioural data were collected between 9:30am and 2:30pm, and distributed approximately evenly to minimize the effect of time of day on feeding (Zemke-White, Choat & Clements 2002). Fine-scale foraging mobility of target individuals was estimated using two metrics: (1) intra-foray distance; and (2) inter-foray distance; where a foray was defined as a

cluster of feeding bites separated from the previous cluster of bites by elevation of the fish's head greater than 45 degrees from the substratum and a period of active swimming (following Nash *et al.* 2012). A focal individual was identified and followed until it commenced feeding. To estimate inter-foray distance, markers were dropped at the last bite of the first foray taken by the fish, and the first bite of the next foray. To estimate intra-foray distance, markers were placed at the location of the two most distant bites within the second foray. The distance between markers was measured. Inter-foray distance is therefore an integration of all movements between successive forays, whereas intra-foray distance is the maximum linear dimension covered by all movements within a foray. The benthos on which the fish fed (e.g. EAM, macroalgae, soft coral) identified by each marker, was recorded. A single observation of intra- and inter-foray distance were recorded for each individual, and where possible, these observations were repeated for 30 individuals of each species at each site (Appendix B Table S1). Two strategies were used to minimize the chance of sampling the same individual more than once: (1) observers moved linearly along the reef, after each observation, away from the area used by individuals that had already been sampled; and (2) where members of the same species were targeted sequentially, fish of different body sizes were chosen. Where the population size of a species was too small to allow the desired degree of replication without resampling individuals, smaller sample sizes were used (Appendix B Table S1).

When estimating the foraging range metrics, a distance of at least 2.5m was maintained from all fish, although this distance was increased to 5m for some of the larger, more mobile species due to increased flight initiation distances for larger individuals (Januchowski-Hartley *et al.* 2011a). Data were discarded where fish showed signs of disturbance by the observer or where a constant visual fix on the individual could not be maintained. Accuracy of observer estimations of fish body length were tested daily using lengths of PVC pipe, prior to the start of data collection, with estimates consistently within 10% of actual lengths.

3.3.5 Data analysis

The relationship between body size and the two foraging metrics (intra- and inter-foray distance) were analysed using ordinary least squares regression as this approach is more suitable when: (1) there is a clear predictor and dependent variable in the relationship; and (2) residuals will be used for further analysis (Warton *et al.* 2006; Smith 2009). The error structure of the data was determined using the guidelines provided by Xiao *et al.* (2011); likelihood analysis indicated that the data showed log-normal error and was therefore suitable for analysis using regression on log-transformed data (Xiao *et al.* 2011). Analysis of covariance (ANCOVA) and log-likelihood ratio tests were used to compare the slopes and elevations of relationships among

sites (Warton *et al.* 2006). Data were back-transformed to allow presentation of the relationship between foraging metrics and body size on the arithmetic scale: a slope of >1 in log-log space represents an upwards concave relationship in arithmetic space, whereas a slope of <1 represents a downwards concave relationship in arithmetic space. Residuals were calculated for each species. To assess the influence of functional group membership on the relationship between body size and the foraging metrics, the analysis was repeated with function as a categorical variable for those groups which had sufficient species (farmers, grazer/detritivores, and scraper/excavators). Phylogenetic relationships may confound interspecific relationships due to non-independence of data points, therefore the analysis was repeated at the family-level (Martin, Genoud & Hemelrijk 2005), and the results compared to the species-level analysis.

To evaluate the potential effects of fishing on scales of functional impact provided by herbivorous fishes, the relationship between scales of foraging movements and vulnerability to fishing were analysed using correlations. Data on the vulnerability of each species to fishing pressure were extracted from FishBase (Froese & Pauly 2012), and are based on an index developed by Cheung *et al.*, (2005) using a fuzzy logic expert system. This index combines information on eight life-history traits of fish species that affect susceptibility to fishing (maximum length, age at maturity, growth rate, natural mortality, maximum age, geographic range, fecundity, and aggregative behaviour). It has been shown to provide sound predictions for species from a range of marine systems (Reynolds *et al.* 2005). Spearman rank correlations between both intra- and inter-foray distance, and fishing vulnerability were calculated.

3.4 RESULTS

3.4.1 *Benthic cover and herbivore abundance*

Benthic cover was primarily composed of live hard coral and epilithic algal matrix (EAM) at all of the three sites. However, the structural complexity and coral cover were slightly higher, and the EAM cover lower at the lagoonal Big Vickies (Complexity: $3.7 \pm 0.2\text{SE}$; Coral: $36.2\% \pm 4.9\text{SE}$; EAM: $34.3\% \pm 2.5\text{SE}$) compared to the fringing reefs at Mermaid and Turtle (Complexity: $2.9 \pm 0.1\text{SE}$; Coral: $24.6\% \pm 3.0\text{SE}$; EAM: $52.9\% \pm 5.3\text{SE}$ and Complexity: $2.8 \pm 0.2\text{SE}$; Coral: $26.6\% \pm 6.9\text{SE}$; EAM: $46.0\% \pm 5.3\text{SE}$ respectively). Macroalgal cover was less than 1% at each of the three sites. The density of herbivorous fishes varied between 21.1 100m^{-2} at Turtle, to 33.5 100m^{-2} at Mermaid, but at all sites, grazer/detritivores were the most common herbivores (over 10 100m^{-2}), and browsers the least common (under 2.0 100m^{-2}).

Table 3-1: A) Density of fish ($100\text{m}^{-2} \pm \text{SE}$) within the four herbivorous functional groups at each site, and B) the proportion of functional group abundance represented by species assessed for foraging metrics and included in Fig. 3-2. Data based on UVC counts, pooled to site level, and incorporating all size classes.

Site	Browser	Farmer	Grazer/Detritivore	Scraper/Excavator	Total Herbivores
A) Density					
Big Vickies	0.4 \pm 0.1	5.9 \pm 1.1	12.6 \pm 1.4	10.2 \pm 1.6	29.0 \pm 3.2
Mermaid	1.6 \pm 0.4	7.3 \pm 1.5	16.2 \pm 2.7	8.4 \pm 1.0	33.5 \pm 2.9
Turtle	1.2 \pm 0.4	4.5 \pm 1.1	10.6 \pm 2.1	4.9 \pm 0.5	21.1 \pm 2.7
B) Proportion of functional group					
Big Vickies	42.9	63.6	86.1	79.3	78.6
Mermaid	46.4	73.4	96.1	84.4	85.8
Turtle	69.6	65.2	94.3	84.7	84.6

(Table 3-1A). The species studied in the behavioural observations accounted for over 75% of all herbivore individuals at each site, although this proportion was lower for browsers (over 40% of individuals) than for the other three herbivorous functional groups (Table 3-1B).

Table 3-2: Summary of scaling parameters for the relationship between body length and A) Intra-foray distance, and B) Inter-foray distance, where parameters represent $y=\alpha x^\beta$.

Site	$\alpha(\pm 95\%CI)$	$\beta(\pm 95\%CI)$	R^2	p-value
A) Intra-foray Distance				
Big Vickies	0.01 (0.00-0.06)	2.35 (1.89-2.83)	0.86	<0.001**
Mermaid	0.01 (0.00-0.08)	2.48 (1.81-3.14)	0.77	<0.001**
Turtle	0.10 (0.03-0.34)	1.81 (1.40-2.21)	0.83	<0.001**
Common parameters	0.03 (0.01-0.06)	2.19 (1.89-2.49)	0.79	<0.001**
Common Slope: Likelihood ratio statistic of 4.54, 2 d.f., p=0.10				
Common Elevation: Wald statistic of 5.75, 2 d.f., p=0.06				
B) Inter-foray Distance				
Big Vickies	0.44 (0.15-1.31)	1.99 (1.63-2.35)	0.88	<0.001**
Mermaid	0.18 (0.05-0.70)	2.35 (1.89-2.80)	0.87	<0.001**
Turtle	0.36 (0.12-1.10)	2.09 (1.72-2.46)	0.89	<0.001**
Common parameters	0.34 (0.17-0.62)	2.12(1.91-2.34)	0.87	<0.001**
Common Slope: Likelihood ratio statistic of 2.53, 2 d.f., p=0.37				
Common Elevation: Wald statistic of 2.41, 2 d.f., p=0.30				

3.4.2 Behavioural metrics

Both log intra-foray distance and inter-foray distance were positively, linearly related to log fish body length at all three sites (Fig. 3-2i; Table 3-2), therefore as body size increases among species, the fine-scale movements made by foraging fish increase exponentially in length (Fig. 3-2ii). The slope and elevation of the linear relationship between log foraging metric and log body size was not significantly different between sites (Table 3-2), giving common parameters of $\alpha=0.03$ and $\beta=2.19$ for intra-foray distance, and $\alpha=0.34$ and $\beta=2.12$ for inter-foray distance, where parameters represent $y=\alpha x^\beta$ in the back-transformed data (i.e. showed upward concave relationships; Fig. 3-2ii). The four herbivorous functional groups were not evenly spread across the scales of movement for either metric (Fig. 3-2ii); farming species had small intra- and inter-foray distances, grazer/detritivores species exhibited mid-size foraging movements, while scraper/excavators and browsers showed mid- to large-size foraging movements (Fig. 3-2Aii).

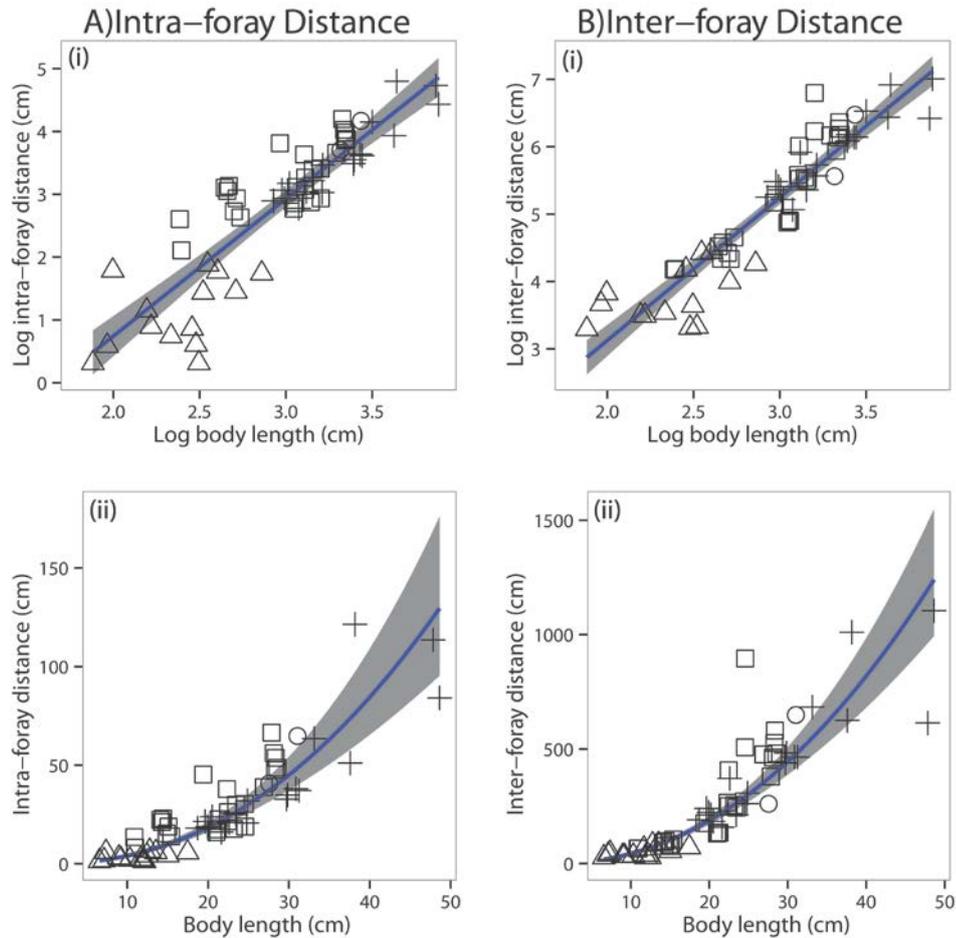


Figure 3-2: Relationship between body length and A) Intra-foray distance or B) Inter-foray distance for herbivorous reef fish, presented in i) log-log scales and ii) back-transformed to arithmetic scales. Lines represent significant relationships ($\pm 95\%$ CI) based on OLS regression, showing common slope and intercept among sites for both variables. Symbols indicate functional group: triangle-Farmer, square-Grazer/Detritivore, circle-Browser, cross-Scrapper/Excavator.

The residuals for these relationships varied among functional groups (Fig. 3-3). Residuals were predominantly negative for farmers with respect to both intra- and inter-foray distance (mean of -0.28 and -0.14 respectively), and for scraper/excavators with respect to intra-foray distance (-0.05), indicating these groups were generally moving shorter distances than predicted by the regressions. In contrast predominantly positive residuals were recorded for both foraging metrics for grazer/detritivores (mean of 0.12 and 0.06 respectively), and for browsers with respect to intra-foray distance (0.08), indicating generally larger movements than predicted. Members of all the four herbivorous functional groups fed primarily on EAM (over 85% of bites; Appendix B Table S2). No browsers were observed feeding on macroalgae; those species that did feed on macroalgae were primarily farmers or scraper/excavators.

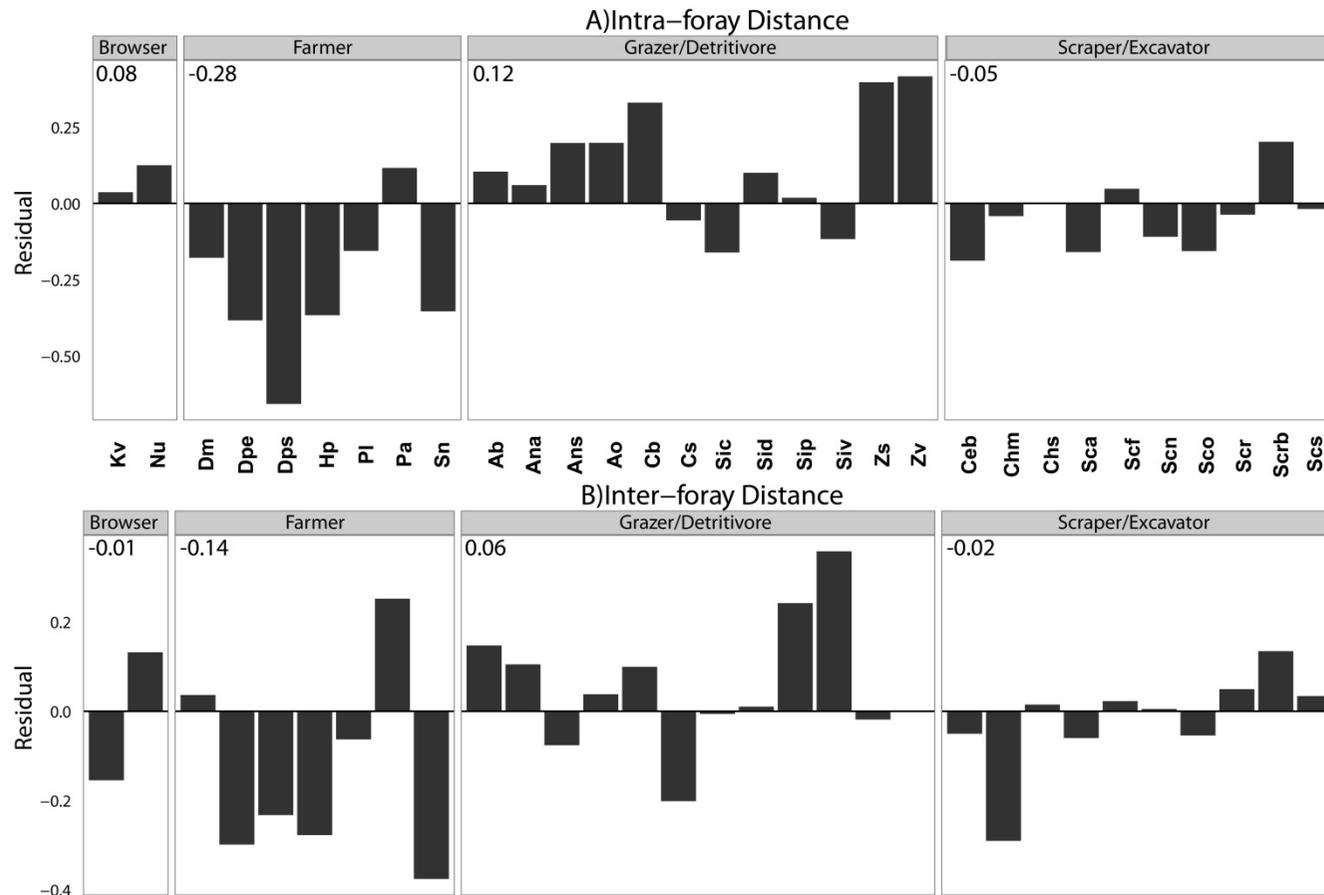


Figure 3-3: Residuals for relationship between body length and A) Intra-foray distance or B) Inter-foray distance for species of herbivorous reef fish. Bars represent mean value across sites where species was observed at multiple sites. Numbers provide mean residual for functional group. Species: Kv-*Kyphosus vaigiensis*; Nu-*Naso unicornis*; Dm- *Dischistodus melanotus*; Dpe- *Dischistodus perspicillatus*; Dps- *Dischistodus psuedochrysopecilus*; Hp- *Hemiglyphidodon plagiometopon*; Pl- *Plectroglyphidodon lacrymatus*; Pa- *Pomacentrus adelus*; Sn- *Stegastes nigricans*; Ab- *Acanthurus blochii*; Ana- *Acanthurus nigricauda*; Ans- *Acanthurus nigrofuscus*; Ao- *Acanthurus olivaceus*; Cb- *Centropyge bicolor*; Cs- *Ctenochaetus striatus*; Sic- *Siganus corallinus*; Sid- *Siganus doliatus*; Sip- *Siganus punctatus*; Siv- *Siganus vulpinus*; Zs-*Zebrasoma scopas*; Zv- *Zebrasoma veliferum*; Ceb- *Cetoscarus bicolor*; Chm- *Chlorurus microrhinus*; Chs- *Chlorurus sordidus*; Sca- *Scarus altipinnis*; Scf- *Scarus flavipectoralis*; Scn- *Scarus niger*; Sco- *Scarus oviceps*; Scr- *Scarus rivulatus*; Scrb- *Scarus rubroviolaceus*; Scs- *Scarus schlegeli*.

When analysed at the functional group level, the relationship between body size and the two foraging metrics was non-significant for farmers, but was strongly positive for both the grazer/detritivores and the scraper/excavators (Appendix B Table S3). However, the intercepts varied among groups for intra-foray distance, and the slopes varied for inter-foray distance (Appendix B Table S3). There was insufficient data on browsing species to incorporate this group into the analysis. The results produced from the family-level analysis were both qualitatively and quantitatively similar to those at the species level, for both α and β (Appendix B Table S4 & Fig. S1), therefore, the species-level data were used for the remaining analyses.

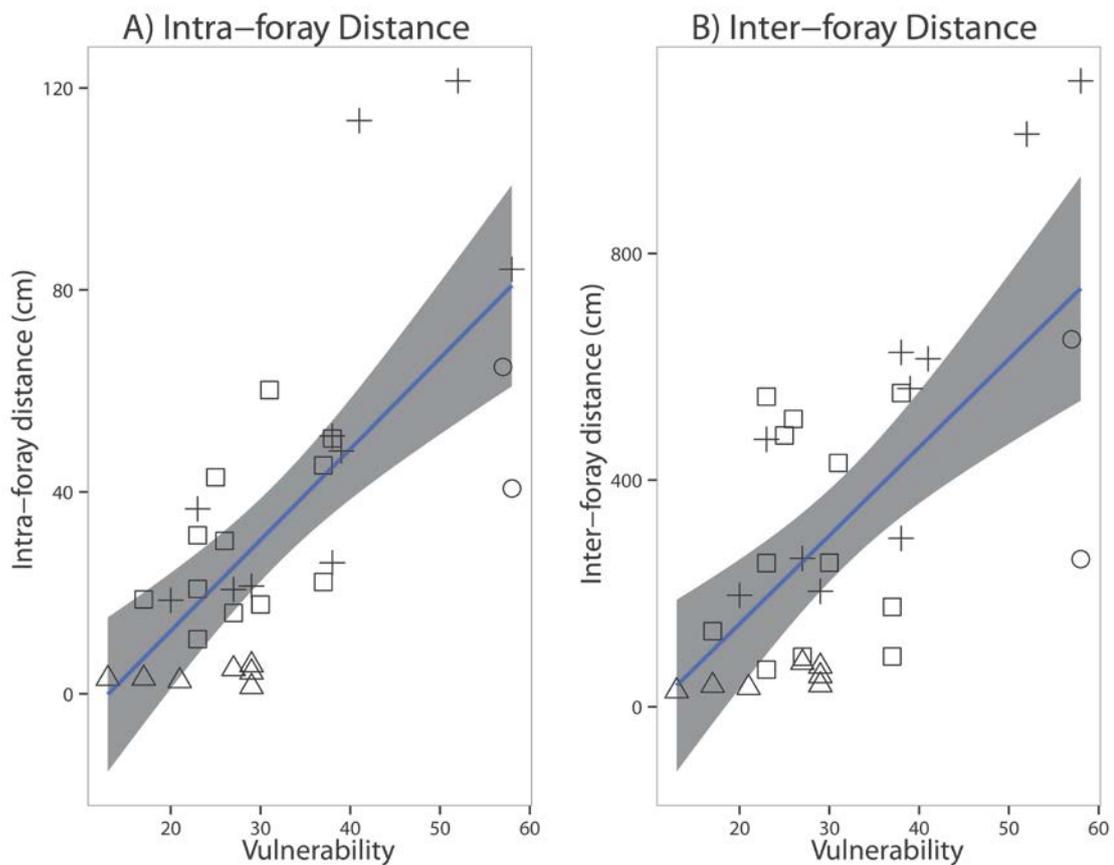


Figure 3-4: Correlation between vulnerability to fishing pressure (based on index by Cheung et al. 2005), and A) Intra-foray distance (spearman $\rho=0.69$, $p<0.001$) or B) Inter-foray distance (spearman $\rho=0.62$, $p<0.001$). Intra-foray and inter-foray data for each species are pooled across sites. Symbols indicate functional group: triangle-Farmer, square-Grazer/Detritivore, circle-Browser, cross-Scraper/Excavator.

There was a strong positive correlation between vulnerability to fishing and both intra- and inter-foray distance ($\rho=0.69$, $p<0.001$ and $\rho=0.62$, $p<0.001$, respectively), therefore those species that moved further whilst foraging, were also more vulnerable to fishing (Fig. 3-

4). Members of grazer/detritivores and scraper/excavator functional groups showed a range of vulnerabilities to fishing, and foraged over a range of spatial scales. Farmers showed low vulnerability to fishing and low movement distances, in contrast the browser species targeted in the foraging observations were highly vulnerable to fishing, and travelled mid-range distances whilst foraging.

3.5 DISCUSSION

This study empirically tests the allometric relationships between foraging movements and the body length of herbivorous reef fishes, indicating that body size is a good proxy for scale of functional impact in these species. Large species operate and deliver their functional role over larger areas than small herbivorous fish species. This finding has important ramifications for the redundancy of function in reef fishes. Analysis of different herbivorous functional groups suggests that although there is cross-scale redundancy for herbivorous fishes as a whole, there is the lack of redundancy in some of the more narrowly defined functional groups within the herbivore classification such as macroalgae browsers. Furthermore, vulnerability of certain species to fishing indicates that fish assemblages may lose function at certain scales in the face of overfishing, and this loss is not limited to the function provided by large species. This highlights the need for management actions that support functions at scales used by relatively few, or vulnerable, herbivore species.

3.5.1 *Allometric relationships*

The positive relationships between body size and both metrics of foraging movement, indicate that small species forage over smaller scales than large species. This pattern may be expected as swimming speed and cost of transport decreases with increasing body size in fish (McMahon & Bonner 1983) suggesting that large fish are more able to exploit resources at larger scales. In addition, large individuals require more resources and therefore are likely to forage over greater distances to meet energy requirements (Harestad & Bunnell 1979).

The allometric relationships were exponential in form indicating that larger species not only feed at larger scales than smaller species, but that small changes in size among species at the larger end of the body size spectrum result in a greater jump in the scale of foraging movements (i.e. similarly sized species feed over a wider range of scales). This suggests that larger species have a broader range of functional roles than smaller species with regards to space use. The importance of large herbivorous fish species for delivering function is mirrored by terrestrial herbivore species, where grazing by large species has been shown to drive habitat structure and functioning (Gordon, Hester & Festa-Bianchet 2004). Species experience

ontogenetic changes in function, and there is evidence that larger individuals may exhibit exponentially higher grazing rates (Lokrantz *et al.* 2008) and remove greater volumes of algae (Bonaldo & Bellwood 2008) than small individuals. My study specifically focused on interspecific allometric patterns of space use whilst foraging. Further work is needed to look at intraspecific patterns of function and space use to understand if these mirror the positive relationships found between body size and grazing rates or bite volume within herbivorous species (Bonaldo & Bellwood 2008; Lokrantz *et al.* 2008).

The slopes of the relationships between body size and both intra- and inter-foray distance were similar giving upwards concave relationships on an arithmetic scale, indicating that interspecific patterns may be comparable at different levels of the foraging decision hierarchy, for example for within or between patch movements. Furthermore, the results mirror those found for the relationship between body size and home range (Kramer & Chapman 1999), suggesting that these comparisons may be made among levels of movement relating to foraging and other activities. The slopes and intercepts of the allometric relationships were not significantly different among sites, although the intercept was only slightly non-significant among sites for intra-foray distance. The three sites were chosen due to their similar benthic composition and geographic location. Changing habitat condition, and therefore resource availability and distribution, is likely to result in changes to both the intercept and slope of these relationships; Nash *et al.* (2012) reported reduced inter-foray distances of parrotfishes in response to increasing coral cover but the shape of this decrease differed among species. Further work is needed to analyse whether these variations among species result in stronger or weaker allometric foraging relationships, in the face of habitat degradation. Additionally, the effect of school size on foraging range was not assessed. Group size has been shown to be positively related to home range in mammal species (e.g. Dias & Strier 2003). Research is needed to analyse the effect of school size on the allometry of function and space use in herbivorous reef fishes.

Foraging decisions, at the scale relating to choice of specific EAM components, were not explicitly studied. However, consistency in the positive or negative nature of residuals within functional groups suggests that although all species fed primarily on the EAM, different components of the algal matrix may have been selected for by species within the four functional groups (Crossman, Choat & Clements 2005; Nash *et al.* 2012). The quality and composition of EAM varies over space (Purcell & Bellwood 2001), therefore differences in the distribution of constituents has the potential to influence the variation around the predicted allometric relationships for members of each functional group (Holling 1992). Farming species exhibited large, primarily negative residuals, signifying that these species cover smaller distances than

expected based on body size. This is likely due to their ability to manipulate resource availability, concentrating food resources into a small patch through farming activities (Ceccarelli 2007), therefore they are less reliant on existing resource distributions. This supposition is further supported by the pattern of large negative residuals recorded for farming species that are known to have a greater influence on benthic composition (intensive/extensive farmers), compared with the positive residuals of *Pomacentrus adelus* which exerts less influence on the benthos (an indeterminate farmer; Emslie *et al.* 2012).

The relationships between body size and the foraging metrics estimated for all species were qualitatively similar to those calculated for the separate functional groups, although these relationships were not significant for farming species, suggesting body size is less critical within this group. Farmers are territorial and as such, space use may be limited by the costs arising from defending a territory (Brown 1964). The relationships between body size and the foraging metrics were quantitatively similar between species level and family level analyses suggesting these patterns hold at a number of taxonomic levels, and is not an artefact of phylogenetic relationships. Therefore, the scale of functional impact of herbivorous reef fishes is positively and exponentially related to body size, although the rate of increase in spatial scale across body sizes depends on functional group membership.

3.5.2 *Cross-scale patterns*

Foraging movements of herbivores, and scraper/excavators in particular, cover a wide range of scales, suggesting the potential for redundancy in the face of disturbances occurring at a given scale (Peterson, Allen & Holling 1998; Elmqvist *et al.* 2003), i.e. impacts deriving from the disturbance may be ameliorated by herbivores which are foraging at scales that do not coincide with the scale of the disturbance. The scraper/excavator group is composed of parrotfish species, therefore this finding supports the well-described importance of parrotfishes for providing herbivory on coral reefs (Choat, Robbins & Clements 2004; Mumby 2006; Adam *et al.* 2011). Grazer/detritivores and farmers were somewhat more constrained in the scales of their movements, being restricted to mid- and small-scales, respectively. Siganids appear to extend the range of grazer/detritivores somewhat, as indicated by the large positive residual of *Siganus vulpinus*, a pattern that appears to be widespread in siganids (Fox & Bellwood 2013). In contrast, the range of scales over which farmers move is likely constrained by the costs associated with defending territories at larger scales (Brown 1964). Most surprisingly, browsers were limited to mid-scale movements. This finding may be a function of the low numbers of browsers studied (2 species), however, individuals of these two species represented between 42% and 70% of browser abundance at the three sites. A maximum of 5 browsing species were

observed at any one site and mean density was less than $1.6 \text{ } 100\text{m}^{-2}$ at all sites, therefore both cross-scale redundancy and abundance of this functional group appears to be low. This suggests that in the face of disturbances, which affect species operating at mid-scales, there may be ecologically significant declines in the delivery of the browsing function. Demarcation of the scales across which the four functional groups operate highlight the relative potential for redundancy in each group. Similar multi-scale foraging patterns have been modelled in terrestrial herbivore communities, driven by interspecific body size variation (Illius & Gordon 1987; Ritchie & Olff 1999; Cumming & Cumming 2003), suggesting corresponding potential for cross-scale redundancy in certain taxa (Peterson, Allen & Holling 1998; Cromsigt & Olff 2006; Laca *et al.* 2010).

Eighty five percent of forays by members of each functional group were observed targeting the EAM, including 100% of forays by browsers. Browsers are defined as species which primarily target macroalgae and are therefore important for reversing shifts to a macroalgal-dominated state (Bellwood, Hughes & Hoey 2006). Browsers targeting EAM, rather than macroalgae, is likely a consequence of the limited cover of macroalgae at the study sites (<1%), and supports the contention that herbivores exhibit feeding versatility in response to changing availability of resources (Bellwood *et al.* 2006b). This has positive implications for control of EAM cover, but doesn't necessarily infer the same positive consequences for control of macroalgae, unless members of other functional groups will switch to feeding on macroalgae when it is abundant, e.g. *Platax pinnatus* (Bellwood, Hughes & Hoey 2006). Work by Chong-Seng *et al.* (2014) indicates the potential for such plasticity in browsing species suggesting the capacity for higher levels of browsing function than were implied by the findings of this study.

Although certain functional groups appear to show low levels of redundancy across scales, this is not necessarily due to past disturbances or impacts such as overfishing, occurring over ecological time scales. The study sites at Lizard Island have been closed to all fishing for 8 years, prior to which there were restrictions on fishing for over 25 years. The presence of low redundancy and a high number of specialized functions within the herbivores is likely driven by relatively low variation in abiotic factors over evolutionary timescales (Walker, Kinzig & Langridge 1999), rather than due to recent impacts reducing cross-scale redundancy. If this is the case, then the distributions of functional groups observed in this study may be representative of relatively unexploited reefs, and therefore present a best case scenario for managers of reef systems. Reefs subject to high fishing pressure are likely to have experienced erosion of redundancy within functional groups and thus be characterized by a more depauperate cross-scale herbivore assemblage.

A number of caveats apply to the interpretation of cross-scale patterns of foraging movements by functional groups: (1) Assignment of functional groups necessarily results in relatively coarse classifications. As a result, feeding behaviours specific to individual species (e.g. Fox & Bellwood 2013) are not accounted for, potentially overestimating redundancy, across scales; (2) The predominant role a species plays may change over time. This may have both negative consequences e.g. herbivorous urchins driving significant bioerosion with increasing population abundance (McClanahan & Shafir 1990), or positive impacts e.g. the invertivore *Platax pinnatus* removing macroalgae in experimental phase-shifts (Bellwood, Hughes & Hoey 2006). Nevertheless, the future delivery of a particular function is not guaranteed (Nyström 2006).

The spatial patterns of foraging by herbivores suggest that the four functional groups exhibit different degrees of cross-scale redundancy. The next step is to assess how foraging areas overlap among members of a functional group operating at different scales to provide this redundancy. In boreal forests, birds foraging over a wide range of scales help control spruce budworm outbreak: different sized species of bird forage for budworm at different scales during an outbreak, with larger species switching to this prey item as budworm becomes more aggregated over larger scales (Peterson, Allen & Holling 1998). Similar research, examining the effect of broad vs. narrow ranges of foraging scales provided by members of herbivorous functional groups, is needed to understand the importance of redundancy mechanisms on coral reefs and how this redundancy interacts with environmental factors (Cheal *et al.* 2013).

3.5.3 Vulnerability of cross-scale patterns to fishing

The positive relationship between vulnerability to fishing and the scale of foraging movements indicates that overfishing has the potential to reduce the range of scales over which herbivores are providing function, by removing species operating at larger spatial scales. There is a strong correlation between species size and vulnerability to fishing (Jackson *et al.* 2001; Friedlander & DeMartini 2002). This is perhaps not surprising considering that the vulnerability metric used incorporates size as just one of eight traits (Cheung, Pitcher & Pauly 2005). However, some species were more vulnerable than their body size alone would suggest, e.g. browsers. Characteristics of a species, other than size, contribute to their relative susceptibility to being caught and the likelihood of populations rebounding from a given fishing pressure, both of which contribute to fishing vulnerability. Variability in the influence of different traits on hunting risk has been explored in terrestrial systems; large body size has been shown to be positively correlated with hunting risk in Australian mammal species (e.g. Cardillo & Bromham 2001), whereas work on African bushmeat exploitation has emphasized the

importance of large population sizes and species' behaviour (Fa, Ryan & Bell 2005). Indeed, behavioural changes in response to predation pressure, adds considerable complexity to assessments of species' vulnerability to exploitation. Predation risk may affect foraging behaviour in communities subject to natural predators (e.g. in baboons: Cowlshaw 1997; and coral reef fishes: Madin, Madin & Booth 2011), but there is also potential for behavioural modifications in response to hunting, which may affect vulnerability to being caught (Thiel *et al.* 2007). For example, recent work on coral reefs has demonstrated that herbivorous fishes flee from spearfishers earlier when they are in locations that experience greater fishing pressure (Januchowski-Hartley *et al.* 2011a). Furthermore, where fishing preferentially targets predatory species, there may be indirect consequences for foraging movements; specifically Madin, Gaines and Warner (2010) showed that high number of predators may suppress the size of foraging movements. In this instance, removal of predators through fishing may increase the range of scales over which other species, including herbivorous taxa, forage. An increased understanding of the vulnerability of herbivorous fishes to fishing, and the indirect effects of fishing, and how this is likely to vary under different fishing pressures and management contexts, should improve our understanding of how the delivery of herbivorous functions across spatial scales are likely to change over time.

Loss of function at specific scales may proceed unnoticed if metrics of function, such as herbivore abundance, are used to monitor essential ecosystem processes (Bellwood *et al.* 2004). Where species are large and vulnerable to fishing, there are the compound issues of losing species operating over large scales and losing species that contribute most to functional impact via higher grazing rates and volumes (Bonaldo & Bellwood 2008; Lokrantz *et al.* 2008). These large species are primarily scraper/excavators and there is therefore the potential for losing a critical component of the herbivore assemblage responsible for algal control and bioerosion, even in areas subject to moderate fishing pressure (Bellwood, Hoey & Hughes 2012). Where fishing reaches greater levels, we may see a subsequent reduction in grazer/detritivores, which are foraging at mid-scales. Cross-scale redundancy has the potential to counteract some of the impact of losing species operating at certain scales. For example, the positive effects of small individuals have been seen in Moorea, where large numbers of small parrotfishes controlled algal growth (Adams *et al.* 2011). However, there is evidence that species operating over small scales may be less effective at compensating for loss at larger scales than vice versa, particularly in the face of large scale disturbances. For example, assemblages of small-scale mammalian seed dispersers are unable to provide dispersal at scales sufficient to maintain tree populations when faced by large scale disturbances, a problem that does not occur in assemblages with both large- and small-scale dispersers (Peterson, Allen & Holling 1998). These contrasting findings suggest that caution needs to be taken when predicting the consequences of cross-scale

redundancy for the continuation of ecosystem processes in the face of different disturbance regimes. There is a need to assess cross-scale patterns of function in concert with future levels of overfishing and the scale of disturbance regimes, to make predictions about the usefulness of current cross-scale redundancy patterns for the ongoing maintenance of coral-dominated reefs.

Vulnerability to fishing is not limited to large species; the browsers exhibit significant susceptibility. When this vulnerability is considered in conjunction with: (i) the low number of browsing species found at the three sites, (ii) the low abundance of these species, and (iii) the narrow range of spatial scales over which they operate, there is a clear need for concern regarding the redundancy of function within this group, and thus the ongoing delivery of browsing function in the face of future change. However, in highlighting the susceptibilities of certain functional groups and spatial scales of function, this study provides managers with the fundamental knowledge needed to plan mitigation measures to counteract fishing pressure that undermines ecosystem processes at critical scales. There is an emerging body of work describing targeted mitigation strategies, such as gear based management, which may minimize catches of important or susceptible species, including herbivores (Cinner *et al.* 2009; Johnson 2010). My study provides the key first step to enable managers to select from these mitigation strategies appropriate tools to maintain function across scales. Due to the local to regional nature of fisheries management, there is the potential to implement such actions in a timely manner, resulting in relatively quick responses within the fish community (Graham *et al.* 2013).

3.5.4 Conclusions

The small-scale movement metrics used in my study reveal the tight relationship between fish body size and space use, at scales appropriate to the functional impact of herbivorous reef species. The results indicate that body size is a useful proxy for scale of foraging and functional impact among species, and that functional groups are not evenly distributed across scales. The influence of fishing pressure on cross-scale distributions of function is of significant concern for two key reasons: (1) fishes operating over large scales (primarily scraper/excavators) and which likely exhibit greater grazing impacts, are particularly susceptible to exploitation; and (2) the few species that act as browsers, targeting mature macroalgae, provide their role over a narrow range of spatial scales and are extremely vulnerable to fishing. This study identifies the scales at which herbivorous function is at risk, and therefore provides critical information needed to inform management actions to support function at specific scales and the provision of the key ecosystem process of herbivory.

Chapter 4: Influence of habitat condition and competition on foraging behaviour of parrotfishes³

4.1 ABSTRACT

Metrics of foraging by herbivorous reef fish has been shown to vary across space and time, and among species. However, little work has explicitly assessed how fish use space within their foraging ranges, or characterised relative foraging mobility in response to habitat condition. This knowledge is fundamental to understanding the functional impact of reef herbivores, and how spatially explicit functional roles may be modified by future reef degradation. In this study, I assess the influence of among-site variation in habitat condition, competition and potential predation risk on the short-term foraging range of two species of parrotfish, *Scarus niger* and *Scarus frenatus*, on mid-shelf reefs of the Great Barrier Reef. Foraging ranges were evaluated using three metrics: inter-foray distance, and the area, and shape of the short-term foraging range. The primary predictor of these metrics of foraging behaviour was coral cover. Inter-foray distance decreased with increasing coral cover for both *S. niger* and *S. frenatus*, and foraging ranges became more circular with increasing coral cover. Competitor abundance was a secondary driver of foraging behaviour, whereas potential predation had no detectable effect. This research provides a fine-scale understanding of how habitat condition and competition among herbivores shapes the spatial scales at which herbivores interact with their environment in the short-term, and at which they perform functions essential for coral reef resilience. Critically, the study suggests that predicted changes in coral cover are likely to alter the way reef herbivores forage, and will shape the extent to which they can compensate for declining habitat condition through changes in their feeding behaviour.

4.2 INTRODUCTION

Herbivores contribute to the resilience of coral reefs by influencing the balance of competition between corals and other benthic species, such as algae (Hughes *et al.* 2007a). In doing so, they may aid in maintaining reefs in a coral dominated state by prevention or reversal of phase shifts to macroalgal dominance (Hughes 1994; Bellwood, Hughes & Hoey 2006),

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thereby preserving the delivery of ecosystem services. Foraging by herbivores may therefore represent a core ecosystem process on coral reefs (Hatcher 1997). Reductions in herbivore abundance have been shown to drive increases in macroalgal cover (Hughes *et al.* 2007a), however, studies from both the Caribbean and the Indo-Pacific have indicated that simple quantification of total herbivore densities may not reflect control of macroalgal cover, even in relatively unexploited herbivore communities (Williams, Polunin & Hendrick 2001); certain herbivorous functional groups e.g. browsers, may be more critical for control of macroalgae, than others (Cheal *et al.* 2010). An in-depth understanding of variations in herbivore roles and foraging behaviour both among and within species is clearly needed (Cheal *et al.* 2010).

Recent work has provided significant progress in the characterisation of herbivory on coral reefs, showing heterogeneity in the herbivorous function of fish with respect to a range of factors: herbivore biomass or abundance may not reflect grazing intensity (Hoey & Bellwood 2009); function is not uniformly distributed among herbivorous species (Bellwood, Hughes & Hoey 2006); functional impact varies non-linearly with body size (Lokrantz *et al.* 2008); and foraging behaviour may vary both spatially and temporally (e.g. Bennett & Bellwood 2011; Lefevre & Bellwood 2011). To date, studies examining differences in fish foraging behaviour have primarily focused on changes in bite rate, area and volume, among body sizes or locations (e.g. Bonaldo & Bellwood 2008; Lokrantz *et al.* 2008; Francini *et al.* 2010). However, the spatial area covered by foraging individuals, or their use of space whilst feeding, has not been explicitly considered in this context.

There is considerable evidence that many reef fish are relatively site attached, with predictable home range sizes (Kramer & Chapman 1999). Use of space within a home range may be partitioned among a variety of activities, such as foraging, reproduction and resting (Eristhee & Oxenford 2001; Claisse *et al.* 2011). Although variations in the home ranges of fish have been linked to a series of factors, such as body size (Jones 2005), habitat composition (Chapman & Kramer 2000), and fish abundance (Mumby & Wabnitz 2002), the use of space by fish when they are actively foraging has not been comprehensively explored, although some work has looked at foraging movements in smaller, territorial species, particularly damselfish (Souza, Ilarri & Rosa 2011). As a result, variation in foraging ranges and the driving mechanisms for these variations are poorly understood. The capacity of a herbivore assemblage to control algal growth may be reduced at sites with low coral cover, as grazing effort is diluted over a larger area of algal-covered reef (Williams, Polunin & Hendrick 2001). It follows that variation in the size of fish foraging ranges may influence the distribution of grazing effort of herbivores across space, directly affecting spatial intensity of function. A need therefore exists,

to explicitly assess the functional implications of foraging behaviour as it pertains to space use and movement.

Foraging behaviour may be influenced by both habitat and fish-community level factors. Variation in foraging behaviour in response to aspects of habitat condition has been demonstrated in a wide range of mobile organisms, including seabirds (McLeay *et al.* 2010), marine mammals (Auge *et al.* 2011), and fish (Hoey & Bellwood 2011). A more in-depth understanding of foraging behaviour for coral reef fishes is critical in light of existing degradation of reefs (e.g. Gardner *et al.* 2003), and projected future loss of coral through increasing anthropogenic pressures (Hughes *et al.* 2003; Veron *et al.* 2009). There are three potential outcomes of the interaction between foraging behaviour and declining reef condition: (1) Foraging by herbivorous fish is unaffected by a changing habitat, an unlikely outcome considering past research (e.g. Francini *et al.* 2010); (2) A positive feedback between foraging behaviour and reef condition arises, such that declining habitat drives behaviour that leads to further degradation; (3) A negative feedback develops between foraging and reef condition, where declining habitat condition drives fish behaviour that helps compensate for degradation. Variations in herbivore foraging intensity are often invoked as mechanistic explanations for differences in reef condition (Duran & Claro 2009; Stockwell *et al.* 2009). However, the potential for reef condition to affect fish behaviour suggests there is a need for improved understanding of the response of herbivore foraging behaviour to different reef conditions.

Fish community characteristics have also been shown to influence foraging behaviour, particularly the degree of competition (Robertson & Gaines 1986), and predation risk (Madin, Gaines & Warner 2010). Because these factors can potentially co-vary with habitat condition (Hixon & Menge 1991), it is critical to tease apart their respective influences on foraging behaviour. This would clarify the primary drivers of fish behaviour, and allow herbivore function to be quantified with respect to changes in habitat and community variables; replacing more generalised measures of function.

The aims of this study were to use short-term assessments of foraging range to i) quantify space use by foraging parrotfish; and ii) compare use of space by feeding fish among sites with varying reef condition, parrotfish abundance (competition), and predation risk. This will help us to understand the spatial intensity of herbivory, how future changes in reef condition may modify foraging behaviour, and inform the development of appropriate and targeted mitigation measures.

4.3 MATERIALS AND METHODS

4.3.1 Study sites

To compare foraging behaviour at sites along a gradient of benthic and fish community parameters, locations were selected at five reefs with different disturbance and recovery histories (Sweatman *et al.* 2008). All reefs were on the mid-shelf Great Barrier Reef in the Townsville region (18°23'S, 146°47'E to 18°48'S, 147°39'E). Two of the reefs (Davies and Wheeler) have been largely un-impacted by major disturbances since the 1980's and had relatively high coral cover (Sweatman *et al.* 2008; AIMS 2011); 2 reefs (John Brewer and Trunk) had very low coral cover (<5%), having experienced multiple, large-scale disturbances (Crown of Thorns (COTs) outbreaks and bleaching) since the early 1980s (Pratchett *et al.* 2008a; Sweatman *et al.* 2008; AIMS 2011); 1 reef (Rib) had been severely impacted by COTs outbreaks, but has been showing recovery with coral cover increasing from 3% in 2003 to 23% in 2010 (AIMS 2011). To provide a range of habitat characteristics, surveys were carried out at three exposed sites, and three sheltered sites on each reef. All surveys were carried out concurrently between November 2010 and January 2011 to avoid potential effects of season on foraging behaviour (Lefevre & Bellwood 2011).

4.3.2 Study species

The initial phases of two scraping parrotfish (*Scarus niger* and *S. frenatus*) were selected for study. Only initial phase individuals of these two species were targeted due to their high relative abundance at the sites, and to remove the potentially confounding effect of reproductive behaviour of terminal phase individuals interacting with foraging behaviour. These species are important components of the mid-shelf herbivore assemblage (Hoey & Bellwood 2008), and are both diurnal home-ranging, scraping herbivores, that feed predominantly on the epilithic algal matrix (EAM) (Bellwood & Choat 1990). Some characteristics vary between the two species: the bite rate of *S. niger* is almost double that of *S. frenatus* (Bellwood & Choat 1990); *S. niger* inhabits deeper slope regions while *S. frenatus* predominantly occupies the reef crest (Russ 1984); and *S. frenatus* displays more territorial behaviour than *S. niger* with respect to other parrotfish (Bellwood 1985). These variations suggest there is potential for contrasting patterns of foraging movement and different responses to reef condition and fish community parameters. To allow comparability among reefs, a single size class was selected for each species (*S. niger*: 15-20cm, *S. frenatus*: 18 - 23cm [Total Length - TL]). *S. niger* were targeted on the reef slope and *S. frenatus* on the reef crest, to reflect their dominant spatial distributions.

4.3.3 Behavioural studies

All behavioural data collection was carried out by a single observer (K. L. N.), and distributed between morning and afternoon to minimise the effect of time of day on feeding (Bonaldo & Bellwood 2008). Fish behaviour may be affected by the presence of observers, and the distance at which fish will flee from an approaching diver (flight initiation distance or FID; Blumstein 2003) may be influenced by the protective status of a reef and the distance to available refuge (Gotanda, Turgeon & Kramer 2009). To account for among-site differences affecting diver-fish interactions and thus potentially influencing foraging range estimations, at each site FID was estimated (see Appendix C Text S1).

Delineation of foraging areas requires in-situ observations (Fox *et al.* 2009). Short-term assessments of mobility using observations of focal individuals have been used to characterise and compare movement paths among labrids with different swimming abilities (Fulton & Bellwood 2002). Such rapid assessments provide a useful tool for assessing the foraging mobility of herbivorous species. Foraging mobility of target individuals was therefore estimated using 3 distinct metrics: (1) inter-foray distance; (2) foraging range over a two minute period; and (3) shape of the foraging range. A foray was defined as a cluster of feeding bites separated from the previous cluster of bites, by elevation of the fish's head greater than 45 degrees from the substratum and a period of active swimming. Inter-foray distance is an integration of all movements between successive forays, whereas foraging range is a subset of the total area covered by a fish and as such delineates only the space used for feeding over the two minute period. Two minute observation periods were chosen after extensive piloting of the methods for two main reasons. First, observations collected over this time period were robust with respect to showing differences in behaviour among sites. Second, longer time periods resulted in some incomplete observations, biasing the data set towards individuals that moved slower and over shorter distances, and therefore were more likely to be kept within visual contact for the entire observation period. Due to the short time period of observations it was not my intention to determine total foraging range but rather to record a measure of relative fish mobility with respect to foraging, among sites.

A focal individual was identified and followed until it commenced feeding. A marker was dropped at each foray taken by the fish over a two minute period. At the end of the time the markers were mapped: the distances between consecutive forays were measured (Metric 1) and the minimum convex polygon area covered by the markers estimated (Metric 2). This area was determined by measuring the distance and compass direction between all pairs of markers, calculating triangular areas ($\frac{1}{2}$ base * height) between sets of three markers on the boundaries of the area, and summing to calculate the total area. The shape of the foraging range was defined

as a measure of compactness and was the ratio between the perimeter of the foraging range and a circle, where the two shapes have the same surface area (Metric 3). On average three individuals of each species were observed at each site. This number was lower at sites with low densities of the target species, e.g. *Scarus frenatus* were not seen at Trunk sheltered sites.

When estimating the foraging range metrics, a distance of at least 2.5m was maintained from all fish. For species where FID had been estimated to be greater than 2.5m for at least one individual at a site, a distance 50cm greater than the longest flight initiation distance was maintained from all fish of that species. Data were discarded where fish showed signs of disturbance by the observer or where a constant visual fix on the individual could not be maintained. Body size (TL) of each individual, and depth of observation were recorded. Accuracy of observer estimations of fish body length were tested daily using lengths of PVC pipe, prior to the start of data collection, with estimates consistently within 8% of actual lengths.

4.3.4 Fish and benthic censuses

Fish abundance of diurnally active non-cryptic species were estimated at each site using instantaneous underwater visual census (UVC) along eight 50m transects; 4 transects were located on the reef slope and 4 on the reef crest. All species ($\geq 5\text{cm}$) were recorded in a 5m swath as the transect was laid. The same observer conducted all fish counts (N.A.J.G.). Replicates were haphazardly arranged along the reef, with a minimum of 15m separating neighbouring transects. The percent cover of different coral lifeforms (branching and submassive, massive and encrusting, foliose, plating, and free-living) and EAM were recorded along each transect using the point intercept method (every 50cm). Structural complexity was estimated for each transect using a six-point visual scale (Wilson, Graham & Polunin 2007).

4.3.5 Data analysis

To estimate the abundance of potential competitors and predators, fish recorded in the UVC were assigned to different functional groups (Wilson *et al.* 2008; Green & Bellwood 2009). Competitors were defined as the combined abundance of ‘scrapers/small excavators’ and ‘large excavators’. All these species were parrotfish, therefore hereafter competitor abundance is termed parrotfish abundance. Parrotfish abundance was collinear with total herbivore abundance on both the crest and slope ($\rho = 0.7$ and 0.9 respectively). Abundance of predators was estimated from all predominantly piscivorous fish that had a gape size larger than the body depth of the fish studied (following Madin, Gaines & Warner 2010). Predator gape size has been shown to correspond to the size of prey selected by predators (Wainwright & Richard 1995), and although optimal prey size is likely to be less than the gape size of the predator, fish

are capable of feeding on prey that are as large as the predator's gape (Werner 1974; Wainwright & Richard 1995). The body depths of *Scarus niger* and *S. frenatus* were calculated from length:depth ratios provided by Graham et al. (2007). Gape sizes of piscivorous species were calculated from length:gape ratios provided by Goatley and Bellwood (2009).

The behavioural data were aggregated to site level to allow for comparison with fish and benthic census data, and assessed for collinearity. Collinearity between the explanatory variables was assessed by plotting pairwise relationships of the covariates, and calculating the variance inflation factor (VIF) for all variables. Variables with VIF values greater than 3 were removed from the analysis (Zuur, Ieno & Smith 2007). All explanatory variables recorded on the reef slope were included in analysis of *Scarus niger* foraging. EAM cover on the reef crest was negatively collinear with both coral cover ($r=-0.8$) and to a lesser extent structural complexity ($r=-0.5$), and was removed from analysis of the *S. frenatus* data.

The relationships between reef condition and the foraging range metrics were assessed by modelling each metric at the site level, as a function of the factor exposure, and covariates coral cover, structural complexity, EAM cover, and, to account for potential alternative drivers of foraging behaviour, predator and parrotfish abundance (Francini *et al.* 2010; Madin, Gaines & Warner 2010). Generalised Linear Models (GLM) with identity link functions and normal errors were fitted to the data, except where plots between explanatory and response variables suggested non-linearity, in which case Generalised Additive Models (GAM) were used. Because multiple sites were located within each reef, the GLMs and GAMs were extended to incorporate mixed effects (Generalised Linear Mixed Models (GLMM) and Generalised Additive Mixed Models (GAMM)), with reef as a random effect (nlme and mgcv packages in R for linear and additive models respectively; Zuur, Ieno & Smith 2007). Parrotfish abundance was log transformed to improve the spread of the data, and reduce the influence of outliers. Residual plots were reviewed for violation of assumptions; alpha values were lowered to 0.01 to account for heteroskedasticity in the data. The best-fit fixed model was chosen by fitting multiple models using the six explanatory variables, removing the least significant term over each iteration and comparing Akaike Information Criterion corrected for small sample sizes (AICc). These models were fitted using maximum likelihood (ML) estimation, to allow comparison of the nested models. The top three models based on AICc values are presented, detailing change in AICc with respect to the top ranked model ($\Delta AICc$), AICc weights ($wAICc$), and adjusted R^2 values.

Where coral cover was shown to be a significant explanatory variable in the analyses of foraging behaviour, the best-fit model was re-run using lifeform data (branching and submassive, massive and encrusting, foliose, plating, and free-living) to determine if particular

types of corals were driving the observed results. Due to collinearity among cover provided by the different lifeforms, these models were run separately for each lifeform, and the alpha value corrected for multiple comparisons using the Bonferroni correction.

4.4 RESULTS

4.4.1 Site-specific benthic cover and fish abundance

Site level coral cover varied from 7.4% (± 1.1 SE) to 74.3% (± 4.0 SE) on the slope and 14.0% (± 2.1 SE) to 77.0% (± 1.9 SE) on the crest. The sites exhibiting highest coral cover were located at Davies, Rib and Wheeler reef, on both the crest and slope of exposed and sheltered sides ($>29.2\%$), whereas the coral cover on John Brewer and Trunk was lower ($<27.8\%$). Branching and submassive corals were the most prevalent colony lifeforms at all but three sites (locations along Davies sheltered slope, where massive and encrusting colonies dominated), composing over 38.0% of coral cover at every site. Plate colonies were more common on the reef crest (23.0% ± 2.0 SE of total coral cover) than on the slope (11.0% ± 1.0 SE of total coral cover), whereas massive and encrusting lifeforms were more common on the reef slope (27.0% ± 2.0 SE of total coral cover), than on the crest (12.0% ± 2.0 SE of total coral cover). Cover of EAM was predominantly higher on both the crest and slope of exposed and sheltered sites at John Brewer, Rib and Trunk reefs (15.9 ± 2.5 SE to 56.0% ± 2.5 SE), and lower on sites at Wheeler and Davies reefs (1.5% ± 1.2 SE to 36.6 % ± 2.7 SE).

Site specific densities of *Scarus niger* varied from 0.1 100 m⁻² ± 0.2 SE to 3.8 100 m⁻² ± 1.7 SE, and were generally higher at sites on Wheeler and Davies reefs. *S. frenatus* were less abundant than *S. niger*; densities ranged from 0.1 100 m⁻² ± 0.1 SE to 2.1 100 m⁻² ± 2.7 SE. All initial phase *S. frenatus* in the foraging behaviour study were observed in a group with one terminal phase and one or two other initial phase *S. frenatus*, whereas initial phase *S. niger* were observed alone or in loose, variable groups with other individuals and scarid species. Site-specific density for all parrotfish species varied from 1.5 100m⁻² ± 0.6 SE to 15.7 100m⁻² ± 1.3 SE, on the crest and slope. There was no correlation between parrotfish abundance and either coral cover or EAM cover for either species. The density of predators with gape sizes of sufficient magnitude to consume focal *Scarus niger* and *S. frenatus* individuals was extremely low across all sites (0.01 100m⁻²), with no site exceeding 0.07 100m⁻².

4.4.2 Inter-foray distance

The inter-foray distance of *Scarus niger* was significantly related to coral cover (Table 4-1A); the inter-foray distance decreased sharply as coral cover increased at low levels of coral

cover (<20%), and was consistently low at higher levels of coral cover (Fig. 4-1A; see Appendix C Fig. S1A for plots of raw data). Coral cover was selected in all the best models for predicting inter-foray distance (Table 4-1A); the model containing coral cover as a single explanatory variable was the best-fit model and explained 77% of the variance in the inter-foray distance. The inter-foray distance of *S. frenatus* was not significantly related to any of the explanatory variables (Table 4-1B), although coral cover was included in the best-fit model for predicting inter-foray distance. The best model only explained 6% of the variance, indicating that inter-foray distance decreased as coral cover increased (Fig. 4-1B; see Appendix C Fig. S1B for plots of raw data). Of the corals, the abundance of branching and submassive corals explained most of the variance in inter-foray distance for both species. Models incorporating these lifeform groups instead of coral cover as a single explanatory variable, explained 72% of the variance in inter-foray distance for *Scarus niger* and 7% of the variance in inter-foray distance for *S. frenatus* (Appendix C Table S1).

Table 4-1: Best-fit models for predicting inter-foray group distance of A) *Scarus niger* and B) *Scarus frenatus*. Models presented are those with lowest AICc values from GAMM and GLMM that evaluate the influence of exposure, structural complexity, coral cover, EAM cover, parrotfish abundance and large piscivore abundance. Significant predictors are in bold ($\alpha = 0.01$).

A. <i>Scarus niger</i>				
Model	AICc	ΔAICc	wAICc	Adj. R^2
Coral cover	382.11	0.00	0.82	0.77
Coral cover , EAM cover	385.20	3.10	0.17	0.76
Coral cover , EAM cover, Structural complexity	392.31	10.21	0.01	0.75
B. <i>Scarus frenatus</i>				
Model	AICc	ΔAICc	wAICc	Adj. R^2
Coral cover	330.22	0.00	0.68	0.06
Coral cover, Structural complexity	332.46	2.24	0.22	0.06
Coral cover, Structural complexity, Exposure	334.54	4.32	0.08	0.06

4.4.3 Short-term foraging range

The mean short-term foraging range of *Scarus niger* varied from $4.9 \text{ m}^2 \pm 3.6\text{SE}$ on John Brewer sheltered sites to $33.5 \text{ m}^2 \pm 5.9\text{SE}$ on Davies sheltered sites, whereas the foraging range of *S. frenatus* ranged from $3.8 \text{ m}^2 \pm 1.3\text{SE}$ on John Brewer sheltered sites, to $34.5 \text{ m}^2 \pm 10.0\text{SE}$ on Davies sheltered sites. The short-term foraging range of both species was poorly explained by the explanatory variables, with only 17% of the variance in foraging by *S. niger* and 3% of the variance in foraging by *S. frenatus* explained by the best-fit models (Appendix C Table S2).

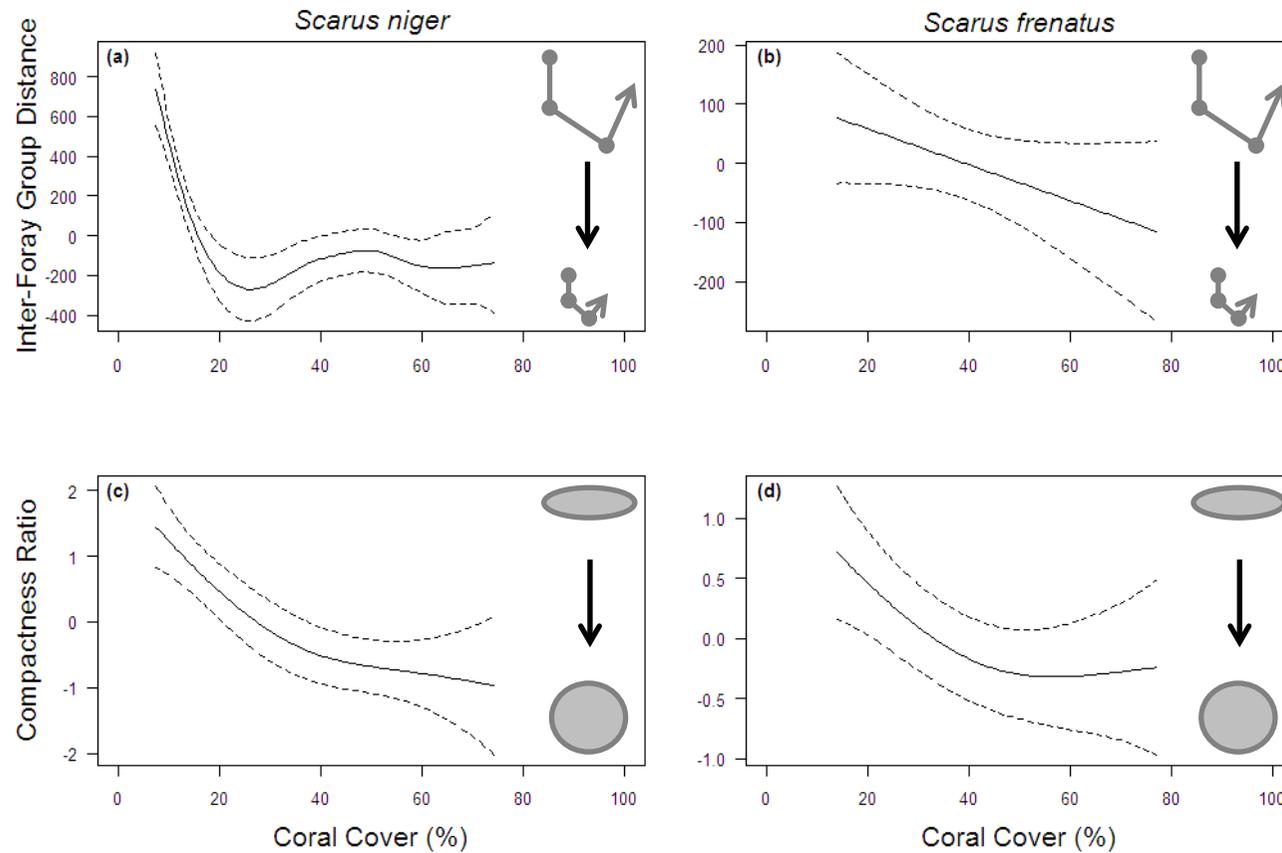


Figure 4-1: The relationship between coral cover and inter-foray group distance for a) *Scarus niger* and b) *Scarus frenatus*, and with shape of foraging range for c) *Scarus niger* and d) *Scarus frenatus*. The data are plotted showing fitted GAM smoothers \pm 95% confidence intervals for the best-fit model, identified using AICc values. X axes are percent coral cover, y axes are centred scales showing partial effect of coral cover on foraging metrics in the respective models.

Smoothing parameters are 5.49, 1, 2.03 and 2.05, respectively for the four plots. Grey graphics in a) and b) represent relative distances between foray groups, where dots depict foray groups and connecting lines depict inter-foray group distance; grey graphics in c) and d) represent relative shapes of short term foraging range represented by different values of compactness ratio.

Table 4-2: Best-fit models for predicting shape of foraging range (compactness ratio) of A) *Scarus niger* and B) *Scarus frenatus*. Models presented are those with lowest AICc values from GAMM that evaluate the influence of exposure, structural complexity, coral cover, EAM cover, parrotfish abundance and large piscivore abundance. Significant predictors are in bold ($\alpha = 0.01$).

<i>A. Scarus niger</i>				
Model	AICc	Δ AICc	wAICc	Adj. R^2
Coral cover, ln(Parrotfish abundance)	81.84	0.00	0.55	0.61
Coral cover, ln(Parrotfish abundance), Exposure	83.52	1.68	0.24	0.64
Coral cover, ln(Parrotfish abundance), Exposure, Piscivore abundance	84.31	2.47	0.16	0.69
<i>B. Scarus frenatus</i>				
Model	AICc	Δ AICc	wAICc	Adj. R^2
Coral cover	41.40	0.00	0.76	0.50
Coral cover, ln(Parrotfish abundance)	44.11	2.70	0.20	0.70
Coral cover, ln(Parrotfish abundance), Structural complexity	47.26	5.86	0.04	0.66

4.4.4 Shape of short-term foraging range

The compactness ratio of both *Scarus niger* and *S. frenatus* was significantly related to coral cover (Table 4-2, Fig. 4-1 C&D); the shape of the foraging range became more circular as coral cover increased, although the influence of changing coral cover on shape was greater at lower levels of coral (Fig. 4-1C&D; see Appendix C Fig. S1C&D for plots of raw data). Coral cover was included in all of the best models for predicting compactness ratios for both species (Table 4-2). Branching and submassive corals were the key drivers of the relationship between coral cover and shape of the foraging range for both species. Models incorporating these lifeforms instead of coral cover as a whole, explained 61% of the variance in shape of foraging range for *S. niger* and 48% of the variance in shape of foraging range for *S. frenatus* (Appendix C Table S3). EAM cover was negatively collinear with coral cover, therefore the shape of the foraging range of *S. frenatus* became more elongate as EAM cover increased.

Parrotfish abundance was a significant predictor of the shape of foraging area for *Scarus niger*, but was only present in the second and third best models for *S. frenatus* (Table 4-2). The foraging range of *S. niger* became more elongate in shape as parrotfish abundance increased (Fig. 4-2A; see Appendix C Fig. S2A for plots of raw data), whereas the foraging range of *S. frenatus* became slightly more circular as parrotfish abundance increased from low to moderate abundances, but then became more elongate at higher parrotfish abundances (Fig. 4-2B; see Appendix C Fig. S2B for plots of raw data). These differences were only apparent when differences in coral cover were accounted for in the model.

Although the same explanatory variables explained the shape of foraging range for both *Scarus niger* and *S. frenatus*, the two species oriented their foraging ranges in different ways. Individuals of *S. niger* displaying more elongate foraging ranges were not consistent in orienting the longest axis either along or down the reef slope, as evidenced by no trend in the depth range of individuals across different shaped foraging ranges ($\rho = 0.37$, $p = \text{N.S.}$). *S. frenatus* individuals displaying more elongate foraging ranges consistently oriented the longest axis along the reef crest, as evidenced by a narrower depth range for more elongate compared with circular foraging ranges ($\rho = 0.54$, $p = 0.01$).

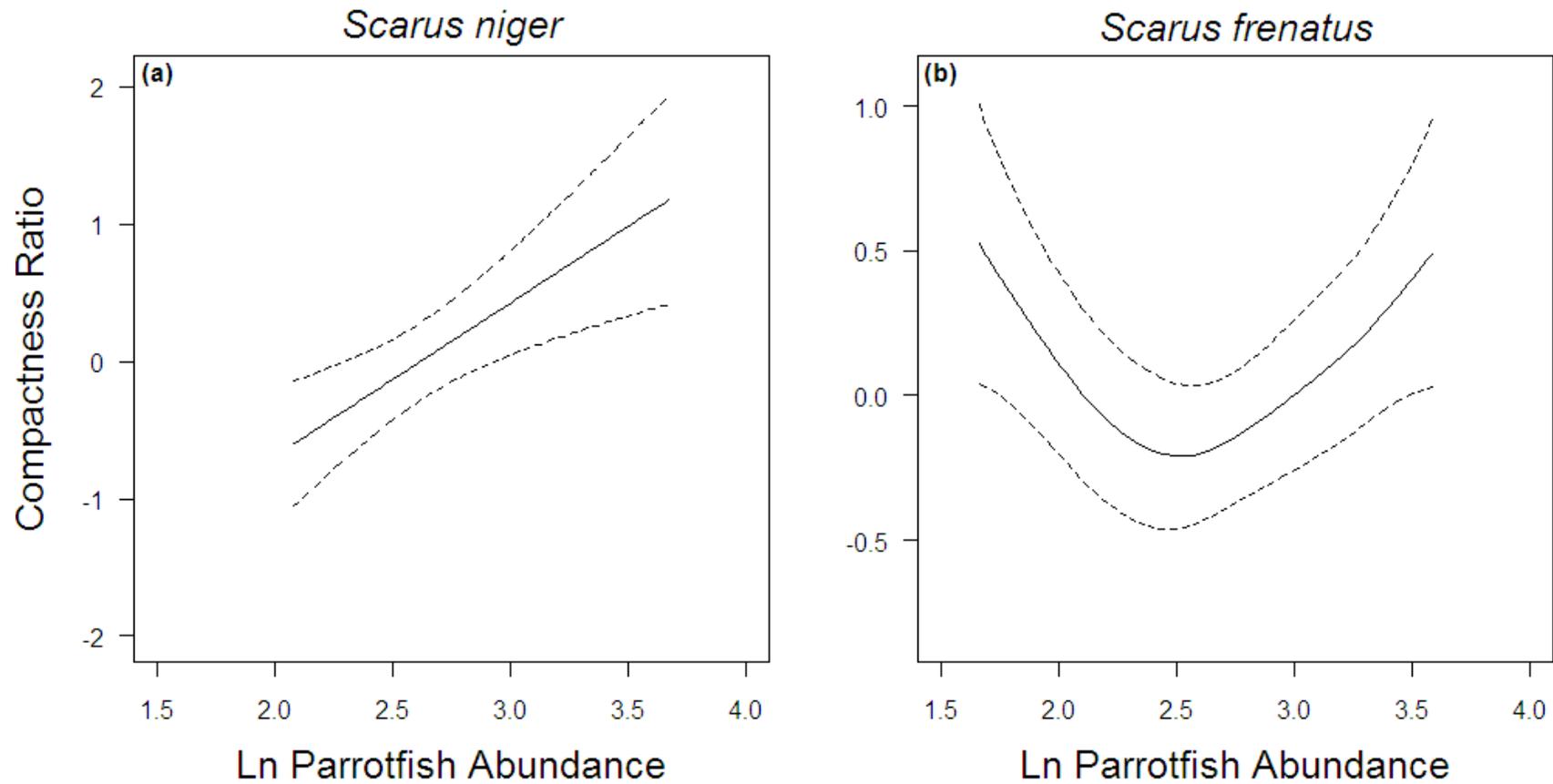


Figure 4-2: The relationship between ln parrotfish abundance and shape of foraging range (compactness ratio) for a) *Scarus niger* and b) *Scarus frenatus*. The data are plotted showing fitted GAM smoothers \pm 95% confidence intervals for the best-fit model, identified using AICc values. X axes are percent coral cover, y axes are centred scales showing partial effect of coral cover on foraging metrics in the respective models. Smoothing parameters are 1 and 2.64, respectively for the two plots.

4.5 DISCUSSION

Determining how herbivorous fish use space when foraging, and what may influence this mobility, are critical for understanding constraints on ecosystem function. Of the variables examined, coral cover and abundance of parrotfish were the key explanatory variables in the models of short term feeding behaviour, although the behavioural responses to these variables varied between the two focal species. In contrast, my estimates of predation risk were not significantly related to foraging. In both species, low levels of coral cover corresponded to more elongate short-term foraging ranges, and greater travel distances between forays, although this relationship was only statistically significant for *Scarus niger*. However, the area covered by individual fish over a two minute period was highly variable within sites for both species. The three metrics of behaviour therefore responded to habitat and fish community variables in different ways. Similar variability has also been found in other organisms (e.g. birds; Pichegru *et al.* 2010), highlighting the importance of characterising foraging behaviour using a range of metrics.

4.5.1 *Habitat condition*

Among the explanatory variables, coral cover showed the strongest relationship with spatial differences in feeding behaviour; it was present in the best-fit model based on AICc values, for inter-foray distance and shape of the foraging range for both species; although the influence of coral cover cannot be separated from that of EAM cover (on reef crest) for *Scarus frenatus* due to negative collinearity. Travelling between resource patches represents a potential energetic cost to foragers (MacArthur & Pianka 1966), suggesting that the decrease in inter-foray distance as coral cover increases, represents a positive influence of coral on individual fish. This may also indicate concentration of foraging effort and therefore function over smaller distances. Williams *et al.* (2001) reported similar patterns, with more intense grazing pressure on algal turfs in higher coral cover areas.

Past research has found greater biomass and abundance of herbivores (e.g. Krajewski & Floeter 2011), and altered foraging behaviour exhibited by reef fish, in areas with high coral cover. The refuge supplied by coral structures has predominantly been invoked as the driver for this relationship (Randall 1965; Graham *et al.* 2006; Madin, Gaines & Warner 2010), but structural complexity was not selected in any of my best models of foraging behaviour. Branching and submassive colonies were the principal components of coral cover at almost all sites and their percent cover was collinear with total cover, therefore it is not possible to determine whether the importance of these lifeforms in the models presented in this study, were

due to the fish responding to coral cover *per se*, or the availability of branching and submassive lifeforms. If it is the latter, this suggests that structural complexity at the scale of the coral colony is important for foraging behaviour, even though the broader scale visual measure of structural complexity was not. The visual scale provides a rapid assessment of complexity, correlating well with availability of holes (>10cm) and vertical relief (Wilson, Graham & Polunin 2007), but it may not reflect colony level rugosity, as reef complexity has been shown to vary non-linearly across spatial scales (Bradbury, Reichelt & Green 1984). Positive relationships between branching coral cover and foraging by herbivores have been found for territorial, farming species (Jones, Santana & McCook 2006; Johnson *et al.* 2011), but negative relationships have been documented for roving herbivores (Bennett, Vergés & Bellwood 2010). Further work is needed to explore the nature of the relationship between corals and foraging behaviour.

Collinearity between coral and EAM cover on the reef crest means that it is not possible to tease apart the relative influences of these two factors on foraging behaviour of *Scarus frenatus*. Coral cover and EAM cover were negatively correlated, indicating that inter-foray distance became greater as algal cover increased. This seems counter-intuitive and conflicts with predictions from optimal foraging theory that predicts smaller, concentrated foraging areas in locations with more resources (Ford 1983; Börger, Dalziel & Fryxell 2008). However, availability of EAM resources may be assessed in a number of ways: standing stock, detrital content, productivity and community composition. Only EAM cover was estimated in this study and it may be that nutritional value or productivity of resources varied among sites, and either individually or interactively, are more closely tied with foraging behaviour than percent cover (Ford 1983), as has been observed for herbivore demographics on reefs (Russ 2003; Nemeth & Appeldoorn 2009).

Parrotfish feed on both algal and detrital elements of the EAM (Choat, Clements & Robbins 2002), however detrital components appear to be selected for as the key constituent that is processed and digested (Crossman, Choat & Clements 2005). The differences in response of *Scarus niger* and *S. frenatus* to EAM may reflect variation in the detrital content between reef crest and slope; particulate material in the crest EAM contains relatively more detritus and less sediment than on the slope, although small-scale variability appears to be highest on the crest (Purcell & Bellwood 2001). It may be this small-scale patchiness in EAM composition that the parrotfishes are reacting to and which explains the differences between the two study species. Further work is needed to assess the influence of both among- and within-zone variability in EAM nutritional quality and productivity, on foraging behaviour.

Recent work by Goatley & Bellwood (2011), examining the importance of a ‘canopy effect’ in benthic monitoring on coral reefs, provides an alternative explanation. The use of planar transects may result in EAM cover being underestimated by up to 67% due to canopy forming corals effectively hiding algae from observers (Goatley & Bellwood 2011). Therefore EAM cover may have been greater than estimated at each of the sites, and the reduced travel distance among forays on reefs with high branching cover may simply represent fish travelling between patches of algae in close proximity to coral cover.

4.5.2 Predation risk

Predation risk has been shown to influence foraging behaviour by decreasing the distance of foraging excursions (Madin, Gaines & Warner 2010). The study found little evidence of predation risk affecting foraging behaviour. However, my results need to be interpreted in light of predator abundances recorded at the study sites; densities of individuals with mouth gapes capable of feeding on the size class of focal *Scarus niger* and *S. frenatus* were low and fairly consistent across sites. This may be the result of low abundance of predators, or transect sizes that were appropriate for determining abundance of parrotfish, but were too small to capture abundance of large mobile predators (Samoilys & Carlos 2000). The study by Madin et al. (2010) was undertaken across an extreme gradient in predator abundance, and densities at all sites in my study were at the lower end of predator densities recorded by Madin et al. (2010). This suggests there may have been insufficient predation pressure to drive changes in foraging behaviour of the focal parrotfish in this study. The low predation pressure may also explain why the visual measure of structural complexity was not a key driver of foraging behaviour, as refuge from predation may not have been of critical importance on the reefs studied.

4.5.3 Competition

I found evidence that spatial differences in parrotfish abundance play a role in modifying foraging behaviour, once the influence of coral cover had been partitioned out. Differences in the shape of the foraging ranges exhibited by *Scarus niger* and *S. frenatus* in response to total parrotfish abundance, is likely to reflect their relative aggression and territoriality with respect to other scraping and excavating herbivores. Work by Bellwood (1985) showed that *S. frenatus* are more predisposed to show antagonistic behaviour in response to other scarids, compared with *S. niger*. Foraging range size of *Scarus niger* decreased with increasing total parrotfish abundance. This negative relationship suggests that parrotfish are competing with *S. niger*, rather than benefiting target fish through group foraging driven reductions in predation risk. These findings are consistent with the outcomes of other studies that have found competitive dominance (Robertson & Gaines 1986) and competition (White &

Warner 2007), may influence feeding behaviour of coral reef fish, and constrain foraging ranges in marine birds (Zavalaga, Halls & Dell'Omo 2010). However, as with other studies (e.g. Francini *et al.* 2010) the influence of competition on foraging behaviour was weak.

4.5.4 Broader implications

This study indicates that the short-term mobility of the parrotfish community is likely to be modified by the cover of coral on a reef, coral community composition, and the density of parrotfish. This extends prior research, which has shown that the geomorphology of a reef may affect use of space (Holland, Lowe & Wetherbee 1996), and that the substratum can influence foraging activity (Krajewski *et al.* 2011) and intensity (Welsh & Bellwood 2012b). However, the strong relationship found between foraging behaviour and coral cover rather than estimates of complexity, does appear somewhat at odds with other work that have primarily found factors such as structural complexity and exposure to drive changes in fish behaviour (e.g. Madin, Gaines & Warner 2010; Krajewski *et al.* 2011). These differences may be the result of scale-specific variation in the influence of environmental characteristics on fish behaviour. The foraging metrics used in this study were short-term, fine-scale assessments and therefore are likely to respond to fine-scale environmental changes (Wiens 1989).

Care needs to be taken when extrapolating from small scale, individual-based observations to broad scale population or community level effects (Peckarsky, Cooper & McIntosh 1997), as individuals may show significant variation in use of space (Kie *et al.* 2002). Additionally, further testing is warranted to assess if these small scale movement patterns integrate up to broad-scale use of space. If these results do reflect broader-scale community effects, the relationship between coral cover, EAM cover, parrotfish densities, and foraging has a number of implications with respect to ecosystem function.

Insufficient grazing pressure has been presented as a key causal factor in macroalgal growth on reefs (Williams, Polunin & Hendrick 2001), but heterogeneous spatial distribution of foraging due to the arrangement of circular or elongate foraging ranges within reef zones may also potentially result in refuges for algae. This suggests that assumptions of uniform foraging effort by reef fish across space (Sandin & McNamara 2011) do not hold for estimates of grazing function.

The relationship between coral cover and short-term behaviour means we cannot expect herbivory processes to continue unaltered, either in the wake of short term pulse disturbances, or in response to predicted, ongoing degradation of coral reefs, both of which will affect coral cover or cause shifts in coral community composition from branching to more massive or

encrusting lifeforms (Hughes *et al.* 2003; Arthur, Done & Marsh 2005; Pratchett *et al.* 2011). The variation in shape of foraging range and inter-foray distance with coral cover suggests that grazing parrotfish are able to make fine-scale changes to the area over which they deliver their functional role in response to loss of coral cover, where reefs are impacted by external disturbances. Whether these fine-scale shifts in behaviour represent a compensatory mechanism that will control algal growth on newly available substratum at site or reef scales, also depends on other factors, such as demographic variables (e.g. herbivore biomass) and behavioural characteristics (e.g. bite rate), which influence grazing intensity across space. Nevertheless, there is room for optimism; by increasing inter-foray distances and changing the shape of foraging areas over short temporal scales, herbivores may be able to modify their broad-scale, spatially explicit functional role in a compensatory manner in response to predicted declines in reef condition. Research examining the interplay between foraging mobility, herbivore community characteristics, and bite rates are now needed to determine how these factors interact to support herbivore function, and to quantify the strength of feedbacks between short-term foraging and reef condition.

Chapter 5: Cross-scale habitat structure drives fish body size distributions on coral reefs⁴

5.1 ABSTRACT

Despite a large number of studies focusing on the complexity of coral reef habitats and the characteristics of associated fish assemblages, the relationship between reef structure and fish assemblages remains unclear. The textural discontinuity hypothesis, which proposes that multi-modal body size distributions of organisms are driven by discontinuous habitat structure, provides a theoretical basis that may explain the influence of habitat availability on associated organisms. In this study I use fractal techniques to characterize patterns of cross-scale habitat complexity, and examine how this relates to body-depth abundance distributions of associated fish assemblages over corresponding spatial scales. My study demonstrates that: (1) Reefs formed from different underlying substrata exhibit distinct patterns of cross-scale habitat complexity; (2) The availability of potential refuges at different scales correlates with patterns in fish body depth distributions, but habitat structure is more strongly related to the relative abundance of fish in the body depth modes, rather than to the number of modes; (3) As reefs change from coral- to algal-dominated states, the complexity of the underlying reef substratum may change, presenting a more homogenous environment to associated assemblages; (4) Individual fish body depth distributions may be multi-modal, however, these distributions are not static characteristics of the fish assemblage and may change to uni-modal forms in response to changing habitat condition. In light of predicted anthropogenic changes, there is a clear need to improve our understanding of the scale of ecological relationships to anticipate future changes and vulnerabilities.

5.2 INTRODUCTION

There is an extensive body of literature examining the influence of habitat complexity on associated organisms. These relationships are of increasing importance on coral reefs where broad-scale declines in complexity have been recorded (Alvarez-Filip *et al.* 2009), driving considerable research focusing on the interactions between complexity and reef fish communities. Many of these studies have shown greater fish abundance and species richness on

⁴ Published as: Nash KL, Graham NAJ, Wilson SK, Bellwood DR. 2013. Cross-scale habitat structure drives fish body size distributions on coral reefs. *Ecosystems* 16: 478-490.

reefs with greater complexity (e.g. Friedlander *et al.* 2003; Emslie *et al.* 2008; Bejarano, Mumby & Sotheran 2011). The strength of this relationship, however, is variable, with methodological, ontogenetic and species-specific effects influencing research outcomes (e.g. Bergman, Ohman & Svensson 2000; Wilson *et al.* 2008). Inconsistencies in the relationship may occur for three key reasons: i) Data arising from the wide range of methods used to assess complexity, such as chain-and-tape, number and size of refuge holes, colony morphology and visual indices (reviewed by Kovalenko, Thomaz & Warfe 2012), may measure different aspects of complexity and are not all directly comparable (Tokeshi & Arakaki 2012); ii) Studies tend to focus on complexity at a particular spatial scale, reinforcing the implicit assumption that complexity at the chosen resolution is homologous to complexity at all scales, which may not be the case (Bradbury, Reichelt & Green 1984; Martin-Garin *et al.* 2007); iii) The metrics used to characterize fish assemblages (for example biomass) are often not related to mechanistic explanations for the association between habitat structure and fish assemblages, preventing explicit linkage between the two (Robson, Barmuta & Fairweather 2005). For example, access to refuge mediates predation risk, therefore availability of shelter of different sizes has the potential to control the abundance of fish of body sizes that can use available holes (Hixon & Beets 1993). Only fish with body depths smaller than structural openings can utilize these refuges for shelter, therefore if fish assemblages are influenced by habitat complexity at different scales, it is predicted that body depth distributions will reflect this relationship.

5.2.1 Analytic framework

Fractal methods, which examine patterns at different scales (spatial or temporal), may address these issues because they allow the relationship between habitat and associated assemblages to be explicitly examined across scales. In this context, cross-scale patterns in habitat structure refer to estimates of complexity measured at a specific range of spatial scales (for example 1cm, 1m, 10m), which are quantified using the fractal dimension (D). D is an ecologically meaningful metric, representing the increase in space available to smaller versus larger organisms (Sugihara & M. May 1990); D measures the rate of increase in distance between two points on a curve as the unit of measurement used to estimate that distance decreases in magnitude (Fig. 5-1; Mandelbrot 1982). This change occurs because smaller units of measurement more closely follow all corrugations of a curve. For a Euclidean line, such as a smooth arc ($D=1$), the estimated distance between two points approximates the true length, therefore the same amount of surface is available to organisms of all sizes (Table 5-1A). In contrast, for a fractal curve (D approaching 2), as the unit of measurement tends to zero, the estimated distance will increase towards infinity, and smaller organisms will have more available space compared with larger organisms; for a tenfold decrease in step length, the

increase in space available scales at 10^D (Table 5-1B; Sugihara & M. May 1990; Martin-Garin *et al.* 2007). Alternatively, complexity may vary across spatial scales, either in the form of smooth changes, or with scales of consistent D (termed ‘scale domains’ by Wiens 1989) separated by increases or decreases in the fractal dimension that indicate discontinuities in habitat structure (Table 5-1C; Bradbury, Reichelt & Green 1984). Fractal methods therefore present a useful framework to examine complexity across scales, and provide a null model of scale invariant habitat complexity against which discontinuities in complexity may be identified (Bradbury, Reichelt & Green 1984; Hartley *et al.* 2004). Importantly, this approach allows explicit predictions regarding scales of habitat structure and the organism body size distributions that would be expected to be associated with this structure (Table 5-1).

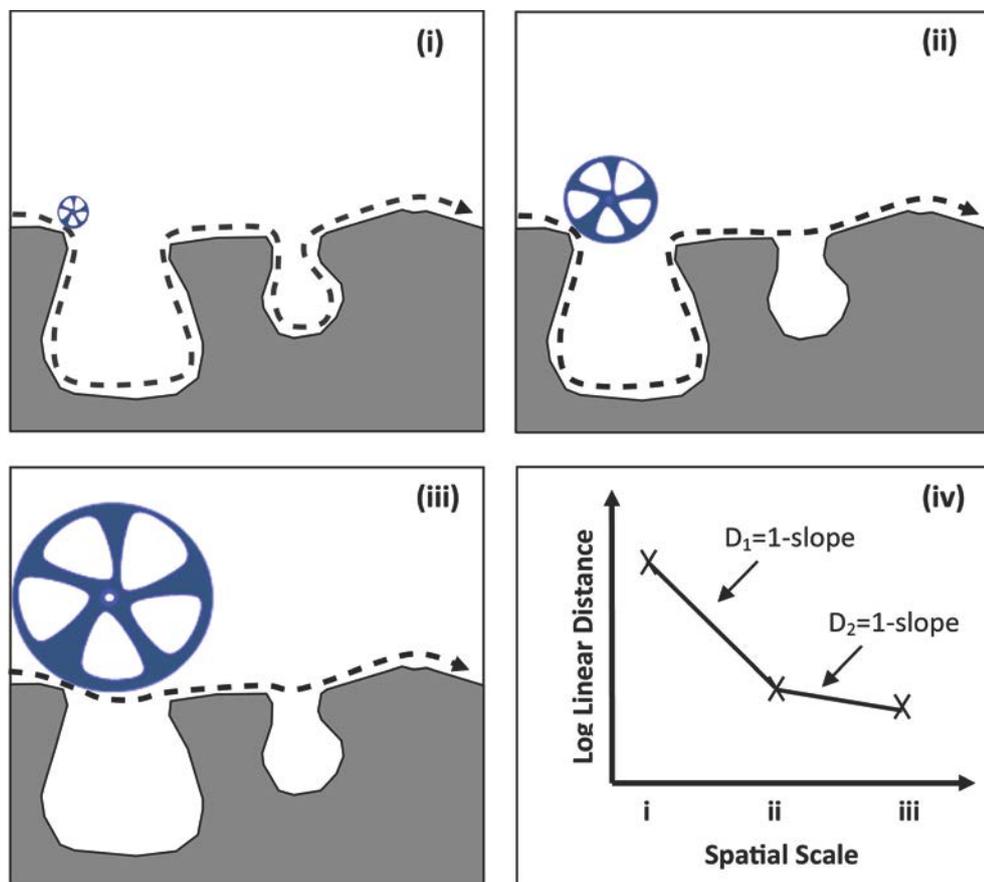


Figure 5-1: Estimation of linear distance by wheels of different diameters. Wheel with small diameter (i) fits into more holes in the reef than mid-sized (ii) or large wheels (iii), thus measuring a greater linear distance (iv). The fractal dimension (D ; 1-slope of the log distance against log spatial scale) provides an indication of the availability of refuges of different sizes (complexity across spatial scales).

Table 5-1: Expected relationships between cross-scale patterns of habitat complexity and associated fish body depth distributions.

	Habitat Complexity Across Scales	Description of Habitat Complexity Across Scales	Predicted Body Depth Distributions	Description of Predicted Body Depth Distributions
A		D=1; Habitat is a Euclidean surface, complexity is constant across scales.		Habitat is a Euclidean curved surface that provides the same surface area to fish of all body sizes. Body depth distributions predicted to be uniformly distributed (for example Brown and Nicoletto 1991).
B		D~2; Habitat is a fractal surface, complexity is constant across scales.		Fractal dimension represents rate of change in available space with decreasing scale. More space (shelter) is available to organisms with smaller body sizes and therefore expect a negative power law distribution with decreasing number of fish as body depth increases (for example Morse and others 1985). However, at very small scales substrate may be too complex to support many individuals (Tokeshi and Arakaki 2012).
C		D varies with scale; Habitat complexity varies linearly or nonlinearly (illustrated) across scales.		Habitat complexity changes across scales such that scales with higher complexity provide greater surface area to fish, and therefore expect higher abundance. ‘Discontinuities’ or sharp drops in complexity may drive troughs in body depth distributions due to lack of shelter or resources at these spatial scales (illustrated; Holling, 1992).

5.2.2 *Theoretical framework*

The textural discontinuity hypothesis (TDH) provides a useful theoretical framework for analysing the cross-scale relationship between reef complexity and fish assemblages. This hypothesis proposes that multi-modal body size distributions of organisms are driven by discontinuous habitat structure and availability of resources across temporal and spatial scales. Furthermore, habitats formed from large or coarse grained structures will be characterized by larger individuals than habitats with fine structures (Holling 1992; Gagné, Proulx & Fahrig 2008). This link between habitat and body size may be accounted for via a range of mechanisms depending on the resource or habitat characteristic in question (Robson, Barnuta & Fairweather 2005), but all are based on the concept that organisms perceive and interact with their environment as a function of their body size (Wiens 1989; Levin 1992).

To date, little research has explicitly examined the links between cross-scale habitat structure and multi-modal body size distributions as outlined in the TDH (but see Leaper *et al.* 2001). Where studies have examined this relationship, estimations of structural complexity have either been qualitative (e.g. Fischer, Lindenmayer & Montague-Drake 2008), or correlations between body size distributions and habitat structure have been made among locations rather than among scales (e.g. Yamanaka *et al.* 2012). Fractals have been used to measure structural complexity on coral reefs over small (e.g. corallite shape; Martin-Garin *et al.* 2007) and large scales (e.g. remotely-sensed reef topography; Purkis & Kohler 2008). However, no attempt has been made to quantitatively evaluate the TDH by explicitly linking fractal cross-scale patterns in coral reef habitat structure to body size distributions of associated ecological assemblages such as fish.

5.2.3 *Aims*

The reefs of the Seychelles provide a unique environment in which to study the relationship between complexity and fish assemblages at a range of scales and in different reef habitats. Two main substrata are found in the inner islands: granitic and carbonate based reefs. The mass bleaching event of 1998 caused significant damage to these reefs, resulting in up to 90% loss of coral cover in some areas (Wilkinson 2000). Subsequent differences in the rate of recovery among reefs, has resulted in sites of varying condition and complexity, with some reefs now dominated by macroalgal cover (Graham *et al.* 2006; Ledlie *et al.* 2007).

This study aims to characterize the complexity of reefs on different underlying substrata (carbonate and granitic), within coral- and algal-dominated states, and across local (within-reef) scales using a fractal approach, and to explore the relationship between these patterns and the

shape of individual body depth distributions of fish assemblages. Specifically, the following questions are addressed: 1) Is coral reef habitat complexity discontinuously distributed across spatial scales, and how does this vary among reef states and substrata? 2) Do scale domains and discontinuities in reef complexity correspond to modes and troughs, respectively, in fish body depth distributions? 3) Are coarse grained habitats characterized by fish with larger body depths compared with fine grained habitats?

5.3 METHODS

5.3.1 Materials

Organisms perceive their environment and therefore habitat structure as a function of body size (e.g. Levin 1992). Fish abundance has been shown to be positively related to availability of refuges with an aperture diameter corresponding to fish body size; larger holes are less attractive to fish as potential predators may also access these refuges (Hixon & Beets 1993), therefore habitat complexity was examined at a range of scales that correspond to the body depths of non-cryptic fish species (2cm to 64cm). Reef complexity was estimated at these scales using a distance measuring device with interchangeable wheels of different diameters, where diameter is equivalent to the spatial scale of measurement or resolution, and wheel circumference provides the step length (Fig. 5-1; after Wilding, Rose & Downie 2007). The circumferences (and diameters) followed a six step-length geometric series (6.6cm to 200.4 cm circumference; 2.1cm to 63.8cm diameter) to allow equal spacing of data points (log scale) used to calculate the fractal dimension (see Data Analysis; Klinkenberg 1994). Each wheel was marked to allow the length of incomplete rotations of the wheel to be quantified. To prevent the wheels slipping on the reef surface or sediment, grip tape was attached to the edge of each wheel. The wheels were calibrated by making a fractal curve, of known dimension, from a piece of plywood (see Supplementary Materials; following Wilding, Rose & Downie 2007). The smallest wheel in the series (2.00 cm) was replaced by a wheel 2.94cm in diameter due to slippage of the smaller wheel on sediment underwater.

5.3.2 Field methods

Ten carbonate sites and 5 granitic sites were surveyed during April 2011 using SCUBA. At each site 8 replicate areas were surveyed along the reef slope, separated by at least 15m. The linear distance over the reef surface was estimated by rolling the measuring wheels along a 5m transect, in a random selection of 5 of these replicate areas. Five areas were chosen due to logistical constraints to obtain robust data from all wheel sizes (Wilding, Rose & Downie 2007).

The transect line was pulled taut across the reef substratum and each wheel was rolled along the length of the line, carefully ensuring the wheel conformed to all the corrugations of the benthos (Fig. 5-1). The number of complete rotations was recorded, and the proportion of the wheel turned for any incomplete rotation noted. Perceived linear distance (L) was then calculated as:

$$L = (R + I) * C \quad (1)$$

where R is number of complete rotations, I is the proportion of the wheel needed for the final incomplete rotation (for example 0.75), and C is circumference of the wheel. All wheel data were collected by the same observer (K.L.N.).

The percent cover of different benthic components was estimated using a line intercept transect along 10m transects within each of the 8 replicate areas, by a single observer (S.K.W) (see Wilson, Graham & Polunin 2007 for details). Fish abundance and individual body length (to the nearest centimetre) of diurnally active non-cryptic species were estimated at each site using instantaneous underwater visual census (UVC) in 7m radius point counts in all replicate areas. Larger, mobile species were recorded before smaller, more site attached species to minimize bias caused by diver effects (see Graham *et al.* 2006 for details). The same observer conducted all fish counts (N.A.J.G.), and the accuracy of fish body length estimations were assessed daily using lengths of PVC pipe, prior to the start of data collection, with estimates consistently within 9% of actual lengths.

5.3.3 Data analysis

Reefs composed of different substrata (granitic and carbonate) provide distinct reef environments (Jennings, Grandcourt & Polunin 1995). It was predicted that contrasting benthic communities at carbonate sites would exhibit different patterns of complexity across scales. Groupings of carbonate sites, based on benthic cover, were evaluated using hierarchical cluster analysis with a Euclidian distance matrix. Clustering (similarity distance = 4) indicated two groups (coral- and algal-dominated). To test the validity of grouping sites into three habitat classifications (fine grained: coral-dominated ($n=6$) and algae-dominated ($n=4$) (carbonate sites) and coarse grained granitic boulder reefs ($n=5$)), differences in the benthic communities of sites were assessed using one-way Analysis of Similarity (ANOSIM) with habitat as a factor (performed in PRIMER; Clarke 1993).

Log-log plots of distance measured against diameter were plotted for each wheel on each transect (Fig. 5-1 iv). Using traditional regression analysis to estimate fractal dimension (D) from data collected at multiple scales along the same transect introduces problems of non-

independence of data points (Halley *et al.* 2004). Therefore, D was calculated between consecutive pairs of scales using:

$$D = 1 - \beta \quad (2)$$

where β is the slope of the line between consecutive scales on the log-log plot. This approach provides slope values (and thus D values) that are independent between treatments (pairs of scales; Halley *et al.* 2004).

Differences in fractal dimension among scales and sites (values of D were averaged across transects within sites) were then compared in R using Monte Carlo simulations (n=5000) within an ANOVA framework (Gotelli & Ellison 2004; R Development Core Team 2011), with post-hoc testing of mean differences corrected for multiple comparisons using the false discovery rate (Benjamini & Hochberg 1995). The range of wheel sizes incorporated in this analysis allowed identification of changes in the fractal dimension of the reef at ecologically relevant scales, corresponding to the range of fish body depths found within each habitat. However, they did not permit classification of the reef as a true fractal; constant D over 3 or more orders of magnitude is required to confirm self-similarity and therefore statistically fractal behaviour (Halley *et al.* 2004).

The body depths of individuals were estimated from recorded body lengths using length: depth ratios provided by Graham *et al.* (2007) and Januchowski-Hartley (unpublished data). Mean body depth was compared among sites using Analysis of Variance (ANOVA) and a post-hoc Tukey's test. To evaluate the relationship between resource and body size distributions, the latter may be assessed for either multi-modality or discontinuities, i.e. a concentration of individuals at a particular body size, or gaps in the distribution. The fractal methods characterize the complexity at different scales and changes in complexity among scales, and therefore focus on the availability of resources rather than identifying scales without resources; as a result a multi-modal approach is more appropriate in this context. The shape of the distribution of log fish abundance across log body depths were tested for using Generalized Additive Models (GAMs) with a Gaussian error structure and identity link function (following Fewster *et al.* 2000; Buckland *et al.* 2005). The degree of smoothing (degrees of freedom, d.f.) defined in the GAM models will influence the modality detected in the data, therefore guidelines provided by Fewster *et al.* (2000; d.f.=no. of size classes*0.3), aimed at finding larger scale trends rather than small-scale fluctuations in abundance among size classes, were used to set the d.f. to 7 in the models. Location was included in the model as a fixed explanatory variable, to account for among-location differences in distributions.

GAMs were fitted to replicate (n=400) body depth distributions sampled with replacement, in the R package *mgcv* (Wood 2006). To identify modes and troughs in the distribution, the second derivatives of the predicted curves for each replicate were estimated. Ninety five percent confidence intervals were calculated for the curves and second derivatives, and significant turning points identified where 95% confidence intervals of the derivatives did not cross zero. Significant negative derivatives bounded by two greater derivatives represent a peak or mode (\cap) in the distribution, whereas significant positive derivatives bounded by two smaller derivatives identify troughs (\cup) in the body size distribution (Fewster *et al.* 2000; Vergnon, Dulvy & Freckleton 2009). Where distributions were found to be multi-modal, significant differences in abundance among modes were assessed using Monte Carlo simulation (n=5000) corrected for multiple comparisons using the false discovery rate (Benjamini & Hochberg 1995).

5.4 RESULTS

5.4.1 *Benthic community and habitat classification*

The benthic communities of all three habitat classifications (coral-dominated carbonate, algal-dominated carbonate and Granitic, hereafter Coral, Algae and Granitic) were significantly different from each other (Table 5-2). Algae sites were characterized by high macroalgal cover ($37.3\% \pm 13.3\text{SE}$) and low coral cover ($2.8\% \pm 0.7\text{SE}$). In contrast, Granitic and Coral sites were both characterized by relatively low algae cover ($0.3\% \pm 0.3\text{SE}$ and $1.4\% \pm 1.6\text{SE}$ respectively) and high coral cover ($20.4\% \pm 2.7\text{SE}$ and $28.7\% \pm 4.8\text{SE}$ respectively), however nonliving substrata at Coral sites was dominated by sand and rubble ($10.9\% \pm 2.1\text{SE}$ and $41.0\% \pm 4.0\text{SE}$), whereas at Granitic sites, rock in the form of large boulders was more prevalent ($55.9\% \pm 5.3\text{SE}$). Coral, Algae and Granite habitat groupings were used for all analyses.

5.4.2 *Cross-scale habitat complexity*

The linear distance measured by the different wheels followed a decreasing trend with increasing scale at small to mid-scales in Coral habitats (8231cm to 5730cm; Fig. 5-2A i). Linear distance was more variable at Algae and Granitic (Fig. 5-2A ii&iii) versus Coral sites, and was generally lower in the Algae habitat (6068cm) compared with both Coral and Granitic sites at small scales (8231cm and 8550cm respectively).

Table 5-2: Analysis of similarity (ANOSIM) among sites of different habitat type.

Factor	Global R	Significance
Habitat	0.84	<0.01
Pairwise Comparison		
Algae, Coral	1.00	<0.01
Algae, Granite	1.00	<0.01
Coral, Granite	0.59	<0.01

D varied across scales in Coral and Algae habitats, but also varied among Algae sites (Table 5-3). In contrast D varied among sites but was consistent across scales in the Granitic habitat (Table 5-3). Post-hoc testing indicated three groupings or ‘scale domains’ of consistent D values separated by discontinuities within the Coral habitat (Fig. 5-2B i): D was significantly greater at the smallest scales (2.94-3.94cm wheel diameter: D of 1.5) compared with mid-scales (3.94-15.80cm wheel diameter: D of 1.13-1.17), and significantly greater at mid-scales than at the largest scales (15.80-63.80cm wheel diameter: D of 1.05). The habitat fractal dimension of Algae sites also varied among scales (D of 1.0-1.3), but there were no clear discontinuities in D, rather there was declining complexity across scales with an overlap in D between small and mid scales, and between mid and large scales (Fig. 5-2B ii). The fractal dimension estimated for Coral sites was greater than that of Algal sites at the smallest scale (Fig. 5-2B i&ii). D was consistent across scales at the Granitic sites (D of 1.1-1.2; Fig. 5-2B iii), and was lower than that of the smallest scale on Coral sites, but overlapped with D at the smallest scale of Algal sites.

5.4.3 Fish individual body depth distributions

Fewer fish were observed at Algae sites (mean of 476 individuals per site) than at Granitic (599 per site) and Coral sites (758 per site). Mean body depth varied among habitat types ($F=111.82$, $d.f.=2$, $p<0.01$); fish were significantly larger at Granitic sites (5.2 cm mean body depth) than at Coral or Algae sites (4.3 cm mean body depth).

Two peaks were identified in both the Coral and Granitic fish body depth abundance distributions (Fig. 5-2C i&iii - grey indicator bars). These modes were located at similar body depths, but were wider at Granitic sites (extended over 0.15-0.2 log cm) compared with Coral sites (extended over 0.1-0.15 log cm). Only a single mode was found in the fish body depth

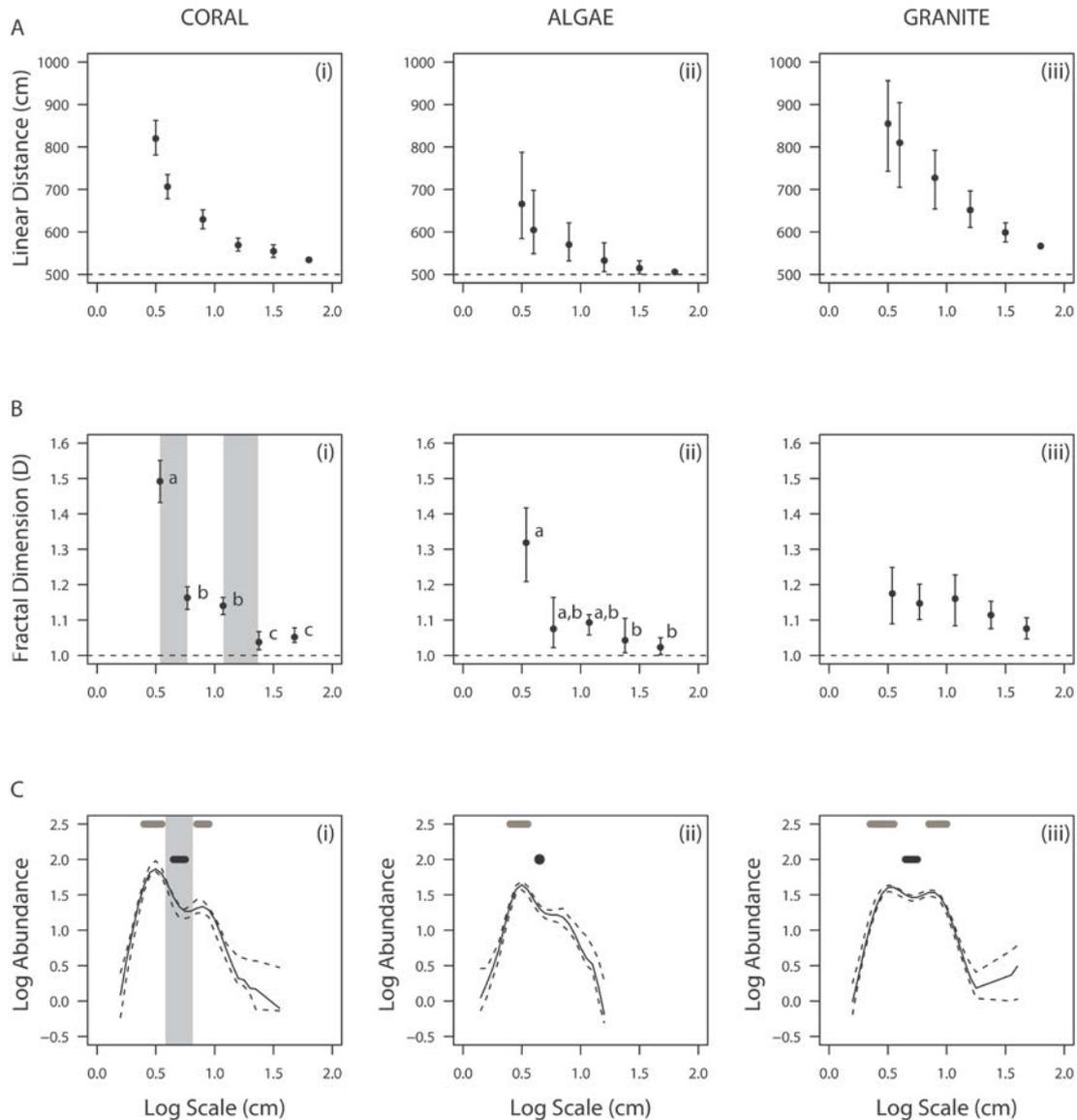


Figure 5-2: A) Mean linear (perceived) distance measured along transects using wheels of different step lengths for i) Coral, ii) Algae, and iii) Granitic sites. Dotted lines represent linear distance along transect (500cm). B) Mean fractal dimension (D) of substrate estimated at different spatial scales for i) Coral, ii) Algae, and iii) Granitic sites. Error bars represent bootstrapped non parametric 95% confidence intervals. Shading indicates location of breaks in D with scale (scale breaks); lowercase letters represent significant groupings assessed using Monte Carlo simulation of mean differences corrected for multiple comparisons. Dotted lines represent fractal dimension for straight Euclidean curve (D=1). C) Distribution of fish abundance across body depth size classes for i) Coral, ii) Algae, and iii) Granitic sites. Dotted curves represent bootstrapped 95% confidence intervals. Grey and black bars identify locations of significant peaks and troughs in abundance respectively, identified using 95% confidence intervals of bootstrapped second derivatives of GAM abundance smoothers. Shading represents location of breaks in abundance identified as modes with significantly different abundances, using Monte Carlo simulation. Note, log scale on x axis represents wheel diameter (cm) in A) and B) and body depth (cm) in C).

Table 5-3: Results of Monte-Carlo simulation of differences in fractal dimension among sites and scales for each habitat.

Habitat	Factor	F-value	Significance
Coral	Site	1.4	NS
	Scale	89.70	<0.01
Algae	Site	4.83	<0.05
	Scale	16.90	<0.01
Granitic	Site	3.63	<0.05
	Scale	2.20	NS

distribution at Algae sites, located at similar body depths (0.4-0.6 log body depth (cm)) as the lower mode in the other two habitats. There was a significant difference in abundance between peaks at the Coral sites (mean difference = 0.68, $p < 0.01$), but not Granitic sites (mean difference = 0.14, $p = \text{NS}$), with numbers decreasing from smaller to larger body depth modes. The abundance of fish in the smallest body depth mode was greater at Coral sites than at Algae or Granitic sites (Fig. 5-2C).

5.5 DISCUSSION

5.5.1 *Evaluation of the textural discontinuity hypothesis*

This study provides a characterization of the cross-scale relationship between habitat complexity and fish body depth distributions, and is the first quantitative evaluation of the textural discontinuity hypothesis (TDH) in a high diversity ecosystem. The differences in fish body depth distributions among habitats provides evidence for the core predictions of the TDH that i) discontinuous cross-scale habitat structure drives patterns of modality in the body size of associated assemblages, and ii) larger organisms are associated with habitats characterized by coarse-grained structure (Granite habitat) compared with those characterized by fine-grained structure (Coral & Algae habitat; Holling 1992; Gagné, Proulx & Fahrig 2008). Furthermore, there was a shift from a multi-modal to a uni-modal fish body depth distribution, between the more complex Coral, and the structurally simpler, degraded Algae habitat type. This aligns with findings of homogenization of habitats correlating with reduced modality in body size distributions in terrestrial systems (Fischer, Lindenmayer & Montague-Drake 2008).

However, the link between complexity and fish body depth distributions is not clear cut. Differences in complexity may more strongly influence the distribution of individuals among modes in the fish body depth distributions, and thus the relative abundance of individuals within modes, rather than the number or location of modes as proposed by the TDH. Differences in abundance among modes would explain variations in the body depth distributions amongst all habitats. Peak abundance at Algae sites coincided with the lower mode at Coral and Granitic sites; few fish were observed at Algae sites in larger body depth classes. Fish body depth distributions were bimodal in both Coral and Granitic habitat types; however, the abundance of individuals were more uniformly distributed among broader modes at Granitic sites where habitat complexity was approximately Euclidean in character, and therefore provided similar space to fish of all sizes (Table 5-1A). In contrast, at Coral sites, a significantly greater number of individuals were found in the lower mode (smaller individuals) compared with the upper mode (larger individuals). This peak in abundance corresponds to the scale at which D was higher, and therefore significantly more space was available to small versus large individuals. This outcome directly corresponds with predictions of a more uniform distribution of organisms among size classes in habitats with a more uniform size distribution of refuges (Tokeshi & Arakaki 2012), and a shift in the balance of body sizes from small to large, with a corresponding shift from fine- to coarse-grained structures (Holling 1992).

There was no mode found at large fish body depths at Coral sites, to coincide with the third scale domain in habitat complexity. This may be a function of low numbers of large fish, limiting the power of the GAMs to locate a mode at larger size classes, or may reflect reduced predation risk with increasing body size (Munday & Jones 1998), thus fish are less reliant on refuge and therefore habitat complexity at these larger scales. Further studies, which incorporate more sites and a greater number of fish point counts at each site, are needed to clarify this.

There are a number of other potential drivers of body size distributions such as biogeographical constraints and community interactions (reviewed by Allen *et al.* 2006). These proposed mechanisms are not necessarily mutually exclusive, and differentiation between the relative importance of drivers may be made partly on a basis of spatial and temporal scale, because the mechanisms are often scale specific. For example, the TDH is relevant at local-regional spatial scales and ecological time scales (Allen *et al.* 2006). My study sites were located within a single region, so broader scale mechanisms such as phylogenetic constraints or regional habitat characteristics may be more influential than local-scale refuge availability, in determining mode location in assemblage distributions across all reef habitats (Havlicek & Carpenter 2001; Allen *et al.* 2006). However, my key findings provide significant support for

the TDH on coral reefs: (1) strong links were found between cross-scale patterns of habitat complexity and fish individual body depth distributions, and (2) the fish assemblage associated with the coarse-grained Granite habitat type was characterized by larger individuals than the fish assemblage observed at the finer-grained Coral sites.

5.5.2 *Fish body depth distributions*

Body size distributions can be assessed at the individual or species level (White *et al.* 2007). To date, much of the work studying the textural discontinuity hypothesis has been undertaken at the species level, using a mean body size for each species and no measure of abundance (but see Ernest 2005; and Thibault *et al.* 2011). However, resource or habitat use by organisms of different body sizes occurs at the individual level and is inextricably linked to individual abundance (White *et al.* 2007). Therefore the individual body size distributions present a robust method for investigating the link between body size and habitat structure across spatial scales (Thibault *et al.* 2011) in my study. Fish body depth distributions varied among habitats, exhibiting both uni-modal and bimodal forms, however for all habitats, abundances were low in the tails of the distribution. Low abundances at small body depths are likely to be a function of progressive, size-related under-sampling, as only non-cryptic species were surveyed (Blackburn & Gaston 1994; Ackerman & Bellwood 2000). In contrast, low abundances at large body sizes is typical of taxa across a range of ecosystems (e.g. Greenwood *et al.* 1996; Cohen, Jonsson & Carpenter 2003; Ackerman, Bellwood & Brown 2004), a phenomenon that is likely exacerbated on coral reefs by selective fishing pressure targeting larger individuals (Jennings, Greenstreet & Reynolds 1999; Friedlander & DeMartini 2002).

Fish assemblage body size distributions have traditionally been studied using linear regression. This approach may be appropriate when looking at the distribution of biomass across size classes in aquatic taxa (Cattaneo 1993), or as a metric of the change in abundance between small and large individuals as a function of fishing pressure (Graham *et al.* 2005). However, multi-modal body size distributions have been found in an increasing array of aquatic environments (Havlicek & Carpenter 2001; Stead *et al.* 2005; Dornelas, Connolly & Hughes 2006). Specifically, reef fish assemblages may have non-linear individual body size distributions, an observation that has been made in this study using visual censuses, and in other work using stereo cameras (Watson *et al.* 2010), and combined rotenone and visual surveys (Ackerman, Bellwood & Brown 2004). My findings suggest that fish assemblages' size frequency distributions are multi-modal but that these distributions may be dynamic in nature, potentially changing from multi-modal to uni-modal forms as reef habitats shift from coral to algal-dominated state. Furthermore, even where the location of a mode remains constant as

habitats change, peak abundances may decline for small non-cryptic fish. Clearly, temporal changes in complexity and fish data are needed to test these suppositions further, however, this outcome supports predictions of negative impacts on small individuals following habitat decline (Pratchett *et al.* 2008b), and is indicative of the specific scale of habitat loss that drives a reduction in numbers of small, non-cryptic individuals. Whether these patterns in body size distributions hold for cryptic and less refuge-reliant species, which may be influenced less by habitat loss (Bellwood *et al.* 2006a), needs to be determined. Regardless, varying drivers of mortality may result in differential size distributions of fish; whereas fishing targets larger individuals, which shifts the size spectra of the assemblage in favour of smaller fish (Graham *et al.* 2005), habitat modification is more likely to negatively impact the abundance of small individuals (Olden, Hogan & Zanden 2007). Therefore, the dual impacts of exploitation and habitat degradation may result in a narrowing of body size distributions (Wilson *et al.* 2010).

5.5.3 *Cross-scale habitat complexity*

Analysing the fractal dimension of habitats provides an objective characterization of complexity across spatial scales (Bradbury, Reichelt & Green 1984). However, complexity is a multi-dimensional phenomenon (Tokeshi & Arakaki 2012), thus it is important to explicitly consider the aspects of habitat structure assessed using a specific method, in order to understand the link between structure and associated organisms.

My approach assesses the relative availability of space in holes or crevices at different spatial scales (range of wheel diameters). Reefs with less surface area at small scales (Algae habitat) can therefore exhibit a greater fractal dimension than reefs with greater surface areas (Granitic habitat) at small scales, because the relative complexity is more evenly distributed across scales in the latter compared with the former. This habitat complexity may represent potential refuges in the reef, although it should be noted that their specific dimensions will influence their suitability as shelter for different sized fish (Friedlander & Parrish 1998; Bartholomew & Shine 2008; Tokeshi & Arakaki 2012). Granitic reefs are composed of boulders of varying sizes that provide a large but variable surface area to inhabitants; the approximate Euclidean nature of these reefs (consistent $D \sim 1.1-1.2$ over scales measured; Davenport 2004) indicates a similar surface area is available to organisms of all sizes. Concavities at Granitic sites therefore have wide openings, decreasing their suitability as shelter for small individuals hiding from predators (Hixon & Beets 1993). The apparent lack of small aperture holes at the study sites may be a function of the shift from branching to encrusting coral lifeforms on granitic substratum since the 1998 bleaching event (Wilson *et al.* 2012),

changing cross-scale patterns in complexity to a coarser grained and more spatially homogenous environment.

Discontinuities in the fractal dimension of a surface may represent a change in the dominant fractal population between spatial scales. The break between small and mid-scales in the Coral habitat corresponded to one of the complexity ‘transition zones’ identified by Bradbury (1984) on the Great Barrier Reef, indicating that this discontinuity may be widely characteristic of coral-dominated carbonate reefs. This break occurs between the small scales of intra-colony architecture, where the dominant fractal population is likely to be the shape of colony branches and corrugations, and mid-scales at which colony size distributions are drivers of the fractal dimension (Bradbury, Reichelt & Green 1984). The second discontinuity found at Coral sites, may represent a further change in the dominant fractal population, from colony size distributions to broader scale reef topography. Delineation of these scale domains provides an indication of the scales at which specific processes operate, and importantly signals appropriate scales of observation and analysis for specific research questions that are not dependent on arbitrary methodological choices (Wiens 1989).

Prior to the 1998 bleaching event the carbonate reefs of the Seychelles were coral-dominated, however differential recovery among the reefs since this disturbance, has resulted in macroalgal domination at some locations (Graham *et al.* 2006). All Coral, and some Algae sites, had D values greater than 1 at the smallest scales, suggesting greater relative availability of space in concavities with small rather than large openings. Two discontinuities in reef complexity were found for Coral sites; in contrast Algae sites showed a shallow decline in complexity with increasing scale, signifying a more uniform, hard benthic environment than found in the Coral habitat. Furthermore, the surface area (linear distance) available on Coral sites was greater than that available on Algae sites at small-mid scales, suggesting that the absolute availability of holes for refuge-dependent, small and mid-sized fish declines as the reef degrades. The differences in cross-scale patterns between Algae and Coral habitats in my study may therefore indicate the specific scales at which reef structure degrades in response to disturbance, and as reefs change from a coral- to an algal-dominated state.

The wheels estimated the complexity of hard substrata, and did not account for the structure of macroalgal stands. Three dimensional algal habitat has been shown to affect associated fish assemblages in temperate algal beds (Levin & Hay 1996), just as refuges in solid substrata do, although the form of this effect may be different (Hoey & Bellwood 2011). The application of fractals may be extended to meet this demand for a method that may be applied to hard and soft structure, as robust techniques are available to measure complexity of

macrophytes (e.g. McAbendroth *et al.* 2005). Fractals, therefore, provide a metric for measuring structure that is comparable among habitats.

The reefs of the inner Seychelles were subject to a bleaching event, which resulted in coral mortality, but did not immediately cause loss of reef structure (Graham *et al.* 2007). Other forms of disturbances such as hurricanes, which directly impact reef substrata, drive varying patterns of degradation and recovery (e.g. Kaufman 1983; Andres & Rodenhouse 1993), and are likely to result in distinct cross-scale variation in patterns of habitat complexity. In addition, the scale, frequency and intensity of a disturbance will influence temporal trajectories of complexity at different spatial scales (O'Neill *et al.* 1986). This variability across scales will have implications for the availability of a wide range of resources, including refugia, for associated assemblages (Peterson, Allen & Holling 1998). Erosion of habitat structure, fragmentation and decline are not limited to coral reefs, and have been reported over large areas in both marine and terrestrial environments (Silliman *et al.* 2005; Alvarez-Filip *et al.* 2009). In the face of projected anthropogenic pressures, and their potential for driving disturbance regimes and phase shifts (Tilman *et al.* 2001; Hughes *et al.* 2007b), the dynamics of cross-scale habitat need to be explored across ecosystems.

5.5.4 Conclusions

The fractal approach used in this study identifies discontinuities in reef structure in coral-dominated habitats and the spatial scales at which this structure is lost as reefs degrade. Comparing this fractal evaluation of complexity with individual body size distributions provides a mechanism for quantitatively linking habitat structure and fish assemblages across scales, and provides support for the textural discontinuity hypothesis in the context of coral reefs. Variations in cross-scale structure among habitats is associated with different patterns in body size distributions, such that more uniform fish size distributions are associated with homogenous versus heterogeneous environments.

Chapter 6: Discontinuities, cross-scale patterns and the organization of ecosystems⁵

6.1 ABSTRACT

Ecological structures and processes occur at specific spatio-temporal scales, and interactions that occur across multiple scales mediate scale-specific (e.g. individual, community, local or regional) responses to disturbance. Despite the importance of scale, explicitly incorporating a multi-scale perspective into research and management actions remains a challenge. The discontinuity hypothesis provides a fertile avenue for addressing this problem, by linking measurable proxies to inherent scales of structure within ecosystems. Here I outline the conceptual framework underlying discontinuities, and review the evidence supporting the discontinuity hypothesis in ecological systems. Next I explore the utility of this approach for understanding cross-scale patterns and the organization of ecosystems by describing recent advances for examining non-linear responses to disturbance, and phenomena such as extinctions, invasions, and resilience. To stimulate new research, I present methods for performing discontinuity analysis, detail outstanding knowledge gaps, and discuss potential approaches for addressing these gaps.

6.2 INTRODUCTION

Toward the end of the 20th Century, ecology underwent a conceptual shift from a linear, continuous view of ecosystem processes and structures, to one that emphasized non-linearity and the discontinuous nature of many variables and processes (Wiens 1989; Solé & Bascompte 2006). Ecosystems are strongly influenced by biotic and abiotic processes that operate over different spatial and temporal scales (Levin 1992; Peterson, Allen & Holling 1998; Peters, Bestelmeyer & Turner 2007). Therefore, although small-scale observations provide an important route to explore ecosystem dynamics, it is critical to understand how patterns and processes observed at finer scales represent those operating over broader spatiotemporal scales, and similarly, how large-scale processes correspond to small-scale phenomena (Levin 1992; Cooper *et al.* 1998; Scheffer & van Nes 2007). These multi-scale patterns will affect the manner in which ecosystems respond to disturbance operating over different scales (Peters, Bestelmeyer

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& Turner 2007), and therefore knowledge of how pattern-process relationships are distributed across scales is crucial for a better understanding of the current state of ecosystems, and to make predictions of their response to change.

Despite this interest in scale-specific patterns, effective implementation of a multi-scale approach in theoretical and empirical research, remains elusive (Wheatley & Johnson 2009). This is primarily due to the difficulties of identifying appropriate scales and the logistics of targeting multiple scales during data collection (Addicott *et al.* 1987). Analysis of discontinuities (Table 6-1) found within a range of abiotic and biotic variables, such as habitat structure, body mass and range size (e.g. Fischer, Lindenmayer & Montague-Drake 2008; Gunderson 2008; Restrepo & Arango 2008), offers a fertile avenue for examining processes and interactions in a multi-scale context. This approach allows the identification of scale-specific relationships among ecosystem drivers and processes, habitat structure, resource availability, and organisms. Here, I outline and evaluate evidence for a conceptual framework that accounts for discontinuities within ecosystems, and draw links to work in other ecological and biological fields such as hierarchy theory. Second, I provide and describe tools for evaluating discontinuities across a range of data types. Third, I explore the emerging literature incorporating discontinuity analysis. I illustrate how this approach may be used to address a range of ecological questions regarding cross-scale patterns in abundance, function, diversity, and organismal traits as they relate to that pattern, as well as to emergent phenomena such as resilience. Finally, I highlight the potential limits of applying discontinuity theory and analyses to specific systems and the current gaps in knowledge, providing stimulus for new research.

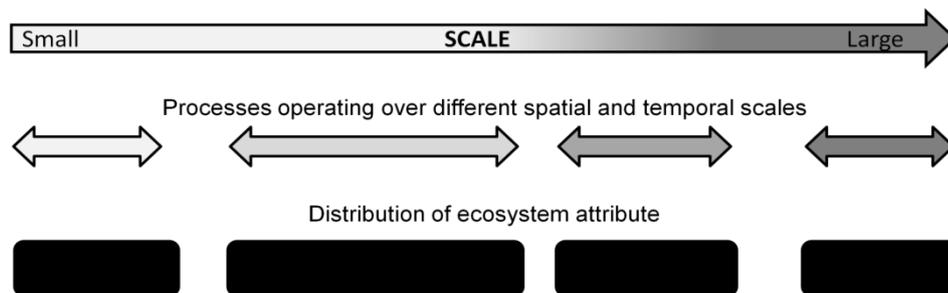


Figure 6-1: Multi-scale relationship between processes occurring over different, discrete spatial and temporal scales, and the resulting discontinuous distribution of an ecosystem attribute, such as physical habitat structure. The distribution of processes over discrete scale ranges, and the landscape patterns they produce represent the ‘intrinsic’ scales (Table 6-1) of a system (adapted from Wiens 1989). Discontinuities, or zones of low or variable resource availability lie between these ‘intrinsic’ scales.

6.3 DISCONTINUITIES: FRAMEWORK, EVIDENCE AND EXTENSIONS

6.3.1 *Conceptual framework*

The discontinuity approach is derived from hierarchy theory (Appendix D Table S1). Growing evidence from nature and ecological modelling suggests that ecosystem structure and dynamics are dominated by the influence of a small set of plant, animal, and abiotic processes operating at specific temporal periodicities and spatial scales, forming a hierarchy (O'Neill *et al.* 1986; Holling 1992). Each level in this nested hierarchy of variables is controlled by processes sufficiently different in speed and size to introduce discontinuities in the distribution and pattern of ecosystem attributes such as habitat structure and resource availability (Allen & Starr 1982; Fig. 6-1; O'Neill *et al.* 1986; Kolasa 1989). Thus ecological structure varies with scale, and reflects the actions of the particular processes operating at a given scale. Such discontinuous hierarchical patterns of processes, structure, and resources were first proposed in systems theory over fifty years ago (Simon 1962). Some thirty years later, ecologists began applying these concepts to describe and understand a range of aquatic and terrestrial ecosystems (Levin 1992; Gillson 2004; Gunderson 2008). For example, the scales of food and shelter afforded by the physical structures of a coral reef ecosystem vary from individual coral branches up to multi-reef complexes, with implications for the abundance of associated organisms (Fig. 6-2a; Nash *et al.* 2013). Discontinuous, hierarchical structure is being used to assess hydro-geomorphic processes in fluvial systems (Poole 2002), and the concept underpins considerable work in landscape ecology (e.g. Kolasa 1989; Pavlacky & Anderson 2007; Johnson 2009).

A number of theoretical frameworks have linked patterns in habitat structure to attributes of associated communities (MacArthur & Wilson 1967; Milne *et al.* 1992; Brown 1995; Ritchie 1998). The discontinuity hypothesis, as originally framed by Holling (1992), proposed that where ecosystem patterns are persistent over ecological timescales, biological processes unrelated to the original structuring processes will become entrained by and adapted to the pattern across scales. For example, life history, behavioural and morphological attributes of animals may adapt to the discontinuous landscape pattern as this pattern reflects opportunities for shelter, food and resources (Fauchald & Tveraa 2006). However, these opportunities are mediated by the scales at which individuals interact with the landscape and exploit resources (Holling 1992; Haskell, Ritchie & Olf 2002), and the scale of these interactions are positively correlated with body size (Peters 1983).

Table 6-1: Glossary of terms.

Term	Definition
Aggregation	Clusters of measurements in the distribution of a variable. In a body size distribution an aggregation is a cluster of species that are of similar size. Synonymous with lump or mode in the distribution and driven by the underlying pattern of resource availability or habitat structure, although a focus on modality differs from one on discontinuity in that the expected mechanisms are different (see Discontinuous and Multi-modal distribution below). An aggregation is separated from its neighbor by a discontinuity.
Cross-scale dynamics	Interactions among processes and variables occurring at discrete spatial and temporal scales, causing non-linear patterns and thresholds. These interactions may result in smaller-scale processes propagating up to influence larger scale processes or variables, or larger-scale processes constraining smaller-scale processes and variables.
Discontinuity	Break in the distribution of a variable. In a body size distribution this would be a region of the distribution with no species. Synonymous with gap and driven by underlying break between ‘intrinsic’ scales (see Appendix D Table S1 for further detail). Discontinuities split aggregations in the distribution.
Discontinuous distribution	The distribution of a variable where measurements are clustered in groups along the axis, and clusters are separated from each other by gaps (cf. multi-modal distribution). For example a body mass distribution, where species of similar size are clustered in aggregations separated from species of different size by gaps or discontinuities in body mass. Methods aimed at evaluating distributions for discontinuities look for gaps rather than aggregations.
Ecological resilience	A measure of the amount of change needed to transform an ecosystem from one set of processes and structures to a different set. An ecosystem with high resilience would require a substantial amount of energy to transform, whereas a low resilience system would transform with a relatively small amount of energy.
Intrinsic scales	Sections of the scale spectrum where process-pattern relationships are consistent, i.e. they are homogeneous or change monotonically, and persist over the timescale of interest (Stallins 2006). Also termed scale domains (see Appendix D Table S1). A domain is separated from neighboring domains by breaks, which are zones of variability where there is a change in the dominant processes.
Multi-modal distribution	The distribution of a variable where measurements are clustered along the axis. Clusters may be separated from each other by gaps <i>or</i> troughs in the distribution (cf. discontinuous distribution). Methods aimed at evaluating modality of a distribution look for modes rather than gaps.
Process	In this context, process includes endogenous processes such as herbivory and exogenous drivers such as a storm. These processes and drivers operate over a discrete range of spatial and temporal scales forming ‘intrinsic’ scales within a system.

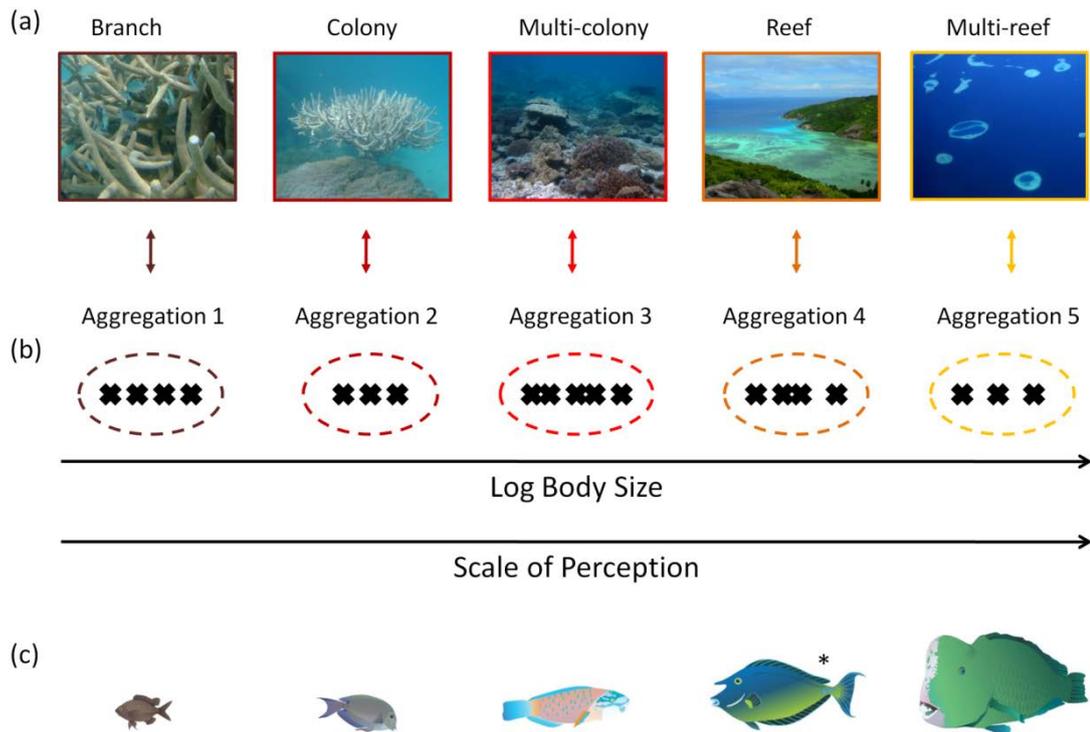


Figure 6-2: The relationship between scales of habitat structure and discontinuities in body size distributions. A) Discontinuous hierarchy of scale for structure and resources within a reef ecosystem, from the individual branches of coral colonies to multi-reef scales. B) A discontinuous fish body size distribution. Crosses represent individual species; aggregations (dashed circles) of similarly sized species operate at similar scales, and are separated from neighboring aggregations by discontinuities. Body size correlates with scale of perception, such that larger species operate over larger scales. C) Representative species from each of the 5 aggregations. For example the blue spine unicornfish (indicated by *) is a member of aggregation 4, and perceives and interacts with its habitat at the reef scale. (Multireef image courtesy of James Oliver: <http://www.reefbase.org>; fish vector graphics courtesy of, from right to left, Tracey Saxby, Joanna Woerner, Joanna Woerner, Christine Thurber, and Tracey Saxby: Integration and Application Network, <http://ian.umces.edu/imagelibrary/>).

Holling (1992) found a correlation between breaks in distributions of animal body masses and discontinuities in structures and processes in the boreal forest of Canada. At about the same time, similar hypotheses were presented in palaeontology (Legendre 1986; Trouvillon & Legendre 2009). Aggregations of species (or modes; Table 6-1) along body mass distributions indicate scales at which resources and structure are available to organisms and persist within a given landscape over ecological time scales (Fig. 6-2). In contrast, gaps (discontinuities or troughs) in the distribution reflect the transition to a new set of structuring processes, and therefore few and highly variable resources (Wardwell & Allen 2009). Because animals themselves often strongly modify their environment, such interactions facilitate and reinforce the resources and structure at specific scales (e.g. Bozec *et al.* 2012).

6.3.2 *Modeling and empirical evidence*

Discontinuous and multi-modal body size distributions (Table 6-1) have been observed in numerous ecological systems, including both terrestrial and aquatic ecosystems. Studied taxa include birds (Fischer, Lindenmayer & Montague-Drake 2008; Skillen & Maurer 2008; Thibault *et al.* 2011), reptiles and amphibians (Allen, Forsy & Holling 1999), fish and plankton (Havlicek & Carpenter 2001), and mammals (Lambert 2006; Rodríguez, Olalla-Tárraga & Hawkins 2008; Wardwell *et al.* 2008). Separate work looking at other species and community attributes, such as species' abundances and biomass (Angeler, Drakare & Johnson 2011), richness (Warwick, Dashfield & Somerfield 2006), range size (Restrepo & Arango 2008) and occupancy patterns (Hartley *et al.* 2004) across spatial and temporal scales, show similar discontinuous distributions (Table 6-1).

Similarities in body size distributions among different taxa within a single ecosystem (and that are thus exposed to the same habitat structure), and body size distributions of a single taxa among structurally similar systems, have been presented as evidence of the influence of habitat on body size distributions (Holling 1992; Sendzimir 1998). However, the specific mechanisms driving the link between body size and hierarchical habitat structure need explicit exploration (Robson, Barmuta & Fairweather 2005). Szabó & Mészéna (2006) modelled competitive interactions among species of different sizes and showed that the positive relationship between body size and the scale at which species perceive and use resources (Peters 1983; Laca *et al.* 2010), will produce discontinuous body size distributions where resources are heterogeneously distributed across scales. Empirical studies exploring the link between habitat structure and body size distributions provide further indications of the importance of scaling of the perception of resources with body size. For example, the distributions of food and habitat resources at different spatial and temporal scales have been shown to influence body size distributions in deserts (Borthagaray, Arim & Marquet 2012), forests (Fisher, Anholt & Volpe 2011) and transition zones between rainforest and savannah habitats (Smith *et al.* 1997), while availability of shelter to different sized fish has been linked to body depth distributions in reef ecosystems (Nash *et al.* 2013). Similarly, thinning of tree stands, reducing the fine scale complexity of forest habitats, influences bird body size distributions, resulting in smaller mean body size (De la Montaña, Rey-Benayas & Carrascal 2006). In contrast, research investigating the influence of habitat structure on invertebrate body size distributions has produced mixed results (Gunnarsson 1992). Marine intertidal communities show evidence of distributions driven by sediment structure (Schwinghamer 1981), whereas seasonal and spatial changes in body size distributions are significant in freshwater sediment infaunal communities, suggesting that habitat structure is less important in this context (Stead *et al.* 2005).

The discontinuity hypothesis represents one of a number of proposed drivers of body size distributions (e.g. Brown, Marquet & Taper 1993; Hubbell 2001; Scheffer & van Nes 2006). However, these drivers are, by and large, complementary as they reflect multiple mechanisms operating at distinct scales. Hypotheses such as community interaction, biogeographical, phylogenetic, and the discontinuity hypothesis explain pattern and allometry at distinctly different spatial and temporal scales (reviewed in Allen *et al.* 2006). The phylogenetic hypothesis, for example, is appropriate at continental scales (Cassey & Blackburn 2004), while the discontinuity hypothesis is relevant at regional scales (Allen *et al.* 2006).

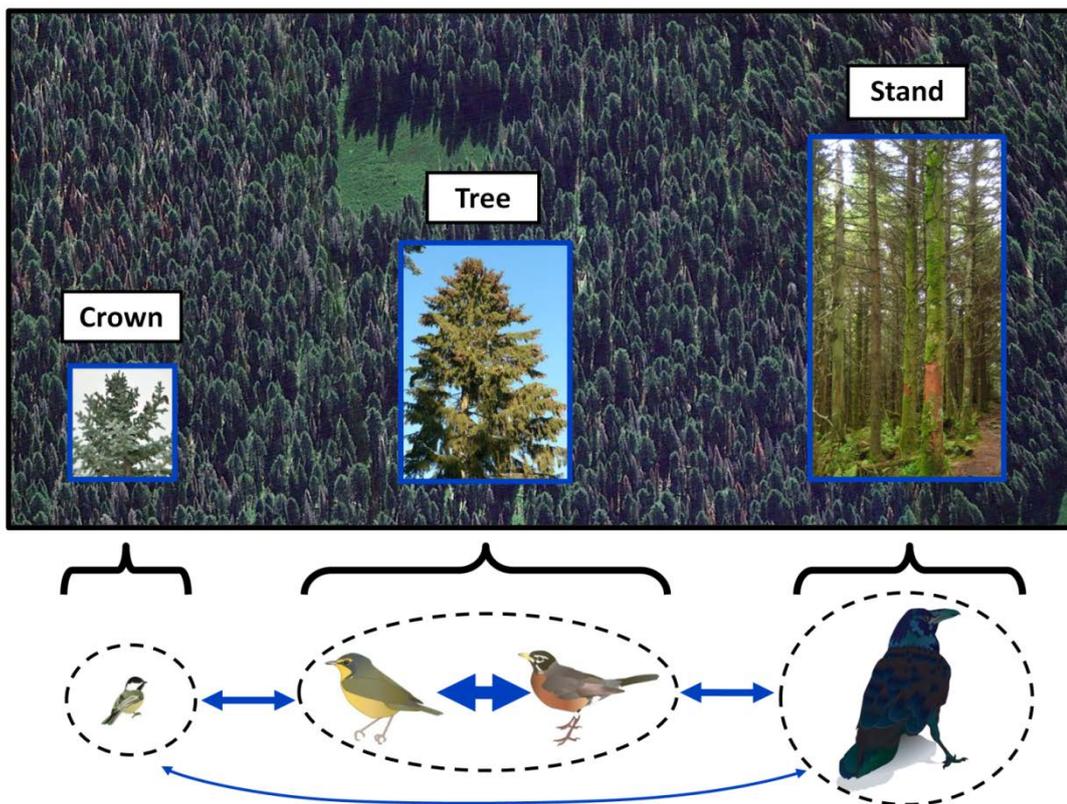


Figure 6-3: The strength of competitive interactions among species using similar resources at different scales. The range of scales at which birds in different body size aggregations perceive and feed on spruce budworm extend from the crown of a fir to a stand of trees, and these sit within larger spatial scales (forest). Blue arrows represent the relative strength of competitive interactions among these species. When species are located within the same body size aggregation (dashed circles) they forage over similar scales and thus experience relatively strong competitive interactions (thick arrow) compared with species in different body size aggregations that are foraging at different scales (thinner arrows). (Tree aerial photo courtesy of Google Earth, spruce tree image courtesy of Rosendahl, <http://www.public-domain-image.com/>; chickadee, warbler and robin graphics courtesy of Tracey Saxby: Integration and Application Network, <http://ian.umces.edu/imagelibrary/>; crow image ©Can Stock Photo Inc. / Birchside).

There has been some debate regarding the relative importance of the discontinuity hypothesis versus emergent neutrality in driving discontinuous distributions at similar scales. The latter hypothesis proposes that competitive interactions alone can generate a discontinuous body mass distribution, although the locations of the modes are the result of stochasticity and so differ from community to community (Scheffer & van Nes 2006). This contrasts to the discontinuity hypothesis, which proposes that the location of modes is driven by biota interacting with habitat structure, and therefore would be similar among sites characterized by the same habitat. Thibault et al. (2011) examined biomass size spectra of breeding and overwintering birds at multiple scales and found strong consistency in the number and location of the modes, suggesting non-stochastic structuring processes at work. In contrast, Vergnon et al. (2012) found evidence supporting emergent neutrality in plankton communities, though their treatment of migrants may not be applicable to terrestrial systems, and their representation of the discontinuity hypothesis should be modified; the discontinuity hypothesis predicts weaker interactions among species operating at different scales compared with those operating at similar scales (Fig. 6-3); this is contrary to the idea of no interaction as suggested by Vergnon et al. (2012). These contrasting results may be a function of the relative complexity of the different ecosystems under study; more work is needed to understand the mechanisms responsible for body size distributions at defined scales and in a wider range of ecosystems, to assess scale and system specific factors that may influence this relationship (Sendzimir *et al.* 2003; Robson, Barmuta & Fairweather 2005; Yvon-Durocher *et al.* 2011).

6.3.3 Extensions to original framework

Coincident with the growing body of evidence for discontinuities in numerous ecological systems, a number of species' attributes have been shown to be associated with discontinuous body mass patterns. These include invasion, extinction, high population variability, migration, and nomadism (Allen, Forsy & Holling 1999; Allen & Holling 2002; Wardwell & Allen 2009). Additionally, the roles species play and the distribution of the functional attributes of these species within and across scales may strengthen the resilience of ecological systems (Peterson, Allen & Holling 1998; Walker, Kinzig & Langridge 1999). Peterson et al. (1998) expanded upon Holling's (1992) discontinuity hypothesis by proposing that functional diversity within body mass aggregations and redundancy of functional groups across body mass aggregations (i.e., scales) supports system resilience (see 'Applications' section below). Despite these advances, much of the potential of evaluating discontinuities and their implications for addressing a broad range of ecological questions remains unexplored.

Table 6-2: Practical tools for detecting discontinuities. Several methods have been described for identifying discontinuities and multi-modality within the distributions of variables such as body size or biomass. The suitability of these methods varies with respect to the type of data available and the research question. All techniques have their biases (reviewed in Stow, Allen & Garmestani 2007), therefore a combination of methods, followed by triangulation of their respective results, has been identified as the most robust approach. To date mean body mass has been primarily used as a measure of body size, though for species with indeterminate growth other metrics may be more appropriate. The list of platforms specified is not exhaustive.

Method	Discontinuities or modality	Data	Platform	Description	Example References
Bayesian Classification and Regression Trees (BCART)	Discontinuities	Mean values*	Executable file: www.rob-mcculloch.org/code/CART/index.html	Identifies groups using successive partitions of the data	(Chipman, George & McCulloch 1998; Stow, Allen & Garmestani 2007)
Gap Rarity Index (GRI)	Discontinuities	Mean values*	BASIC; R code is currently under development.	Observed distributions are compared with continuous null distribution and significant gaps identified	(Restrepo, Renjifo & Marples 1997; Allen & Saunders 2006)
Hierarchical Cluster Analysis	Discontinuities	Mean values*	R: hclust in the stats library	Identifies groups using successive partitions of the data	(Fischer <i>et al.</i> 2007)
Multi-variate time-series modeling	Discontinuities	Species abundance	R: quickPCNM in the PCNM library	Identifies groups of species exhibiting different temporal trends	(Angeler, Viedma & Moreno 2009; Angeler, Allen & Johnson 2012)
Fractal analysis	Discontinuities	Various	Various	Identifies groups based on changes in fractal dimension across scales	(Krummel <i>et al.</i> 1987)
Kernel-density estimation	Modality	Mean values ^{*^}	R: density within the stats library	Estimates probability density function of a variable	(Havlicek and Carpenter 2001)
Mixture models	Modality	Mean values ^{*+}	R: OpenBUGS	Uses MCMC estimation to model modality	(Xu <i>et al.</i> 2010)

Notes: * Other descriptive statistics, such as mode, median or maximum value may be used, depending on the research question and data. ^ May incorporate a measure of dispersion. + May be modified to incorporate abundance.

6.4 APPLICATIONS OF DISCONTINUITY ANALYSIS

Evaluating and analysing data for discontinuous patterns (Table 6-2) has two primary uses. First, it is an independent method for identifying ‘intrinsic’ scales (Table 6-1; Fig. 6-1) of pattern and process in ecosystems. Second, it provides a platform from which to assess the distribution of key traits or processes within and across the scales of any given system. As a result, it may be used to explain cross-scale patterns such as abundance, functionality, diversity and organismal traits as they relate to that pattern, as well as emergent phenomena such as resilience.

6.4.1 Identification of scales

Incorporating a multi-scaled perspective into empirical research remains a key issue, with choice of discrete scales often being arbitrary (Levin 1992; Wheatley & Johnson 2009). Such subjectivity introduces two problems. First, the scales chosen may be relevant for a subset of focal species or ecological processes, but may not be suitable for all species or processes of interest (Davidson *et al.* 2012). Second, the relevance of theoretical models to empirical results may be masked due to a scale mismatch (Addicott *et al.* 1987; Roubicek *et al.* 2010), with the inherent danger that findings are an artefact of ad hoc scale choices and effects (Wiens 1989; McGeoch & Gaston 2002; Halley *et al.* 2004; Lechner *et al.* 2012).

Selecting scales for investigation and analysis that are relevant to the particular individual, population or community is, therefore, a goal of effective ecological research. This has resulted in the development of a range of multi-scale methods for identifying ‘intrinsic’ scales in ecosystems, largely arising out of work on hierarchy theory in landscape ecology (Wu & Li 2006). However, the information needed to make such informed decisions is often considerable (Addicott *et al.* 1987). Discontinuity analysis provides a method for detecting underlying scales of process and structure in a system, which is not dependent on arbitrary methodological choices and is relatively data inexpensive, using simple proxies such as animal body size (Appendix D Table S2; Holling 1992; Wardwell & Allen 2009) or how patterns change across scales (Bradbury, Reichelt & Green 1984; Hartley *et al.* 2004).

Such analyses present a number of important opportunities, including the ability to: i) differentiate between systems exhibiting scale invariance of variables and processes (i.e. consistent patterns across scales) versus those with discrete, ‘intrinsic’ scales (see ‘power laws’ and ‘scale domains’ in Appendix 2; Wiens 1989; Kerkhoff & Enquist 2007); ii) reduce the arbitrariness of scale selection and increase the likelihood of designing effective multi-scale studies (Wheatley & Johnson 2009); iii) delimit the appropriate scales for ecological surrogates

(Hartley *et al.* 2004; Januchowski-Hartley *et al.* 2011b); iv) predict congruence in the response of species to disturbance or environmental drivers (Peterson, Allen & Holling 1998; Chen *et al.* 2011); and v) partition out variance associated with scale effects prior to running other analyses. An example of such an analytical integration is seen in tests for priority effects in Hawaiian avifauna (Allen & Moulton, unpublished data). Inhibitory priority effects describe the negative influence of species already present at a site, on the colonizing ability of new species (Belyea & Lancaster 1999). The strength of the negative relationship between the number of species present in the Hawaiian bird community and the success of introduced species was strengthened when body size was accounted for, i.e. membership within a specific body size aggregation was used as a blocking factor in the analysis of variance. This outcome is linked to scale-specific competitive interactions; species within the same aggregation are predicted to experience greater inter-specific competition than with species in other aggregations (Fig. 6-3; Peterson, Allen & Holling 1998). As a result, priority effects are stronger in aggregations containing greater numbers of species (Allen & Moulton, unpublished data).

Evaluations of discontinuities in body size distributions are based on links between body size and patterns of habitat structure, driven by the scale at which species interact with their environment (Szabó & Meszéna 2006; Fisher, Anholt & Volpe 2011; Nash *et al.* 2013). The drivers of discontinuities in other traits or community characteristics, such as biomass, are less clear and need further exploration. Nevertheless, such investigations present the opportunity to identify 'the 'intrinsic' scales within a system, and develop clear testable hypotheses regarding mechanisms driving these hierarchies.

6.4.2 Identification of nonlinearities and regime shifts

Interactions among processes operating at different temporal and spatial scales can generate nonlinear behaviour (Burkett *et al.* 2005; Peters, Bestelmeyer & Turner 2007). To model these dynamics and minimize 'ecological surprises' at local and system-wide scales, development of robust methods for detecting and evaluating nonlinearities is essential (Peters *et al.* 2004). Discontinuity analysis may be used to explicitly identify non-linear patterns within social and ecological systems. For example, these methods have highlighted non-linearities in both city size and plankton biomass distributions (Garmestani *et al.* 2007; Angeler, Allen & Johnson 2012). This approach can be extended to characterize non-linear temporal behaviour at the system-level, to detect impending regime shifts (Allen *et al.* 2014).

The capacity for leading indicators, such as recovery rate, rising variance, skewness or 'flickering', to reveal approaching regime shifts has generated considerable interest (e.g. Scheffer *et al.* 2009; Wang *et al.* 2013). Nonetheless, there is concern that proposed metrics

may provide an inadequate warning period to allow policy changes in time to address and counteract forecasted shifts (Biggs, Carpenter & Brock 2009). Discontinuity analysis may contribute to regime shift detection using existing indicators, by highlighting more sensitive variables that will provide earlier warning signals. For example, rising variance has been presented as a prospective leading indicator (Carpenter & Brock 2006). However, some populations, communities and abiotic variables are likely to show greater variability than others, thus a method of selecting appropriate variables is needed to inform the design of monitoring programs developed to highlight ecosystem changes (Carpenter & Brock 2006; Wardwell & Allen 2009). Wardwell & Allen (2009) found rising variance in bird population abundance close to discontinuities in body mass distributions (Fig. 6-4), and proposed that this type of analysis could be used to highlight which variables are likely to show increased variance prior to a regime shift (Wardwell & Allen 2009).

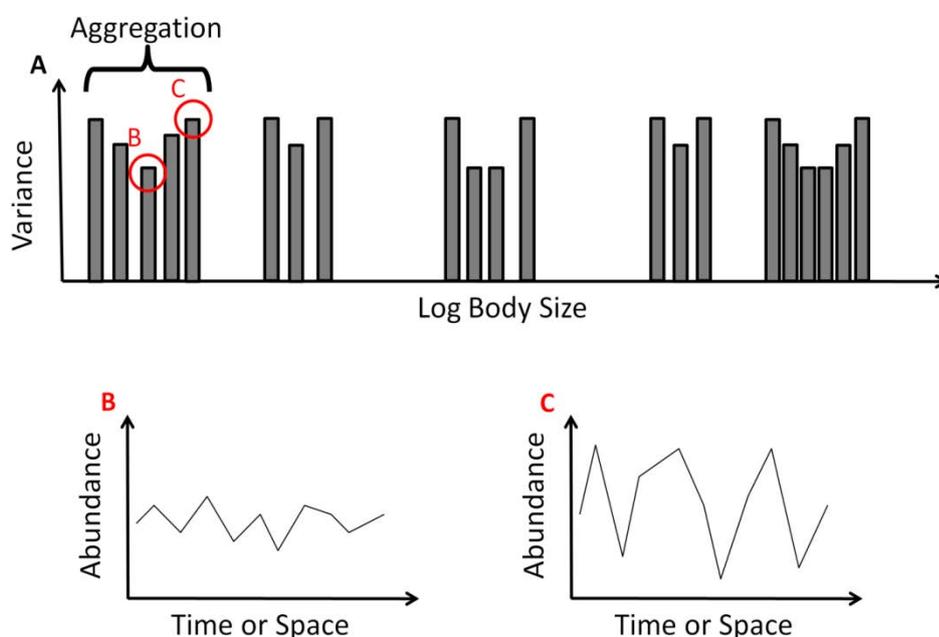


Figure 6-4: A) Patterns of variance in abundance of species located in body mass aggregations. Those species at the centre of aggregations exhibit lower variance in abundance (B), than those at the edges of aggregations (C). N.B. Body size and abundance are used as an example. Other variables may show similar patterns of aggregation and variability.

Spanbauer et al. (in press) present a novel regime shift indicator based on analysis of discontinuities in species abundances over time. Multivariate time series analysis (Angeler, Drakare & Johnson 2011) was used to successfully delimit regime shifts in lakes using paleo-diatom data. Where large spatial and temporal datasets are not available (Biggs, Carpenter & Brock 2009), other indicators based on discontinuity analysis that require comparatively little

data are proposed. The cross-scale pattern of habitat structure and body size distributions is driven by dominant processes and drivers operating over specific spatial and temporal scales (Holling 1992). Therefore, changes in the number or location of discontinuities within habitat or body size distributions over time, would indicate changes in the dominant processes driving these discontinuous patterns, i.e. provide evidence of a regime shift (Holling 2001). Such changes have been observed spatially in bird communities, among sites experiencing differing levels of landscape modification (Fischer *et al.* 2007). Temporal changes in the structure of body size distributions could be used to forewarn of reorganization within a system leading to a new regime. In light of research highlighting the need for robust multi-metric early warning frameworks (Lindgren *et al.* 2012), discontinuities present an innovative method with which existing metrics can be compared and combined.

6.4.3 Functional distributions, macroecology and resilience

Species may be grouped according to the functional role they play in the environment. Functions performed by vertebrate and invertebrate species include pollination, grazing, nitrogen fixation, seed dispersal, decomposition, soil nutrient generation, modification of water flows, opening up patches and modifying environmental gradients within the landscape (Folke *et al.* 2004). Body size is a proxy for the scale at which species operate (Peters 1983), therefore body size distributions can be combined with functional classifications to describe and enumerate the distribution of members of functional groups within and across scales, i.e. the range of scales over which each group delivers its functional role. This information is of direct interest to two fields of ecology: macroecology and resilience (Kerkhoff & Enquist 2007).

There has been an increasing recognition that competitive and other forms of intra- and inter-specific interactions need to be incorporated into macroecological studies (Araújo & Luoto 2007), but to date there has been a lack of clarity regarding the influence of competition on local assembly (Gotelli, Graves & Rahbek 2010). Where studies have incorporated competition, the strength of interactions has been inferred from membership within species or functional groups (e.g. Gotelli, Graves & Rahbek 2010). Peterson *et al.* (1998) predict that species using similar resources could minimize competitive interactions via differentiation of the scales at which they operate (Fig. 6-3). Therefore, members of a functional group are more likely to be distributed across scales (and thus body size aggregations) than expected by chance. This non-random pattern has been demonstrated in bird and mammal populations (Wardwell *et al.* 2008), suggesting that functionally similar species within the same body size aggregation are subject to stronger interactions than those operating at different scales (Peterson, Allen & Holling 1998). As a result macroecological studies that group species according to body size aggregation would

provide a clearer picture of the likely strength of competitive interactions among species using similar resources, and may help resolve some of the current uncertainties. The effectiveness of this approach is illustrated in the discussion on Hawaiian avifauna priority effects, above.

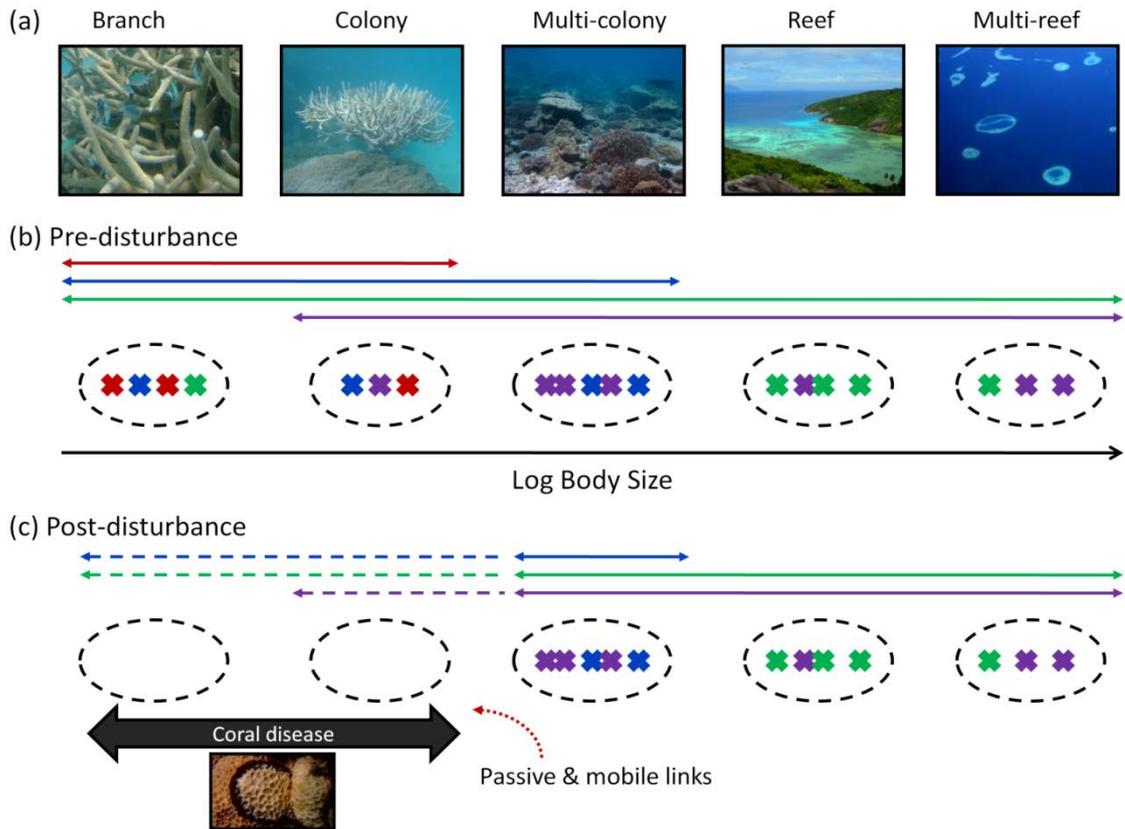


Figure 6-5: Influence of disturbance on the distribution of functional groups across scales. A) The range of scales at which fish perceive, interact with and use resources on the reef, from the individual branches of coral colonies to multi-reef scales. B) Pre-disturbance: discontinuous fish body size distribution, where crosses represent individual species and colors indicate functional group membership. Colored arrows indicate the range of scales over which each group operates and therefore provides its function: the green functional group operates over a wide range of scales, whereas the red functional group only operates over small scales. C) Post-disturbance: coral disease provides a small scale disturbance that affects fish species operating at the branch and colony scales (empty aggregations). Those functional groups with redundancy across spatial scales (blue, green and purple groups) may compensate for loss of species at these small scales (dashed arrows), whereas those functional groups with low cross-scale redundancy (red group) are reliant on passive links (recruitment) or mobile links (adult fish) recolonizing from neighbouring regions (red dotted arrow) for maintenance of function. (Multireef image courtesy of James Oliver: <http://www.reefbase.org>).

Redundancy of species within functional groups is thought to underpin ecological resilience, as it reflects the potential for each group to compensate for the loss of one or multiple species in the face of disturbance, and thus continue to drive ecological processes. But the

value of this redundancy is misleading if each species responds to a disturbance in a similar manner. Species interacting with their environment at different scales are likely to respond to disturbances differently (Fig. 6-5 b-c; Elmqvist *et al.* 2003), therefore the scale-specific distribution of functions may be used to quantify the degree of cross- and within-scale redundancy of an assemblage (Allen, Gunderson & Johnson 2005). This approach, known as the cross-scale resilience model, has been tested on bird community data from south-eastern Australia, providing promising results that indicate reduced resilience of modified landscapes (Fischer *et al.* 2007). However there is a need to evaluate these metrics in a wider range of ecosystems and taxa. Furthermore, opportunities remain to examine the effects of abundance on functional redundancy (Walker, Kinzig & Langridge 1999), and to incorporate trait-based functional categorization that transcend the relatively coarse nature of some functional classifications (Fischer *et al.* 2007).

The distribution of functional groups in time and space may indicate the scales at which species are fulfilling their role, however the relative impact of organisms of different body sizes is inextricably linked to individual abundance (White *et al.* 2007). Therefore decline in the abundance of common species, which may form habitat structure within an ecosystem and/or drive key processes (Gaston & Fuller 2008), has significant implications for functional impact at different spatial and temporal scales, which is not quantified by functional distributions alone. The role of species abundance in resilience is largely unexplored, except in the general sense that minor species can sometimes be functional substitutes for more dominant species whose populations are depressed after a disturbance (Walker, Kinzig & Langridge 1999). To date, the cross-scale resilience model and empirical evaluations of this model have not incorporated abundance and its influence on the functions species perform (Peterson, Allen & Holling 1998; Fischer *et al.* 2007). There is a clear need to address this gap through the addition of abundance into current models relating biological diversity to resilience.

A more detailed characterization of species roles, other than simple functional groups, is possible through the use of multi-dimensional functional space indices. This approach has been used to examine drivers of community assembly (Ackerly & Cornwell 2007), the delivery of ecosystem processes (Pakeman 2011), and has been proposed as a way of predicting the response of communities to specific disturbances (Mouillot *et al.* 2012). Mouillot *et al.* (2012) discuss body size as one of a number of possible traits that may vary in response to disturbance. Therefore, classifying species according to body mass aggregation in a functional trait-based analysis would explicitly group species operating at similar scales and thus incorporate scale-specific response to disturbance, increasing the sensitivity of such analyses.

The resilience of an ecosystem to specific disturbances may relate to connectivity among habitat patches. This connectivity may be passive (e.g. propagules) or due to mobile links, i.e. individuals moving between areas (Nystrom & Folke 2001). Characterizing distributions of function across scales will highlight the likely spatial extent of mobile links, and identify vulnerabilities due to a narrowing of the range of scales over which an assemblage is functionally effective (Nyström 2006). For example, large reef fish are subject to extreme fishing pressure in certain areas, resulting in the removal of those species that operate over large scales and thus provide critical linkages among locations across the broader seascape (Jackson *et al.* 2001; McCauley *et al.* 2012). This loss has significant implications for the connectivity and spatial resilience of coral reefs, and limits the likelihood of mobile links connecting undamaged reefs with those impacted by disturbance (Fig. 6-5).

6.4.4 Extinctions and invasions

The rising number of invasions by non-indigenous species and extinctions in terrestrial and aquatic environments are of serious concern (Pimentel, Zuniga & Morrison 2005; Vié, Hilton-Taylor & Stuart 2009). These changes are often associated with significant modifications to habitats and food webs, with important ramifications for the delivery of ecosystem services and the maintenance of key ecosystem processes (Simberloff *et al.* 2013). For example, in New Zealand, functional extinction of some bird species has significantly reduced pollination of endemic plant species, leading to reduced plant density (Anderson *et al.* 2011). The cost associated with the impact of invasive species in the United States alone, is estimated to exceed \$100 billion per annum (Pimentel, Zuniga & Morrison 2005).

Predicting the likelihood of a species either becoming extinct, or being introduced and then successfully establishing a breeding population, is critical for management and for mitigation efforts. However, such prediction is extremely difficult due to the range of species, community and habitat level factors influencing the decline of species and the success of invasions (Brook, Sodhi & Bradshaw 2008; Hayes & Barry 2008; Harnik *et al.* 2012). Nonetheless, proximity to the edge of body mass aggregations has been found to be a significant predictor of invasion success for both bird and mammal species, and of extinction risk among mammals (Allen, Forsys & Holling 1999; Allen *et al.* 2006). Edges of body mass aggregations are associated with increased variability in abundance (Wardwell & Allen 2009), and are linked to less predictable resource availability (Fig. 6-4; Wiens 1989). Consequently, these edges represent locations where species may be more susceptible to extinction or more able to exploit opportunities (Allen, Forsys & Holling 1999; Allen *et al.* 2006). The strength of using proximity to a discontinuity in the body mass distribution as a predictor is that it incorporates both

community and habitat level factors. Specifically it indicates the likely level of competition experienced by an invading species (Fig. 6-3) and the scales at which resources are available to species, because body mass distributions are thought to reflect underlying habitat structure. In ecosystems where body size aggregations are demonstrated to reflect the underlying scales of pattern-process relationships (Borthagaray, Arim & Marquet 2012), the distribution of extinctions and invasions across body mass distributions can also be used to identify scales particularly vulnerable to change and impact (Cardillo & Bromham 2001; Petchey & Gaston 2002; Woodward *et al.* 2005). In addition, proximity to discontinuities can be used to predict extinctions or the likely success of invasions of introduced species, prior to their occurrence or establishment, respectively. Considering the global threats of extinction and invasion, for example 56 species of amphibians and reptiles have successfully invaded and established breeding populations in Florida alone (Krysko *et al.* 2011), such a predictive ability is of considerable importance. There is however, a clear need to assess the relationship between discontinuities and invasions or extinctions among taxa other than birds and mammals.

6.5 FUTURE DIRECTIONS

The discontinuity hypothesis provides a conceptual framework, arising from hierarchy theory, within which to examine the organization of ecosystems. However, much of the potential of this framework is unexploited and presents a fertile arena for original research in a wide range of ecological fields. To date, discontinuity research has primarily focused on adult body size as the variable of interest. Performing such studies on plants and modular organisms with no discrete body size, or in species that experience significant ontogenetic changes and indeterminate growth such as fish, remains a challenge that invites innovative approaches. For example, work by Angeler *et al.* (2013) used multivariate time series modelling of invertebrate species abundance in subarctic lakes as a novel way to examine patterns of function and resilience multiple scales, which did not rely on body size metrics. To broaden the utility of discontinuity analysis, similar efforts are needed to address this challenge across the range of potential applications. Furthermore, although there is an emerging literature on the mechanistic links between habitat and body size distributions, additional studies are needed to understand the mechanisms driving discontinuities in variables such as species biomass (Angeler, Drakare & Johnson 2011), richness (Warwick, Dashfield & Somerfield 2006) and occupancy (Hartley *et al.* 2004).

My discussion of modelling and empirical evidence illustrates the range of studies providing support for the discontinuity hypothesis. However, to date there has been little exploration of those systems where discontinuities are less likely to be found. The discontinuity

hypothesis links cross-scale habitat structure to community attributes, such as body size, over ecological time scales. In ecosystems where such structure is less consistent over time, e.g. pelagic systems with dynamic oceanographic conditions and boundaries, discontinuous signals may not be evident. Some work has looked at discontinuities in the body mass (Havlicek & Carpenter 2001), biomass (Angeler, Allen & Johnson 2012) and abundance (Angeler, Drakare & Johnson 2011) distributions of lake system communities, however, little work has investigated discontinuities in marine pelagic systems (but see Vergnon, Dulvy & Freckleton 2009). It therefore remains to be seen whether, in comparatively dynamic pelagic environments; discontinuities consistently arise and may be detected.

Discontinuity analysis offers a powerful tool for investigating cross-scale interactions, as it identifies scale-specific relationships between ecosystem drivers and processes, habitat structure, resource availability, and organisms. As a consequence, it provides a platform from which to assess the distribution of key traits or processes within and across the scales of any given ecosystem, e.g., the distribution of ecological function or invasive species. There is considerable scope to broaden the application of discontinuity analysis across ecosystems and taxa, and beyond its current focus on body size applications.

Chapter 7: Habitat structure and body size distributions: cross-ecosystem comparison for taxa with determinate and indeterminate growth⁶

7.1 ABSTRACT

Habitat structure across multiple spatial and temporal scales has been proposed as a key driver of body size distributions for associated communities. Thus, understanding the relationship between habitat and body size is fundamental to developing predictions regarding the influence of habitat change on animal communities. Much of the work assessing the relationship between habitat structure and body size distributions has focused on terrestrial taxa with determinate growth, and has primarily analysed discontinuities (gaps) in the distribution of species mean sizes (species size relationships or SSRs). The suitability of this approach for taxa with indeterminate growth has yet to be determined. I provide a cross-ecosystem comparison of bird (determinate growth) and fish (indeterminate growth) body mass distributions using 4 independent data sets. I evaluate three size distribution indices: SSRs, species size-density relationships (SSDRs) and individual size-density relationships (ISDRs), and two types of analysis: looking for either discontinuities or abundance patterns and multi-modality in the distributions. To assess the respective suitability of these three indices and two analytical approaches for understanding habitat-size relationships in different ecosystems, I compare their ability to differentiate bird or fish communities found within contrasting habitat conditions. All three indices of body size distribution are useful for examining the relationship between cross-scale patterns of habitat structure and size for species with determinate growth, such as birds. In contrast, for species with indeterminate growth such as fish, the relationship between habitat structure and body size may be masked when using mean summary metrics, and thus individual-level data (ISDRs) are more useful. Furthermore, ISDRs, which have traditionally been used to study aquatic systems, present a potentially useful common currency for comparing body size distributions across terrestrial and aquatic ecosystems.

⁶ Nash KL, Allen CR, Barichiev C, Nystrom M, Sundstrom SM, Graham NAJ. 2014 Habitat structure and body size distributions: cross-ecosystem comparison for taxa with determinate and indeterminate growth. *Oikos* 123: 971-983.

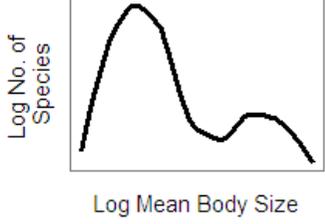
7.2 INTRODUCTION

The complexity of community dynamics has driven the search for simple proxies of key life history and ecological traits, measurable across multiple taxa (e.g. White *et al.* 2007). This has led to considerable interest in body size, which correlates with a broad range of species' traits such as home range, dispersal, trophic level, metabolism and extinction risk (Blackburn & Gaston 1994; Woodward *et al.* 2005). Body size distributions have been used to quantify energy transfer and biogeochemical cycling in ecosystems (Yvon-Durocher & Allen 2012), to examine the division of resources within a community (White *et al.* 2007), and to quantify the relative resilience of different communities (Peterson, Allen & Holling 1998).

Habitat and resource availability are thought to be fundamental drivers of body size distributions over ecological timescales (Holling 1992). Consequently, habitat degradation and land use modification will have implications for body size distributions, with knock-on effects for community interactions, ecosystem processes and resilience (Peterson, Allen & Holling 1998). The discontinuity hypothesis proposes that the interaction between patterns of habitat structure and resources at different scales, and the scale at which species interact with their environment, influences body size distributions within a community (Holling 1992). Such an interaction occurs because resources are patchily distributed so their availability varies among spatial and temporal scales (Wiens 1989), and the scale or spatio-temporal resolution at which an organism perceives its environment and procures resources is a function of its size (Peters 1983). Species are expected to be clustered in aggregations (or modes) along a body size axis corresponding to scales where resources are available, and separated from neighbouring body size aggregations by discontinuities (gaps or troughs), corresponding to scales where resources are limited (Holling 1992).

To date, the discontinuity hypothesis has primarily been tested in terrestrial ecosystems on mammal and avian fauna (e.g. Fischer, Lindenmayer & Montague-Drake 2008). These studies have predominantly analysed patterns in the distribution of species' mean body masses (hereafter species size relationships (SSRs); Table 7-1A), and have provided evidence to support the discontinuity hypothesis (reviewed in Nash *et al.* 2014a). Evaluating SSRs demonstrates how patterns of habitat structure influence associated communities via the availability of niches for different sized species (Robson, Barmuta & Fairweather 2005). However, species size relationships do not account for species' abundances. Distributions quantifying the abundance of different sized species provide an alternative index (hereafter termed species size-density relationships (SSDRs; Table 7-1B; White *et al.* 2007). This approach allows examination of how resources are distributed among species, or which size

Table 7-1: Different indices of body size distribution considered in this study. Key features and their value in examining the distribution of resources within communities are presented.

Body Mass Distribution Indices	Description	Distribution of resources
<p>1. Species size relationship (SSR)</p> 	<ul style="list-style-type: none"> • Size is aggregated at the species-level • Species-level presence-absence data • Greater relative weight given to species identity versus individual size 	<p>Examines how resources are distributed across size classes, providing niches and driving the number of species within different size classes.</p>
<p>2. Species size-density relationship (SSDR)</p> 	<ul style="list-style-type: none"> • Size is aggregated at the species-level • Species-level abundance data • Greater relative weight given to species identity versus individual size 	<p>Examines how resources are distributed across size classes, driving abundance of species within different size classes.</p>
<p>3. Individual size-density relationship (ISDR)</p> 	<ul style="list-style-type: none"> • Size is presented at the individual-level • Individual-level abundance data • Greater relative weight given to individual size versus species identity. 	<p>Examines how resources are distributed across size classes, driving abundance of individuals within each size class.</p>

classes predominantly drive energy flow within a system (Ernest 2013). This is important as incorporating abundance and examining how resources are apportioned among size classes may provide a more appropriate test of the discontinuity hypothesis (Thibault *et al.* 2011).

There are two key assumptions to using both SSRs and SSDRs: 1) summarising size information at the species-level is more informative than using individual-level size data for understanding community structure (Doledec & Statzner 1994), and 2) mean body mass is an appropriate metric to represent the size of a species. The first assumption has underpinned much of the terrestrial body size literature, and is appropriate where there are close ties between species identity, and key life history and ecological traits such as size and mobility, meaning that species-level data is representative of individuals within a population (Doledec & Statzner 1994). The second assumption should hold for taxa with determinate growth and where parental care means that predominantly adults are interacting directly with resources available in their environment, giving a narrow range of body sizes from which to calculate the summary metric. Importantly, variation in the mean body masses among species must exceed size variability within species (Robson, Barmuta & Fairweather 2005).

Little research regarding the discontinuity hypothesis has been carried out in aquatic systems or for taxa exhibiting indeterminate growth such as fish (but see Havlicek & Carpenter 2001; Nash *et al.* 2013), despite considerable evidence that habitat is important in structuring fish communities (e.g. Graham & Nash 2013). It is unlikely that the assumptions underlying SSRs and SSDRs will hold for fish: there has been considerable research suggesting that aquatic communities are strongly size structured, and that individual size may be more informative than species-level data in understanding the functioning of aquatic ecosystems (e.g. Shurin, Gruner & Hillebrand 2006). Unlike many terrestrial vertebrates, individual fish may vary over orders of magnitude in length during the course of their life, although how dispersed this growth is across age classes is taxa dependent (Choat & Robertson 2002; Webb *et al.* 2011). Furthermore, fishes undergo significant ontogenetic changes in habitat and resource requirements (Green & Bellwood 2009), and fish often do not exhibit any form of parental care (Smith & Wootton 1995). Thus, size variability within species may exceed variation among species (see Choat & Robertson 2002; Webb *et al.* 2011 for examples) such that species' mean body size may not be an appropriate metric to represent the size of individuals within a population. As a result, there is a need to investigate appropriate indices for use when examining the relationship between habitat and the shape of fish size distributions.

In studies of fish where species identity is of interest, maximum and asymptotic species' body sizes have been suggested as appropriate alternatives to mean size (Jennings *et al.* 2001). These metrics may be particularly useful in the context of evaluating habitat-body size relationships, as maximum size is likely to be directly influenced by habitat structure in taxa

with indeterminate growth (Cumming & Havlicek 2002). However, two issues arise from using maximum length, 1) fish exhibit growth patterns driven by location, latitude and exposure to fishing pressure (Choat & Robertson 2002; DeMartini *et al.* 2008), so obtaining maximum size data from published sources may introduce bias, and 2) species' maximum size is a summary metric and may not represent intra-specific size variability any better than species' mean size.

For communities where greater relative weight is given to individual body size rather than species-specific traits, a distribution quantifying the abundance of different sized individuals may be a more appropriate body size index (hereafter termed individual size-density relationships (ISDRs; Table 7-1C; White *et al.* 2007). This approach examines how resources are divided among individuals within different size classes regardless of an individual's taxonomic affinity. Individual- versus species-level indices have often been applied to different sides of a marine-terrestrial disciplinary divide (size versus species, respectively), and are not generally compared within studies (but see Reuman *et al.* 2008). As a result, there has been a lack of clarity regarding the shape of body size distributions and reinforcement of the perspective that marine and terrestrial systems are fundamentally different (White *et al.* 2007; Webb *et al.* 2011). This problem has been compounded by a dearth of comparative studies examining body size patterns across multiple ecosystems (but see Petchey & Belgrano 2010; Webb *et al.* 2011), or among taxa with determinate versus indeterminate growth patterns (but see Forsy & Allen 2002).

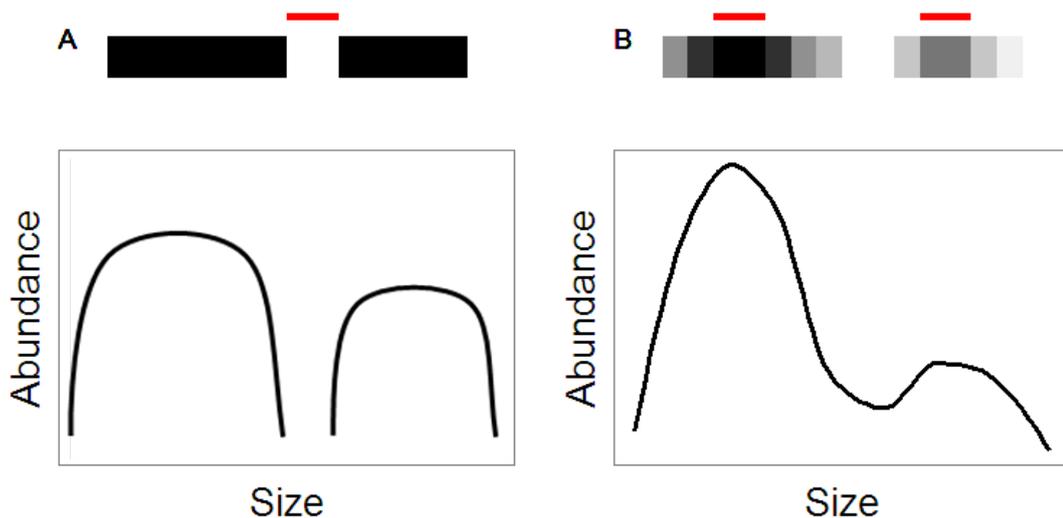


Figure 7-1: Different analytical approaches for evaluating patterns in body size distributions. A) Analysis looks for the presence of discontinuities or gaps (red bar) in size distributions. This approach may be used for either distributions that incorporate abundance information (e.g. ISDRs) or those that do not (SSRs) because abundance information is ignored; the analysis solely searches for gaps in the distribution. B) Analysis evaluates abundance patterns, looking for modes (red bar) and the distribution of abundances across size classes. This approach may only be used for distributions that incorporate abundance information (SSDRs and ISDRs).

After selecting the appropriate size distribution index (Table 7-1), patterns in the size distributions may be analysed in a number of ways (Nash *et al.* 2014a). In the context of the discontinuity hypothesis, studies have primarily looked for discontinuities within size distributions (Fig. 7-1A; e.g. Holling 1992). This approach may be used on either species- or individual-level data, and any abundance information (if present) is ignored; the analysis purely searches for gaps in the distribution. However, an alternative approach is to assess modality patterns in size distributions that incorporate abundance information (Fig. 7-1B; e.g. Xu *et al.* 2010). These two analytical approaches represent contrasting ways of evaluating body size distributions because they focus on different hypotheses regarding the mechanisms driving the patterns. Multi-modality suggests a concentration of available resources within each mode providing an attractor allowing greater abundances within size classes that utilise resources at coincident scales (Xu *et al.* 2010). In contrast, discontinuities suggest scales where resources are absent and thus body size classes that utilize resources at those scales are empty (Holling 1992). The relevance of the two approaches (Fig. 7-1) in the context of the three size distribution indices (Table 7-1) has significant implications for understanding what drives community body size distributions, and has not been adequately assessed to date.

The aim of my cross-ecosystem study is to assess if determinate versus indeterminate growth patterns influence the appropriateness of the three different size distribution indices and two distinct analysis methods for detecting habitat effects on body size distributions. Specifically, I examine whether bird or fish communities in habitats of contrasting condition are better differentiated by species-level size data analysed for discontinuities, species-level size and abundance data analysed for abundance and modality patterns, individual-level size and abundance data analysed for discontinuities, or individual-level size and abundance data analysed for abundance and modality patterns (Table 7-2). My results may be used to develop predictions regarding community, species and individual responses to future environmental change such as habitat degradation and land use modification; specifically the vulnerability of particular size classes and species. Although I focus on habitat as a driver of body size distributions, the approaches may be applicable to research looking at a range of contrasting and complementary drivers such as competitive interactions and biogeography (Allen *et al.* 2006).

7.3 MATERIALS AND METHODS

Two woodland bird (Mount Lofty Ranges and Borneo Upland Forest) and two coral reef fish (Seychelles and the Great Barrier Reef, GBR) datasets were used in the study. Each dataset detailed the bird or fish communities found within multiple habitat types of a particular

Table 7-2: Combinations of the three size distribution indices and two analytical approaches used in the four analyses comparing body size distributions among different habitat types.

		Analytical approach	
		Discontinuity patterns	Abundance patterns
Distribution Index	Species size relationship (SSR) ^a	Analysis 1	^b
	Species size-density relationship (SSDR) ^a	^c	Analysis 2
	Individuals size-density relationship (ISDR)	Analysis 3	Analysis 4

^a Distributions were based on either mean mass, maximum mass recorded in the literature, or maximum observed mass.

^b Abundance data is not present in species size relationships and thus abundance patterns could not be evaluated.

^c Analysing discontinuity patterns in species size-density relationships is equivalent to analysing discontinuity patterns in species size relationships (Analysis 1), therefore this combination of approaches was redundant.

ecosystem. The Mount Lofty Ranges bird data encompassed two habitat types (stringybark and gum; Possingham, Field & Possingham 2004). The Borneo Upland Forest bird data covered three habitat types (unlogged, logged in 1993, and logged in 1989; Cleary *et al.* 2007). The Seychelles coral reef fish data incorporated three habitat types (coral dominated, algal dominated, granitic reefs; Nash *et al.* 2013), whereas the GBR coral reef fish data encompassed three habitat types (undisturbed, disturbed, recovering; Graham *et al.* 2014). Full details of the datasets, the habitats, and the methods used to collect them are provided in the Supplementary Material (Appendix E Text S1). The various habitat types possessed distinct patterns of cross-scale habitat structure. The body mass distributions of communities from sites within the same habitat type, and thus with similar cross-scale patterns of structure, were expected to be more similar than those from habitats with different structural patterns.

Bird and fish communities were chosen because: 1) they are dominant, species-rich vertebrate groups in their respective ecosystems; 2) they have been the focus of complimentary studies on body mass distributions examining occupancy and abundance patterns (Webb *et al.* 2011); and 3) my aim was to determine the appropriateness of different approaches for detecting habitat effects on body size distributions rather than to test the discontinuity hypothesis *per se*, thus it was important to choose taxa and systems where habitat is known to have a strong influence on body size, and thus the signature of habitat effects should be evident within the size distributions. Most research on the discontinuity hypothesis has been performed on birds, so their relationship to habitat and patterns of discontinuities are well studied. Furthermore, examples from the wider literature have shown that woodland birds are influenced by physical habitat structure (e.g. De la Montaña, Rey-Benayas & Carrascal 2006). Similarly, the influence of habitat structure on coral reef fish communities has been particularly well documented (e.g. Graham & Nash 2013), and the availability of habitat correlates with fish size (Nash *et al.* 2013).

7.3.1 Data analysis

Body mass was used for all size measurements in the analyses. Individual body sizes were not recorded in the bird surveys, and indeed are rarely assessed in bird studies (Ernest 2013) due to the difficulty of estimating the sizes of cryptic species. Therefore, mean body mass data for each bird species were sourced from the Handbook of Avian Body Masses, averaging across estimates where separate male and female records were presented (Dunning Jr. 2008). In addition, maximum recorded body mass of each species were sourced from Dunning Jr. (2008), where available. Thibault *et al.* (2011) present a method for constructing individual size distributions for bird communities using published mean size and variance data for each

species. Information on the variance of some species is not provided by Dunning Jr. (2008), therefore species mean body mass data were used to calculate the variance of the mass for each species using the scaling relationship $\text{var}(\text{mass})=0.0055*\text{mean}(\text{mass})^{1.98}$. This relationship is based on the mean-variance relationship of 376 bird species ($R^2 = 0.92$; Thibault *et al.* 2011). Individual body sizes were generated for each dataset by randomly drawing the observed number of individuals from a normal distribution with the estimated mean and variance values of each species. As this method assumes normal distributions and is based on summary statistics it only provides an estimation of the likely size distribution within a community. However, by accounting for intraspecific variability it is more representative of individual size distributions than mean data alone, and this approach has successfully been used to highlight consistency in the shape of bird community ISDRs at macroecological scales (Thibault *et al.* 2011). For fish, individual length data were recorded in the field, therefore individual, mean and maximum observed body masses were calculated using length:body mass conversions available from FishBase (Froese & Pauly 2012). In addition, maximum recorded body mass of each species were sourced from FishBase (Froese & Pauly 2012).

A critical issue when studying body size distributions is how to effectively compare different distributions. Traditionally, such comparisons have relied on visual assessments (e.g. Holling 1992), which are subjective and may not detect key similarities and differences. More recently, comparisons have been made using nested mixture models (Xu *et al.* 2010) but these rely on *a priori* decisions regarding the shape of the distributions, or using univariate approaches such as phi correlations (Forys & Allen 2002) and distribution overlap indices (Ernest 2005). Non-metric multidimensional scaling (nMDS) is a multivariate approach that is commonly used to compare either presence-absence or abundance of species among sites. In this study this approach was extended to allow a comparison of the patterns in the body size distributions among sites. Analysis of similarities (ANOSIM) was used to statistically test for differences in size classes among sites of distinct habitat types (following Hua *et al.* 2013).

Four groups of analyses were conducted on each dataset, comparing either fish or bird communities among sites of different habitat types, for example comparing the size distributions of bird communities among sites in stringybark and gum habitat (Lofty Ranges dataset). These four groups of analyses evaluated different combinations of the three types of body mass distribution and the two analytical approaches (Table 7-2). ANOSIM significance values will be influenced by the number of replicates within each analysis, therefore Global R values from the ANOSIM results were used to provide a comparative measure of the strength of the differentiation between habitat types for each analysis (Clarke & Warwick 2001).

7.3.1.1 Analysis 1 and 3

For each dataset, discontinuities (Fig. 7-1A) were evaluated in the species size relationships (Analysis 1) or the individual size-density relationships (Analysis 3) of either the bird or fish community at each site, using the Gap Rarity Index (GRI). The GRI compares the differences between body masses of observed data with those of a null model to assess whether there are significant discontinuities or ‘gaps’ in the observed size distribution. The null model is produced by fitting a kernel density estimate to the observed rank-ordered log-transformed body masses, using the smallest bandwidth that results in a smoothed, continuous, unimodal null distribution (Silverman 1986). The kernel density estimate is transformed to a rank order vs. body mass distribution by multiplying the densities by the number of species in the observed dataset. Differences in the mass between consecutive, rank ordered body masses from the observed dataset are compared to the change in rank among similar differences in body mass from the unimodal null model. This comparison generates a measure of the probability of the difference between consecutive masses in the observed dataset being significantly different from that expected from the null distribution, and thus whether the difference can be considered a discontinuity. Clusters of species between significant discontinuities are defined as aggregations. Further details of the GRI method may be found in Restrepo et al. (1997), and Wardwell et al. (2008).

For each of the datasets, a matrix of sites (columns) by log mean body mass (rows) was developed. Values of log body mass (to three decimal places) between the minimum and maximum for the community were included as separate rows. The matrix was populated using the GRI results, with 0s for discontinuities between aggregations, and 1s within aggregations (Table 7-3A). Patterns of discontinuities and aggregations were compared among sites using nMDS in PRIMER (Clarke 1993). ANOSIM was then used to test for statistical differences in discontinuity and aggregation patterns between sites of defined habitat types (e.g. unlogged, logged_89, logged_93 in the Borneo dataset). Euclidean distances were used to calculate the distance matrices to ensure that double zeroes were included as a basis for comparing among sites, because I was interested in the discontinuity structure of the sites’ respective communities (Legendre & Legendre 1998). For the Lofty Ranges bird dataset, Analysis 1 was also performed using maximum body mass from the literature (Dunning Jr. 2008). This was not possible for the Borneo dataset due to lack of maximum mass data. For the two fish datasets, Analysis 1 was also performed using both maximum body mass from FishBase and maximum observed body mass.

Table 7-3: Matrix setup for different analyses using example data. Row labels are log₁₀ body sizes, column titles are habitat type (Y or Z) and site number (1, 2 or 3). A) Analysis 1 (species-level data) and 3 (individual-level data), where data represent discontinuities (0) and aggregations (1) identified by the Gap Rarity Index (GRI), B) Analysis 2 (species-level data) and 4 (individual-level data), where data represent log₁₀ (abundance +1).

A	Y_1	Y_2	Y_3	Z_1	Z_2	Z_3	B	Y_1	Y_2	Y_3	Z_1	Z_2	Z_3
0.150	0	1	0	0	0	0	0.150	0	0.3	0	0	0	0
0.151	0	1	0	0	1	0	0.151	0	0.3	0	0	0.3	0
0.152	0	1	0	1	1	0	0.152	0	0.3	0	1.5	0	0
0.153	1	1	0	1	1	0	0.153	0.3	1.5	0	0.3	0	0
0.154	1	1	0	1	1	1	0.154	0.8	0.8	0	0	0	1.5
0.155	1	1	0	1	1	1	0.155	0.8	1.4	0	1.6	0	0.3
0.156	1	1	0	1	1	1	0.156	0	0.3	0	0	1.6	1.8
0.157	1	1	0	1	0	1	0.157	0	0	0	0	0	0
0.158	1	1	0	1	0	1	0.158	0	0.3	0	0.3	0	0.6
0.159	1	0	0	1	0	0	0.159	0.3	0	0	1.5	0	0
⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮
4.123	0	0	0	1	0	0	4.123	0	0	0	0.3	0	0
4.124	0	1	0	1	0		4.124	0	0.8	0	0	0	0.8
4.125	0	1	0	1	0	1	4.125	0	0	0	1.5	0	0.9
4.126	0	1	0	0	0	1	4.126	0	0	0	0	0	0.3
4.127	0	1	1	0	0	1	4.127	0	0	0.3	0	0	0
4.128	0	1	1	0	0	1	4.128	0	0	0.4	0	0	0
4.129	0	1	1	0	0	1	4.129	0	0	0	0	0	0.3
4.130	0	1	1	0	0	0	4.130	0	0	0	0	0	0
4.131	0	1	1	0	0	0	4.131	0	0.8	0.5	0	0	0

7.3.1.2 Analysis 2 and 4

For each dataset the abundance and modality patterns (Fig. 7-1B) were compared in the species size-density distribution (Analysis 2) or the individual size-density relationships (Analysis 4), of either the bird or fish communities, among sites of different habitat type using ANOSIM. For each dataset a matrix of sites (columns) by log body mass (rows) was developed. Values of log body mass (to three decimal places) between the minimum and maximum for the community were included as separate rows. The matrix was populated by assigning either the species' (Analysis 2) or individual' (Analysis 4) log₁₀ (abundance+1) to its respective body mass value (Table 7-3B). Patterns of abundance of different body sizes were then compared among sites using nMDS and ANOSIM. Chord distances were used to calculate

the distance matrices, because this allowed comparison of the proportion of individuals recorded within body mass classes (Legendre & Legendre 1998). Pairs of sites that have peaks (and troughs) in abundance in the same size classes as well as similar proportions of individuals within size classes give the smallest chord distances, while pairs of sites that do not share overlapping modes in the abundance distribution or similar proportions of individuals in size classes give the largest distances. For the Lofty Ranges bird dataset, Analysis 2 was also performed using maximum body mass from the literature. This was not possible for the Borneo dataset due to lack of information. For the two fish datasets, Analysis 2 was also performed using both maximum body mass from FishBase and maximum observed body mass.

7.4 RESULTS

7.4.1 *Analysis 1: discontinuity patterns across species size relationships (SSRs)*

The ANOSIM results and nMDS plots show a differentiation in bird mean body size discontinuity patterns between sites in gum (black circles) and stringybark (green triangles) habitats in the Lofty Ranges dataset (Table 7-4A & Fig. 7-2A). Differences were also found between sites in logged_93 (green triangles) and unlogged (blue squares) habitats in the Borneo dataset, but not between remaining pairwise comparisons (Table 7-4B & Fig. 7-2B). The discontinuity patterns in fish mean species size relationships were not significantly different among habitats for either dataset (Table 7-4C&D & Fig. 7-2C&D). When using maximum species body mass data recorded in the literature, the Lofty Ranges bird communities showed significant differences among the two habitats (Appendix E Table S1A; Fig. S2A). The Seychelles fish communities showed no significant differences among habitats for either maximum mass recorded in FishBase, or for observed maximum mass (Appendix E Table S1C; Fig. S1B & S2A). For the GBR dataset, there were significant differences among disturbed reefs (black circles), and both undisturbed (blue squares) and recovering (green triangles) reefs using species size relationships based on maximum mass recorded in FishBase (Appendix E Table S1D; Fig. S1C). However the R value for the disturbed-undisturbed reef comparison was extremely low ($R=0.097$) suggesting there is little real separation between these two groups. Differences were only found among disturbed (black circles) and undisturbed (blue squares) habitats using maximum observed species body mass distributions (Appendix E Table S1D; Fig. S2B).

Table 7-4: Analysis of Similarities (ANOSIM) comparing the size distributions of communities for sites of different habitat type for A) Lofty Ranges bird, B) Borneo bird, C) Seychelles fish, and D) Great Barrier Reef fish communities. Analysis 1: Comparison of discontinuities in species mean size relationships (SSRs). Analysis 2: Comparison of abundance in species mean size-density distributions (SSDRs). Analysis 3: Comparison of discontinuities in individual size-density relationships (ISDRs). Analysis 4: Comparison of abundance across individual size-density relationships (ISDRs). The resemblance matrices were calculated using Euclidean distances for Analyses 1 and 3, and chord distances for Analyses 2 and 4.

Factor	Analysis 1		Analysis 2		Analysis 3		Analysis 4	
	R	Significance	R	Significance	R	Significance	R	Significance
A) Birds - Lofty Ranges								
Habitat	0.115	0.001	0.271	0.001	0.205	0.001	0.212	0.001
B) Birds - Borneo								
Habitat	0.128	0.015	0.326	0.001	0.114	0.014	0.268	0.001
Logged_93,Logged_89	0.107	0.084	0.210	0.006	0.085	0.129	0.080	0.106
Logged_93, Unlogged	0.237	0.004	0.472	0.001	0.218	0.001	0.442	0.001
Logged_89, Unlogged	0.005	0.379	0.274	0.001	0.015	0.341	0.224	0.004
C) Fishes - Seychelles								
Habitat	0.084	0.223	0.141	0.128	0.425	0.005	0.658	0.001
Algae, Granite					0.600	0.018	0.867	0.018
Algae, Coral					0.427	0.050	0.825	0.008
Granite, Coral					0.380	0.013	0.523	0.001
D) Fishes - GBR								
Habitat	0.045	0.052	0.016	0.236	0.098	0.001	0.173	0.001
Undisturbed, Disturbed					0.132	0.001	0.143	0.001
Undisturbed, Recovering					0.111	0.034	0.294	0.001
Disturbed, Recovering					0.025	0.298	0.112	0.037

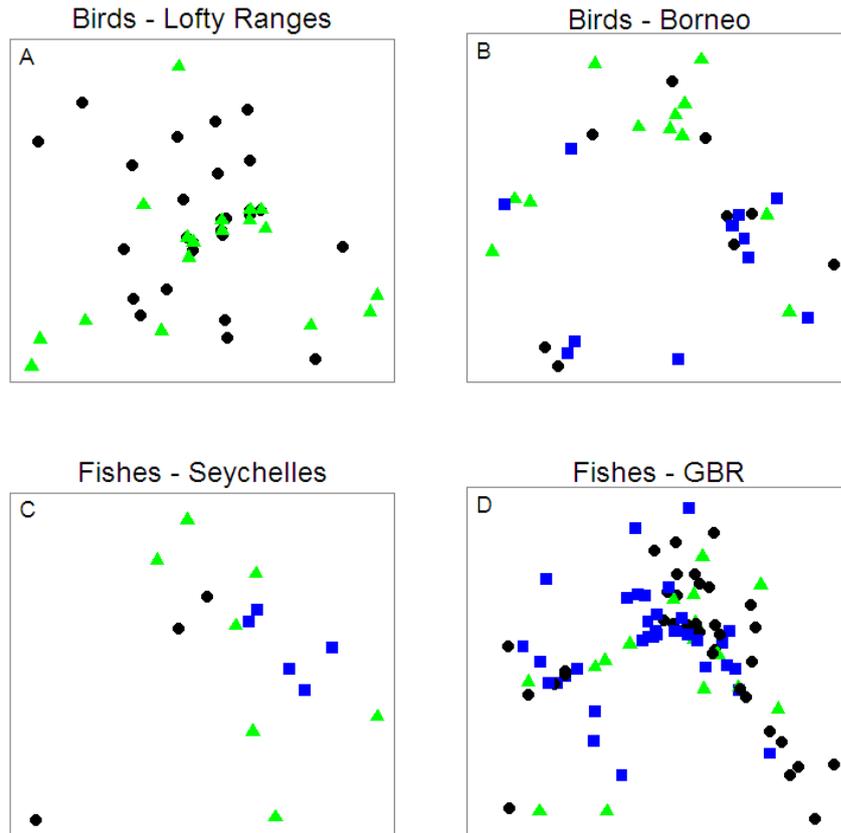


Figure 7-2: Non-metric multi-dimensional scaling (nMDS) comparing size distributions of communities for sites of different habitat type. Comparison of discontinuities in species size relationships (SSRs; Analysis 1) for A) Lofty Ranges bird, B) Borneo bird, C) Seychelles fish, and D) Great Barrier Reef fish communities. The resemblance matrices were calculated using Euclidean distances. Symbols in A: black circles – gum woodland, green triangles – stringybark woodland; symbols in B: black circles – logged₈₉ forest, green triangles – logged₉₃ forest, blue squares – unlogged forest; symbols in C: black circles – algal-dominated carbonate reef, green triangles – coral-dominated carbonate reef, blue squares – granitic reef; symbols in D: black circles – disturbed reef, green triangles – recovering reef, blue squares – undisturbed reef.

7.4.2 Analysis 2: abundance patterns across species size-density relationships (SSDRs)

The ANOSIM results and nMDS plots show a stronger differentiation among sites of different habitat type when the species size-density relationships of bird communities were analysed for abundance patterns (Analysis 2), compared to assessment of species size relationships for discontinuity patterns (Analysis 1). This outcome holds among all habitats for both the Lofty Ranges and Borneo datasets (R values of 0.271 versus 0.115, and 0.326 versus 0.128, respectively; Table 7-4A&B; Fig. 7-3A&B). No significant differences were found among habitats in either fish dataset (Table 7-4C&D, Appendix E Fig. S1C&D). When using maximum species body mass data recorded in the literature, the Lofty Ranges bird communities showed significant differences among the two habitats (Appendix E Table S1A; Fig. S3A), although this differentiation was not as strong as when mean data were used (R values of 0.217

versus 0.271). The Seychelles fish communities showed differences among all habitats for both maximum mass recorded in FishBase and observed maximum mass (Appendix E Table S1C; Fig. S3B & S4A). In addition, global R values were higher compared with Analysis 2 based on mean data (R values of 0.454 and 0.337 for maximum mass in FishBase and maximum observed mass, versus 0.141 for mean data). For the GBR dataset, differences were found among undisturbed reefs (blue squares), and both disturbed (black circles) and recovering (green triangles) reefs using either maximum mass recorded in FishBase or maximum observed species body mass (Appendix E Table S1D; Fig. S3C & S4B). However R values were very low for the pairwise comparison between undisturbed and disturbed reefs (0.092 and 0.081 for maximum mass recorded in FishBase and observed maximum mass, respectively).

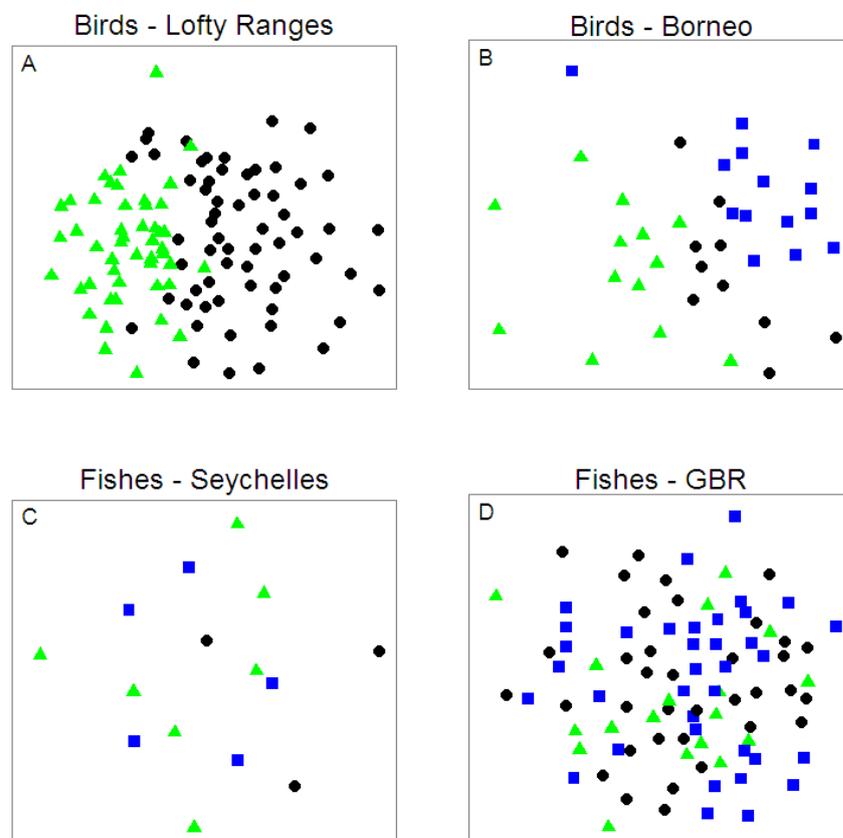


Figure 7-3: Non-metric multi-dimensional scaling (nMDS) comparing size distributions of communities for sites of different habitat type. Comparison of abundance patterns in species size-density relationships (SSDRs; Analysis 2) for A) Lofty Ranges bird, B) Borneo bird, C) Seychelles fish, and D) Great Barrier Reef fish communities. The resemblance matrices were calculated using chord distances. Symbols in A: black circles – gum woodland, green triangles – stringybark woodland; symbols in B: black circles – logged₈₉ forest, green triangles – logged₉₃ forest, blue squares – unlogged forest; symbols in C: black circles – algal-dominated carbonate reef, green triangles – coral-dominated carbonate reef, blue squares – granitic reef; symbols in D: black circles – disturbed reef, green triangles – recovering reef, blue squares – undisturbed reef.

7.4.3 Analysis 3: discontinuity patterns across individual size-density relationships (ISDRs)

The ANOSIM results and nMDS plots show a significant differentiation in individual bird body size discontinuity patterns between the two habitats in the Lofty Ranges dataset (Table 7-4A & Fig. 7-4A). However this differentiation was slightly weaker than for Analysis 2 (R values of 0.205 versus 0.271). Differences were also found between logged_93 (green triangles) and unlogged (blue squares) habitats in the Borneo dataset, but not between other pairwise habitat comparisons (Table 7-4B & Fig. 7-4B), and the global R value was lower than for either Analysis 1 or 2 (0.114 vs. 0.128 and 0.326). There was an overall significant differentiation in individual fish body size discontinuity patterns between habitats for both datasets. For the Seychelles dataset, the ANOSIM pairwise comparisons highlight significant differences between the fish community discontinuity patterns of granite (blue squares) and both algae (black circles) and coral (green triangles) sites, but was just barely non-significant between algae (black circles) and coral (green triangles) sites (Table 7-4C; Fig. 7-4C). Furthermore, the global R value (0.425) was higher than all previous analyses, except Analysis 2 using maximum mass from the literature (0.454). Pairwise comparisons indicate significant differences in the discontinuity patterns of undisturbed (blue squares) and both disturbed (black circles) and recovering (green triangles) sites for the GBR dataset (Table 7-4D; Fig. 7-4D). The global R for the GBR dataset was greater than all previous analyses, however, it was still quite low (0.098).

7.4.4 Analysis 4: abundance patterns across individual size-density relationships (ISDRs)

The ANOSIM results and nMDS plots show significant differences in the abundance patterns and modality of individual body size-density relationships between all habitats for the Lofty Ranges bird, and the Seychelles and GBR fish datasets (Table 7-4A,C&D; Fig. 7-5A,C&D). There were also significant differences between the Borneo bird communities of unlogged (blue squares) and both logged_89 (black circles) and logged_93 (green triangles) sites, but not between logged_89 and logged_93 sites (Table 7-5B, Fig. 7-5B). The differentiation among habitats for Analysis 4 was greatest compared to the other three Analyses for both fish datasets (R values of 0.658 and 0.173 for the Seychelles and GBR respectively). In contrast the differentiation among habitats for Analysis 4 was greater compared to Analysis 3 for the bird datasets (R values of 0.212 versus 0.205, and 0.268 versus 0.114 for the Lofty Ranges and Borneo respectively), but were lower than for Analysis 2 (R values of 0.271 and 0.326 for the Lofty Ranges and Borneo respectively).

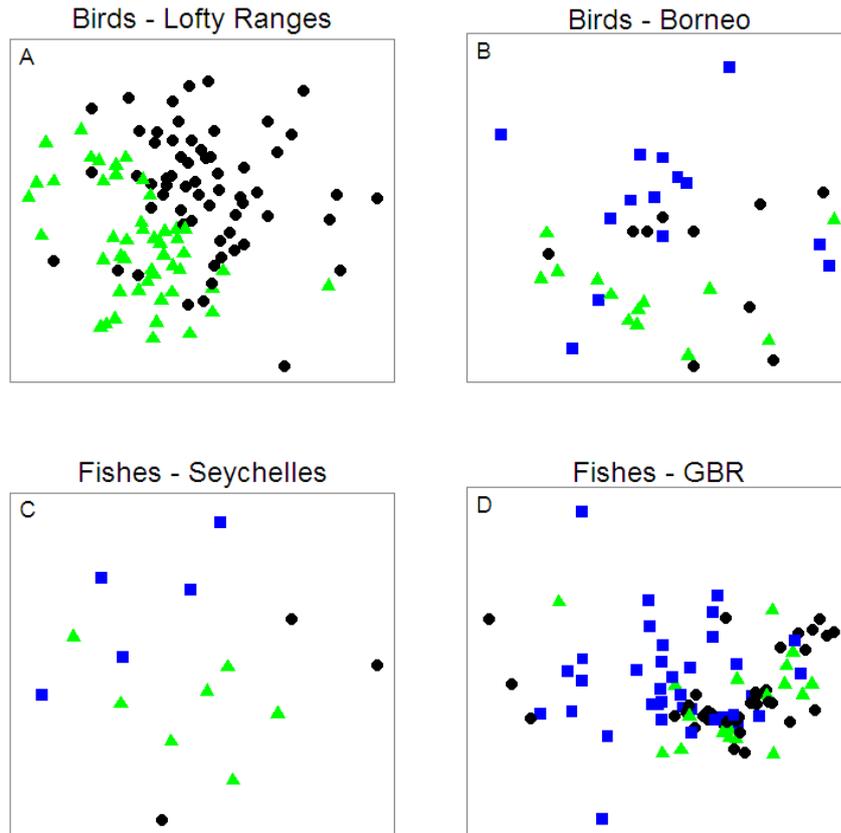


Figure 7-4: Non-metric multi-dimensional scaling (nMDS) comparing size distributions of communities for sites of different habitat type. Comparison of discontinuities in individual size-density relationships (ISDRs; Analysis 3) for A) Lofty Ranges bird, B) Borneo bird, C) Seychelles fish, and D) Great Barrier Reef fish communities. The resemblance matrices were calculated using Euclidean distances. Symbols in A: black circles – gum woodland, green triangles – stringybark woodland; symbols in B: black circles – logged_89 forest, green triangles – logged_93 forest, blue squares – unlogged forest; symbols in C: black circles – algal-dominated carbonate reef, green triangles – coral-dominated carbonate reef, blue squares – granitic reef; symbols in D: black circles – disturbed reef, green triangles – recovering reef, blue squares – undisturbed reef.

7.5 DISCUSSION

This study provides a cross-ecosystem comparison of the suitability of different body size distribution indices and analyses for assessing the relationship between habitat structure and the size distributions of animal communities. Individual- or species-level size data may be used to examine this relationship in bird communities. In contrast, although there was some evidence for species-level patterns in the fish data when using maximum size metrics, the patterns were more consistent and stronger when using individual-level data. Abundance data either at the species- (SSDRs) or individual- (ISDRs) level provides closer ties between the habitat structure and the concomitant body size distributions than when relying on species

presence-absence data alone (SSRs). Significantly, individual size-density relationships (ISDRs) provide a potentially useful index for comparing drivers of body size across habitats and among taxa exhibiting determinate or indeterminate growth.

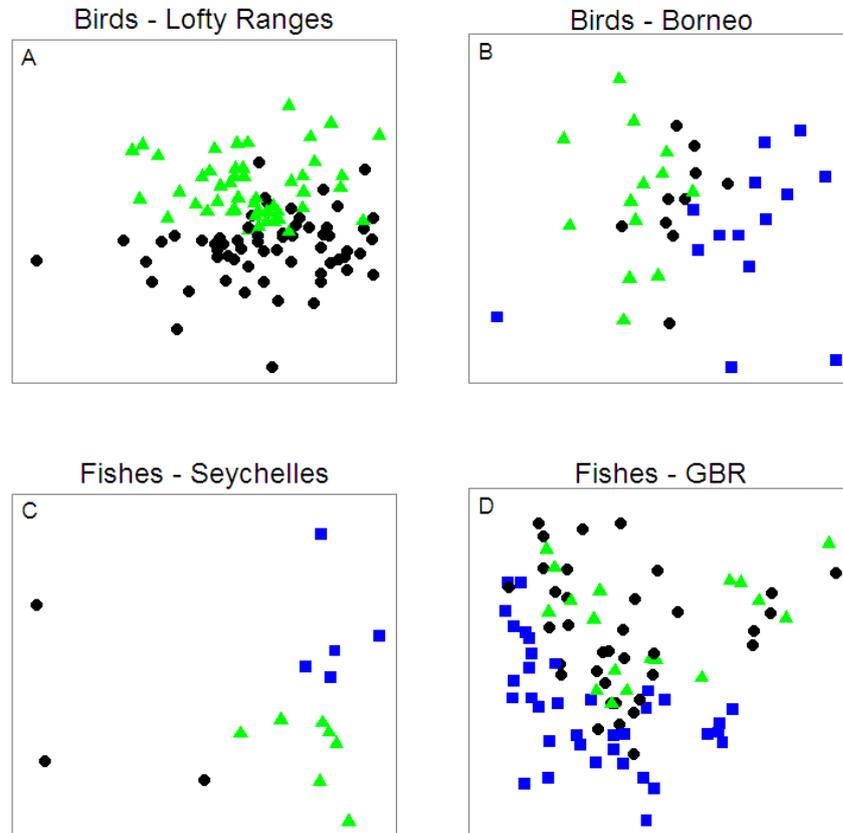


Figure 7-5: Non-metric multi-dimensional scaling (nMDS) comparing size distributions of communities for sites of different habitat type. Comparison of abundance patterns in individual size-density relationships (ISDRs; Analysis 4) for A) Lofty Ranges bird, B) Borneo bird, C) Seychelles fish, and D) Great Barrier Reef fish communities. The resemblance matrices were calculated using chord distances. Symbols in A: black circles – gum woodland, green triangles – stringybark woodland; symbols in B: black circles – logged_89 forest, green triangles – logged_93 forest, blue squares – unlogged forest; symbols in C: black circles – algal-dominated carbonate reef, green triangles – coral-dominated carbonate reef, blue squares – granitic reef; symbols in D: black circles – disturbed reef, green triangles – recovering reef, blue squares – undisturbed reef.

7.5.1 *Body size distributions: choice of index and analysis*

In line with previous work evaluating terrestrial body size distributions (e.g. White *et al.* 2007), the outcomes of this study suggest that species' mean body size provides a useful descriptive summary for bird communities. There is also potential for species' maximum body size to provide a similarly useful summary metric, although this needs further exploration with more than the single dataset (Lofty Ranges) presented in my study. There was stronger differentiation between habitat types for species size-density distributions (SSDRs) analysed for

abundance patterns (Analysis 2; Table 7-2) compared with species size relationships (SSRs) analysed for discontinuities (Analysis 1; Table 7-2) in both the Borneo and Lofty Ranges dataset. This suggests that species' abundance may provide more discriminatory power with respect to habitat imposed differences in body size patterns than solely looking at species' presence-absence data (Nash *et al.* 2013). This finding held for species size-density relationships based on both mean and maximum mass data.

The results for the species-level fish analyses were less consistent than for birds (Analyses 1&2). Overall, however, they suggest that mean mass does not provide a useful summary metric for fish communities when examining the relationship between habitat and body size distributions. In contrast, maximum mass observed and particularly maximum mass recorded in FishBase provide useful metrics for examining the relationship between habitat and size-density distributions (Analysis 2). The inappropriateness of mean body size is not surprising considering the wide intra-specific size ranges of fish (Choat & Robertson 2002). The better performance of the maximum size metrics corresponds to existing work presenting maximum size as a good alternative to the mean as a summary metric to describe species with indeterminate growth (Jennings *et al.* 2001; Cumming & Havlicek 2002). There have been recent calls to study individual size-density relationships (ISDRs) in terrestrial systems (Thibault *et al.* 2011). Mammal research often collects individual size data, however current bird (and other terrestrial animal taxa) surveys primarily collect data on species abundance, rather than information on individual size (Ernest 2013). The methods described by Thibault *et al.* (2011) and used in this study, extrapolating intra-specific size distributions from published mean and variance information, provide a technique for producing ISDRs without survey-derived individual size data. My results suggest the relationships between habitat and ISDRs of birds may be detected (albeit more weakly than for the SSDRs) when assessing distribution patterns of modality within size distributions (Analysis 4; Fig. 7-1B), despite using model-simulated individual data. However, the weaker performance of the ISDR analyses in relation to the SSDR analyses may be a function of the simulated nature of the individual-level data. Indeed, a clear caveat of this approach is that these data were based on recorded statistics of size distributions as opposed to real data from the two locations. Importantly,, the assumptions used in generating the individual-level data using Thibault *et al.*'s (2011) approach may bias results. For example, published estimates of mean size and variance may be affected by local or latitudinal variability (Ashton 2002) resulting in deviations from the mean-variance scaling relationship employed in the method. Furthermore, individual sizes simulated in this manner may mask real discontinuities in body size distributions thus limiting the potential of discontinuity analyses on ISDRs (Analysis 3), or may result in shifts in abundance along the size class axis, providing apparent differences among sites when calculating the distance

matrices, which are a result of the simulation as opposed to real differences (Analysis 4). Therefore my results indicate the potential for ISDRs to examine the relationship between habitat and body size distributions in bird communities, but further work is needed using survey-collected, individual size data, where available, to explore this potential further. It should be noted that despite the fact that maximum body size was only evaluated for one bird dataset, this summary metric of size showed promise for both birds and fishes, and represents a logistically more economical alternative to measuring sizes of all individuals within a field sample. Therefore, further work looking at the efficacy of using maximum body size to explore the effects of habitat on size distributions in different taxa across a broader range of datasets, is recommended.

The relationships between habitat and fish size distributions were strongest when evaluating ISDRs (Analysis 3&4; Table 7-2). This corresponds to a wide literature examining size spectra in marine communities (e.g. Jennings *et al.* 2001), and indicates that ISDRs are not only useful for understanding the effects of fisheries exploitation (Rice 2000), but also the potential influence of habitat change. Analyses of discontinuities within ISDRs, which ignore abundance information (Analysis 3; Table 7-2), showed weaker relationships with habitat structure compared to analyses of abundance within ISDRs (Analysis 4; Table 7-2), for both bird and fish communities. This corresponds to Holling's (1992) original supposition that individual-level data may mask discontinuities within body size distributions. It therefore appears that research questions and analyses aimed at examining abundance patterns and modality are more appropriate when using individual-level data (Nash *et al.* 2014a). Nevertheless, a critical question remains regarding the mechanisms responsible for the patterns observed in size distributions. Modality and discontinuities support very different hypotheses regarding the drivers underlying the observed patterns. Multi-modality suggests a central attractor within each mode (where abundance would be greatest), whereas discontinuities suggest the existence of "forbidden" sizes where resources are absent, and the lack of a central attractor within size classes such that abundance is randomly distributed within the size classes separated by discontinuities (Holling 1992; Xu *et al.* 2010). Rigorous tests of these two hypotheses for multiple taxa are currently absent.

Three important considerations apply to the interpretation of my results. It is critical to tailor the choice of index and analysis to the research question, as different distributions and methods provide contrasting information regarding the distribution of resources among either individuals or species (Table 7-1; Robson, Barmuta & Fairweather 2005). Equally, the range of drivers affecting body size distributions need to be considered. At the habitat-level scale of my analyses, competitive interactions will also influence body size distributions, and as such may

mask the influence of habitat structure (Scheffer & van Nes 2006). This may partially explain why habitat effects were not seen when using certain distribution indices and analyses. Larger scale, regional datasets may provide clearer patterns across indices and analyses, and should be considered for future research. Finally, although I specifically chose taxa and systems where habitat is known to have a strong influence on body size of associated taxa, and thus the signature of habitat effects should be evident within the size distributions, it is possible that where no effect was found, that this was a function of a genuine absence of a habitat-body size relationship as opposed to a poorly performing index or analysis (suggestions of approaches to quantitatively test this further are presented in the supplementary material; Appendix E Text S2). I suggest that the use of multiple datasets, with consistent results within the two fish and within the two bird datasets provide support for the interpretations presented. Furthermore, these outcomes support complimentary work within the terrestrial and marine literature. As a result, I suggest that the key outcome of this study is the identification of ISDRs as a potential common currency with which to examine the relationship between habitat structure and community assembly in both terrestrial and marine systems, and among taxa exhibiting indeterminate and determinate growth. ISDRs permit cross-ecosystem comparisons, allowing clarification of the differences and similarities among marine and terrestrial systems unbiased by discipline specific approaches, and which may be more sensitive to habitat change (Ernest 2013).

7.5.2 *Size and vulnerability*

Predicting species' vulnerabilities to disturbance is of significant interest to managers as this would allow the development of appropriate mitigation strategies. Size has been presented as one trait that influences this vulnerability: large body size correlates with vulnerability to human activities such as hunting, whereas small species may be particularly susceptible to habitat loss (Owens & Bennett 2000). However, the loss of habitat structure at particular scales is likely to influence the decline of particular size classes (De la Montaña, Rey-Benayas & Carrascal 2006). Once Analysis of Similarities (ANOSIM) has been used to identify differences in the size distributions of communities associated with different habitat types, Similarity Percentages (SIMPER; Clarke 1993) may be performed on the same distance matrices used for the ANOSIM, identifying which size classes contribute to similarity among sites of a particular habitat type, and thus allow interpretation of the differences found using ANOSIM. This would allow finer scale discrimination of whether certain body sizes are likely to be susceptible to specific types of habitat change, such as losing structure at a particular scale (Nash *et al.* 2013). In fish communities, where individuals cover large size ranges over the course of their life (Choat & Robertson 2002), such discrimination is particularly important

Inherent to the relationship between scale-specific disturbance of habitat and size-based vulnerability is the concept of response time, whereby different species and individuals may respond to disturbance over different time scales (Hughen *et al.* 2004). The body size distribution of a community is a dynamic trait, and therefore the relationship between size and vulnerability to habitat change needs ongoing evaluation (Nash *et al.* 2013). For example, fishes may exhibit differential loss from coral reefs in response to bleaching events: initial community changes caused by an immediate loss of live coral may be followed by distinct modifications to the community through the gradual loss of habitat structure (Graham *et al.* 2006). As a result, temporal studies of body size distributions are needed, in addition to the type of spatial study presented here. Once again, testing for the presence of differences among communities over time (ANOSIM) could then be followed by evaluation of which size classes are causing these changes (SIMPER).

7.5.3 *Conclusions and future directions*

There has been recent interest in comparing body size distributions across ecosystems, coincident with the desire to reconcile approaches placing greater relative weight on either size or taxonomic affinity (Petchey & Belgrano 2010). I show that size distributions of terrestrial taxa exhibiting determinate growth may be evaluated at the species or the individual-level, but incorporating abundance data across size classes adds to the robustness of these analyses. In contrast habitat driven patterns in the size distributions of aquatic taxa with indeterminate growth may be masked when using mean data. Maximum summary metrics and individual size-density relationships represent more appropriate approaches in this context. Importantly, individual size-density relationships provide a potential useful common currency with which to compare the influence of habitat structure among ecosystems. However, many questions regarding ecosystem specific differences remain unanswered. For example, there is a need to tease apart the relative influence of terrestrial versus aquatic factors compared to that of the two growth patterns. Possible examples which would allow the separation of these drivers are comparing body size distributions in insects within terrestrial soils and marine sediments (e.g. Wall *et al.* 2005) to understand ecosystem effects, and contrasting bird and reptile communities to assess the impact of growth pattern within a single ecosystem (Woodward *et al.* 2005). Other potential directions include: exploring the relationships between the different body size distribution indices (Table 7-1), particularly for those taxa exhibiting indeterminate growth (Reuman *et al.* 2008). Finally, there remains considerable scope for exploration of the shape of different body size distribution indices in response to other drivers besides habitat structure, such as community interactions and phylogeny, which may be evident at different spatial or temporal scales (Allen *et al.* 2006).

Chapter 8: Herbivore cross-scale redundancy supports response diversity and coral reef recovery

8.1 ABSTRACT

The range of responses species exhibit to perturbations (response diversity) is thought to underpin the ongoing maintenance of important ecosystem processes that species provide, e.g. pollination and herbivory. The cross-scale resilience model proposed that the scale at which an individual provides its function will influence its response to scale-specific disturbances. Thus, the presence of species operating at different scales within a community (cross-scale redundancy), should be a useful indicator of resilience, if it provides for a high degree of response diversity. Coral reefs are diverse systems that provide key ecosystem services, and are subject to increasing anthropogenic disturbance. Herbivorous reef fish are critical for maintaining reefs within coral-dominated states, through the grazing and removal of algae, which competes with coral for space. Prior work has explicitly indicated the potential for response diversity in herbivorous fish communities, but there has been no evaluation of the traits responsible for this range of responses to environmental change. I assessed the effectiveness of cross-scale redundancy in herbivores as an indicator of response diversity and benthic recovery on reefs monitored through a major climatic disturbance event (coral bleaching) that caused widespread coral mortality. The distribution (redundancy) of herbivores operating across a broader range of spatial scales prior to the coral bleaching corresponded with increased reef recovery post-disturbance. Analysis of the change in biomass across size classes indicated that response diversity, whereby a decline in small herbivores was compensated for by increases in large herbivores, drove an increase in the overall herbivore biomass at recovering sites. These compensatory mechanisms were not found at sites with herbivores operating over a narrower range of spatial scales. This study highlights the need to manage herbivores, and the function they provide on reefs by supporting the delivery of herbivory across spatial scales. The importance of large individuals for controlling algae and providing compensation for the loss of smaller size classes emphasizes the necessity for effective fisheries management and strategies to reduce pressure on larger species. Importantly, cross-scale redundancy provides managers with a measurable indicator of resilience and an avenue to support the ongoing delivery of herbivore function.

8.2 INTRODUCTION

The resilience of an ecosystem can be broadly defined as its capacity to adapt to changing conditions whilst maintaining core processes, resisting shifts to different dynamic regimes, and continuing to provide critical ecosystem services (Holling 1973; Carpenter *et al.* 2001; Walker *et al.* 2006). Despite the usefulness of resilience as a framework to conceptualise ecosystem dynamics (Carpenter *et al.* 2001), operationalising resilience into a quantitative measure or set of measures has proved harder to achieve because reduced resilience is often only apparent when thresholds are reached and the system moves into an alternate state (Bellwood *et al.* 2004). Nonetheless, due to the significant logistical and monetary costs associated with reversing regime shifts, it is critical for managers to anticipate and adapt to change before shifts occur (Scheffer *et al.* 2001; Biggs, Carpenter & Brock 2009). To date there has been much discussion regarding drivers of resilience within different ecosystems, presenting an array of potentially measurable indicators (Folke *et al.* 2004; Nyström *et al.* 2008); however, there is a lack of empirical studies assessing these indicators' abilities to predict a system's trajectory to recovery or regime shift (Carpenter, Westley & Turner 2005; Thrush *et al.* 2009).

The functional composition of communities provides one prospective avenue of study for the assessment of resilience (Walker *et al.* 2006). Species provide a range of functions driving key ecosystem processes, for example seed dispersal, pollination, herbivory and decomposition (Folke *et al.* 2004). Thus, functional diversity within a community ensures the delivery of a range of important processes and underpins ecosystem performance (Walker, Kinzig & Langridge 1999; Hooper *et al.* 2005). Such diversity may be explored by assessing the presence and distribution of effect traits among species, i.e. those life history and ecological traits that support specific ecosystem functions; for example, in rangeland plants, nitrogen fixation may be considered an effect trait (Chillo, Anand & Ojeda 2011).

Ecosystems are dynamic, experiencing a range of natural and anthropogenic impacts; to allow system recovery and renewal, ecosystem processes need to be buffered to ensure their maintenance in the face of disturbance. Multiple species with a similar functional role should give a degree of redundancy, because the decline of one species in response to a disturbance may be compensated for by other species increasing their contribution to that function (Nyström 2006). Nonetheless, this redundancy is only of value if the different species respond to a disturbance in distinct ways (response diversity); if they all respond similarly, having multiple species within the functional group will not provide the anticipated insurance value (Elmqvist *et al.* 2003). Response diversity may be explored by assessing the presence and distribution of response traits among species, i.e. those life history and ecological traits that are likely to support different responses to environmental change; for example, in rangeland plants,

palatability and the presence of thorns may be considered response traits in relation to grazing pressure (Chillo, Anand & Ojeda 2011).

Peterson, Allen & Holling (1998) proposed the cross-scale resilience model, suggesting that if members of a functional group operate at different spatial scales, they are likely to respond differently to scale-specific disturbances impacting their habitat, providing cross-scale redundancy. This range of responses should ensure the continued delivery of the function, promoting recovery of the habitat post-disturbance (Mori, Furukawa & Sasaki 2012; Nash *et al.* 2014a). Therefore, the range of spatial scales over which species within a community provide a particular function should be suggestive of response diversity and the potential for a site to recover after a perturbation, and as a consequence provides a measureable indicator of ecosystem resilience (Fig. 8-1; Peterson, Allen & Holling 1998; Pope, Allen & Angeler 2014).

To date the cross-scale resilience model has undergone little testing (e.g. Fischer *et al.* 2007; Sundstrom, Allen & Barichievsky 2012). To my knowledge, no studies have empirically assessed whether cross-scale redundancy within important functional groups supports the recovery of a system through a major disturbance event. Therefore the usefulness of cross-scale redundancy as a resilience indicator and predictor of recovery is, as yet, unevaluated. Coral reefs are high diversity systems that provide key ecosystem services such as fisheries and coastal protection (Duffy 2002; Hughes *et al.* 2010). However, human impacts are causing significant and ongoing degradation on reefs (Gardner *et al.* 2003), with increasing evidence of shifts from coral to algal-dominated reefs in response to drivers such as bleaching events and overfishing (e.g. Hughes 1994; Hoegh-Guldberg *et al.* 2007). Herbivorous reef fishes have been identified as critical for mediating this competition between coral and macroalgae (Mumby *et al.* 2006; Ledlie *et al.* 2007), thus these fish play key functional roles on reefs, and provide an important focus for testing the cross-scale resilience model.

The acknowledged importance of herbivores on reefs has generated an extensive literature examining functional diversity and effect traits within these species. Herbivorous fish species may be split into grazer/detritivores, scraper/excavators, and browsers (Bellwood *et al.* 2004). Grazer/detritivores feed on the epilithic algal matrix (EAM), which is composed of turf algae, detritus, microbes, sediment, and invertebrates (Wilson & Bellwood 1997), whereas scraper/excavators remove both components of the EAM and the underlying substrate, and thus contribute to bioerosion (Green & Bellwood 2009). These groups help reduce colonization by young macroalgae. In contrast, browsers feed on mature macroalgae and as such are critical for reversing shifts from coral to macroalgal dominance (Bellwood *et al.* 2006).

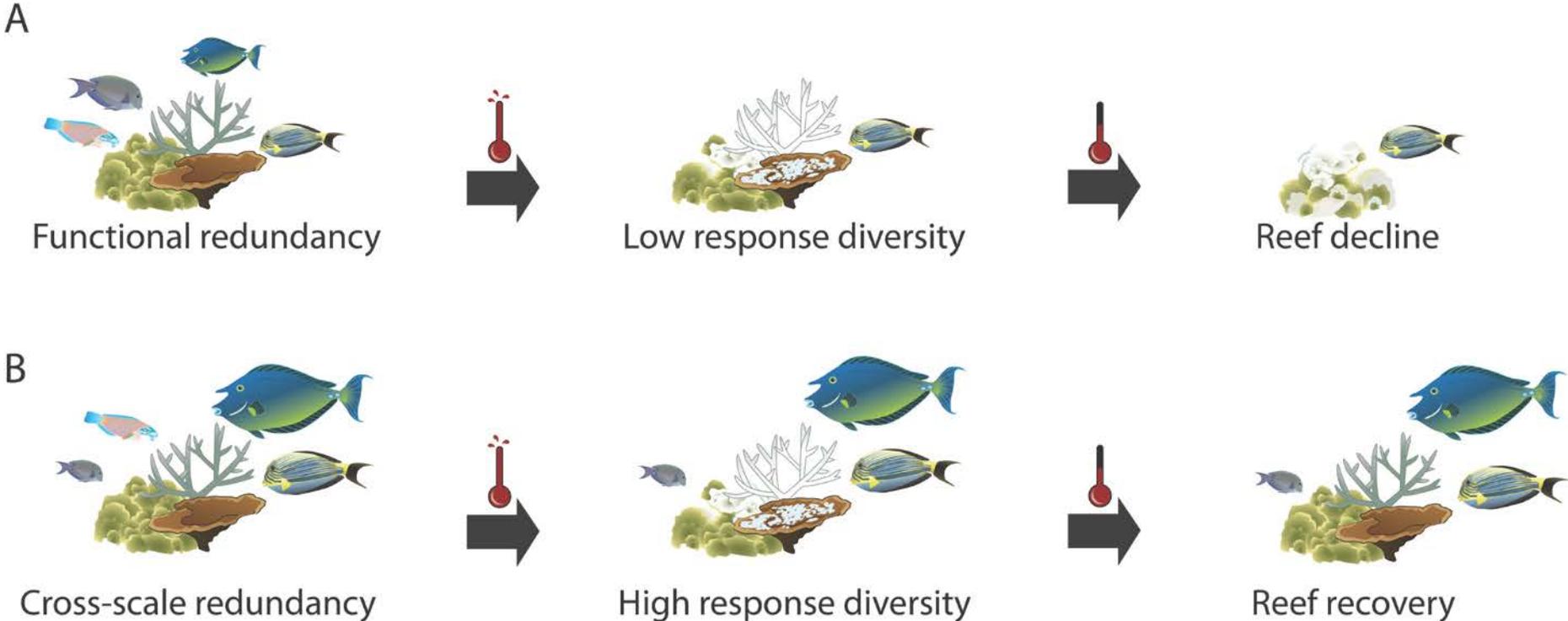


Figure 8-1: A coral reef experiencing high water temperatures driving a bleaching event (illustrated with thermometers). The proposed influence of A) herbivore functional redundancy (multiple species providing the same role) and B) herbivore cross-scale functional redundancy (multiple species providing the same role but at different spatial scales as indicated by variable body sizes; Nash et al. 2013) on community response diversity, leading to either reef recovery or decline. Both communities have the same total herbivore biomass and functional diversity prior to the disturbance.

There has been considerably less work focused on response diversity within herbivorous fishes. Thibaut, Connolly & Sweatman (2011) found evidence of compensatory mechanisms driving stability in herbivore abundance on the Great Barrier Reef, and primarily attributed this stability to response diversity. Nevertheless, to date there has been no exploration of the traits that support this range of responses to environmental change. The cross-scale resilience model provides a means of evaluating the importance of body size in reef herbivores as a driver of response diversity. The model is based on two assumptions. First, that the trait body size is a good proxy for the scale at which a species operates and provides its function, i.e. larger species operate at larger scales than smaller species (Calder 1984). Second, habitat condition influences the body size distribution of associated animal communities (Holling 1992). Recent studies exploring the relationship between body size and the scale of functional impact in herbivorous reef fish communities (Nash, Graham & Bellwood 2013), and the effect of habitat condition on fish body size distributions (Nash *et al.* 2013; Rogers, Blanchard & Mumby 2014) support the underlying assumptions of the cross-scale resilience model, and are suggestive of the suitability of reef fish as a test case for the model.

The 1998 bleaching event had a significant impact on the reefs of the inner Seychelles islands, causing up to 90% mortality of corals in certain areas (Wilkinson 2000). Subsequently, some reefs have shown signs of recovery, whereas other areas now appear to be shifting to an algal-dominated state, resulting in sites of varying benthic condition (Chong-Seng *et al.* 2012). The Seychelles, therefore, provide a unique environment in which to assess the application of the cross-scale resilience model in relation to a disturbance event and subsequent recovery or degradation of the reef. This study aims to: (1) Determine the efficacy of cross-scale redundancy as an indicator of recovery and thus resilience, relative to that provided by functional diversity and redundancy in the absence of body size data; (2) Evaluate the degree of response diversity indicated by the best performing herbivore functional redundancy metrics and examine how this relates to overall delivery of the herbivore function over time; and (3) Determine whether levels of redundancy within sites are retained across the disturbance event or if they vary over time.

8.3 METHODS

8.3.1 *Field methods*

The study is based on ecological surveys of the fish and benthic community of the Seychelles, carried out in 1994, 2005 and 2011, at 21 sites within the inner granitic islands. Summaries of the surveys and key changes in the benthic and fish community are presented.

More detailed descriptions may be found in Jennings, Grandcourt & Polunin (1995), Graham *et al.* (2006), and Wilson *et al.* (2012).

Fish abundance and individual body length (to the nearest centimeter) of diurnally active non-cryptic herbivorous species (37 species from 4 families) were estimated within each replicate survey area (7m radius measured with a precut length of rope) using instantaneous underwater visual census (UVC). Larger, mobile species were recorded before smaller, more site attached species to minimize bias caused by diver effects. The accuracy of fish body length estimations were assessed daily using lengths of PVC pipe, prior to the start of data collection, with estimates consistently within 5% of actual lengths. After the UVCs were completed, the percent cover of different benthic components (macroalgae, hard coral, soft coral and non-living substrata) and the structural complexity of the reef (six point visual scale), were estimated by a diver hovering 2m above the substrate. This method provided rapid estimates of percent cover and complexity within the survey areas and has been shown to provide similar results to methods such as line intercept transects of benthic cover and the linear versus contour rugosity measure (Wilson, Graham & Polunin 2007). In 1994 and 2005, 16 replicate areas were surveyed at each site, whereas in 2011, 8 replicates were surveyed as power analyses indicated that surveying 16 replicates did not significantly alter the percentage change detectable among years in either coral cover or fish biomass (Appendix F Table S1).

8.3.2 Data analysis

8.3.2.1 Benthic condition

Variation in the benthic composition among sites and time periods was assessed using principal component analysis (PCA) in the statistical software PRIMER (Clarke 1993). PCA axis 1 values (hereafter PCA1), which separated sites with high coral cover and complexity (positive values) from those with high macroalgal cover (negative values), were extracted for each site as an index of benthic condition.

8.3.2.2 Redundancy metrics

The body mass of individual fish were estimated from recorded body lengths using published length-mass relationships (Froese & Pauly 2012). The herbivorous fishes were assigned to one of the following functional groups: browser, grazer/detritivore and scraper/excavator (Green & Bellwood 2009). I calculated two sets of redundancy metrics for each site and year. The first set solely incorporated the categorical trait 'functional group' (browser, grazer/detritivore, scraper/excavator) and consisted of the two complementary metrics functional dispersion and functional evenness, which have been developed to look at the

Table 8-1: Description of the two sets of redundancy metrics used in the analyses.

A) Functional group metrics	
i. Dispersion	<i>Dispersion = Mean distance of each species, weighted by biomass, to the centre (biomass weighted mean trait value of whole fish community) of the occupied trait space.</i>
Traits:	
• Functional group	Quantifies how dispersed the species, weighted by their biomass, are distributed through trait space. High values represent high dispersion, and thus high functional diversity. Low values represent low dispersion, and thus little diversity of functional groups.
ii. Evenness	<i>Evenness = Regularity of species within trait space, weighted by biomass</i>
Traits:	
• Functional group	Quantifies how evenly the species, weighted by their relative biomass, are distributed through trait space. High values represent a regular distribution of biomass across occupied trait space, and thus redundancy within each functional group. Low values represent an irregular distribution of biomass across occupied trait space, and thus low redundancy within at least one of the functional groups.
<p>These two complementary metrics indicate the level of diversity and redundancy within functional groups. For example, a combination of high dispersion and high evenness (Fig. 8-2B) would indicate that biomass is distributed evenly among all the functional groups (browsers, grazer/detritivores, and scraper/excavators). In contrast, low dispersion and low evenness (Fig. 8-2C) would indicate few of the functional groups were represented at the sites, and biomass was concentrated into only some of the functional groups.</p>	
B) Function & size metrics	
i. Dispersion	<i>Dispersion= Mean distance of individual species-size groupings, weighted by biomass, to the centre (biomass weighted mean trait value of whole fish community) of the occupied trait space.</i>
Traits:	
• Functional group	Quantifies how dispersed the species-size groupings, weighted by their biomass, are distributed through trait space. High values represent high dispersion, and thus high functional diversity and redundancy across scales. Low values represent low dispersion, and thus low functional diversity and little redundancy across scales.
• Mean body length within species-size groupings	
ii. Evenness	<i>Evenness = Regularity of species-size groupings within trait space, weighted by biomass</i>
Traits:	
• Functional group	Quantifies how evenly the species-size groupings, weighted by their relative biomass, are distributed through trait space. High values represent a regular distribution of biomass across occupied trait space, and thus redundancy within-scales and functional groups. Low values represent an irregular distribution of biomass across occupied trait space, and thus low redundancy within most scales and at least one functional group.
• Mean body length within species-size groupings	
<p>These two complementary metrics indicate the level of functional diversity, redundancy and cross-scale redundancy within the communities. For example, a combination of high dispersion and high evenness (Fig. 8-2B) would indicate that biomass is distributed evenly among the functional groups (browsers, grazer/detritivores, and scraper/excavators) and across size classes giving complementarity and cross-scale redundancy. In contrast, low dispersion and low evenness (Fig. 8-2C) would indicate few functional groups and size classes were represented at the sites, and biomass was unevenly distributed amongst the represented trait combinations. This indicates low complementarity and cross-scale redundancy.</p>	

distribution of function within trait space (see Villéger, Mason & Moullot 2008 for further details; Laliberté & Legendre 2010). Functional dispersion is the mean distance of each species to the mean trait value weighted by biomass. Higher values indicate biomass is dispersed among all the functional groups (Table 8-1Ai). Functional evenness is the regularity by which fish biomass is distributed across trait space, such that higher values indicate biomass is more evenly distributed among functional groups (Table 8-1Aii). Together these metrics indicate the degree of functional group diversity, and redundancy within these groups (Fig. 8-2). To calculate the metrics, two data matrices were developed: sites*species, populated with biomass data, and species*trait, populated with trait attributes (Appendix F Table S2). Calculation of functional dispersion and evenness were performed in the FD package in R (Laliberté & Legendre 2010).

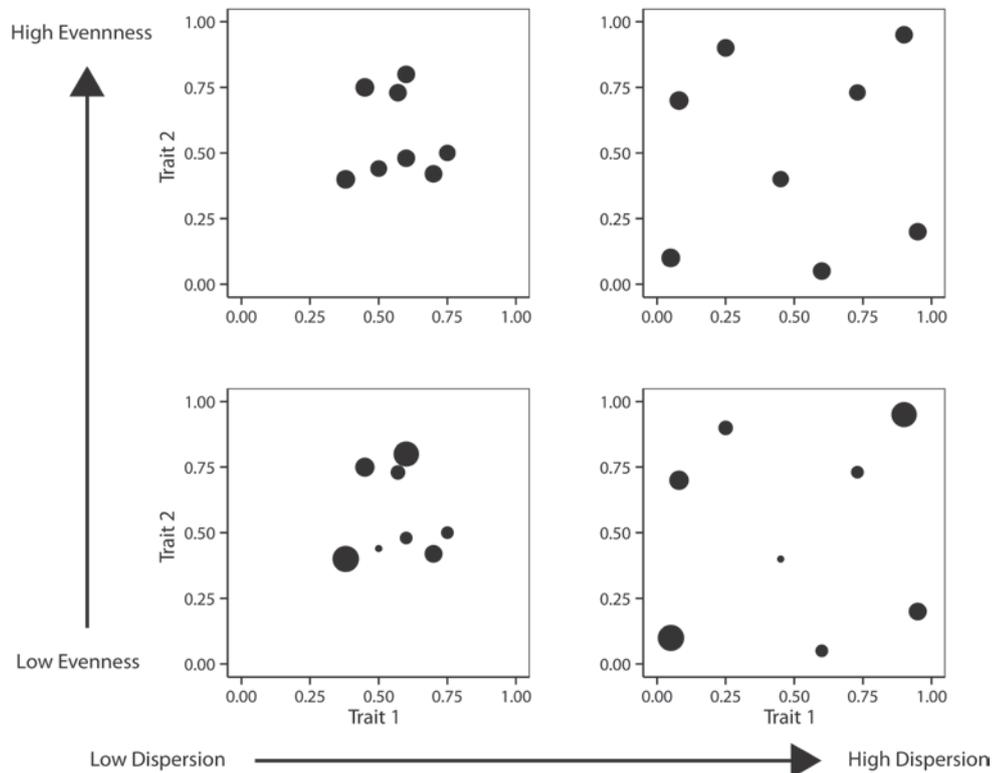


Figure 8-2: Example distribution of species-size groupings in trait space, with relative biomass indicated by bubble size. Individual plots illustrate differences between communities with same number of species and total biomass but exhibiting varying levels of dispersion and evenness. For illustrative purposes, only two trait axes are shown. For the metrics calculated solely from the function information, trait axes would be developed from dummy variables representing each functional group. For the metrics calculated from function and size information, trait axes would be body size and dummy variables representing each functional group. In this latter situation, those sites with high dispersion and evenness possess high cross-scale redundancy and functional diversity, whereas those sites with low dispersion and evenness possess low cross-scale redundancy and functional diversity. Those sites with high dispersion but low evenness have high dispersion across trait space, but the low evenness reduces the inherent redundancy. Sites with low dispersion and high evenness have little dispersion across trait space and thus low functional diversity and cross-scale redundancy, but redundancy within the represented trait combinations.

The second set of metrics incorporated the categorical trait ‘functional group’ and the continuous trait ‘size’ (body length, as a proxy for scale of operation; Nash, Graham & Bellwood 2013), and once again consisted of the complementary metrics functional dispersion and functional evenness. In this instance higher values of functional dispersion indicate biomass is more dispersed among functional groups and size classes (Table 8-1Bi), whilst higher values of functional evenness indicate biomass is more evenly distributed among functional groups and size classes (Table 8-1Bii). Together these metrics indicate the degree of functional group diversity and cross-scale redundancy for a community (Fig. 8-2). Intraspecific variability in body length is thought to be important for size structured aquatic communities (Shurin, Gruner & Hillebrand 2006), and for examining interactions between habitat and reef fishes (Nash *et al.* 2014b). To incorporate intraspecific size variability into estimation of the metrics, each species was split into 5cm size classes (hereafter referred to as species-size categories) and I developed two data matrices based on these species-size categories: sites*species-size categories, populated with biomass data, and species-size categories* traits populated with trait attributes (Appendix F Table S3).

8.3.2.3 Redundancy as an indicator of reef resilience

To evaluate if redundancy metrics are useful indicators of resilience, metrics calculated for 1994 were assessed for their ability to predict the post disturbance benthic trajectory. Change in benthic condition (position on the PCA1) post-disturbance (2005-2011) was first modelled as a function of the two sets of redundancy metrics: functional dispersion 1994 + functional evenness 1994, function & size dispersion 1994 + function & size evenness 1994, and the null model. An information-theoretic approach was used to compare the models. Akaike Information Criteria (AIC) adjusted for small sample sizes (AICc) are presented for the models, detailing change in AICc with respect to the top ranked model ($\Delta AICc$), and AICc weights ($wAICc$) (AICcmodavg package in R; Mazerolle 2013). To understand the relative importance of the two explanatory variables in the best-fit model, a second model selection step evaluated the relative performance of all possible models within the global model (function & size dispersion 1994 + function & size evenness 1994). Prior to fitting the models the explanatory variables were checked for collinearity. The data and residuals were checked to ensure they met the assumptions of the models. The explanatory variables in the best-fit model were used in the remaining analyses.

Herbivorous reef fish are targets of small-scale artisanal fisheries in the Seychelles. Some of the sites were located in no-take marine reserves (n=9), whereas others were located in fished areas (n=12). There has been little recorded differences in the herbivore communities between fished and unfished areas in the Seychelles (Graham *et al.* 2007), potentially due to

compliance issues (Daw *et al.* 2011), nevertheless it was important to evaluate the potential effect of fishing pressure on the analysis. The analysis was repeated incorporating the level of protection (no-take vs. fished) into the models, to see if accounting for fishing pressure influenced the outcomes of the models and the findings of the model comparison.

8.3.2.4 Redundancy as an indicator of response diversity

I did further analyses using those metrics that successfully predicted benthic trajectories. First, I evaluated how these metrics were associated with the maintenance of the herbivore function through time (before and following the disturbance event). Thus, herbivore biomass (a proxy for herbivore function) in 1994, 2005 and 2011 were modelled in relation to the function & size dispersion and evenness in 1994. Herbivore biomass was square root transformed to ensure assumptions of the models were met. Second, for those redundancy metrics that were also related to the maintenance of the herbivore function I investigated patterns of response diversity among size classes; this provided an understanding of how response diversity supports herbivore function. For the analysis, I grouped sites according to low, mid and high redundancy in 1994 (equal groupings with 7 sites in each category), and calculated mean change in herbivore biomass within size classes, across the disturbance (1994-2005) and post-disturbance (2005-2011). Bootstrapped 95% confidence intervals were calculated for each mean change.

8.3.2.5 Redundancy over time

Finally, for those metrics that successfully predicted benthic trajectories, I wanted to evaluate whether values of the metrics were retained across the disturbance event or varied over time. This would allow us to understand whether recovery of the benthos after the disturbance event was reflective of consistent redundancy within the herbivore community, or masked fluctuations in redundancy. Thus, the function & size metrics in 2005 were modelled against their respective values in 1994, in 2011 against values in 2005, and in 2011 against values in 1994.

8.4 RESULTS

8.4.1 Benthic condition

Benthic cover varied among the 21 reefs over the three time periods (Fig. 8-3). The first principle component axis (PCA1) explained 35.9% of the variation among sites and time periods, and differentiated between high coral cover and complexity at positive PCA1 scores, and high macroalgal cover at negative PCA1 scores. The second axis (PCA2) explained 24.4% of the variation among sites and time periods, and differentiated between high rubble and sand

at negative PCA2 scores and high rock cover at positive PCA2 scores. In 1994, sites were located at positive values on PCA1 (high coral cover and complexity and low algal cover, mean of $0.35 \pm 0.14SE$). In 2005 (after the bleaching event in 1998) sites had spread out, moving varying distances in a negative direction along PCA1 (mean of $-0.43 \pm 0.31SE$). By 2011, sites were even more dispersed along PCA1, with some sites returning to a similar location on PCA1 as the sites in 1994, whereas some moved further towards the negative end of PCA1 with high macroalgal cover and low coral cover and complexity (mean of $-0.57 \pm 0.45SE$).

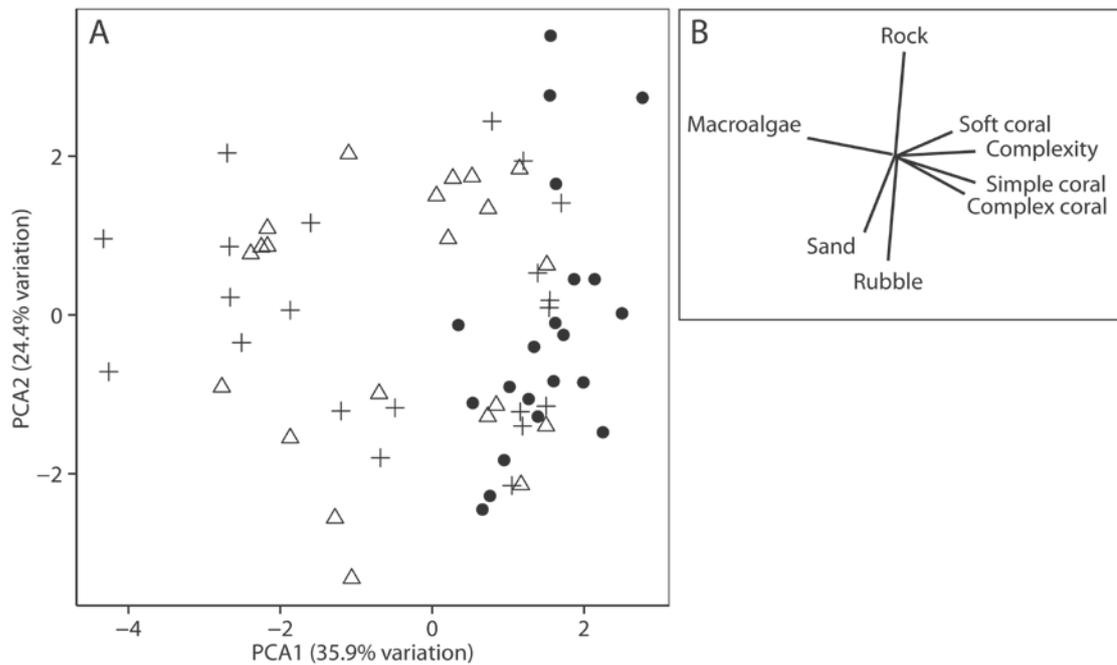


Figure 8-3: Principal component analysis of benthic habitat variables in 1994 (circles), 2005 (triangles) and 2011 (crosses). A) Variation in the benthic habitat among sites shown for the first two axes of a principal component analysis. B) Relative contribution of the benthic variables to the variation in benthic condition.

8.4.2 Redundancy as an indicator of reef resilience

Change in benthic condition post-disturbance was best explained by a model incorporating the function & size metrics (Table 8-2A), with 0.75 of the AICc weight supporting this model. There was most support for the function & size model incorporating dispersion and evenness over one solely including dispersion (Table 8-2B; AICc weight of 0.60). The best-fit model explained 26% of the variation in changing benthic condition, with sites with greater dispersion and evenness in 1994 showing significantly greater recovery post-

disturbance (larger positive change on benthic PCA1 between 2005 and 2011; $F_{2,18} = 4.51$; $p=0.03$; Adj. $R^2 = 0.26$; Fig. 8-4).

The outcome of the analysis for models incorporating fishing pressure was qualitatively similar to those ignoring fishing pressure. Specifically, change in benthic condition post-disturbance was still explained by a model incorporating the function and size metrics (Appendix F Table S4A), and this model performed less well with the inclusion of fishing pressure (Appendix F Table S4B). Therefore, fishing pressure was not included in the remaining analyses.

Table 8-2: Model selection comparing the utility of the different redundancy metrics in 1994 as predictors of reef benthic trajectories from 2005 to 2011. A) Step 1 evaluated the performance of the metrics from the functional group and the functional & size approaches, and B) Step 2 evaluated the performance of models combining different metrics arising from the functional & size approach.

Model	K	AICc	Δ AICc	AICc Wt
A				
Functional group & size dispersion + Functional group & size evenness	4	62.2	0.00	0.75
Null	2	64.9	2.70	0.20
Functional group dispersion + Functional group evenness	4	67.7	5.42	0.05
B				
Functional group & size dispersion + Functional group & size evenness	4	62.2	0.00	0.60
Null	2	64.9	2.70	0.17
Functional group & size dispersion	3	65.2	2.96	0.14
Functional group & size evenness	3	65.6	3.42	0.11

8.4.3 Redundancy as an indicator of response diversity

The evaluation of the maintenance of herbivore function over time, in relation to the best performing redundancy metrics, showed a positive relationship between function & size dispersion in 1994 and herbivore biomass in 1994, 2005 and 2011 (Table 8-3A; Fig. 8-5). Sites with low dispersion in 1994 had little change in biomass over time, whereas sites with high dispersion in 1994 experienced an increase in biomass over time (Fig. 8-5). In contrast, there was no relationship between function & size evenness in 1994 and herbivore biomass in 1994, 2005 and 2011 (Table 8-3B).

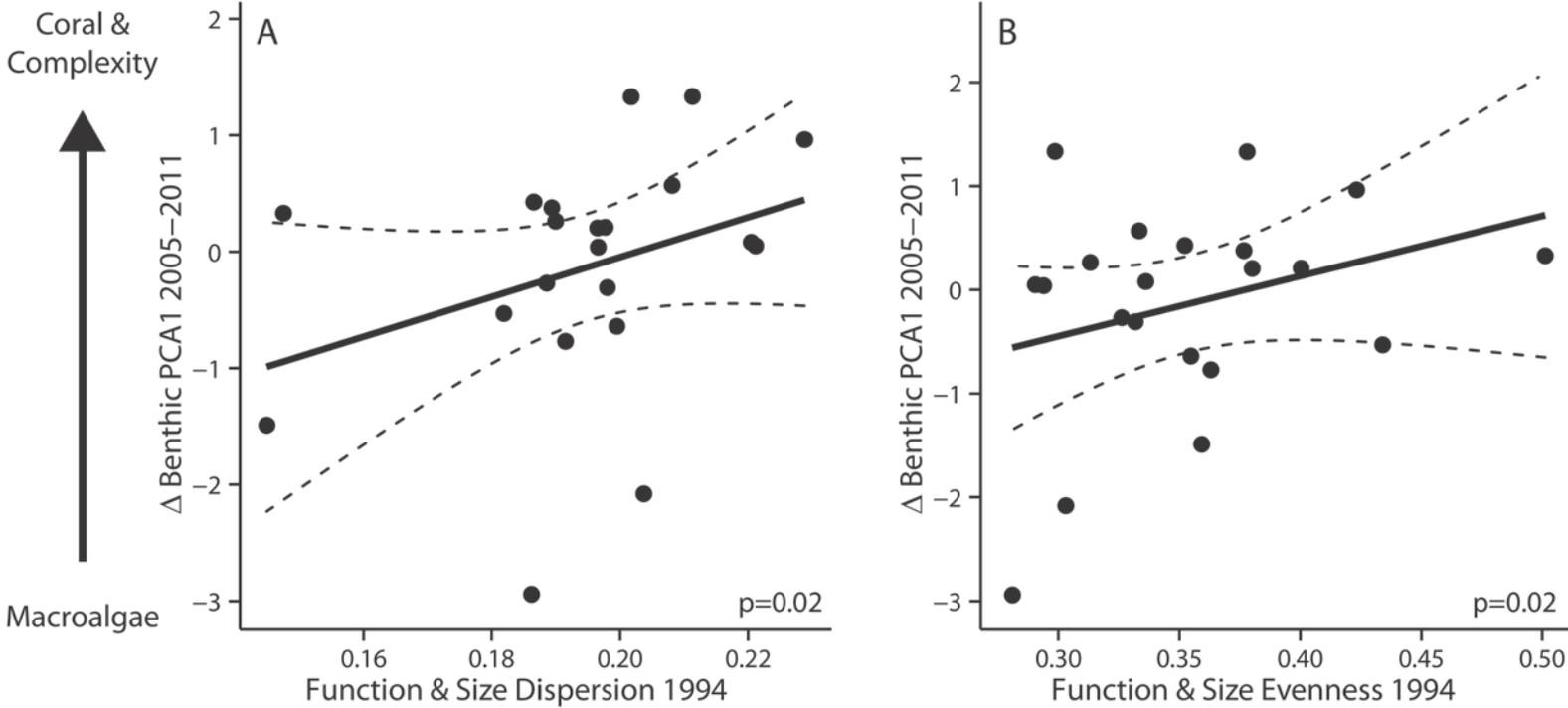


Figure 8-4: The relationship ($\pm 95\%$ CI) between change in benthic condition (position on PCA1) from 2005 to 2011 and A) function & size dispersion and B) function & size evenness. $F_{2,18} = 4.51$; $p = 0.03$; $Adj. R^2 = 0.26$.

Table 8-3: Models of relationships between herbivore biomass in the different years and A) functional & size dispersion, and B) functional & size evenness. Significant relationships are shown in bold. Herbivore biomass was square root transformed to meet model assumptions.

Model	F	P value	Adj. R ²
A			
Sqrt Herbivore Biomass 94 ~ Functional group & size dispersion 94	12.06	<0.01	0.36
Sqrt Herbivore Biomass 05 ~ Functional group & size dispersion 94	8.83	<0.01	0.28
Sqrt Herbivore Biomass 11 ~ Functional group & size dispersion 94	7.96	0.01	0.26
B			
Sqrt Herbivore Biomass 94 ~ Functional group & size evenness 94	3.89	0.06	0.17
Sqrt Herbivore Biomass 05 ~ Functional group & size evenness 94	2.48	0.13	0.07
Sqrt Herbivore Biomass 11 ~ Functional group & size evenness 94	1.44	0.24	0.02

The investigation of the patterns of response diversity among size classes for different levels of function & size dispersion in 1994, indicated that across the disturbance (1994-2005) there was a decline in biomass in the smallest size classes for sites with low, mid and high function & size dispersion in 1994 (Fig. 8-6). There were concurrent increases in biomass at mid-large size classes for those sites with mid and high dispersion in 1994. This increase was only replicated within some mid-size classes at sites with low function & size dispersion in 1994. Post-disturbance (2005-2011) there was considerable variability in biomass trends among sites (shown by wide 95% confidence intervals), however, there were some consistent increases in biomass at small-mid size classes across all sites.

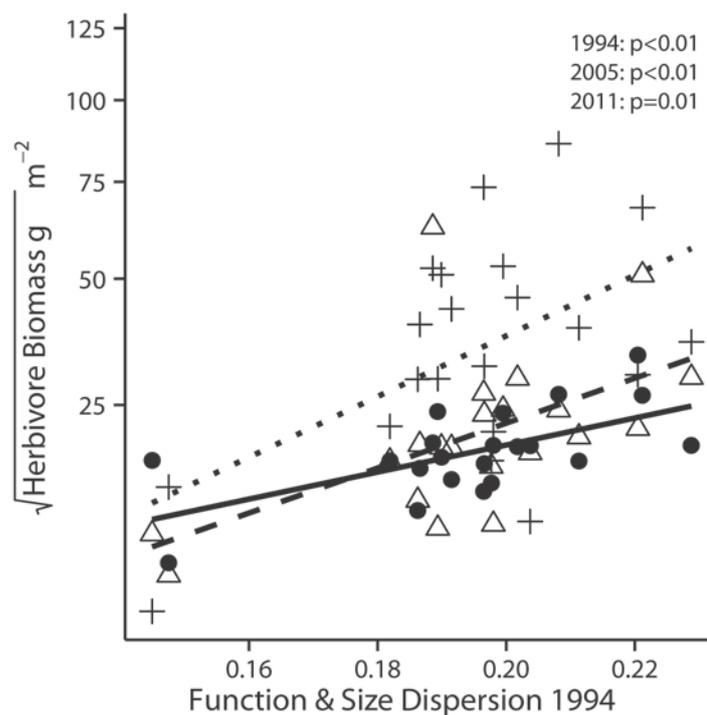


Figure 8-5: Relationships between log herbivore biomass in 1994 (circles, solid line), 2005 (triangles, dashed line) and 2011 (crosses, dotted line) and function & size dispersion in 1994.

8.4.4 Redundancy over time

There was no evidence of predictable patterns in the redundancy metrics over time. Specifically, there was no relationship between function & size dispersion in 1994 and 2005, 2005 and 2011 or 1994 and 2011 (Appendix F Table S5A). Similarly, no relationships were found for function & size evenness between the same year combinations (Appendix F Table S5B).

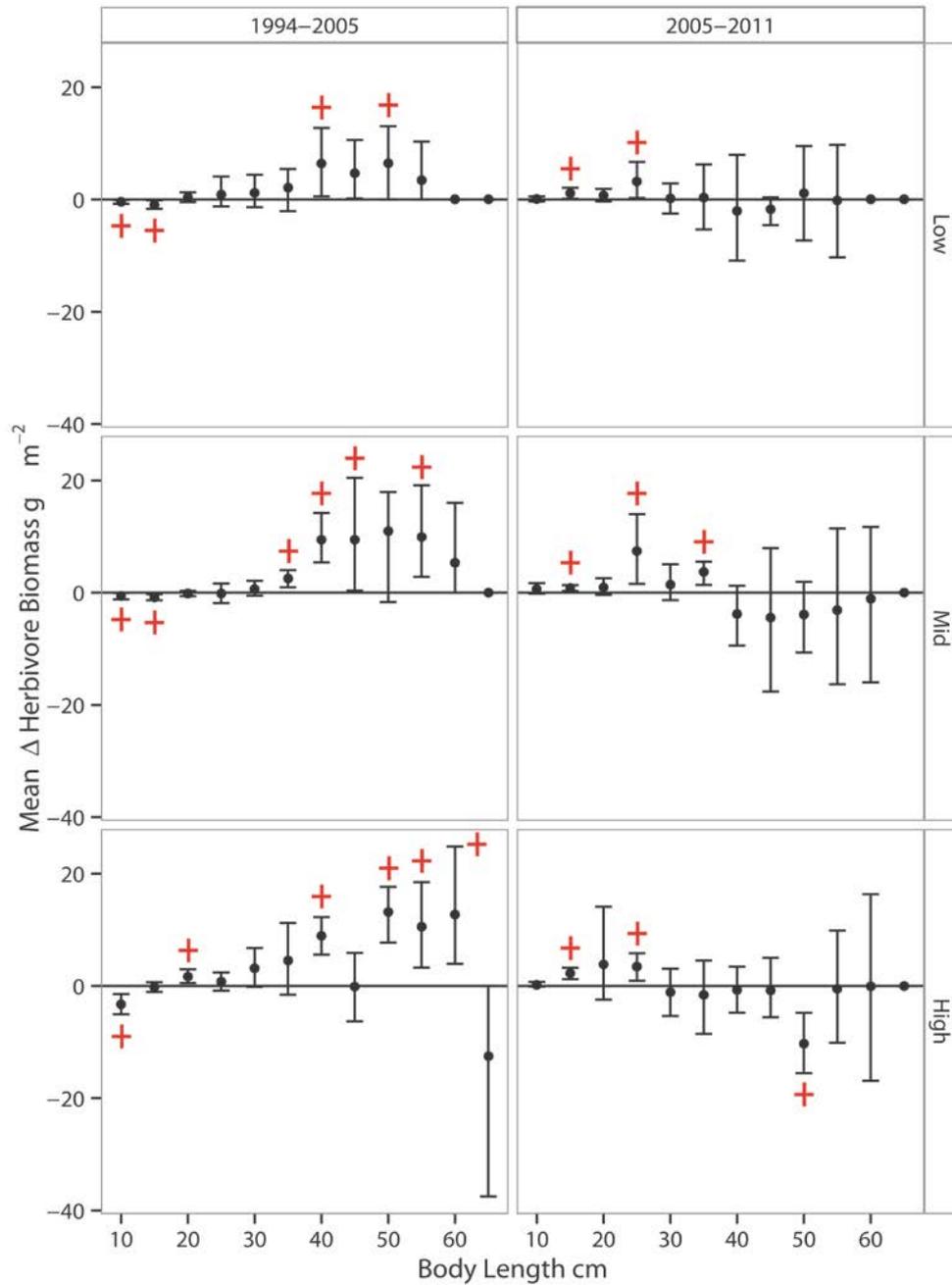


Figure 8-6: Mean change ($\pm 95\%$ CI) in herbivore biomass within size classes between 1994-2005 and 2005-2011 for sites with low, mid or high functional & size dispersion in 1994. Red crosses represent confidence intervals that are significantly different from zero. Note, change in biomass for large size classes may be driven by few individuals due to their large mass, e.g. non-significant decline of individuals $>65\text{cm}$ between 1994 and 2005 at sites with high function & size dispersion is driven by loss of 1 large individual.

8.5 DISCUSSION

This study empirically tested the utility of cross-scale redundancy as an indicator of resilience on coral reefs. The research outcomes demonstrate that greater dispersion and evenness of herbivores across size classes and functional groups supports reef recovery, whereas sites with low dispersion and evenness before a disturbance event are more likely to shift to a macroalgal dominated state. I document size-based response diversity, with small individuals being more negatively impacted by the bleaching event in 1998, but loss of the function provided by these individuals appears to have been compensated for through increases in the biomass of large individuals. Patterns of cross-scale redundancy were not retained across the disturbance event and had not recovered to pre-disturbance levels by 2011, suggesting fish community regeneration may take several decades.

8.5.1 *Redundancy as an indicator of response diversity and reef resilience*

The function metrics incorporating the distribution of herbivore biomass across both functional groups and across size classes (and therefore spatial scales; Nash, Graham & Bellwood 2013), performed considerably better as predictors of reef recovery than those solely describing the distribution of species' biomass across functional groups. This outcome strongly supports Peterson, Allen & Holling's (1998) cross-scale resilience model, i.e. that the distribution of a function across scales indicates the potential for a community to continue to drive ecosystem processes in the face of disturbance. In this model, consistent delivery of important functions leads to regeneration and renewal of the system (Walker, Kinzig & Langridge 1999), and in my example maintenance of the reef in a coral-dominated state.

Exploration of the change in biomass across size classes indicates that this conservation of the herbivore function was a consequence of the breadth of responses by different sized individuals to the 1998 bleaching event, as predicted by the cross-scale resilience model (Peterson, Allen & Holling 1998). The proximate driver of decline in small individuals is likely to be habitat and structural loss across all sites (Bellwood *et al.* 2006a; Graham *et al.* 2006). Increases in large herbivore biomass may result from the proliferation of algae growing in newly open space following coral, leading to growth of individuals and consequent increases in total herbivore biomass (Pratchett *et al.* 2008b). Graham *et al.* (2007) first reported these patterns using data up to 2005, my results suggest that increases in herbivore biomass are maintained through time, but recovery of smaller individuals started to occur post-2005. A similar decline in small herbivores, coincident with stability or increases of large herbivore species following bleaching events, were recorded at Scott Reef in the eastern Indian Ocean (Halford & Caley 2009) and in Fiji (Wilson *et al.* 2008; Wilson *et al.* 2010). Such coherence

indicates that this size-based diversity of responses is likely a general phenomenon of herbivore communities following bleaching events. Critically, recovery was reliant on the contribution of large herbivores providing the important element for reorganisation back towards coral-domination (Steneck, Arnold & Mumby 2014). In contrast, on degraded reefs, similar increases in the biomass of large individuals were lacking, presumably due to a dearth of large herbivores pre-disturbance. Such patterns are not limited to reefs; in tropical forests large trees that remain after a disturbance may play a central role in renewal and recovery (Elmqvist *et al.* 2002).

Large bodied herbivore individuals provide greater functional impact due to exponential relationships found between size and scraped area per unit time (Lokrantz *et al.* 2008), bite volume (Bonaldo & Bellwood 2008), and functional breadth (Green & Bellwood 2009). Thus large herbivores are likely to favour coral growth over macroalgal expansion (Steneck, Arnold & Mumby 2014). As a consequence, body size of reef fish appears to act as both an effect and a response trait, in that it reflects the magnitude of ecosystem function and the likely responses to disturbance (Laliberté *et al.* 2010). The bias in functional impact towards large individuals does mean that cross-scale redundancy may not prove as effective an indicator of resilience in instances where large rather than small individuals respond negatively to a disturbance. However, Adam *et al.* (2011) provided evidence that very high densities of small herbivores were able to control algal growth and open up space for coral recruits following a crown of thorns starfish outbreak. Nevertheless, this uncertainty presents a need to explore patterns of cross-scale response diversity among different herbivore species following a wider range of natural and anthropogenic disturbances (Winfree 2013).

8.5.2 Redundancy over time

It is critical to move beyond assessing resilience at a single time step, and to integrate changes in resilience indicators over time (Hughes *et al.* 2005). In my study, I found no relationship between either redundancy metric pre- and post-disturbance. Furthermore, neither metric recovered to pre-disturbance levels for those sites showing recovery of the benthic community back to coral-dominance. Surprisingly, the highest level of cross-scale redundancy in 2011 was at a site with high macroalgal cover. This suggests that cross-scale redundancy of herbivores may help prevent phase shifts but does not necessarily promote reversal of shifts once they have occurred.

At recovering sites the compensatory increases in herbivore biomass in large size classes across and subsequent to the disturbance event effectively masked the unpredictable patterns in dispersion and evenness, such that the coral community is recovering and herbivore function appears to be sufficient at these sites. However, further disturbances that occur before

cross-scale patterns of function return to pre-disturbance levels may not be withstood in a similar manner to the 1998 bleaching event for two key reasons: (1) Due to the loss of small individuals across the disturbance event, mortality of large individuals over time is unlikely to be compensated for through the growth and maturation of smaller cohorts of fish, such that the increase in large herbivores represents only a temporary buffer for the herbivore function (Graham *et al.* 2007); and (2) I solely examined response diversity in relation to a bleaching event, whereas other types of disturbance e.g. cyclones or coastal development, may result in different response capabilities among fish size classes (Graham, Nash & Kool 2011; Winfree 2013). The concealed losses in the potential ongoing delivery of function are a significant cause for concern where monitoring programs and management actions rely on biomass or abundance of important species as indicators of a functionally intact and resilient system (Hughes *et al.* 2010).

Work on other isolated Indian Ocean reefs showed recovery of coral cover after twelve years (Chagos Reef; Sheppard *et al.* 2012; Scott Reef; Gilmour *et al.* 2013) years following the 1998 bleaching event, but community composition differed to starting conditions. A study on the Great Barrier Reef found that fish communities have not returned to pre-bleaching composition more than 16 years after the 1998 bleaching (Bellwood *et al.* 2012). Thus, it is perhaps not surprising that although the Seychelles reefs were showing signs of recovery 11 years after the 1998 bleaching event, neither coral nor fish communities were showing pre-disturbance composition across all sites, with implications for cross-scale redundancy. In light of the potential for more frequent disturbances with rising climate change and anthropogenic pressures, this emphasises the need for careful management of the herbivore community to help sustain their function into the future.

8.5.3 Management implications

Reversing phase shifts, whilst not impossible (Graham *et al.* 2013), certainly presents significant logistical and economic challenges (Hughes *et al.* 2010; McClanahan, Muthiga & Coleman 2011). Thus, it is important for managers to have the tools to help prevent regime shifts (Nyström *et al.* 2008). My findings indicate that sustaining robust and functional herbivore communities through the maintenance or rebuilding of cross-scale redundancy provides a proactive avenue for managers to support reef resilience to face future disturbances and prevent shifts to macro-algal dominated states. Non-random loss of herbivores, following the bleaching event, suggests that it is not enough for management actions to support redundancy, they also need to target the response diversity underpinning this redundancy. This

could be achieved by moving beyond strategies aimed at protecting specific species, to management actions that sustain broad size spectra within species.

Whilst it is important to protect large individuals, such an objective is likely to be difficult to achieve due to fishing efforts directed at larger-bodied fish (Bellwood, Hoey & Choat 2003; Hawkins & Roberts 2004). There is evidence that loss of herbivores may not be reversed through marine parks alone (McClanahan, Muthiga & Coleman 2011), a pattern supported in the Seychelles where compliance with no-take areas is mixed (Daw *et al.* 2011). Thus, a multi-pronged management strategy may best address the impacts of fishing on herbivorous fish communities, blending approaches such as controls on fishing effort, with controls on the types of gears used by fisherman and access rights (Hilborn 2007). Combinations of these non-traditional management techniques are more likely to not only protect species, but also specific size classes within species, supporting cross-scale herbivore redundancy (McClanahan & Hicks 2011; Nash, Graham & Bellwood 2013).

Despite the apparent importance of cross-scale redundancy as an indicator of reef resilience, I am not advocating specific thresholds for function and size dispersion in herbivore communities for two reasons: (1) There is a need to be cautious about basing management actions on response diversity with respect to a single disturbance type, due to the range of pressures acting on coral reefs and the likely variability in response diversity to different disturbances (Mori, Furukawa & Sasaki 2012). (2) Cross-scale redundancy needs to be considered in relation to reef context. For example low levels of cross-scale redundancy within specific functional groups may arise due to the evolutionary history of a region, such as relatively low variation in abiotic drivers over time (Walker, Kinzig & Langridge 1999; Bellwood *et al.* 2004), rather than be the result of recent recurrent impacts. Thus setting targets for cross-scale redundancy globally, would not signify baseline conditions in different regions, and are likely to present unattainable objectives in many locations.

The best-fit model examining reef recovery explained 26% of the variability in benthic condition. To exploit the full potential of supporting cross-scale redundancy for enhancing resilience, this redundancy needs to be managed in concert with other factors related to geomorphology, connectivity, and coral community composition that may also influence the resilience of the coral-dominated state (McClanahan *et al.* 2012). Nevertheless, whilst among site variation means that local factors are important, my results provide clear evidence for the potential of the cross-scale resilience model to be employed on coral reefs as a framework for predicting resilience.

Chapter 9: General Discussion

Current and projected anthropogenic impacts on coral reefs (Hoegh-Guldberg *et al.* 2007), combined with the extensive reliance of human communities on the ecosystem services provided by reef systems (Moberg & Folke 1999; Teh, Teh & Sumaila 2013), has generated a serious need to understand how to sustain and manage processes that maintain reefs within coral-dominated states. Herbivory is a critical component within feedback loops that are thought to support coral-based regimes (Mumby 2009), and as such, knowledge of how herbivores provide their function and respond to habitat context, is essential for effective reef management (Bellwood, Hughes & Hoey 2006).

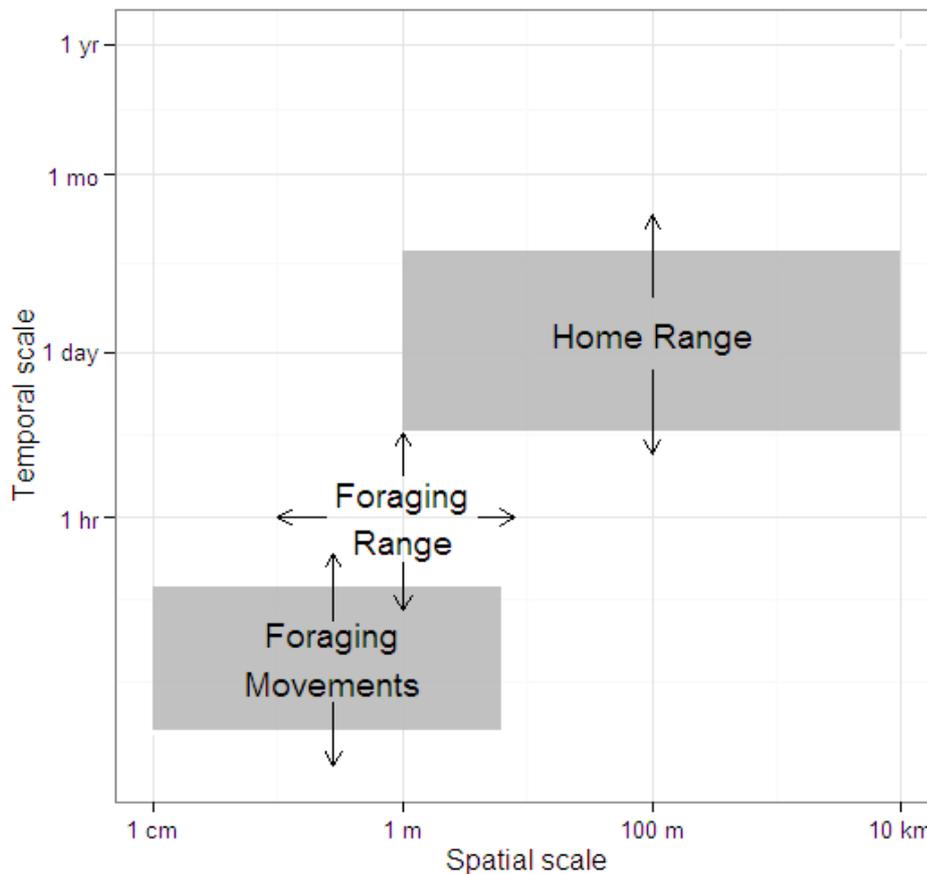


Figure 9-1: Spatial scales of home range and foraging movements reviewed and quantified in this thesis, where foraging movements are small-scale feeding movements within the broader foraging range. Scales of foraging ranges, and the temporal scales of these movements are as yet unestablished (arrows indicate uncertainty). Note spatial scale of foraging movements relate to herbivorous species only.

In response to this need, Part 1 of the thesis characterised the spatial ecology of reef fish, and herbivores in particular, moving beyond single species approaches by quantifying patterns across communities (Fig. 9.1). Specifically, the study showed that positive allometry of movement in reef fish occurs at both the level of home range (Chapter 2) and at the smaller scales of individual foraging movements (Chapter 3). This research updates existing work on home range allometry in reef fish (Kramer & Chapman 1999), which relied primarily on older studies using visual tracking of fish before telemetry methods came to the fore. The work on foraging movements provides a similar analysis to that of home range allometry but at a spatial scale that had, to date, not been explored.

Movement and body size scaling relationships cannot be viewed independently of fishing pressure and habitat context. Browsing species were found to cover a small range of spatial scales whilst foraging and are particularly vulnerable to fishing, indicating the potential for a very narrow breadth of spatial scales over which the browsing function may be delivered (Chapter 3). These findings are particularly worrisome considering: (1) the relatively few species that appear to be capable of reversing phase shifts once they have occurred, by acting as browsers and consuming macroalgae (Bellwood, Hughes & Hoey 2006); and (2) the increasing evidence of overfishing of herbivores in many areas (Edwards *et al.* 2014). Benthic condition was also found to influence the size of foraging movements and the scale at which fish provide their function (Chapter 4). With the current uncertainty regarding coral reef trajectories in response to disturbance events (Hughes *et al.* 2012; Zhang *et al.* 2014), this plasticity of foraging behaviour means that managers are faced with the unenviable task of trying to support herbivory to help mitigate impacts, even as the herbivore function provided by species changes over time and space (Francini *et al.* 2010; Bennett & Bellwood 2011; Chong-Seng *et al.* 2014). Finally, in Part 1, quantification of the relationship between habitat patterns across scales and the body depth distributions of reef fish, identified the close ties between the changing availability of shelter due to disturbance events and consequent modifications in fish size distributions (Chapter 5). This has implications for changes in the delivery of function across scales, and provides a strong mechanistic basis for the variation in the relationships between structural complexity and fish communities recorded in the literature (reviewed in Graham & Nash 2013). Part 1 of the thesis informed studies within Part 2, providing fundamental knowledge to apply and evaluate the cross-scale resilience model on coral reefs, identifying the benefits of this approach as an indicator of resilience.

The current state of knowledge on discontinuity theory and the cross-scale resilience model was reviewed with key research gaps identified (Chapter 6). This chapter brought together disparate strands of research from a range of fields such as macroecology (Gotelli,

Graves & Rahbek 2010), invasion ecology (Allen, Forsy & Holling 1999), hierarchy theory (Allen & Starr 1982) and resilience science (Peterson, Allen & Holling 1998), providing important links between the different areas. One key research gap highlighted in the study was the need for appropriate size metrics to explore the influence of habitat structure on body size distributions for taxa with indeterminate growth (White *et al.* 2007), a critical step needed to implement the cross-scale resilience model for reef fish communities. Individual size and abundance metrics were found to be suitable for evaluating habitat effects on fish communities (Chapter 7). The methods developed in this chapter may also be used for a broader range of applications such as indicating the relative vulnerability of specific size classes to different, scale specific disturbances (Owens & Bennett 2000; De la Montaña, Rey-Benayas & Carrascal 2006). Perhaps, most promisingly, the study outcomes indicated a common method (individual size-density relationships) for exploring body size distribution patterns across taxa. Such a method supports current interest to break down the terrestrial-aquatic divide in the approaches used by various ecological fields (Webb 2012). Finally, the outcomes of Chapter 7 led to the development of new metrics for applying the cross-scale resilience model in the context of coral reef fish (Chapter 8). The findings of this ultimate study suggested that the distribution of the herbivore function across scales is associated with response diversity and recovery of the benthos towards coral-domination. These outcomes provide managers with a mechanism to support reef resilience and prevent phase shifts to macroalgal domination, which are likely to prove logistically difficult and extremely costly to reverse (Hughes *et al.* 2010).

9.1 CONTRIBUTIONS TO METHODOLOGY

This thesis has contributed a number of novel methods for exploring scale-specific function in reef fish. Intra-foray and inter-foray distance provide ways of quantifying movement at small scales, relevant to the provision of the herbivore function on reefs (Chapter 3 and 4). These metrics complement more traditional approaches such as home range, and require little in the way of equipment, thus lending themselves to a range of settings.

A number of methods have been modified and repurposed in this thesis, expanding their application and providing new ways of examining the interaction between habitat availability and the body size distributions of associated communities. In Chapter 5, an existing rocky shore method (Wilding, Rose & Downie 2007) was adapted to assess the fractal complexity of reef habitats. This provides an accessible method for examining cross-scale patterns in structural complexity, giving important insights into the dynamic nature of these patterns and their relationship with changing fish body size distributions.

Body size distributions have commonly be compared using methods that require *a priori* decisions about the shape of the distributions (Xu *et al.* 2010) or are limited to univariate data (Forys & Allen 2002). Calculating distance matrices for use in Analysis of Similarities from body size distribution data, rather than traditional species abundance information, provides a way of statistically comparing size distributions without these constraints (Chapter 7). Finally, modifying existing trait-based functional diversity metrics to incorporate information on size classes within species, provides a way of incorporating intraspecific variability into these metrics (Chapter 8). This helps to address a significant methodological gap that has been identified in the literature (e.g. Petchey & Gaston 2006).

9.2 MANAGEMENT IMPLICATIONS

There are a number of key findings from this thesis that provide fundamental knowledge needed by managers to effectively support fish and herbivore populations on coral reefs under pressure from anthropogenic driven disturbances and change. The problems associated with quantifying allometry of home range in reef fish arising from the evolution of tracking methods (Chapter 2), suggest extreme caution needs to be exercised when using home range–body size scaling relationships as a basis for marine reserve design. However, the combination of relatively small home ranges of reef fish and the documented reluctance of individuals to cross open-areas (Chapman & Kramer 2000; Turgeon *et al.* 2010), indicates that where marine reserve objectives focus on species’ protection, then reserve placement should exploit the fragmented nature of the broader reefscape to maximise retention of fish within reserve boundaries.

Investigations targeting smaller scale foraging movements highlighted the vulnerability of the browsing function (Chapter 3): its delivery is limited to a small range of spatial scales, and is provided by few species that are highly susceptible to fishing (Cheung, Pitcher & Pauly 2005). These findings indicate that management efforts need to support the browsing function through reduction of fishing effort, potentially through gear management (Gomes, Erzini & McClanahan 2013; Graham *et al.* 2013). Furthermore, the changing spatial behaviour of fish (Chapter 4) and modifications in fish body depth distributions (Chapter 5) in response to habitat condition, highlight the dynamic nature of both foraging behaviour and community function as a whole. This suggests that management of reefs requires adaptive strategies that can respond quickly and effectively to the changing fish community and behaviour, as reefs follow different benthic trajectories. In highlighting the importance of redundancy within the herbivore group, Chapter 8 further emphasises the need to manage and support herbivore function across space. This clearly indicates that mitigation strategies that support biodiversity rather than

function, may not be sufficient to ensure the effective provision of herbivory by the fish community (Mouillot *et al.* in press).

9.3 FUTURE RESEARCH DIRECTIONS

Part 1 of the study goes a long way to characterise the spatial scales at which fish provide their function and interact with the reef (Fig. 9.1). However, a number of key research gaps remain: (1) The slope of the positive relationship between home range and body size in reef fish is, as yet, undetermined, and the relative strengths and weaknesses associated with different methods for estimating home range in reef fish are poorly understood (Chapter 2). Further studies are needed to estimate home ranges of reef fish using a range of methodologies. (2) The spatial scale of reef fish movements post-recruitment have been quantified at large (home range, reviewed in Chapter 2), and small scales (foraging movements for herbivores, Chapter 3 and 4; Fig. 9.1). However, there has been little done to quantify mid-scale functional movements such as foraging range (but see Welsh & Bellwood 2012b). The positive allometry between body size and movements at large and small scales suggests that similar patterns may be found for functional range, nevertheless, this hypothesis needs empirical testing. (3) Work by Lefevre and Bellwood (2011) suggests that there may significant temporal dynamics in foraging behaviour, but there has been a lack of studies characterising the temporal scales at which fish provide their function (Fig. 9.1). (4) Chapter 4 highlighted the plasticity of foraging behaviour in relation to habitat condition, with foraging movements increasing in size in response to reduced coral cover. However, the concentration or overlap of foraging effort and movements among individuals and species across the reefscape was not determined. These patterns have significant consequences for the spatial delivery of the herbivory function by fish communities as a whole. The potential for herbivory effort to be diluted due to low coral cover has been demonstrated in the Caribbean (Williams, Polunin & Hendrick 2001). There is now a need to bring together information on grazing effort and the scale of herbivore movements to determine broad scale patterns in functional impact across space.

Part 2 of the study applies the cross-scale resilience model on coral reefs. Empirical testing of the model has been somewhat limited to date (Chapter 6), suggesting that more work, beyond that presented in this thesis, is ultimately needed to move the model from a conceptual framework to a practical management tool across a broader range of ecosystems. Whilst Chapter 7 provided the metrics needed to effectively implement the cross-scale resilience model for reef fish, it also highlighted other research gaps; specifically, the need to separate out the relative effects of the aquatic environment and indeterminate growth on the influence of habitat on body size distributions. Outcomes of the final chapter indicate that cross-scale redundancy

supports response diversity within the herbivore community, enhancing the resilience of the reef (Chapter 8). There is now a need to understand the relative importance of this resilience indicator compared to other proposed indicators such as recruitment, coral community composition and sedimentation (McClanahan *et al.* 2012). Application of the model to different reef systems would provide an understanding of how the type of disturbance and the reef context influences the effect of cross-scale redundancy on reef recovery. Chapter 8 implemented the model for reefs impacted by a bleaching event and located in a relatively isolated reef ecosystem. Physical disturbances such as hurricanes impact the reef differently to biological disturbances like bleaching, influencing recovery trajectories (Graham, Nash & Kool 2011). In addition, connectivity among reefs is likely to alter the dynamics within the herbivore community through recruitment and mobile links (Nystrom & Folke 2001). As a consequence there is significant scope for research to bring together and understand the interactions between these different variables influencing and supporting reef resilience.

Chapter 10: References

- Ackerly, D.D. & Cornwell, W.K. (2007) A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. *Ecology Letters*, **10**, 135-145.
- Ackerman, J., Bellwood, D. & Brown, J. (2004) The contribution of small individuals to density-body size relationships: examination of energetic equivalence in reef fishes. *Oecologia*, **139**, 568-571.
- Ackerman, J.L. & Bellwood, D.R. (2000) Reef fish assemblages: a re-evaluation using enclosed rotenone stations. *Marine Ecology Progress Series*, **206**, 227-237.
- Adam, T.C., Schmitt, R.J., Holbrook, S.J., Brooks, A.J., Edmunds, P.J., Carpenter, R.C. & Bernardi, G. (2011) Herbivory, connectivity, and ecosystem resilience: response of a coral reef to a large-scale perturbation. *PLoS ONE*, **6**, e23717.
- Adams, V.M., Mills, M., Jupiter, S.D. & Pressey, R.L. (2011) Improving social acceptability of marine protected area networks: A method for estimating opportunity costs to multiple gear types in both fished and currently unfished areas. *Biological Conservation*, **144**, 350-361.
- Addicott, J.F., Aho, J.M., Antolin, M.F., Padilla, D.K., Richardson, J.S. & Soluk, D.A. (1987) Ecological neighborhoods: scaling environmental patterns. *Oikos*, **49**, 340-346.
- Afonso, P., Fontes, J., Holland, K.N. & Santos, R.S. (2008) Social status determines behaviour and habitat usage in a temperate parrotfish: implications for marine reserve design. *Marine Ecology-Progress Series*, **359**, 215-227.
- AIMS (2011) Reef monitoring. Townsville.
- Allen, C.R., Angeler, D.G., Garmestani, A.S., Gunderson, L.H. & Holling, C.S. (2014) Panarchy: theory and application. *Ecosystems*, **17**, 578-589.
- Allen, C.R., Forsy, E.A. & Holling, C.S. (1999) Body mass patterns predict invasions and extinctions in transforming landscapes. *Ecosystems*, **2**, 114-121.
- Allen, C.R., Garmestani, A.S., Havlicek, T.D., Marquet, P.A., Peterson, G.D., Restrepo, C., Stow, C.A. & Weeks, B.E. (2006) Patterns in body mass distributions: sifting among alternative hypotheses. *Ecology Letters*, **9**, 630-643.
- Allen, C.R., Gunderson, L. & Johnson, A.R. (2005) The use of discontinuities and functional groups to assess relative resilience in complex systems. *Ecosystems*, **8**, 958-966.
- Allen, C.R. & Holling, C.S. (2002) Cross-scale morphology. *Encyclopedia of Environmetrics* (eds A.H. El-Shaarawi & W.W. Piegorsch), pp. 450-452. John Wiley & Sons Ltd, Chichester.

- Allen, C.R. & Saunders, D. (2006) Multimodel inference and the understanding of complexity, discontinuity, and nomadism. *Ecosystems*, **9**, 694-699.
- Allen, T.F.H. & Starr, T.B. (1982) Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago.
- Alvarez-Filip, L., Dulvy, N.K., Gill, J.A., Cote, I.M. & Watkinson, A.R. (2009) Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings of the Royal Society B-Biological Sciences*, **276**, 3019-3025.
- Anderson, S.H., Kelly, D., Ladley, J.J., Molloy, S. & Terry, J. (2011) Cascading effects of bird functional extinction reduce pollination and plant density. *Science*, **331**, 1068-1071.
- Andres, N.G. & Rodenhouse, N.L. (1993) Resilience of corals to hurricanes - a simulation-model. *Coral Reefs*, **12**, 167-175.
- Angeler, D.G., Allen, C.R. & Johnson, R.K. (2012) Insight on invasions and resilience derived from spatiotemporal discontinuities of biomass at local and regional scales. *Ecology and Society*, **17**, 32.
- Angeler, D.G., Allen, C.R. & Johnson, R.K. (2013) Measuring the relative resilience of subarctic lakes to global change: redundancies of functions within and across temporal scales. *Journal of Applied Ecology*, **50**, 572-584.
- Angeler, D.G., Drakare, S. & Johnson, R.K. (2011) Revealing the organization of complex adaptive systems through multivariate time series modeling. *Ecology and Society*, **16**, 5.
- Angeler, D.G., Viedma, O. & Moreno, J. (2009) Statistical performance and information content of time lag analysis and redundancy analysis in time series modeling. *Ecology*, **90**, 3245-3257.
- Araújo, M.B. & Luoto, M. (2007) The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography*, **16**, 743-753.
- Arthur, R., Done, T.J. & Marsh, H. (2005) Benthic recovery four years after an El Nino-induced coral mass mortality in the Lakshadweep atolls. *Current Science*, **89**, 694-699.
- Ashton, K.G. (2002) Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. *Global Ecology and Biogeography*, **11**, 505-523.
- Auge, A.A., Chilvers, B.L., Moore, A.B. & Davis, L.S. (2011) Foraging behaviour indicates marginal marine habitat for New Zealand sea lions: remnant versus recolonising populations. *Marine Ecology Progress Series*, **432**, 247-256.
- Avgar, T., Mosser, A., Brown, G.S. & Fryxell, J.M. (2013) Environmental and individual drivers of animal movement patterns across a wide geographical gradient. *Journal of Animal Ecology*, **82**, 96-106.
- Baker, R.R. (1978) *The evolutionary ecology of animal migration*. Hodder & Stoughton, London.

- Barnett, A., Abrantes, K.G., Seymour, J. & Fitzpatrick, R. (2012) Residency and spatial use by reef sharks of an isolated seamount and its implications for conservation. *PLoS ONE*, **7**.
- Bartholomew, A. & Shine, R.L. (2008) Space size relative to prey width (Sp/Py) influences macrofaunal colonization of artificial structures. *Marine Ecology-Progress Series*, **358**, 95-102.
- Barton, K. (2013) MuMIn: Multi-model inference.
- Basset, A. (1995) Body size-related coexistence: an approach through allometric constraints on home-range use. *Ecology*, **76**, 1027-1035.
- Bejarano, S., Mumby, P. & Sotheran, I. (2011) Predicting structural complexity of reefs and fish abundance using acoustic remote sensing (RoxAnn). *Marine Biology*, **158**, 489-504.
- Bellwood, D.R. (1985) The functional morphology, systematics and behavioural ecology of parrotfishes (family Scaridae). PhD, James Cook University.
- Bellwood, D.R., Baird, A., Depczynski, M., González-Cabello, A., Hoey, A., Lefèvre, C. & Tanner, J. (2012) Coral recovery may not herald the return of fishes on damaged coral reefs. *Oecologia*, **170**, 567-573.
- Bellwood, D.R. & Choat, J.H. (1990) A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. *Environmental Biology of Fishes*, **28**, 189-214.
- Bellwood, D.R., Hoey, A.S., Ackerman, J.L. & Depczynski, M. (2006a) Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. *Global Change Biology*, **12**, 1587-1594.
- Bellwood, D.R., Hoey, A.S. & Choat, J.H. (2003) Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecology Letters*, **6**, 281-285.
- Bellwood, D.R., Hoey, A.S. & Hughes, T.P. (2012) Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 1621-1629.
- Bellwood, D.R., Hughes, T.P., Folke, C. & Nystrom, M. (2004) Confronting the coral reef crisis. *Nature*, **429**, 827-833.
- Bellwood, D.R., Hughes, T.P. & Hoey, A.S. (2006) Sleeping functional group drives coral-reef recovery. *Current Biology*, **16**, 2434-2439.
- Bellwood, D.R. & Wainwright, P.C. (2002) The history and biogeography of fishes on coral reefs. *Coral Reef Fishes: Dynamics and diversity in a complex ecosystem* (ed. P.F. Sale), pp. 5-32. Elsevier, San Diego, CA.
- Bellwood, D.R., Wainwright, P.C., Fulton, C.J. & Hoey, A.S. (2006b) Functional versatility supports coral reef biodiversity. *Proceedings of the Royal Society B-Biological Sciences*, **273**, 101-107.

- Belyea, L.R. & Lancaster, J. (1999) Assembly rules within a contingent ecology. *Oikos*, **86**, 402-416.
- Benjamini, Y. & Hochberg, Y. (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, **57**, 289-300.
- Bennett, S. & Bellwood, D.R. (2011) Latitudinal variation in macroalgal consumption by fishes on the Great Barrier Reef. *Marine Ecology Progress Series*, **426**, 241-252.
- Bennett, S., Vergés, A. & Bellwood, D. (2010) Branching coral as a macroalgal refuge in a marginal coral reef system. *Coral Reefs*, **29**, 471-480.
- Bergman, K.C., Ohman, M.C. & Svensson, S. (2000) Influence of habitat structure on *Pomacentrus sulfureus*, a western Indian Ocean reef fish. *Environmental Biology of Fishes*, **59**, 243-252.
- Biggs, R., Carpenter, S.R. & Brock, W.A. (2009) Turning back from the brink: detecting an impending regime shift in time to avert it. *Proceedings of the National Academy of Sciences*, **106**, 826-831.
- Blackburn, T.M. & Gaston, K.J. (1994) Animal body size distributions: patterns, mechanisms and implications. *Trends in Ecology and Evolution*, **9**, 471-474.
- Blumstein, D.T. (2003) Flight-initiation distance in birds is dependent on intruder starting distance. *The Journal of Wildlife Management*, **67**, 852-857.
- Bolden, S.K. (2001) Using acoustic telemetry to determine home range of a coral reef fish. *Electronic tagging and tracking in marine fisheries* (eds J. Sibert & J.L. Nielsen). Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.-S.S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution*, **24**, 127-135.
- Bonaldo, R.M. & Bellwood, D.R. (2008) Size-dependent variation in the functional role of the parrotfish *Scarus rivulatus* on the Great Barrier Reef, Australia. *Marine Ecology Progress Series*, **360**, 237-244.
- Börger, L., Dalziel, B.D. & Fryxell, J.M. (2008) Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecology Letters*, **11**, 637-650.
- Borthagaray, A.I., Arim, M. & Marquet, P.A. (2012) Connecting landscape structure and patterns in body size distributions. *Oikos*, **121**, 697-710.
- Bozec, Y.-M., Yakob, L., Bejarano, S. & Mumby, P.J. (2012) Reciprocal facilitation and non-linearity maintain habitat engineering on coral reefs. *Oikos*, **122**, 428-440.

- Bradbury, R.H., Reichelt, R.E. & Green, D.G. (1984) Fractals in ecology: methods and interpretation. *Marine Ecology Progress Series*, **14**, 295-296.
- Brook, B.W., Sodhi, N.S. & Bradshaw, C.J.A. (2008) Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, **23**, 453-460.
- Brown, J.H. (1995) *Macroecology*. University of Chicago Press, Chicago.
- Brown, J.H., Marquet, P.A. & Taper, M.L. (1993) Evolution of body size: consequences of an energetic definition of fitness. *The American Naturalist*, **142**, 573-584.
- Brown, J.L. (1964) The evolution of diversity in avian territorial systems. *The Wilson Bulletin*, **76**, 160-169.
- Buchmann, C.M., Schurr, F.M., Nathan, R. & Jeltsch, F. (2011) An allometric model of home range formation explains the structuring of animal communities exploiting heterogeneous resources. *Oikos*, **120**, 106-118.
- Buckland, S.T., Magurran, A.E., Green, R.E. & Fewster, R.M. (2005) Monitoring change in biodiversity through composite indices. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **360**, 243-254.
- Buckle, E.C. & Booth, D.J. (2009) Ontogeny of space use and diet of two temperate damselfish species, *Parma microlepis* and *Parma unifasciata*. *Marine Biology*, **156**, 1497-1505.
- Burkett, V.R., Wilcox, D.A., Stottlemeyer, R., Barrow, W., Fagre, D., Baron, J., Price, J., Nielsen, J.L., Allen, C.D., Peterson, D.L., Ruggerone, G. & Doyle, T. (2005) Nonlinear dynamics in ecosystem response to climatic change: case studies and policy implications. *Ecological Complexity*, **2**, 357-394.
- Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretical approach*, 2nd edn. SpringerVerlag, New York.
- Burt, W.H. (1943) Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, **24**, 346-352.
- Calder, W.A. (1984) *Size, function, and life history*. Harvard University Press, Cambridge, MA.
- Cardillo, M. & Bromham, L. (2001) Body size and risk of extinction in Australian mammals. *Conservation Biology*, **15**, 1435-1440.
- Carpenter, S.R. & Brock, W.A. (2006) Rising variance: a leading indicator of ecological transition. *Ecology Letters*, **9**, 311-318.
- Carpenter, S.R., Walker, B., Anderies, J.M. & Abel, N. (2001) From metaphor to measurement: resilience of what to what? *Ecosystems*, **4**, 765-781.
- Carpenter, S.R., Westley, F. & Turner, M. (2005) Surrogates for resilience of social–ecological systems. *Ecosystems*, **8**, 941-944.
- Cassey, P. & Blackburn, T.M. (2004) Body size trends in a Holocene island bird assemblage. *Ecography*, **27**, 59-67.

- Cattaneo, A. (1993) Size spectra of benthic communities in Laurentian streams. *Canadian Journal of Fisheries and Aquatic Sciences*, **50**, 2659-2666.
- Ceccarelli, D. (2007) Modification of benthic communities by territorial damselfish: a multi-species comparison. *Coral Reefs*, **26**, 853-866.
- Ceccarelli, D., Jones, G.P. & McCook, L.J. (2001) Territorial damselfishes as determinants of benthic community structure on coral reefs. *Oceanography and Marine Biology: an annual review*, **39**, 355-389.
- Chapman, M.R. & Kramer, D.L. (2000) Movements of fishes within and among fringing coral reefs in barbados. *Environmental Biology of Fishes*, **57**, 11-24.
- Chase, J. (2003) Community assembly: when should history matter? *Oecologia*, **136**, 489-498.
- Cheal, A.J., Emslie, M., MacNeil, M.A., Miller, I. & Sweatman, H. (2013) Spatial variation in the functional characteristics of herbivorous fish communities and the resilience of coral reefs. *Ecological Applications*, **23**, 174-188.
- Cheal, A.J., MacNeil, M., Cripps, E., Emslie, M., Jonker, M., Schaffelke, B. & Sweatman, H. (2010) Coral-macroalgal phase shifts or reef resilience: links with diversity and functional roles of herbivorous fishes on the Great Barrier Reef. *Coral Reefs*, **29**, 1005-1015.
- Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**, 1024-1026.
- Cheung, W.W.L., Pitcher, T.J. & Pauly, D. (2005) A fuzzy logic expert system to estimate intrinsic extinction vulnerabilities of marine fishes to fishing. *Biological Conservation*, **124**, 97-111.
- Chillo, V., Anand, M. & Ojeda, R. (2011) Assessing the use of functional diversity as a measure of ecological resilience in arid rangelands. *Ecosystems*, **14**, 1168-1177.
- Chipman, H.A., George, E.I. & McCulloch, R.E. (1998) Bayesian CART model search. *Journal of the American Statistical Association*, **93**, 935-948.
- Choat, Clements & Robbins (2002) The trophic status of herbivorous fishes on coral reefs. *Marine Biology*, **140**, 613-623.
- Choat, J.H., Robbins, W.D. & Clements, K.D. (2004) The trophic status of herbivorous fishes on coral reefs. *Marine Biology*, **145**, 445-454.
- Choat, J.H. & Robertson, D.R. (2002) Age-based studies on coral reef fishes. *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem* (ed. P.F. Sale), pp. 57-80. Academic Press, Elsevier Science, San Diego.
- Chong-Seng, K.M., Mannering, T.D., Pratchett, M.S., Bellwood, D.R. & Graham, N.A. (2012) The influence of coral reef benthic condition on associated fish assemblages. *PLoS ONE*, **7**, e42167.

- Chong-Seng, K.M., Nash, K.L., Bellwood, D.R. & Graham, N.A.J. (2014) Macroalgal herbivory on recovering versus degrading coral reefs. *Coral Reefs*, **33**, 409-419.
- Christensen, N.L., Bartuska, A.M., Brown, J.H., Carpenter, S., D'Antonio, C., Francis, R., Franklin, J.F., MacMahon, J.A., Noss, R.F., Parsons, D.J., Peterson, C.H., Turner, M.G. & Woodmansee, R.G. (1996) The report of the Ecological Society of America committee on the scientific basis for ecosystem management. *Ecological Applications*, **6**, 665-691.
- Cinner, J.E., McClanahan, T.R., Graham, N.A.J., Pratchett, M.S., Wilson, S.K. & Raina, J.-B. (2009) Gear-based fisheries management as a potential adaptive response to climate change and coral mortality. *Journal of Applied Ecology*, **46**, 724-732.
- Civantos, E. (2000) Home-range ecology, aggressive behaviour, and survival in juvenile lizards, *Psammodromus algirus*. *Canadian Journal of Zoology*, **78**, 1681-1685.
- Claisse, J., Clark, T., Schumacher, B., McTee, S., Bushnell, M., Callan, C., Laidley, C. & Parrish, J. (2011) Conventional tagging and acoustic telemetry of a small surgeonfish *Zebrafoma flavescens* in a structurally complex coral reef environment. *Environmental Biology of Fishes*, **91**, 185-201.
- Clarke, K.R. (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, **18**, 117-143.
- Clarke, K.R. & Warwick, R.M. (2001) A further biodiversity index applicable to species lists: variation in taxonomic distinctness. *Marine Ecology Progress Series*, **216**, 265-278.
- Claydon, J., McCormick, M. & Jones, G. (2012) Patterns of migration between feeding and spawning sites in a coral reef surgeonfish. *Coral Reefs*, **31**, 77-87.
- Cleary, D.F.R., Boyle, T.J.B., Setyawati, T., Anggraeni, C.D., Loon, E.E.V. & Menken, S.B.J. (2007) Bird species and traits associated with logged and unlogged forest in Borneo. *Ecological Applications*, **17**, 1184-1197.
- Cohen, J.E., Jonsson, T. & Carpenter, S.R. (2003) Ecological community description using the food web, species abundance, and body size. *Proceedings of the National Academy of Sciences*, **100**, 1781-1786.
- Cooper, S.D., Diehl, S., Kratz, K. & Sarnelle, O. (1998) Implications of scale for patterns and processes in stream ecology. *Australian Journal of Ecology*, **23**, 27-40.
- Cowlishaw, G.U.Y. (1997) Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Animal Behaviour*, **53**, 667-686.
- Cromsigt, J.P.G.M. & Olff, H. (2006) Resource partitioning among savanna grazers mediated by local heterogeneity: an experimental approach. *Ecology*, **87**, 1532-1541.
- Crossman, D.J., Choat, J.H. & Clements, K.D. (2005) Nutritional ecology of nominally herbivorous fishes on coral reefs. *Marine Ecology Progress Series*, **296**, 129-142.

- Cumming, D.H.M. & Cumming, G.S. (2003) Ungulate community structure and ecological processes: body size, hoof area and trampling in African savannas. *Oecologia*, **134**, 560-568.
- Cumming, G.S., Barnes, G., Perz, S., Schmink, M., Sieving, K., Southworth, J., Binford, M., Holt, R., Stickler, C. & Van Holt, T. (2005) An exploratory framework for the empirical measurement of resilience. *Ecosystems*, **8**, 975-987.
- Cumming, G.S. & Havlicek, T.D. (2002) Evolution, ecology, and multimodal distributions of body size. *Ecosystems*, **5**, 0705-0711.
- Davenport, J. (2004) Fractal dimension estimation in studies of epiphytal and epilithic communities: strengths and weaknesses. *Handbook of Scaling Methods in Aquatic Ecology* (eds L. Seuront & P.G. Strutton), pp. 245-256. CRC Press, Boca Raton, USA.
- Davidson, Z., Valeix, M., Loveridge, A.J., Hunt, J.E., Johnson, P.J., Madzikanda, H. & Macdonald, D.W. (2012) Environmental determinants of habitat and kill site selection in a large carnivore: scale matters. *Journal of Mammalogy*, **93**, 677-685.
- Daw, T.M., Cinner, J.E., McClanahan, T.R., Graham, N.A.J. & Wilson, S.K. (2011) Design factors and socioeconomic variables associated with ecological responses to fishery closures in the western Indian Ocean. *Coastal Management*, **39**, 412-424.
- De la Montaña, E., Rey-Benayas, J.M. & Carrascal, L.M. (2006) Response of bird communities to silvicultural thinning of Mediterranean maquis. *Journal of Applied Ecology*, **43**, 651-659.
- DeMartini, E.E., Friedlander, A.M., Sandin, S.A. & Sala, E. (2008) Differences in fish-assemblage structure between fished and unfished atolls in the northern Line Islands, central Pacific. *Marine Ecology Progress Series*, **365**, 199-215.
- Dias, L.G. & Strier, K.B. (2003) Effects of group size on ranging patterns in *Brachyteles arachnoides hypoxanthus*. *International Journal of Primatology*, **24**, 209-221.
- Doledec, S. & Statzner, B. (1994) Theoretical habitat templates, species traits, and species richness: 548 plant and animal species in the Upper Rhône River and its floodplain. *Freshwater Biology*, **31**, 523-538.
- Dornelas, M., Connolly, S.R. & Hughes, T.P. (2006) Coral reef diversity refutes the neutral theory of biodiversity. *Nature*, **440**, 80-82.
- Duffy, J.E. (2002) Biodiversity and ecosystem function: the consumer connection. *Oikos*, **99**, 201-219.
- Dunning Jr., J.B. (2008) CRC Handbook of Avian Body Masses. CRC Press, Boca Raton.
- Duran, A. & Claro, R. (2009) The feeding activity of herbivorous fishes and their impact on coral reefs with different levels of anthropogenic degradation. *Revista De Biología Tropical*, **57**, 687-697.

- Edwards, C.B., Friedlander, A.M., Green, A.G., Hardt, M.J., Sala, E., Sweatman, H.P., Williams, I.D., Zgliczynski, B., Sandin, S.A. & Smith, J.E. (2014) Global assessment of the status of coral reef herbivorous fishes: evidence for fishing effects. *Proceedings of the Royal Society B: Biological Sciences*, **281**.
- Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B. & Norberg, J. (2003) Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*, **1**, 488-494.
- Elmqvist, T., Wall, M., Berggren, A.-L., Blix, L., Fritioff, Å. & Rinman, U. (2002) Tropical forest reorganization after cyclone and fire disturbance in Samoa: remnant trees as biological legacies. *Ecology and Society*, **5**.
- Emslie, M.J., Cheal, A.J., Sweatman, H. & Delean, S. (2008) Recovery from disturbance of coral and reef fish communities on the Great Barrier Reef, Australia. *Marine Ecology-Progress Series*, **371**, 177-190.
- Emslie, M.J., Logan, M., Ceccarelli, D., Cheal, A., Hoey, A., Miller, I. & Sweatman, H. (2012) Regional-scale variation in the distribution and abundance of farming damselfishes on Australia's Great Barrier Reef. *Marine Biology*, **159**, 1293-1304.
- Eristhee, N. & Oxenford, H.A. (2001) Home range size and use of space by Bermuda chub *Kyphosus sectatrix* (L.) in two marine reserves in the Soufrière Marine Management Area, St Lucia, West Indies. *Journal of Fish Biology*, **59**, 129-151.
- Ernest, S.K.M. (2005) Body size, energy use, and community structure of small mammals. *Ecology*, **86**, 1407-1413.
- Ernest, S.K.M. (2013) Using size distributions to understand the role of body size in mammalian community assembly. *Animal body size* (eds F.A. Smith & S.K. Lyons). The University of Chicago Press, Chicago.
- Fa, J.E., Ryan, S.F. & Bell, D.J. (2005) Hunting vulnerability, ecological characteristics and harvest rates of bushmeat species in afrotropical forests. *Biological Conservation*, **121**, 167-176.
- Fagan, W.F., Lutscher, F. & Schneider, K. (2007) Population and community consequences of spatial subsidies derived from central-place foraging. *The American Naturalist*, **170**, 902-915.
- Fauchald, P. & Tveraa, T. (2006) Hierarchical patch dynamics and animal movement pattern. *Oecologia*, **149**, 383-395.
- Ferreira, D.E.L., Peret, A.C. & Coutinho, R. (1998) Seasonal grazing rates and food processing by tropical herbivorous fishes. *Journal of Fish Biology*, **53**, 222-235.

- Fewster, R.M., Buckland, S.T., Siriwardena, G.M., Baillie, S.R. & Wilson, J.D. (2000) Analysis of population trends for farmland birds using generalized additive models. *Ecology*, **81**, 1970-1984.
- Fischer, J., Lindenmayer, D., Blomberg, S., Montague-Drake, R., Felton, A. & Stein, J. (2007) Functional richness and relative resilience of bird communities in regions with different landuse intensities. *Ecosystems*, **10**, 964-974.
- Fischer, J., Lindenmayer, D.B. & Montague-Drake, R. (2008) The role of landscape texture in conservation biogeography: a case study on birds in south-eastern Australia. *Diversity and Distributions*, **14**, 38-46.
- Fisher, J.T., Anholt, B. & Volpe, J.P. (2011) Body mass explains characteristic scales of habitat selection in terrestrial mammals. *Ecology and Evolution*, **1**, 517-528.
- Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L. & Holling, C.S. (2004) Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics*, **35**, 557-581.
- Ford, R.G. (1983) Home range in a patchy environment: optimal foraging predictions. *American Zoologist*, **23**, 315-326.
- Forys, E.A. & Allen, C.R. (2002) Functional group change within and across scales following invasions and extinctions in the Everglades ecosystem. *Ecosystems*, **5**, 339-347.
- Fox, R.J. & Bellwood, D.R. (2011) Unconstrained by the clock? Plasticity of diel activity rhythm in a tropical reef fish, *Siganus lineatus*. *Functional Ecology*, **25**, 1096-1105.
- Fox, R.J. & Bellwood, D.R. (2013) Niche partitioning of feeding microhabitats produces a unique function for herbivorous rabbitfishes (Perciformes, Siganidae) on coral reefs. *Coral Reefs*, **32**, 13-23.
- Fox, R.J., Sunderland, T.L., Hoey, A.S. & Bellwood, D.R. (2009) Estimating ecosystem function: contrasting roles of closely related herbivorous rabbitfishes (Siganidae) on coral reefs. *Marine Ecology Progress Series*, **385**, 261-269.
- Francini, R.B., Ferreira, C.M., Coni, E.O., De Moura, R.L. & Kaufman, L. (2010) Foraging activity of roving herbivorous reef fish (Acanthuridae and Scaridae) in eastern Brazil: influence of resource availability and interference competition. *Journal of the Marine Biological Association of the United Kingdom*, **90**, 481-492.
- Freiwald, J. (2012) Movement of adult temperate reef fishes off the west coast of North America. *Canadian Journal of Fisheries and Aquatic Sciences*, **69**, 1362-1374.
- Friedlander, A.M., Brown, E.K., Jokiel, P.L., Smith, W.R. & Rodgers, K.S. (2003) Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. *Coral Reefs*, **22**, 291-305.

- Friedlander, A.M. & DeMartini, E.E. (2002) Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: The effects of fishing down apex predators. *Marine Ecology Progress Series*, **230**, 253-264.
- Friedlander, A.M. & Parrish, J.D. (1998) Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *Journal of Experimental Marine Biology and Ecology*, **224**, 1-30.
- Froese, R. & Pauly, D. (2012) FishBase.
- Fulton, C.J. & Bellwood, D.R. (2002) Patterns of foraging in labrid fishes. *Marine Ecology Progress Series*, **226**, 135-142.
- Gagné, S.A., Proulx, R. & Fahrig, L. (2008) Testing Holling's textural-discontinuity hypothesis. *Journal of Biogeography*, **35**, 2149-2150.
- Gardner, T.A., Cote, I.M., Gill, J.A., Grant, A. & Watkinson, A.R. (2003) Long-term region-wide declines in caribbean corals. *Science*, **301**, 958-960.
- Garmestani, A.S., Allen, C.R., Gallagher, C.M. & Mittelstaedt, J.D. (2007) Departures from Gibrat's Law, discontinuities and city size distributions. *Urban Studies*, **44**, 1997-2007.
- Gaston, K.J. & Fuller, R.A. (2008) Commonness, population depletion and conservation biology. *Trends in Ecology & Evolution*, **23**, 14-19.
- GBRMPA (2002) Biophysical operational principles as recommended by the Scientific Steering Committee for the Representative Areas Program. *Technical Information Sheet #6 Representative Areas Program background and history*, pp. 6. Great Barrier Reef Marine Park Authority.
- Gillingham, M.P., Parker, K.L. & Hanley, T.A. (1997) Forage intake by black-tailed deer in a natural environment: bout dynamics. *Canadian Journal of Zoology*, **75**, 1118-1128.
- Gillson, L. (2004) Evidence of hierarchical patch dynamics in an east african savanna? *Landscape Ecology*, **19**, 883-894.
- Gilmour, J.P., Smith, L.D., Heyward, A.J., Baird, A.H. & Pratchett, M.S. (2013) Recovery of an isolated coral reef system following severe disturbance. *Science*, **340**, 69-71.
- Goatley, C. & Bellwood, D. (2009) Morphological structure in a reef fish assemblage. *Coral Reefs*, **28**, 449-457.
- Goatley, C.H.R. & Bellwood, D.R. (2011) The roles of dimensionality, canopies and complexity in ecosystem monitoring. *PLoS ONE*, **6**, e27307.
- Gomes, I., Erzini, K. & McClanahan, T.R. (2013) Trap modification opens new gates to achieve sustainable coral reef fisheries. *Aquatic Conservation: Marine and Freshwater Ecosystems*, Early View Online.
- Gordon, I.J., Hester, A.J. & Festa-Bianchet, M. (2004) The management of wild large herbivores to meet economic, conservation and environmental objectives. *Journal of Applied Ecology*, **41**, 1021-1031.

- Gotanda, K., Turgeon, K. & Kramer, D. (2009) Body size and reserve protection affect flight initiation distance in parrotfishes. *Behavioral Ecology and Sociobiology*, **63**, 1563-1572.
- Gotelli, N.J. & Ellison, A.M. (2004) *A primer of ecological statistics*. Sinauer Associates Inc, Sunderland, Massachusetts.
- Gotelli, N.J., Graves, G.R. & Rahbek, C. (2010) Macroecological signals of species interactions in the Danish avifauna. *Proceedings of the National Academy of Sciences*, **107**, 5030-5035.
- Graham, N.A.J., Bellwood, D.R., Cinner, J.E., Hughes, T.P., Norström, A.V. & Nyström, M. (2013) Managing resilience to reverse phase shifts in coral reefs. *Frontiers in Ecology and the Environment*, **11**, 541-548.
- Graham, N.A.J., Chong-Seng, K.M., Huchery, C., Januchowski-Hartley, F.A. & Nash, K.L. (2014) Coral reef community composition in the context of disturbance history on the Great Barrier Reef, Australia. *PLoS ONE*, **9**, e101204.
- Graham, N.A.J., Dulvy, N.K., Jennings, S. & Polunin, N.V.C. (2005) Size-spectra as indicators of the effects of fishing on coral reef fish assemblages. *Coral Reefs*, **24**, 118-124.
- Graham, N.A.J. & Nash, K.L. (2013) The importance of structural complexity in coral reef ecosystems. *Coral Reefs*, **32**, 315-326.
- Graham, N.A.J., Nash, K.L. & Kool, J. (2011) Coral reef recovery dynamics in a changing world. *Coral Reefs*, **30**, 283-294.
- Graham, N.A.J., Wilson, S.K., Jennings, S., Polunin, N.V.C., Bijoux, J.P. & Robinson, J. (2006) Dynamic fragility of oceanic coral reef ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 8425-8429.
- Graham, N.A.J., Wilson, S.K., Jennings, S., Polunin, N.V.C., Robinson, J., Bijoux, J.P. & Daw, T.M. (2007) Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. *Conservation Biology*, **21**, 1291-1300.
- Green, A.L. & Bellwood, D.R. (2009) Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience: a practical guide for coral reef managers in the Asia Pacific Region. *IUCN working group on Climate Change and Coral Reefs.*, pp. 70. IUCN, Gland, Switzerland.
- Greenwood, J.J.D., Gregory, R.D., Harris, S., Morris, P.A. & Yalden, D.W. (1996) Relations between abundance, body size and species number in British birds and mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **351**, 265-278.
- Gunderson, L.H. (2008) Biophysical discontinuities in the Everglades system. *Discontinuities in ecosystems and other complex systems* (eds C.R. Allen & C.S. Holling), pp. 83-100. Columbia University Press, New York.

- Gunnarsson, B. (1992) Fractal dimension of plants and body size distribution in spiders. *Functional Ecology*, **6**, 636-641.
- Halford, A.R. & Caley, M.J. (2009) Towards an understanding of resilience in isolated coral reefs. *Global Change Biology*, **15**, 3031-3045.
- Halley, J.M., Hartley, S., Kallimanis, A.S., Kunin, W.E., Lennon, J.J. & Sgardelis, S.P. (2004) Uses and abuses of fractal methodology in ecology. *Ecology Letters*, **7**, 254-271.
- Hamilton, R.J., Potuku, T. & Montambault, J.R. (2011) Community-based conservation results in the recovery of reef fish spawning aggregations in the Coral Triangle. *Biological Conservation*, **144**, 1850-1858.
- Harestad, A.S. & Bunnell, F.L. (1979) Home range and body weight: a reevaluation. *Ecology*, **60**, 389-402.
- Harnik, P.G., Lotze, H.K., Anderson, S.C., Finkel, Z.V., Finnegan, S., Lindberg, D.R., Liow, L.H., Lockwood, R., McClain, C.R., McGuire, J.L., O'Dea, A., Pandolfi, J.M., Simpson, C. & Tittensor, D.P. (2012) Extinctions in ancient and modern seas. *Trends in Ecology & Evolution*, **27**, 608-617.
- Harris, S., Cresswell, W.J., Forde, P.G., Trehwella, W.J., Woollard, T. & Wray, S. (1990) Home-range analysis using radio-tracking data—a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review*, **20**, 97-123.
- Hartley, S., Kunin, W.E., Lennon, J.J. & Pocock, M.J.O. (2004) Coherence and discontinuity in the scaling of species' distribution patterns. *Proceedings of the Royal Society B: Biological Sciences*, **271**, 81-88.
- Haskell, J.P., Ritchie, M.E. & Olf, H. (2002) Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. *Nature*, **418**, 527-530.
- Hatcher, B.G. (1997) Coral reef ecosystems: how much greater is the whole than the sum of the parts? *Coral Reefs*, **16**, S77-S91.
- Havlicek, T.D. & Carpenter, S.R. (2001) Pelagic species size distributions in lakes: are they discontinuous? *Limnology and Oceanography*, **46**, 1021-1033.
- Hawkins, J.P. & Roberts, C.M. (2004) Effects of artisanal fishing on Caribbean coral reefs. *Conservation Biology*, **18**, 215-226.
- Hayes, K. & Barry, S. (2008) Are there any consistent predictors of invasion success? *Biological Invasions*, **10**, 483-506.
- Hendriks, A.J. (2007) The power of size: A meta-analysis reveals consistency of allometric regressions. *Ecological Modelling*, **205**, 196-208.
- Hendriks, A.J., Willers, B.J.C., Lenders, H.J.R. & Leuven, R.S.E.W. (2009) Towards a coherent allometric framework for individual home ranges, key population patches and geographic ranges. *Ecography*, **32**, 929-942.

- Heupel, M.R., Semmens, J.M. & Hobday, A.J. (2006) Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. *Marine and Freshwater Research*, **57**, 1-13.
- Hilborn, R. (2007) Moving to sustainability by learning from successful fisheries. *Ambio*, **36**, 296-303.
- Hixon, M.A. & Beets, J.P. (1993) Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs*, **63**, 77-101.
- Hixon, M.A. & Menge, B.A. (1991) Species diversity: prey refuges modify the interactive effects of predation and competition. *Theoretical Population Biology*, **39**, 178-200.
- Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E., Harvell, C.D., Sale, P.F., Edwards, A.J., Caldeira, K., Knowlton, N., Eakin, C.M., Iglesias-Prieto, R., Muthiga, N., Bradbury, R.H., Dubi, A. & Hatziolos, M.E. (2007) Coral reefs under rapid climate change and ocean acidification. *Science*, **318**, 1737-1742.
- Hoey, A. & Bellwood, D. (2008) Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. *Coral Reefs*, **27**, 37-47.
- Hoey, A. & Bellwood, D.R. (2009) Limited functional redundancy in a high diversity system: single species dominates key ecological process on coral reefs. *Ecosystems*, **12**, 1316-1328.
- Hoey, A.S. & Bellwood, D.R. (2011) Suppression of herbivory by macroalgal density: a critical feedback on coral reefs? *Ecology Letters*, **14**, 267-273.
- Holland, K.N., Lowe, C.G. & Wetherbee, B.M. (1996) Movements and dispersal patterns of blue trevally (*Caranx melampygus*) in a fisheries conservation zone. *Fisheries Research*, **25**, 279-292.
- Holling, C.S. (1973) Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, **4**, 1-23.
- Holling, C.S. (1992) Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecological Monographs*, **62**, 447-502.
- Holling, C.S. (2001) Understanding the complexity of economic, ecological, and social systems. *Ecosystems*, **4**, 390-405.
- Hooper, D.U., Chapin, F.S., III, Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3-35.

- Hua, E., Zhang, Z., Warwick, R., Deng, K., Lin, K., Wang, R. & Yu, Z. (2013) Pattern of benthic biomass size spectra from shallow waters in the East China Seas. *Marine Biology*, **160**, 1723-1736.
- Hubbell, S.P. (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, NJ.
- Hughen, K.A., Eglinton, T.I., Xu, L. & Makou, M. (2004) Abrupt tropical vegetation response to rapid climate changes. *Science*, **304**, 1955-1959.
- Hughes, T.P. (1994) Catastrophes, phase shifts, and large-scale degradation of a caribbean coral reef. *Science*, **265**, 1547-1551.
- Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J.B.C., Kleypas, J., Lough, J.M., Marshall, P., Nystrom, M., Palumbi, S.R., Pandolfi, J.M., Rosen, B. & Roughgarden, J. (2003) Climate change, human impacts, and the resilience of coral reefs. *Science*, **301**, 929-933.
- Hughes, T.P., Bellwood, D.R., Folke, C., Steneck, R.S. & Wilson, J. (2005) New paradigms for supporting the resilience of marine ecosystems. *Trends in Ecology & Evolution*, **20**, 380-386.
- Hughes, T.P., Bellwood, D.R., Folke, C.S., McCook, L.J. & Pandolfi, J.M. (2007a) No-take areas, herbivory and coral reef resilience. *Trends in Ecology & Evolution*, **22**, 1-3.
- Hughes, T.P., Graham, N.A.J., Jackson, J.B.C., Mumby, P.J. & Steneck, R.S. (2010) Rising to the challenge of sustaining coral reef resilience. *Trends in Ecology & Evolution*, **25**, 633-642.
- Hughes, T.P., Linares, C., Dakos, V., van de Leemput, I.A. & van Nes, E.H. (2012) Living dangerously on borrowed time during slow, unrecognized regime shifts. *Trends in Ecology & Evolution*.
- Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschanowskyj, N., Pratchett, M.S., Steneck, R.S. & Willis, B. (2007b) Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology*, **17**, 360-365.
- Illius, A.W. & Gordon, I.J. (1987) The allometry of food intake in grazing ruminants. *Journal of Animal Ecology*, **56**, 989-999.
- Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J. & Warner, R.R. (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science*, **293**, 629-637.

- Januchowski-Hartley, F.A., Graham, N.A.J., Feary, D.A., Morove, T. & Cinner, J.E. (2011a) Fear of fishers: human predation explains behavioral changes in coral reef fishes. *PLoS ONE*, **6**, e22761.
- Januchowski-Hartley, S.R., Hermoso, V., Pressey, R.L., Linke, S., Kool, J., Pearson, R.G., Pusey, B.J. & VanDerWal, J. (2011b) Coarse-filter surrogates do not represent freshwater fish diversity at a regional scale in Queensland, Australia. *Biological Conservation*, **144**, 2499-2511.
- Jennings, S., Grandcourt, E.M. & Polunin, N.V.C. (1995) The effects of fishing on the diversity, biomass and trophic structure of Seychelles' reef fish communities. *Coral Reefs*, **14**, 225-235.
- Jennings, S., Greenstreet, S.P.R. & Reynolds, J.D. (1999) Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *Journal of Animal Ecology*, **68**, 617-627.
- Jennings, S., Pinnegar, J.K., Polunin, N.V.C. & Boon, T.W. (2001) Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. *Journal of Animal Ecology*, **70**, 934-944.
- Jetz, W., Carbone, C., Fulford, J. & Brown, J.H. (2004) The scaling of animal space use. *Science*, **306**, 266-268.
- Johnson, A. (2010) Reducing bycatch in coral reef trap fisheries: escape gaps as a step towards sustainability. *Marine Ecology Progress Series*, **415**, 201-209.
- Johnson, C., Parker, K. & Heard, D. (2001) Foraging across a variable landscape: behavioral decisions made by woodland caribou at multiple spatial scales. *Oecologia*, **127**, 590-602.
- Johnson, C.R. (2009) Natural length scales of ecological systems: applications at community and ecosystem levels. *Ecology and Society*, **14**, 7.
- Johnson, M.K., Holbrook, S.J., Schmitt, R.J. & Brooks, A.J. (2011) Fish communities on staghorn coral: effects of habitat characteristics and resident farmerfishes. *Environmental Biology of Fishes*, **91**, 429-448.
- Jones, G.P., Santana, L. & McCook, L.J. (2006) Resource use and impact of three herbivorous damselfishes on coral reef communities. *Marine Ecology Progress Series*, **328**, 215-224.
- Jones, K.M.M. (2005) Home range areas and activity centres in six species of Caribbean wrasses (Labridae). *Journal of Fish Biology*, **66**, 150-166.
- Jouventin, P. & Weimerskirch, H. (1990) Satellite tracking of Wandering albatrosses. *Nature*, **343**, 746-748.

- Kaufman, L.S. (1983) Effects of Hurricane Allen on reef fish assemblages near Discovery Bay, Jamaica. *Coral Reefs*, **2**, 43-47.
- Kelt, D.A. & Vuren, D.H.V. (2001) The ecology and macroecology of mammalian home range area. *The American Naturalist*, **157**, 637-645.
- Kerkhoff, A.J. & Enquist, B.J. (2007) The implications of scaling approaches for understanding resilience and reorganization in ecosystems. *Bioscience*, **57**, 489-499.
- Kie, J.G., Matthiopoulos, J., Fieberg, J., Powell, R.A., Cagnacci, F., Mitchell, M.S., Gaillard, J.-M. & Moorcroft, P.R. (2010) The home-range concept: are traditional estimators still relevant with modern telemetry technology? *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 2221-2231.
- Kie, J.G., Terry Bowyer, R., Nicholson, M.C., Boroski, B.B. & Loft, E.R. (2002) Landscape heterogeneity at differing scales: Effects on spatial distribution of mule deer. *Ecology*, **83**, 530-544.
- Klinkenberg, B. (1994) A review of methods used to determine the fractal dimension of linear features. *Mathematical Geology*, **26**, 23-46.
- Kolasa, J. (1989) Ecological systems in hierarchical perspective: breaks in community structure and other consequences. *Ecology*, **70**, 36-47.
- Kovalenko, K., Thomaz, S. & Warfe, D. (2012) Habitat complexity: approaches and future directions. *Hydrobiologia*, **685**, 1-17.
- Krajewski, J.P. & Floeter, S.R. (2011) Reef fish community structure of the Fernando de Noronha Archipelago (Equatorial Western Atlantic): the influence of exposure and benthic composition. *Environmental Biology of Fishes*, **92**, 25-40.
- Krajewski, J.P., Floeter, S.R., Jones, G.P. & Leite, F.P.P. (2011) Patterns of variation in behaviour within and among reef fish species on an isolated tropical island: influence of exposure and substratum. *Journal of the Marine Biological Association of the United Kingdom*, **91**, 1359-1368.
- Kramer, D.L. & Chapman, M.R. (1999) Implications of fish home range size and relocation for marine reserve function. *Environmental Biology of Fishes*, **55**, 65-79.
- Krummel, J.R., Gardner, R.H., Sugihara, G., O'Neill, R.V. & Coleman, P.R. (1987) Landscape patterns in a disturbed environment. *Oikos*, **48**, 321-324.
- Krysko, K.L., Burgess, J.P., Rochford, M.R., Gillette, C.R., Cueva, D., Enge, K.M., Somma, L.A., Stabile, J.L., Smith, D.C., Wasilewski, J.A., Kieckhefer, G.N., Granatosky, M.C. & Nielsen, S.V. (2011) Verified non-indigenous amphibians and reptiles in Florida from 1863 through 2010: outlining the invasion process and identifying invasion pathways and stages. *Zootaxa*, 1-64.

- Laca, E.A., Sokolow, S., Galli, J.R. & Cangiano, C.A. (2010) Allometry and spatial scales of foraging in mammalian herbivores. *Ecology Letters*, **13**, 311-320.
- Laliberté, E. & Legendre, P. (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, **91**, 299-305.
- Laliberté, E., Wells, J.A., DeClerck, F., Metcalfe, D.J., Catterall, C.P., Queiroz, C., Aubin, I., Bonser, S.P., Ding, Y., Fraterrigo, J.M., McNamara, S., Morgan, J.W., Merlos, D.S., Vesk, P.A. & Mayfield, M.M. (2010) Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecology Letters*, **13**, 76-86.
- Lambert, W. (2006) Functional convergence of ecosystems: evidence from body mass distributions of North American late Miocene mammal faunas. *Ecosystems*, **9**, 97-118.
- Laver, P.N. & Kelly, M.J. (2008) A critical review of home range studies. *The Journal of Wildlife Management*, **72**, 290-298.
- Lazenby-Cohen, K.A. & Cockburn, A. (1991) Social and foraging components of the home range in *Antechinus stuartii* (Dasyuridae, Marsupialia) *Australian Journal of Ecology*, **16**, 301-307.
- Leaper, R., Raffaelli, D., Emes, C. & Manly, B. (2001) Constraints on body-size distributions: an experimental test of the habitat architecture hypothesis. *Journal of Animal Ecology*, **70**, 248-259.
- Lechner, A.M., Langford, W.T., Jones, S.D., Bekessy, S.A. & Gordon, A. (2012) Investigating species-environment relationships at multiple scales: differentiating between intrinsic scale and the modifiable areal unit problem. *Ecological Complexity*, **11**, 91-102.
- Ledlie, M., Graham, N., Bythell, J., Wilson, S., Jennings, S., Polunin, N. & Hardcastle, J. (2007) Phase shifts and the role of herbivory in the resilience of coral reefs. *Coral Reefs*, **26**, 641-653.
- Lefevre, C.D. & Bellwood, D.R. (2011) Temporal variation in coral reef ecosystem processes: herbivory of macroalgae by fishes. *Marine Ecology Progress Series*, **422**, 239-251.
- Legendre, P. & Legendre, L. (1998) *Numerical Ecology*, 2nd edn. Elsevier Science, Amsterdam.
- Legendre, S. (1986) Analysis of mammalian communities from the late Eocene and Oligocene of southern France. *Palaeovertebrata*, **16**, 191-212.
- Levin, P.S. & Hay, M.E. (1996) Responses of temperate reef fishes to alterations in algal structure and species composition. *Marine Ecology Progress Series*, **134**, 37-47.
- Levin, S.A. (1992) The problem of pattern and scale in ecology: the Robert H. MacArthur Award lecture. *Ecology*, **73**, 1943-1967.

- Lindgren, M., Dakos, V., Gröger, J.P., Gårdmark, A., Kornilovs, G., Otto, S.A. & Möllmann, C. (2012) Early detection of ecosystem regime shifts: a multiple method evaluation for management application. *PLoS ONE*, **7**, e38410.
- Lindstedt, S.L., Miller, B.J. & Buskirk, S.W. (1986) Home range, time, and body size in mammals. *Ecology*, **67**, 413-418.
- Lira, P.K. & Fernandez, F.A.d.S. (2009) A comparison of trapping- and radiotelemetry-based estimates of home range of the neotropical opossum *Philander frenatus*. *Mammalian Biology - Zeitschrift für Säugetierkunde*, **74**, 1-8.
- Lokrantz, J., Nystrom, M., Thyresson, M. & Johansson, C. (2008) The non-linear relationship between body size and function in parrotfishes. *Coral Reefs*, **27**, 967-974.
- Luckhurst, B.E. & Luckhurst, K. (1978) Analysis of influence of substrate variables on coral-reef fish communities. *Marine Biology*, **49**, 317-323.
- MacArthur, R.H. & Pianka, E.R. (1966) On optimal use of a patchy environment. *The American Naturalist*, **100**, 603-609.
- MacArthur, R.H. & Wilson, E. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, N.J.
- Madin, E.M.P., Gaines, S.D. & Warner, R.R. (2010) Field evidence for pervasive indirect effects of fishing on prey foraging behavior. *Ecology*, **91**, 3563-3571.
- Madin, E.M.P., Madin, J.S. & Booth, D.J. (2011) Landscape of fear visible from space. *Scientific Reports*, **1**, 14.
- Makarieva, A.M., Gorshkov, V.G. & Li, B.-L. (2005) Why do population density and inverse home range scale differently with body size?: Implications for ecosystem stability. *Ecological Complexity*, **2**, 259-271.
- Mandelbrot, B.B. (1982) *The fractal geometry of nature*. W.H. Freeman and Company, New York.
- Martin-Garin, B., Lathuiliere, B., Verrecchia, E.P. & Geister, J. (2007) Use of fractal dimensions to quantify coral shape. *Coral Reefs*, **26**, 541-550.
- Martin, R.D., Genoud, M. & Hemelrijk, C.K. (2005) Problems of allometric scaling analysis: examples from mammalian reproductive biology. *Journal of Experimental Biology*, **208**, 1731-1747.
- Mazerolle, M.J. (2013) AICcmodavg: model selection and multimodel inference based on (Q)AIC(c).
- McAbendroth, L., Ramsay, P.M., Foggo, A., Rundle, S.D. & Bilton, D.T. (2005) Does macrophyte fractal complexity drive invertebrate diversity, biomass and body size distributions? *Oikos*, **111**, 279-290.

- McCauley, D.J., Young, H.S., Dunbar, R.B., Estes, J.A., Semmens, B.X. & Micheli, F. (2012) Assessing the effects of large mobile predators on ecosystem connectivity. *Ecological Applications*, **22**, 1711-1717.
- McClanahan, T.R., Donner, S.D., Maynard, J.A., MacNeil, M.A., Graham, N.A.J., Maina, J., Baker, A.C., Alemu I, J.B., Beger, M., Campbell, S.J., Darling, E.S., Eakin, C.M., Heron, S.F., Jupiter, S.D., Lundquist, C.J., McLeod, E., Mumby, P.J., Paddock, M.J., Selig, E.R. & van Woesik, R. (2012) Prioritizing key resilience indicators to support coral reef management in a changing climate. *PLoS ONE*, **7**, e42884.
- McClanahan, T.R. & Hicks, C.C. (2011) Changes in life history and ecological characteristics of coral reef fish catch composition with increasing fishery management. *Fisheries Management and Ecology*, **18**, 50-60.
- McClanahan, T.R., Muthiga, N.A. & Coleman, R.A. (2011) Testing for top-down control: can post-disturbance fisheries closures reverse algal dominance? *Aquatic Conservation-Marine and Freshwater Ecosystems*, **21**, 658-675.
- McClanahan, T.R., Polunin, N. & Done, T. (2002) Ecological states and the resilience of coral reefs. *Conservation Ecology*, **6**, 18.
- McClanahan, T.R. & Shafir, S.H. (1990) Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. *Oecologia*, **83**, 362-370.
- McGeoch, M.A. & Gaston, K.J. (2002) Occupancy frequency distributions: patterns, artefacts and mechanisms. *Biological Reviews*, **77**, 311-331.
- McLeay, L.J., Page, B., Goldsworthy, S.D., Paton, D.C., Teixeira, C., Burch, P. & Ward, T. (2010) Foraging behaviour and habitat use of a short-ranging seabird, the crested tern. *Marine Ecology Progress Series*, **411**, 271-283.
- McMahon, T. & Bonner, J. (1983) *On size and life*. Scientific American Books, Inc., New York.
- McNab, B.K. (1963) Bioenergetics and the determination of home range size. *The American Naturalist*, **97**, 133-140.
- Meyer, C.G., Papastamatiou, Y.P. & Clark, T.B. (2010) Differential movement patterns and site fidelity among trophic groups of reef fishes in a Hawaiian marine protected area. *Marine Biology*, **157**, 1499-1511.
- Milne, B.T., Turner, M.G., Wiens, J.A. & Johnson, A.R. (1992) Interactions between the fractal geometry of landscapes and allometric herbivory. *Theoretical Population Biology*, **41**, 337-353.
- Minns, C.K. (1995) Allometry of home range size in lake and river fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, **52**, 1499-1508.
- Moberg, F. & Folke, C. (1999) Ecological goods and services of coral reef ecosystems. *Ecological Economics*, **29**, 215-233.

- Moffitt, E.A., Botsford, L.W., Kaplan, D.M. & O'Farrell, M.R. (2009) Marine reserve networks for species that move within a home range. *Ecological Applications*, **19**, 1835-1847.
- Mori, A.S., Furukawa, T. & Sasaki, T. (2012) Response diversity determines the resilience of ecosystems to environmental change. *Biological Reviews*, **88**, 349-364.
- Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H. & Bellwood, D.R. (2012) A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, **28**, 167-177.
- Mouillot, D., Villéger, S., Parravicini, V., Kulbicki, M., Arias-Gonzales, J.E., Bender, M.G., Chabanet, P., Floeter, S.R., Friedlander, A., Vigliola, L. & Bellwood, D.R. (in press) Functional over-redundancy and high functional vulnerability in global fish faunas of tropical reefs. *Proceedings of the National Academy of Sciences*.
- Mumby, P. (2009) Phase shifts and the stability of macroalgal communities on Caribbean coral reefs. *Coral Reefs*, **28**, 761-773.
- Mumby, P.J. (2006) The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. *Ecological Applications*, **16**, 747-769.
- Mumby, P.J., Dahlgren, C.P., Harborne, A.R., Kappel, C.V., Micheli, F., Brumbaugh, D.R., Holmes, K.E., Mendes, J.M., Broad, K., Sanchirico, J.N., Buch, K., Box, S., Stoffle, R.W. & Gill, A.B. (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. *Science*, **311**, 98-101.
- Mumby, P.J. & Wabnitz, C.C.C. (2002) Spatial patterns of aggression, territory size, and harem size in five sympatric Caribbean parrotfish species. *Environmental Biology of Fishes*, **63**, 265-279.
- Munday, P.L. & Jones, G.P. (1998) The ecological implications of small body size among coral-reef fishes. *Oceanography and Marine Biology: an annual review*, **36**, 373-411.
- Nakagawa, S. & Schielzeth, H. (2013) A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, **4**, 133-142.
- Nanami, A. & Yamada, H. (2008) Size and spatial arrangement of home range of checkered snapper *Lutjanus decussatus* (Lutjanidae) in an Okinawan coral reef determined using a portable GPS receiver. *Marine Biology*, **153**, 1103-1111.
- Nash, K.L., Allen, C.R., Angeler, D.G., Barichievy, C., Eason, T., Garmestani, A.S., Graham, N.A.J., Granholm, D., Knutson, M.G., Nelson, R.J., Nyström, M. & Stow, C.A.S., S.M. (2014a) Discontinuities, cross-scale patterns and the organization of ecosystems. *Ecology*, **95**, 654-667.

- Nash, K.L., Allen, C.R., Barichievy, C., Nyström, M., Sundstrom, S. & Graham, N.A.J. (2014b) Habitat structure and body size distributions: cross-ecosystem comparison for taxa with determinate and indeterminate growth. *Oikos*, **123**, 971-983.
- Nash, K.L., Graham, N.A.J. & Bellwood, D.R. (2013) Fish foraging patterns, vulnerability to fishing and implications for the management of ecosystem function across scales. *Ecological Applications*, **23**, 1632-1644.
- Nash, K.L., Graham, N.A.J., Januchowski-Hartley, F.A. & Bellwood, D.R. (2012) Influence of habitat condition and competition on foraging behaviour of parrotfishes. *Marine Ecology Progress Series*, **457**, 113-124.
- Nash, K.L., Graham, N.A.J., Wilson, S.K. & Bellwood, D.R. (2013) Cross-scale habitat structure drives fish body size distributions on coral reefs. *Ecosystems*, **16**, 478-490.
- Nemeth, M. & Appeldoorn, R. (2009) The distribution of herbivorous coral reef fishes within fore-reef habitats: the role of depth, light and rugosity. *Caribbean Journal of Science*, **45**, 247-253.
- Nilsen, E., Pedersen, S. & Linnell, J.C. (2008) Can minimum convex polygon home ranges be used to draw biologically meaningful conclusions? *Ecological Research*, **23**, 635-639.
- Nyström, M. (2006) Redundancy and response diversity of functional groups: implications for the resilience of coral reefs. *Ambio*, **35**, 30-35.
- Nystrom, M. & Folke, C. (2001) Spatial resilience of coral reefs. *Ecosystems*, **4**, 406-417.
- Nyström, M., Graham, N.A.J., Lokrantz, J. & Norstrom, A.V. (2008) Capturing the cornerstones of coral reef resilience: linking theory to practice. *Coral Reefs*, **27**, 795-809.
- O'Neill, R.V., DeAngelis, D.L., Waide, J.B. & Allen, T.F.H. (1986) *A hierarchical concept of ecosystems*. Princeton University Press, Princeton, New Jersey.
- Olden, J.D., Hogan, Z.S. & Zanden, M.J.V. (2007) Small fish, big fish, red fish, blue fish: size-biased extinction risk of the world's freshwater and marine fishes. *Global Ecology and Biogeography*, **16**, 694-701.
- Owen-Smith, N., Fryxell, J.M. & Merrill, E.H. (2010) Foraging theory upscaled: the behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 2267-2278.
- Owens, I.P.F. & Bennett, P.M. (2000) Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proceedings of the National Academy of Sciences*, **97**, 12144-12148.
- Paddack, M., Cowen, R. & Sponaugle, S. (2006) Grazing pressure of herbivorous coral reef fishes on low coral-cover reefs. *Coral Reefs*, **25**, 461-472.
- Page, S.E. (2011) *Diversity and Complexity*. Princeton University Press, Princeton, New Jersey.

- Pakeman, R.J. (2011) Multivariate identification of plant functional response and effect traits in an agricultural landscape. *Ecology*, **92**, 1353-1365.
- Palumbi, S.R. (2004) Marine reserves and ocean neighborhoods: the spatial scale of marine populations and their management. *Annual Review of Environment and Resources*, **29**, 31-68.
- Pavlacky, D.C. & Anderson, S.H. (2007) Does avian species richness in natural patch mosaics follow the forest fragmentation paradigm? *Animal Conservation*, **10**, 57-68.
- Peckarsky, B.L., Cooper, S.D. & McIntosh, A.R. (1997) Extrapolating from individual behavior to populations and communities in streams. *Journal of the North American Benthological Society*, **16**, 375-390.
- Petchey, O.L. & Belgrano, A. (2010) Body-size distributions and size-spectra: universal indicators of ecological status? *Biology Letters*, **6**, 434-437.
- Petchey, O.L. & Gaston, K.J. (2002) Extinction and the loss of functional diversity. *Proceedings of the Royal Society B: Biological Sciences*, **269**, 1721-1727.
- Petchey, O.L. & Gaston, K.J. (2006) Functional diversity: back to basics and looking forward. *Ecology Letters*, **9**, 741-758.
- Peters, D.P.C., Bestelmeyer, B.T. & Turner, M.G. (2007) Cross-scale interactions and changing pattern-process relationships: Consequences for system dynamics. *Ecosystems*, **10**, 790-796.
- Peters, D.P.C., Pielke, R.A., Bestelmeyer, B.T., Allen, C.D., Munson-McGee, S. & Havstad, K.M. (2004) Cross-scale interactions, nonlinearities, and forecasting catastrophic events. *Proceedings of the National Academy of Sciences of the United States of America*, **101**, 15130-15135.
- Peters, R.H. (1983) *The ecological implications of body size*. Cambridge University Press, Cambridge.
- Peterson, G.D., Allen, C.R. & Holling, C.S. (1998) Ecological resilience, biodiversity, and scale. *Ecosystems*, **1**, 6-18.
- Pichegru, L., Ryan, P., Crawford, R., van der Lingen, C. & Grémillet, D. (2010) Behavioural inertia places a top marine predator at risk from environmental change in the Benguela upwelling system. *Marine Biology*, **157**, 537-544.
- Pikitch, E.K., Santora, C., Babcock, E.A., Bakun, A., Bonfil, R., Conover, D.O., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E.D., Link, J., Livingston, P.A., Mangel, M., McAllister, M.K., Pope, J. & Sainsbury, K.J. (2004) Ecosystem-based fishery management. *Science*, **305**, 346-347.

- Pimentel, D., Zuniga, R. & Morrison, D. (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics*, **52**, 273-288.
- Poole, G.C. (2002) Fluvial landscape ecology: addressing uniqueness within the river discontinuum. *Freshwater Biology*, **47**, 641-660.
- Pope, K.L., Allen, C.R. & Angeler, D.G. (2014) Fishing for resilience. *Transactions of the American Fisheries Society*, **143**, 467-478.
- Possingham, M.L., Field, S.A. & Possingham, H.P. (2004) Species richness and abundance of birds in Mt Lofty Ranges stringybark habitat: 1999-2000 survey. *South Australian Ornithologist*, **34**, 153-169.
- Pratchett, M., Baird, A.H., McCowan, D.M., Coker, D.J., Cole, A.J. & Wilson, S.K. (2008a) Protracted declines in coral cover and fish abundance following climate induced coral bleaching on the Great Barrier Reef. *International Coral Reef Symposium*, pp. 1309-1313. Ft. Lauderdale, Florida.
- Pratchett, M.S., Munday, P.L., Wilson, S.K., Graham, N.A.J., Cinner, J.E., Bellwood, D.R., Jones, G.P., Polunin, N.V.C. & McClanahan, T.R. (2008b) Effects of climate-induced coral bleaching on coral-reef fishes - Ecological and economic consequences. *Oceanography and Marine Biology: An Annual Review*, Vol 46, pp. 251-296.
- Pratchett, M.S., Trapon, M., Berumen, M.L. & Chong-Seng, K. (2011) Recent disturbances augment community shifts in coral assemblages in Moorea, French Polynesia. *Coral Reefs*, **30**, 183-193.
- Purcell, S.P. & Bellwood, D.B. (2001) Spatial patterns of epilithic algal and detrital resources on a windward coral reef. *Coral Reefs*, **20**, 117-125.
- Purkis, S. & Kohler, K. (2008) The role of topography in promoting fractal patchiness in a carbonate shelf landscape. *Coral Reefs*, **27**, 977-989.
- R Development Core Team (2011) R: a language and environment for statistical computing. R Project for Statistical Computing, Vienna, Austria.
- Raffaelli, D., Solan, M. & Webb, T.J. (2005) Do marine and terrestrial ecologists do it differently. *Marine Ecology Progress Series*, **304**, 283-289.
- Randall, J.E. (1965) Grazing effect on sea grasses by herbivorous reef fishes in the West Indies. *Ecology*, **46**, 255-260.
- Restrepo, C. & Arango, N. (2008) Discontinuities in the geographical range size of North American birds and butterflies. *Discontinuities in ecosystems and other complex systems* (eds C.R. Allen & C.S. Holling), pp. 101-135. Columbia University Press, New York.
- Restrepo, C., Renjifo, L.M. & Marples, P. (1997) Frugivorous birds in fragmented Neotropical montane forests: Landscape pattern and body mass distribution. *Tropical forest*

- remnants: Ecology, Management, and Conservation of Fragmented Landscapes* (eds W.F. Laurance & R.O. Bierregaard Jr.), pp. 171-189. University of Chicago Press, Chicago.
- Reuman, D.C., Mulder, C., Raffaelli, D. & Cohen, J.E. (2008) Three allometric relations of population density to body mass: theoretical integration and empirical tests in 149 food webs. *Ecology Letters*, **11**, 1216-1228.
- Reynolds, J.D., Dulvy, N.K., Goodwin, N.B. & Hutchings, J.A. (2005) Biology of extinction risk in marine fishes. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 2337-2344.
- Rice, J.C. (2000) Evaluating fishery impacts using metrics of community structure. *ICES Journal of Marine Science: Journal du Conseil*, **57**, 682-688.
- Ritchie, M. (1998) Scale-dependent foraging and patch choice in fractal environments. *Evolutionary Ecology*, **12**, 309-330.
- Ritchie, M.E. & Olff, H. (1999) Spatial scaling laws yield a synthetic theory of biodiversity. *Nature*, **400**, 557-560.
- Robertson, D.R. & Gaines, S.D. (1986) Interference competition structures habitat use in a local assemblage of coral reef surgeonfishes. *Ecology*, **67**, 1372-1383.
- Robson, B.J., Barmuta, L.A. & Fairweather, P.G. (2005) Methodological and conceptual issues in the search for a relationship between animal body-size distributions and benthic habitat architecture. *Marine and Freshwater Research*, **56**, 1-11.
- Rodríguez, M.Á., Olalla-Tárraga, M.Á. & Hawkins, B.A. (2008) Bergmann's rule and the geography of mammal body size in the Western Hemisphere. *Global Ecology and Biogeography*, **17**, 274-283.
- Rogers, A., Blanchard, Julia L. & Mumby, Peter J. (2014) Vulnerability of coral reef fisheries to a loss of structural complexity. *Current Biology*, **24**, 1000-1005.
- Roubicek, A.J., VanDerWal, J., Beaumont, L.J., Pitman, A.J., Wilson, P. & Hughes, L. (2010) Does the choice of climate baseline matter in ecological niche modelling? *Ecological Modelling*, **221**, 2280-2286.
- Rudolf, V.H.W., Rasmussen, N.L., Dibble, C.J. & Van Allen, B.G. (2014) Resolving the roles of body size and species identity in driving functional diversity. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20133203.
- Russ, G. (1984) Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. II. Patterns of zonation of mid-shelf and outershelf reefs. *Marine Ecology Progress Series*, **20**, 23-34.
- Russ, G.R. (2003) Grazer biomass correlates more strongly with production than with biomass of algal turfs on a coral reef. *Coral Reefs*, **22**, 63-67.

- Saïd, S. & Servanty, S. (2005) The influence of landscape structure on female roe deer home-range size. *Landscape Ecology*, **20**, 1003-1012.
- Sale, P.F., Cowen, R.K., Danilowicz, B.S., Jones, G.P., Kritzer, J.P., Lindeman, K.C., Planes, S., Polunin, N.V.C., Russ, G.R., Sadovy, Y.J. & Steneck, R.S. (2005) Critical science gaps impede use of no-take fishery reserves. *Trends in Ecology & Evolution*, **20**, 74-80.
- Samoilys, M.A. & Carlos, G. (2000) Determining methods of underwater visual census for estimating the abundance of coral reef fishes. *Environmental Biology of Fishes*, **57**, 289-304.
- Samuel, M.D., Pierce, D.J. & Garton, E.O. (1985) Identifying areas of concentrated use within the home range. *Journal of Animal Ecology*, **54**, 711-719.
- Sandin, S. & McNamara, D. (2011) Spatial dynamics of benthic competition on coral reefs. *Oecologia*, 1-12.
- Savitz, J., Bardygula, L.G., Harder, T. & Stuechli, K. (1993) Diel and seasonal utilization of home ranges in a small lake by smallmouth bass (*Micropterus dolomieu*). *Ecology of Freshwater Fish*, **2**, 31-39.
- Scheffer, M., Bascompte, J., Brock, W.A., Brovkin, V., Carpenter, S.R., Dakos, V., Held, H., van Nes, E.H., Rietkerk, M. & Sugihara, G. (2009) Early-warning signals for critical transitions. *Nature*, **461**, 53-59.
- Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. & Walker, B. (2001) Catastrophic shifts in ecosystems. *Nature*, **413**, 591-596.
- Scheffer, M. & van Nes, E.H. (2006) Self-organized similarity, the evolutionary emergence of groups of similar species. *Proceedings of the National Academy of Sciences*, **103**, 6230-6235.
- Scheffer, M. & van Nes, E.H. (2007) Shallow lakes theory revisited: various alternative regimes driven by climate, nutrients, depth and lake size. *Hydrobiologia*, **584**, 455-466.
- Schoener, T.W. (1968) Sizes of feeding territories among birds. *Ecology*, **49**, 123-141.
- Schoener, T.W. & Schoener, A. (1982) Intraspecific variation in home-range size in some *Anolis* lizards. *Ecology*, **63**, 809-823.
- Scholz, F. & Kappeler, P. (2004) Effects of seasonal water scarcity on the ranging behavior of *Eulemur fulvus rufus*. *International Journal of Primatology*, **25**, 599-613.
- Schwinghamer, P. (1981) Characteristic size distributions of integral benthic communities. *Canadian Journal of Fisheries and Aquatic Sciences*, **38**, 1255-1263.
- Sendzimir, J. (1998) Patterns of animal size and landscape complexity: correspondance within and across scales. PhD PhD, University of Florida.
- Sendzimir, J., Allen, C.R., Gunderson, L.H. & Stow, C.A. (2003) Implications of body mass patterns: linking ecological structure and process to wildlife conservation and

- management. *Landscape ecology and resource management: linking theory with practice* (eds J. Bissonette & I. Storch), pp. 125-152. Island Press, Washington, DC.
- Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E. & Swift, D.M. (1987) Large herbivore foraging and ecological hierarchies. *Bioscience*, **37**, 789-799.
- Seton, E.T. (1909) *Life-histories of northern animals*. Charles Scribner's Sons, New York.
- Shaffer, M.L. (1981) Minimum population sizes for species conservation. *Bioscience*, **31**, 131-134.
- Sheppard, C.R.C., Ateweberhan, M., Bowen, B.W., Carr, P., Chen, C.A., Clubbe, C., Craig, M.T., Ebinghaus, R., Eble, J., Fitzsimmons, N., Gaither, M.R., Gan, C.H., Gollock, M., Guzman, N., Graham, N.A.J., Harris, A., Jones, R., Keshavmurthy, S., Koldewey, H., Lundin, C.G., Mortimer, J.A., Obura, D., Pfeiffer, M., Price, A.R.G., Purkis, S., Raines, P., Readman, J.W., Riegl, B., Rogers, A., Schleyer, M., Seaward, M.R.D., Sheppard, A.L.S., Tamelander, J., Turner, J.R., Visram, S., Vogler, C., Vogt, S., Wolschke, H., Yang, J.M.C., Yang, S.Y. & Yesson, C. (2012) Reefs and islands of the Chagos Archipelago, Indian Ocean: why it is the world's largest no-take marine protected area. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **22**, 232-261.
- Shurin, J.B., Gruner, D.S. & Hillebrand, H. (2006) All wet or dried up? Real differences between aquatic and terrestrial food webs. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 1-9.
- Silliman, B.R., van der Koppel, J., Bertness, M.D., Stanton, L.E. & Mendelsohn, I.A. (2005) Drought, snails, and large-scale die-off of southern U.S. salt marshes. *Science*, **310**, 1803-1806.
- Silverman, B.W. (1986) *Density estimation for statistics and data analysis*. Chapman & Hall/CRC Press.
- Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E. & Vilà, M. (2013) Impacts of biological invasions: what's what and the way forward. *Trends in Ecology & Evolution*, **28**, 58-66.
- Simon, H.A. (1962) The architecture of complexity. *Proceedings of the American Philosophical Society*, **106**, 467-482.
- Skillen, J.J. & Maurer, B.A. (2008) The ecological significance of discontinuities in body-mass distributions. *Discontinuities in ecosystems and other complex systems* (eds C.R. Allen & C.S. Holling), pp. 193-218. Columbia University Press, New York.
- Smith, C. & Wootton, R. (1995) The costs of parental care in teleost fishes. *Reviews in Fish Biology and Fisheries*, **5**, 7-22.

- Smith, R.J. (2009) Use and misuse of the reduced major axis for line-fitting. *American Journal of Physical Anthropology*, **140**, 476-486.
- Smith, T.B., Wayne, R.K., Girman, D.J. & Bruford, M.W. (1997) A role for ecotones in generating rainforest biodiversity. *Science*, **276**, 1855-1857.
- Solé, R.V. & Bascompte, J. (2006) *Self-organization in complex ecosystems*. Princeton University Press, Princeton, New Jersey.
- Souza, A., Ilarri, M. & Rosa, I. (2011) Habitat use, feeding and territorial behavior of a Brazilian endemic damselfish *Stegastes rocasensis* (Actinopterygii: Pomacentridae). *Environmental Biology of Fishes*, **91**, 133-144.
- Spanbauer, T.L., Allen, C.R., Angeler, D.G., Eason, T., Nash, K.L., Fritz, S.C., Stone, J.R. & Garmestani, A.S. (in press) A shift in time: statistical evidence of a slow regime shift from paleoecological data. *PLoS ONE*.
- Stallins, J.A. (2006) Geomorphology and ecology: unifying themes for complex systems in biogeomorphology. *Geomorphology*, **77**, 207-216.
- Stead, T.K., Schmid-Araya, J.M., Schmid, P.E. & Hildrew, A.G. (2005) The distribution of body size in a stream community: one system, many patterns. *Journal of Animal Ecology*, **74**, 475-487.
- Steneck, R.S., Arnold, S.N. & Mumby, P.J. (2014) Experiment mimics fishing on parrotfish: insights on coral reef recovery and alternative attractors. *Marine Ecology Progress Series*, **506**, 115-127.
- Stockwell, B., Jadloc, C.R.L., Abesamis, R.A., Alcalá, A.C. & Russ, G.R. (2009) Trophic and benthic responses to no-take marine reserve protection in the Philippines. *Marine Ecology Progress Series*, **389**, 1-15.
- Stow, C.A., Allen, C.R. & Garmestani, A.S. (2007) Evaluating discontinuities in complex systems: toward quantitative measures of resilience. *Ecology and Society*, **12**, 26.
- Sugihara, G. & May, R. (1990) Applications of fractals in ecology. *Trends in Ecology & Evolution*, **5**, 79-86.
- Sundstrom, S.M., Allen, C.R. & Barichievy, C. (2012) Species, functional groups, and thresholds in ecological resilience. *Conservation Biology*, **26**, 305-314.
- Sweatman, H., Cheal, A., Coleman, G., Emslie, M., Johns, K., Jonker, M., Miller, I. & Osborne, K. (2008) Long-term monitoring of the Great Barrier Reef. *Status Report 8*. Australian Institute of Marine Science, Townsville, Australia.
- Szabó, P. & Meszéna, G. (2006) Spatial ecological hierarchies: coexistence on heterogeneous landscapes via scale niche diversification. *Ecosystems*, **9**, 1009-1016.
- Teh, L.S.L., Teh, L.C.L. & Sumaila, U.R. (2013) A Global Estimate of the Number of Coral Reef Fishers. *PLoS ONE*, **8**, e65397.

- Thibault, K.M., White, E.P., Hurlbert, A.H. & Ernest, S.K.M. (2011) Multimodality in the individual size distributions of bird communities. *Global Ecology and Biogeography*, **20**, 145-153.
- Thibaut, L.M., Connolly, S.R. & Sweatman, H.P.A. (2011) Diversity and stability of herbivorous fishes on coral reefs. *Ecology*, **93**, 891-901.
- Thiel, D., Menoni, E., Brenot, J.-F. & Jenni, L. (2007) Effects of recreation and hunting on flushing distance of capercaillie. *The Journal of Wildlife Management*, **71**, 1784-1792.
- Thrush, S.F., Hewitt, J.E., Dayton, P.K., Coco, G., Lohrer, A.M., Norkko, A., Norkko, J. & Chiantore, M. (2009) Forecasting the limits of resilience: integrating empirical research with theory. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 3209-3217.
- Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R.W., Schindler, D., Schlesinger, W.H., Simberloff, D. & Swackhamer, D. (2001) Forecasting agriculturally driven global environmental change. *Science*, **292**, 281-284.
- Tokeshi, M. & Arakaki, S. (2012) Habitat complexity in aquatic systems: fractals and beyond. *Hydrobiologia*, **685**, 27-47.
- Travouillon, K.J. & Legendre, S. (2009) Using cenograms to investigate gaps in mammalian body mass distributions in Australian mammals. *Palaeogeography Palaeoclimatology Palaeoecology*, **272**, 69-84.
- Turgeon, K., Robillard, A., Grégoire, J., Duclos, V. & Kramer, D.L. (2010) Functional connectivity from a reef fish perspective: behavioral tactics for moving in a fragmented landscape. *Ecology*, **91**, 3332-3342.
- Turner, F.B., Jennrich, R.I. & Weintraub, J.D. (1969) Home ranges and body size of lizards. *Ecology*, **50**, 1076-1081.
- van Rooij, J.M., Kroon, F.J. & Videler, J.J. (1996) The social and mating system of the herbivorous reef fish *Sparisoma viride*: one-male versus multi-male groups. *Environmental Biology of Fishes*, **47**, 353-378.
- Vanni, M.J. (2002) Nutrient cycling by animals in freshwater ecosystems. *Annual Review of Ecology and Systematics*, **33**, 341-370.
- Vaughn, C.C. & Hakenkamp, C.C. (2001) The functional role of burrowing bivalves in freshwater ecosystems. *Freshwater Biology*, **46**, 1431-1446.
- Vergnon, R., Dulvy, N.K. & Freckleton, R.P. (2009) Niches versus neutrality: uncovering the drivers of diversity in a species-rich community. *Ecology Letters*, **12**, 1079-1090.
- Vergnon, R., van Nes, E.H. & Scheffer, M. (2012) Emergent neutrality leads to multimodal species abundance distributions. *Nature Communications*, **3**, 663.
- Veron, J.E.N., Hoegh-Guldberg, O., Lenton, T.M., Lough, J.M., Obura, D.O., Pearce-Kelly, P., Sheppard, C.R.C., Spalding, M., Stafford-Smith, M.G. & Rogers, A.D. (2009) The coral

- reef crisis: The critical importance of <350 ppm CO₂. *Marine Pollution Bulletin*, **58**, 1428-1436.
- Vié, J.-C., Hilton-Taylor, C. & Stuart, S.N. (2009) Wildlife in a changing world – an analysis of the 2008 IUCN Red List of Threatened Species., pp. 180. IUCN, Gland, Switzerland.
- Villéger, S., Mason, N.W.H. & Mouillot, D. (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, **89**, 2290-2301.
- Wainwright, P.C. & Richard, B.A. (1995) Predicting patterns of prey use from morphology of fishes. *Environmental Biology of Fishes*, **44**, 97-113.
- Walker, B.H., Gunderson, L.H., Kinzig, A.P., Folke, C., Carpenter, S.R. & Schultz, L. (2006) A handful of heuristics and some propositions for understanding resilience in social-ecological systems. *Ecology and Society*, **11**, 13.
- Walker, B.H., Kinzig, A.P. & Langridge, J. (1999) Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems*, **2**, 95-113.
- Wall, D.H., Ayres, E., Behan-Pelletier, Covich, A.P. & Snelgrove, P.V.R. (2005) Soils, freshwater and marine sediments: the need for integrative landscape science. *Marine Ecology Progress Series*, **304**, 271-307.
- Wang, R., Dearing, J.A., Langdon, P.G., Zhang, E., Yang, X., Dakos, V. & Scheffer, M. (2013) Flickering gives early warning signals of a critical transition to a eutrophic lake state. *Nature*.
- Wardwell, D. & Allen, C.R. (2009) Variability in population abundance is associated with thresholds between scaling regimes. *Ecology and Society*, **14**, 42.
- Wardwell, D.A., Allen, C.R., Peterson, G.D. & Tyre, A.J. (2008) A test of the cross-scale resilience model: functional richness in Mediterranean-climate ecosystems. *Ecological Complexity*, **5**, 165-182.
- Warton, D.I., Wright, I.J., Falster, D.S. & Westoby, M. (2006) Bivariate line-fitting methods for allometry. *Biological Reviews*, **81**, 259-291.
- Warwick, R.M., Dashfield, S.L. & Somerfield, P.J. (2006) The integral structure of a benthic infaunal assemblage. *Journal of Experimental Marine Biology and Ecology*, **330**, 12-18.
- Watson, D., Harvey, E., Fitzpatrick, B., Langlois, T. & Shedrawi, G. (2010) Assessing reef fish assemblage structure: how do different stereo-video techniques compare? *Marine Biology*, **157**, 1237-1250.
- Webb, T.J. (2012) Marine and terrestrial ecology: unifying concepts, revealing differences. *Trends in Ecology & Evolution*, **27**, 535-541.

- Webb, T.J., Dulvy, N.K., Jennings, S. & Polunin, N.V.C. (2011) The birds and the seas: body size reconciles differences in the abundance–occupancy relationship across marine and terrestrial vertebrates. *Oikos*, **120**, 537-549.
- Welsh, J.Q. & Bellwood, D.R. (2012a) How far do schools of roving herbivores rove? A case study using *Scarus rivulatus*. *Coral Reefs*, 1-13.
- Welsh, J.Q. & Bellwood, D.R. (2012b) Spatial ecology of the steephead parrotfish (*Chlorurus microrhinos*): an evaluation using acoustic telemetry. *Coral Reefs*, **31**, 55-65.
- Welsh, J.Q. & Bellwood, D.R. (2014) Herbivorous fishes, ecosystem function and mobile links on coral reefs. *Coral Reefs*, **33**, 303-311.
- Welsh, J.Q., Goatley, C.H.R. & Bellwood, D.R. (2013) The ontogeny of home ranges: evidence from coral reef fishes. *Proceedings of the Royal Society B: Biological Sciences*, **280**.
- Werner, E.E. (1974) The fish size, prey size, handling time relation in several sunfishes and some implications. *Journal of the Fisheries Research Board of Canada*, **31**, 1531-1536.
- Wheatley, M. & Johnson, C. (2009) Factors limiting our understanding of ecological scale. *Ecological Complexity*, **6**, 150-159.
- White, E.P., Ernest, S.K.M., Kerkhoff, A.J. & Enquist, B.J. (2007) Relationships between body size and abundance in ecology. *Trends in Ecology & Evolution*, **22**, 323-330.
- White, J.W. & Warner, R.R. (2007) Behavioral and energetic costs of group membership in a coral reef fish. *Oecologia*, **154**, 423-433.
- Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology*, **3**, 385-397.
- Wilding, T.A., Rose, C.A. & Downie, M.J. (2007) A novel approach to measuring subtidal habitat complexity. *Journal of Experimental Marine Biology and Ecology*, **353**, 279-286.
- Wilkinson, C.R. (2000) World-wide coral reef bleaching and mortality during 1998: a global climate change warning for the new millenium? *Seas at the millenium: An environmental evaluation* (ed. C.R.C. Sheppard), pp. 43-57. Elseiver Science, Amsterdam.
- Williams, I.D., Polunin, N.V.C. & Hendrick, V.J. (2001) Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize. *Marine Ecology Progress Series*, **222**, 187-196.
- Wilson, S.K. & Bellwood, D.R. (1997) Cryptic dietary components of territorial damselfishes (Pomacentridae, Labroidae). *Marine Ecology Progress Series*, **153**, 299-310.
- Wilson, S.K., Fisher, R., Pratchett, M.S., Graham, N.A.J., Dulvy, N.K., Turner, R.A., Cakacaka, A. & Polunin, N.V.C. (2010) Habitat degradation and fishing effects on the size structure of coral reef fish communities. *Ecological Applications*, **20**, 442-451.

- Wilson, S.K., Fisher, R., Pratchett, M.S., Graham, N.A.J., Dulvy, N.K., Turner, R.A., Cakacaka, A., Polunin, N.V.C. & Rushton, S.P. (2008) Exploitation and habitat degradation as agents of change within coral reef fish communities. *Global Change Biology*, **14**, 2796-2809.
- Wilson, S.K., Graham, N.A.J., Fisher, R., Robinson, J., Nash, K.L., Chong-Seng, K., Polunin, N.V.C., Aumeeruddy, R. & Quatre, R. (2012) Effect of macroalgal expansion and marine protected areas on coral recovery following a climatic disturbance. *Conservation Biology*, **26**, 995-1004.
- Wilson, S.K., Graham, N.A.J. & Polunin, N.V.C. (2007) Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Marine Biology*, **151**, 1069-1076.
- Winfree, R. (2013) Global change, biodiversity, and ecosystem services: What can we learn from studies of pollination? *Basic and Applied Ecology*, **14**, 453-460.
- Wood, S. (2006) *Generalized additive models: an introduction with R*. Taylor & Francis.
- Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A. & Warren, P.H. (2005) Body size in ecological networks. *Trends in Ecology & Evolution*, **20**, 402-409.
- Woolnough, D.A., Downing, J.A. & Newton, T.J. (2009) Fish movement and habitat use depends on water body size and shape. *Ecology of Freshwater Fish*, **18**, 83-91.
- Worton, B.J. (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, **70**, 164-168.
- Wu, J. & Li, H. (2006) Perspectives and methods of scaling. *Scaling and uncertainty analysis in ecology* (eds J. Wu, K.B. Jones, H. Li & O. Loucks), pp. 17-44. Springer Netherlands.
- Xiao, X., White, E.P., Hooten, M.B. & Durham, S.L. (2011) On the use of log-transformation vs. nonlinear regression for analyzing biological power laws. *Ecology*, **92**, 1887-1894.
- Xu, L., Hanson, T., Bedrick, E. & Restrepo, C. (2010) Hypothesis tests on mixture model components with applications in ecology and agriculture. *Journal of Agricultural, Biological, and Environmental Statistics*, **15**, 308-326.
- Yamanaka, T., White, P.C.L., Spencer, M. & Raffaelli, D. (2012) Patterns and processes in abundance-body size relationships for marine benthic invertebrates. *Journal of Animal Ecology*, **81**, 463-471.
- Yvon-Durocher, G. & Allen, A.P. (2012) Linking community size structure and ecosystem functioning using metabolic theory. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**, 2998-3007.

- Yvon-Durocher, G., Reiss, J., Blanchard, J., Ebenman, B., Perkins, D.M., Reuman, D.C., Thierry, A., Woodward, G. & Petchey, O.L. (2011) Across ecosystem comparisons of size structure: methods, approaches and prospects. *Oikos*, **120**, 550-563.
- Zavalaga, C.B., Halls, J. & Dell'Omo, G. (2010) Marine habitat use of Peruvian boobies: a geographic and oceanographic comparison between inshore and offshore islands. *ICES Journal of Marine Science*, **67**, 940-951.
- Zemke-White, L., Choat, J.C. & Clements, K.C. (2002) A re-evaluation of the diel feeding hypothesis for marine herbivorous fishes. *Marine Biology*, **141**, 571-579.
- Zhang, S.Y., Speare, K.E., Long, Z.T., McKeever, K.A., Gyoerkoe, M., Ramus, A.P., Mohorn, Z., Akins, K.L., Hambridge, S.M., Graham, N.A.J., Nash, K.L., Selig, E.R. & Bruno, J.F. (2014) Is coral richness related to community resistance to and recovery from disturbance? *PeerJ*, **2**, e308.
- Zuur, A.F., Ieno, E.N. & Smith, G.M. (2007) *Analysing ecological data*. Springer, New York.
- Zuur, A.F., Ieno, E.N., Walker, N.J.S., A. A. & Smith, G.M. (2009) *Mixed effects models and extensions in Ecology with R*. Springer, New York.

Appendix A: Supplemental information for Chapter 2

Table S1. Details of studies used to assess the relationship between body size and home range in coral reef fishes.

Reference	Location	Species	Trophic Group	Individual Data	n	Tracking Method	Log Body Mass (g)	Log Home Range (m ²) MCP
Low 1971 Ecology	Australia - Heron Island	<i>Pomacentrus chrysurus</i>	Herbivore	N	5	Visual	0.71	0.30
Sale 1971 Copeia	Australia - Heron Island	<i>Dacyllus aruanus</i>	Herbivore	Y	28	Visual	0.45	-1.11
Nursall 1977 Jr Zool	Barbados & Curacao	<i>Ophioblennius atlanticus</i>	Herbivore	N	31	Visual	0.29	-0.29
Gronell 1984 Z. Tierpsychologie	Australia - One Tree	<i>Corythoichthys intestinalis</i>	Predator	N	22	Visual	0.29	1.27
Hourigan 1989 Env Biol Fishes	US Virgin Islands - St. Coix	<i>Holacanthus tricolor</i>	Predator	N	24	Visual	1.87	2.79
Sikkel 1990 Env Biol Fishes	Panama - Akudargana Reef	<i>Canthigaster rostrata</i>	Predator	Y	24	Visual	1.50	1.55
Shpigel and Fishelson 1991 Jr Fish Biol	Gulf Aquaba - Na'ama Bay	<i>Cephalopholis argus</i>	Predator	N	25	Visual	2.67	2.27
		<i>Cephalopholis hemistiktos</i>	Predator	N	16	Visual	2.00	1.08
		<i>Cephalopholis miniata</i>	Predator	N	36	Visual	2.47	1.70
Shapiro 1994 Env Biol Fishes	Puerto Rico	<i>Epinephelus guttatus</i>	Predator	Y	15	Visual	2.28	2.92
van Rooij 1996 Env Biol Fishes	Bonaire	<i>Sparisoma viride</i>	Herbivore	Y	17	Visual	2.90	3.48
Ohnishi et al. 1997 Env Biol	Japan - Shikoku Island	<i>Parapercis snyderi</i>	Predator	N	60	Visual	0.93	0.50

Fishes

Samoilys 1997 Coral Reefs	Australia - Heron Island	<i>Plectropomus leopardus</i>	Predator	Y	16	Visual	3.17	3.26
Zeller 1997 MEPS	Australia - Lizard Island	<i>Plectropomus leopardus</i>	Predator	N	39	Telemetry	3.24	4.17
Meyer et al 2000 Env Biol Fishes	Hawaii - Oahu	<i>Parapeneus porphyreus</i>	Predator	Y	5	Telemetry	3.53	4.23
Muñoz & Motta 2000 Copeia	USA - Florida Keys	<i>Sparisoma chrysopterum</i>	Herbivore	N	7	Visual	2.64	3.64
Bolden 2001 Rev Elec Tagg & Track	Bahamas	<i>Epinephelus striatus</i>	Predator	N	22	Telemetry	3.35	4.26
Eristhee & Oxenford 2001 Jr Fish Biol	St. Lucia - Grand Caille	<i>Kyphosus sectatrix</i>	Herbivore	Y	11	Telemetry	2.97	4.51
Wetherbee et al 2004 Fish Res	Hawaii - Oahu	<i>Caranx ignobilis</i>	Predator	Y	4	Telemetry	2.86	5.62
Jones 2005 Jr Fish Biol	US Virgin Islands - St. Croix	<i>Halichoeres poeyi</i>	Predator	Y	4	Visual	1.18	1.19
		<i>Halichoeres garnoti</i>	Predator	Y	2	Visual	1.35	1.27
		<i>Halichoeres maculpinna</i>	Predator	Y	12	Visual	1.36	1.43
		<i>Thalassoma bifasciatum</i>	Predator	Y	5	Visual	0.74	1.27
Liu & Sadovy 2005 Env Biol Fishes	Hong Kong - Ping Chau Is.	<i>Cephalopholis boenak</i>	Predator	Y	28	Visual	1.49	0.91

Krone 2008 Coral Reefs	Egypt - Ras Mohammed	<i>Ctenochaetus striatus</i>	Herbivore	Y	11	Visual	1.78	1.06
Nanami & Yamada 2008 Mar Biol	Japan - Ishigaki Island	<i>Lutjanus decussatus</i>	Predator	Y	6	Visual	2.43	3.34
Nanami & Yamada 2009 Fish Sci	Japan - Ishigaki Island	<i>Lethrinus harak</i>	Predator	Y	6	Visual	2.53	3.27
Hardman et al. 2010 Aq Cons	Rodrigues	<i>Naso unicornis</i>	Herbivore	Y	7	Telemetry	3.28	4.66
Muñoz et al. 2010 Bull Mar Sci	USA - Florida Keys	<i>Lachnolaimus maximus</i>	Predator	N	24	Visual	2.92	3.09
Farmer and Ault 2011 MEPS	Florida - Dry Tortugas	<i>Epinephelus morio</i>	Predator	Y	28	Telemetry	3.30	6.16
		<i>Lutjanus analis</i>	Predator	Y	1	Telemetry	3.80	6.88
		<i>Mycteroperca bonaci</i>	Predator	Y	2	Telemetry	3.56	5.99
		<i>Ocyurus chrysurus</i>	Predator	Y	5	Telemetry	3.28	6.46
Garcia et al 2011 GCFI	Martinique	<i>Acanthurus chirurgus</i>	Herbivore	Y	1	Telemetry	2.75	3.85
		<i>Sparisoma viride</i>	Herbivore	Y	3	Telemetry	2.34	3.51
Marshall et al 2011 Coral Reefs	Guam	<i>Naso lituratus</i>	Herbivore	Y	8	Telemetry	2.36	4.18
		<i>Naso unicornis</i>	Herbivore	Y	7	Telemetry	2.60	4.13
Welsh & Bellwood 2012a Coral Reefs	Australia - Orpheus Island	<i>Chlorurus microrhinus</i>	Herbivore	Y	7	Telemetry	3.47	3.92
Welsh & Bellwood 2012b Coral Reefs	Australia - Orpheus Island	<i>Scarus rivulatus</i>	Herbivore	Y	18	Telemetry	2.67	4.35
Howard et al 2013 Mar Biol	Hawaii - Wawaloli Reef	<i>Scarus rubroviolaceus</i>	Herbivore	Y	20	Telemetry	3.26	3.46
Welsh et al 2013 Proc R Soc B	Australia - Lizard Island	<i>Chlorurus sordidus</i>	Herbivore	Y	1	Visual	2.48	2.21
		<i>Scarus frenatus</i>	Herbivore	Y	16	Visual	2.96	2.40
		<i>Scarus niger</i>	Herbivore	Y	3	Visual	2.69	2.21

References:

- Bolden, S. K. 2001. Using acoustic telemetry to determine home range of a coral reef fish. - In: Sibert, J. and Nielsen, J. L. (eds.), Electronic tagging and tracking in marine fisheries. Kluwer Academic Publishers.
- Eristhee, N. and Oxenford, H. A. 2001. Home range size and use of space by Bermuda chub *Kyphosus sectatrix* (L.) in two marine reserves in the Soufrière Marine Management Area, St Lucia, West Indies. - J. Fish. Biol. 59: 129-151.
- Farmer, N. A. and Ault, J. S. 2011. Grouper and snapper movements and habitat use in Dry Tortugas, Florida. - Mar. Ecol. Prog. Ser. 433: 169-184.
- Garcia, J., et al. 2010. Herbivorous reef fish movement ability estimation in marine protected areas of Martinique (FWI). 63rd Gulf and Caribbean Fisheries Institute, pp. 254-259.
- Gronell, A. M. 1984. Courtship, spawning, and social organization of the pipefish, *Corythoichthys intestinalis* (Pisces: Syngnathidae), with notes on two congeneric species. - Z. Tierpsychol. 65: 1-24.
- Hardman, E., et al. 2010. Movement of sonically tagged bluespine unicornfish, *Naso unicornis*, in relation to marine reserve boundaries in Rodrigues, western Indian Ocean. - Aquat. Conserv.-Mar. Freshw. Ecosyst. 20: 357-361.
- Hourigan, T., et al. 1989. The feeding ecology of three species of Caribbean angelfishes (family Pomacanthidae). - Environ. Biol. Fishes 24: 105-116.
- Howard, K., et al. 2013. Home range and movement patterns of the Redlip Parrotfish (*Scarus rubroviolaceus*) in Hawaii. - Mar. Biol. 160: 1583-1595.
- Jones, K. M. M. 2005. Home range areas and activity centres in six species of Caribbean wrasses (Labridae). - J. Fish. Biol. 66: 150-166.
- Krone, R., et al. 2008. Defecation behaviour of the Lined Bristletooth Surgeonfish *Ctenochaetus striatus* (Acanthuridae). - Coral Reefs 27: 619-622.
- Liu, M. and Sadovy, Y. 2005. Habitat association and social structure of the chocolate hind, *Cephalopholis boenak* (Pisces: Serranidae: Epinephelinae), at Ping Chau Island, northeastern Hong Kong waters. - Environ. Biol. Fishes 74: 9-18.
- Low, R. M. 1971. Interspecific territoriality in a pomacentridreef fish, *Pomacentrus flavicauda*. - Ecol. 52: 648-654.
- Marshall, A., et al. 2011. Passive acoustic telemetry reveals highly variable home range and movement patterns among unicornfish within a marine reserve. - Coral Reefs 30: 631-642.
- Meyer, C. G., et al. 2000. Movement patterns, habitat utilization, home range size and site fidelity of whitesaddle goatfish, *Parupeneus porphyreus*, in a marine reserve. - Environ. Biol. Fishes 59: 235-242.
- Muñoz, R. C., et al. 2010. Reproduction, habitat utilization, and movements of hogfish (*Lachnolaimus maximus*) in the Florida Keys, USA: comparisons from fished versus unfished habitats. - Bull. Mar. Sci. 86: 93-116.
- Muñoz, R. C., et al. 2000. Interspecific aggression between two parrotfishes (*Sparisoma*, Scaridae) in the Florida Keys. - Copeia 2000: 674-683.
- Nanami, A. and Yamada, H. 2008. Size and spatial arrangement of home range of checkered snapper *Lutjanus decussatus* (Lutjanidae) in an Okinawan coral reef determined using a portable GPS receiver. - Mar. Biol. 153: 1103-1111.
- Nanami, A. and Yamada, H. 2009. Site fidelity, size, and spatial arrangement of daytime home range of thumbprint emperor *Lethrinus harak* (Lethrinidae). - Fish. Sci. 75: 1109-1116.
- Nursall, J. R. 1977. Territoriality in redlip blennies (*Ophioblennius atlanticus* - Pisces: Blenniidae). - J. Zool. Lon. 182: 205-223.
- Ohnishi, N., et al. 1997. Sneaking by harem masters of the sandperch, *Parapercis snyderi*. - Environ. Biol. Fishes 50: 217-223.
- Sale, P. F. 1971. Extremely limited home range in a coral reef fish, *Dascyllus aruanus* (Pisces; Pomacentridae). - Copeia 1971: 324-327.

- Samoilys, M. A. 1997. Movement in a large predatory fish: coral trout, *Plectropomus leopardus* (Pisces: Serranidae), on Heron Reef, Australia. - Coral Reefs 16: 151-158.
- Shapiro, D., et al. 1994. Social system of an inshore stock of the red hind grouper, *Epinephelus guttatus* (Pisces: Serranidae). - Environ. Biol. Fishes 41: 415-422.
- Shpigel, M. and Fishelson, L. 1991. Territoriality and associated behaviour in three species of the genus *Cephalopholis* (Pisces: Serranidae) in the Gulf of Aqaba (Red Sea). - J. Fish. Biol. 38: 887-896.
- Sikkel, P. 1990. Social organization and spawning in the Atlantic sharpnose puffer, *Canthigaster rostrata* (Tetraodontidae). - Environ. Biol. Fishes 27: 243-254.
- van Rooij, J. M., et al. 1996. The social and mating system of the herbivorous reef fish *Sparisoma viride*: one-male versus multi-male groups. - Environ. Biol. Fishes 47: 353-378.
- Welsh, J. and Bellwood, D. 2012. How far do schools of roving herbivores rove? A case study using *Scarus rivulatus*. - Coral Reefs: 1-13.
- Welsh, J. and Bellwood, D. 2012. Spatial ecology of the steephead parrotfish (*Chlorurus microrhinos*): an evaluation using acoustic telemetry. - Coral Reefs 31: 55-65.
- Welsh, J. Q., et al. 2013. The ontogeny of home ranges: evidence from coral reef fishes. - Proc. Royal Soc. B 280.
- Wetherbee, B. M., et al. 2004. Use of a marine reserve in Kaneohe Bay, Hawaii by the giant trevally, *Caranx ignobilis*. - Fish. Res. 67: 253-263.
- Zeller, D. 1997. Home range and activity patterns of the coral trout *Plectropomus leopardus* (Serranidae). - Mar. Ecol. Prog. Ser. 154: 65-77.

Appendix B: Supplemental information for Chapter 3

Table S1: Summary of fish used in behavioural observations at the three sites. Statistics describe size class of fish used in observations (mean, range and standard error of fish lengths (cm)), and density of fish recorded during UVC within these size classes (mean and standard error (100m⁻²)). Where fish within focal size classes were not observed on the UVC transects, density is recorded as <0.05.

1

Family	Full Name	FG	Mean	Size (cm)			Density		
				Min	Max	SE	Mean	SE	
Big Vickies									
Acanthuridae	Acanthurus blochii	Grazer/Detritivore	30	28.30	26	30	0.20	0.75	0.47
Acanthuridae	Acanthurus nigricauda	Grazer/Detritivore	21	28.57	27	31	0.33	<0.05	
Acanthuridae	Acanthurus nigrofuscus	Grazer/Detritivore	30	15.43	14	18	0.22	2.60	0.53
Acanthuridae	Ctenochaetus striatus	Grazer/Detritivore	30	21.00	19	23	0.33	4.45	1.11
Acanthuridae	Zebrasoma scopas	Grazer/Detritivore	30	14.43	12	16	0.27	0.40	0.25
Pomacentridae	Dischistodus melanotus	Intensive farmer	30	11.67	9	13	0.21	0.35	0.14
Pomacentridae	Dischistodus perspicillatus	Intensive farmer	30	17.47	15	19	0.24	0.05	0.05
Pomacentridae	Hemiglyphidodon plagiometopon	Extensive farmer	30	15.03	13	17	0.16	0.30	0.20
Pomacentridae	Plectroglyphidodon lacrymatus	Extensive farmer	31	10.32	8	12	0.24	0.10	0.07
Pomacentridae	Pomacentrus adelus	Indeterminate farmer	30	6.57	6	8	0.13	2.10	0.27
Scaridae	Chlorurus microrhinus	Excavator	13	47.85	45	50	0.48	0.20	0.11
Scaridae	Chlorurus sordidus IP	Scraper	30	21.63	19	23	0.26	0.85	0.28

Scaridae	<i>Scarus altipinnus</i>	Scraper	17	37.59	35	42	0.56	0.15	0.07
Scaridae	<i>Scarus flavipectoralis</i> IP	Scraper	30	20.50	18	22	0.27	0.20	0.13
Scaridae	<i>Scarus niger</i> TP	Scraper	20	31.25	29	33	0.38	0.10	0.07
Scaridae	<i>Scarus rivulatus</i> TP	Scraper	30	29.70	28	32	0.31	0.35	0.21
Scaridae	<i>Scarus schlegeli</i> IP	Scraper	30	23.43	21	25	0.18	0.55	0.35
Siganidae	<i>Siganus corallinus</i>	Grazer/Detritivore	30	23.20	22	26	0.21	0.60	0.21
Siganidae	<i>Siganus doliatus</i>	Grazer/Detritivore	30	22.47	21	25	0.22	0.20	0.11
Siganidae	<i>Siganus vulpinus</i>	Grazer/Detritivore	30	22.47	20	24	0.28	0.35	0.23
Mermaid									
Acanthuridae	<i>Acanthurus nigricauda</i>	Grazer/Detritivore	30	26.90	24	28	0.27	0.07	0.06
Acanthuridae	<i>Acanthurus nigrofuscus</i>	Grazer/Detritivore	30	15.10	14	18	0.19	3.43	0.47
Acanthuridae	<i>Acanthurus olivaceus</i>	Grazer/Detritivore	20	27.85	26	32	0.48	<0.05	
Acanthuridae	<i>Ctenochaetus striatus</i>	Grazer/Detritivore	30	21.20	18	24	0.31	6.46	1.55
Acanthuridae	<i>Naso unicornis</i>	Browser	20	31.05	28	38	0.52	0.17	0.12
Acanthuridae	<i>Zebrasoma scopas</i>	Grazer/Detritivore	30	14.10	11	16	0.29	1.89	0.83
Pomacanthidae	<i>Centropyge bicolor</i>	Grazer/Detritivore	30	10.87	8	14	0.24	0.29	0.19
Pomacentridae	<i>Dischistodus melanotus</i>	Intensive farmer	30	13.53	12	16	0.25	0.29	0.11
Pomacentridae	<i>Dischistodus psuedochrysopecilus</i>	Intensive farmer	30	12.13	10	16	0.25	0.29	0.17
Pomacentridae	<i>Plectroglyphidodon lacrymatus</i>	Extensive farmer	30	9.20	8	12	0.22	1.20	0.51
Pomacentridae	<i>Pomacentrus adelus</i>	Indeterminate farmer	30	7.13	6	9	0.15	1.89	0.69
Pomacentridae	<i>Stegastes nigricans</i>	Intensive farmer	30	11.93	10	13	0.17	0.63	0.40
Scaridae	<i>Chlorurus sordidus</i> IP	Scraper	30	19.63	18	22	0.30	0.46	0.14
Scaridae	<i>Scarus flavipectoralis</i> IP	Scraper	30	19.93	18	22	0.33	<0.05	

Scaridae	<i>Scarus niger</i> TP	Scraper	30	30.87	29	33	0.23	0.34	0.16
Scaridae	<i>Scarus rivulatus</i> IP	Scraper	30	20.20	18	22	0.37	0.34	0.14
Scaridae	<i>Scarus rubroviolaceus</i> IP	Scraper	12	38.17	36	42	0.63	0.11	0.11
Scaridae	<i>Scarus schlegeli</i> IP	Scraper	30	22.60	20	24	0.37	0.57	0.39
Siganidae	<i>Siganus doliatus</i>	Grazer/Detritivore	30	23.47	22	27	0.26	0.46	0.18
Siganidae	<i>Siganus vulpinus</i>	Grazer/Detritivore	12	24.58	22	27	0.43	0.06	0.06
Turtle									
Acanthuridae	<i>Acanthurus blochii</i>	Grazer/Detritivore	30	28.37	26	30	0.22	0.05	0.05
Acanthuridae	<i>Acanthurus nigrofuscus</i>	Grazer/Detritivore	30	14.87	14	18	0.21	1.30	0.42
Acanthuridae	<i>Acanthurus olivaceus</i>	Grazer/Detritivore	31	28.13	26	30	0.24	0.20	0.13
Acanthuridae	<i>Ctenochaetus striatus</i>	Grazer/Detritivore	31	21.29	19	24	0.24	2.20	0.96
Acanthuridae	<i>Zebrasoma scopas</i>	Grazer/Detritivore	30	14.30	12	16	0.25	0.25	0.11
Acanthuridae	<i>Zebrasoma veliferum</i>	Grazer/Detritivore	30	19.40	17	21	0.29	0.15	0.11
Kyphosidae	<i>Kyphosus vaigiensis</i>	Browser	30	27.57	25	30	0.27	0.50	0.25
Pomacanthidae	<i>Centropyge bicolor</i>	Grazer/Detritivore	31	10.97	8	14	0.21	0.25	0.11
Pomacentridae	<i>Dischistodus melanotus</i>	Intensive farmer	30	12.77	11	16	0.24	0.10	0.10
Pomacentridae	<i>Plectroglyphidodon lacrymatus</i>	Extensive farmer	30	8.97	8	12	0.25	0.35	0.26
Pomacentridae	<i>Pomacentrus adelus</i>	Indeterminate farmer	30	7.37	6	9	0.13	1.30	0.43
Pomacentridae	<i>Stegastes nigricans</i>	Intensive farmer	30	12.43	10	14	0.24	0.35	0.23
Scaridae	<i>Cetoscarus bicolor</i>	Excavator	11	48.64	45	55	0.98	0.10	0.10
Scaridae	<i>Chlorurus sordidus</i> IP	Scraper	30	18.70	16	21	0.30	0.05	0.05
Scaridae	<i>Scarus niger</i> TP	Scraper	30	29.83	28	34	0.29	0.05	0.05
Scaridae	<i>Scarus oviceps</i> IP	Scraper	18	24.78	22	26	0.29	0.10	0.07

Scaridae	Scarus rivulatus TP	Scraper	30	33.13	32	34	0.15	0.25	0.11
Scaridae	Scarus schlegeli IP	Scraper	30	24.87	23	27	0.25	0.15	0.07
Siganidae	Siganus doliatus	Grazer/Detritivore	31	22.32	21	24	0.19	0.75	0.19
Siganidae	Siganus punctatus	Grazer/Detritivore	29	24.55	22	26	0.25	0.05	0.05

Table S2: Proportion of bites targeting different benthic types by focal individuals at the 3 sites. CCA-Calcareous coralline algae, DI-Diseased coral, EAM-Epilithic algal matrix, HC-Hard coral, MA-Macroalgae, SA-Sand, SC-Soft coral, SCM –Soft coral mucus.

Family	Full Name	FG	CCA	DI	EAM	HC	MA	SA	SC	SCM
Big Vickies										
Acanthuridae	Acanthurus blochii	Grazer/Detritivore	0.0	0.0	93.3	0.0	0.0	3.3	0.0	3.3
Acanthuridae	Acanthurus nigricauda	Grazer/Detritivore	0.0	0.0	95.2	0.0	0.0	4.8	0.0	0.0
Acanthuridae	Acanthurus nigrofuscus	Grazer/Detritivore	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Acanthuridae	Ctenochaetus striatus	Grazer/Detritivore	0.0	0.0	69.2	30.8	0.0	0.0	0.0	0.0
Acanthuridae	Zebrasoma scopas	Grazer/Detritivore	0.0	0.0	96.7	0.0	0.0	0.0	3.3	0.0
Pomacentridae	Dischistodus melanotus	Intensive farmer	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Pomacentridae	Dischistodus perspicillatus	Intensive farmer	0.0	3.3	93.3	0.0	3.3	0.0	0.0	0.0
Pomacentridae	Hemiglyphidodon plagiometopon	Extensive farmer	0.0	0.0	86.7	0.0	13.3	0.0	0.0	0.0
Pomacentridae	Plectroglyphidodon lacrymatus	Extensive farmer	0.0	0.0	90.0	0.0	10.0	0.0	0.0	0.0
Pomacentridae	Pomacentrus adelus	Indeterminate farmer	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Scaridae	Chlorurus microrhinus	Excavator	0.0	0.0	93.3	0.0	0.0	0.0	6.7	0.0
Scaridae	Chlorurus sordidus IP	Scraper	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Scaridae	Scarus altipinnus	Scraper	0.0	0.0	96.7	0.0	0.0	3.3	0.0	0.0
Scaridae	Scarus flavipectoralis IP	Scraper	0.0	0.0	95.0	5.0	0.0	0.0	0.0	0.0
Scaridae	Scarus niger TP	Scraper	0.0	0.0	96.7	0.0	0.0	3.3	0.0	0.0
Scaridae	Scarus rivulatus TP	Scraper	0.0	0.0	96.7	0.0	0.0	0.0	3.3	0.0
Scaridae	Scarus schlegeli IP	Scraper	0.0	0.0	96.7	3.3	0.0	0.0	0.0	0.0
Siganidae	Siganus corallinus	Grazer/Detritivore	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0

Siganidae	<i>Siganus doliatus</i>	Grazer/Detritivore	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Siganidae	<i>Siganus vulpinus</i>	Grazer/Detritivore	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Mermaid										
Acanthuridae	<i>Acanthurus nigricauda</i>	Grazer/Detritivore	3.3	0.0	90.0	0.0	3.3	3.3	0.0	0.0
Acanthuridae	<i>Acanthurus nigrofuscus</i>	Grazer/Detritivore	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Acanthuridae	<i>Acanthurus olivaceus</i>	Grazer/Detritivore	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Acanthuridae	<i>Ctenochaetus striatus</i>	Grazer/Detritivore	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Acanthuridae	<i>Naso unicornis</i>	Browser	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Acanthuridae	<i>Zebrasoma scopas</i>	Grazer/Detritivore	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Pomacanthidae	<i>Centropyge bicolor</i>	Grazer/Detritivore	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Pomacentridae	<i>Dischistodus melanotus</i>	Intensive farmer	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Pomacentridae	<i>Dischistodus psuedochrysopecilus</i>	Intensive farmer	5.0	0.0	95.0	0.0	0.0	0.0	0.0	0.0
Pomacentridae	<i>Plectroglyphidodon lacrymatus</i>	Extensive farmer	0.0	0.0	96.7	3.3	0.0	0.0	0.0	0.0
Pomacentridae	<i>Pomacentrus adelus</i>	Indeterminate farmer	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Pomacentridae	<i>Stegastes nigricans</i>	Intensive farmer	0.0	0.0	96.7	0.0	3.3	0.0	0.0	0.0
Scaridae	<i>Chlorurus sordidus</i> IP	Scraper	0.0	0.0	96.7	3.3	0.0	0.0	0.0	0.0
Scaridae	<i>Scarus flavipectoralis</i> IP	Scraper	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Scaridae	<i>Scarus niger</i> TP	Scraper	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Scaridae	<i>Scarus rivulatus</i> IP	Scraper	0.0	0.0	93.3	0.0	3.3	3.3	0.0	0.0
Scaridae	<i>Scarus rubroviolaceus</i> IP	Scraper	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Scaridae	<i>Scarus schlegeli</i> IP	Scraper	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Siganidae	<i>Siganus doliatus</i>	Grazer/Detritivore	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Siganidae	<i>Siganus vulpinus</i>	Grazer/Detritivore	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0

Turtle										
Acanthuridae	<i>Acanthurus blochii</i>	Grazer/Detritivore	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Acanthuridae	<i>Acanthurus nigrofuscus</i>	Grazer/Detritivore	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Acanthuridae	<i>Acanthurus olivaceus</i>	Grazer/Detritivore	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Acanthuridae	<i>Ctenochaetus striatus</i>	Grazer/Detritivore	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Acanthuridae	<i>Zebrasoma scopas</i>	Grazer/Detritivore	0.0	0.0	90.9	9.1	0.0	0.0	0.0	0.0
Acanthuridae	<i>Zebrasoma veliferum</i>	Grazer/Detritivore	0.0	0.0	96.7	3.3	0.0	0.0	0.0	0.0
Kyphosidae	<i>Kyphosus vaigiensis</i>	Browser	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Pomacanthidae	<i>Centropyge bicolor</i>	Grazer/Detritivore	0.0	0.0	96.7	0.0	3.3	0.0	0.0	0.0
Pomacentridae	<i>Dischistodus melanotus</i>	Intensive farmer	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Pomacentridae	<i>Plectroglyphidodon lacrymatus</i>	Extensive farmer	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Pomacentridae	<i>Pomacentrus adelus</i>	Indeterminate farmer	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Pomacentridae	<i>Stegastes nigricans</i>	Intensive farmer	0.0	0.0	96.7	3.3	0.0	0.0	0.0	0.0
Scaridae	<i>Cetoscarus bicolor</i>	Excavator	0.0	0.0	94.4	0.0	5.6	0.0	0.0	0.0
Scaridae	<i>Chlorurus sordidus</i> IP	Scraper	0.0	0.0	96.7	0.0	3.3	0.0	0.0	0.0
Scaridae	<i>Scarus niger</i> TP	Scraper	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Scaridae	<i>Scarus oviceps</i> IP	Scraper	0.0	0.0	93.5	0.0	0.0	3.2	3.2	0.0
Scaridae	<i>Scarus rivulatus</i> TP	Scraper	0.0	0.0	86.2	0.0	13.8	0.0	0.0	0.0
Scaridae	<i>Scarus schlegeli</i> IP	Scraper	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Siganidae	<i>Siganus doliatus</i>	Grazer/Detritivore	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Siganidae	<i>Siganus punctatus</i>	Grazer/Detritivore	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0

Table S3: Summary of scaling parameters for the relationship in herbivorous fish functional groups between body length and A) Intra-foray distance, and B) Inter-foray distance, where parameters represent $y=\alpha x^\beta$.

Site	$\alpha(\pm 95\%CI)$	$\beta(\pm 95\%CI)$	R^2	p-value
A) Intra-foray Distance				
Farmer	0.58 (0.01→36.06)	0.70 (-0.96→2.36)	0.19	0.329
Grazer/Detritivore	0.48 (0.04→5.86)	1.32 (0.51→2.15)	0.56	0.004**
Scraper/Excavator	0.04 (0.00→0.42)	2.01 (1.35→2.66)	0.86	<0.001**
Common parameters		1.46 (0.96→1.96)	0.89	<0.001**
Common Slope: Likelihood ratio statistic of 5.26, 2 d.f., p=0.07				
Common Elevation: Wald statistic of 32.86, 2 d.f., p<0.001**				
B) Inter-foray Distance				
Farmer	0.14 (0.32→153.46)	0.76 (-0.49→2.00)	0.32	0.179
Grazer/Detritivore	0.15 (0.02→1.41)	2.42 (1.69→3.16)	0.84	<0.001**
Scraper/Excavator	1.08 (0.15→7.76)	1.76 (1.19→2.34)	0.86	<0.001**
Common Slope: Likelihood ratio of 10.63, 2 d.f., p=0.005**				
Common Elevation: NA				

Table S4: Summary of scaling parameters for the relationship in herbivorous fish families between body length and A) Intra-foray distance, and B) Inter-foray distance, where parameters represent $y=αx^β$.

Site	$α(± 95\%CI)$	$β(± 95\%CI)$	R^2	p-value
A) Intra-foray Distance				
Big Vickies	0.00 (0.00→2.45)	2.97 (0.66→5.27)	0.94	0.03*
Mermaid	0.04 (0.00→55.72)	2.15 (1.81→3.14)	0.71	0.07
Turtle	0.06 (0.01→0.45)	1.97 (1.31→2.63)	0.95	0.001**
Common parameters	0.03 (0.00→0.21)	2.17 (1.52→2.81)	0.79	<0.001**
Common Slope: Likelihood ratio statistic of 6.50, 2 d.f., p=0.33				
Common Elevation: Wald statistic of 1.91, 2 d.f., p=0.38				
B) Inter-foray Distance				
Big Vickies	0.15 (0.00→38.90)	2.37 (0.55→4.20)	0.94	0.030*
Mermaid	0.11 (0.01→1.82)	2.58 (1.62→3.55)	0.96	0.003**
Turtle	0.48 (0.05→4.42)	2.02 (1.28→2.77)	0.93	0.002**
Common parameters	0.27 (0.08→0.87)	2.23(1.83→2.63)	0.91	<0.001**
Common Slope: Likelihood ratio statistic of 14.50, 2 d.f., p=0.23				
Common Elevation: Wald statistic of 2.73, 2 d.f., p=0.26				

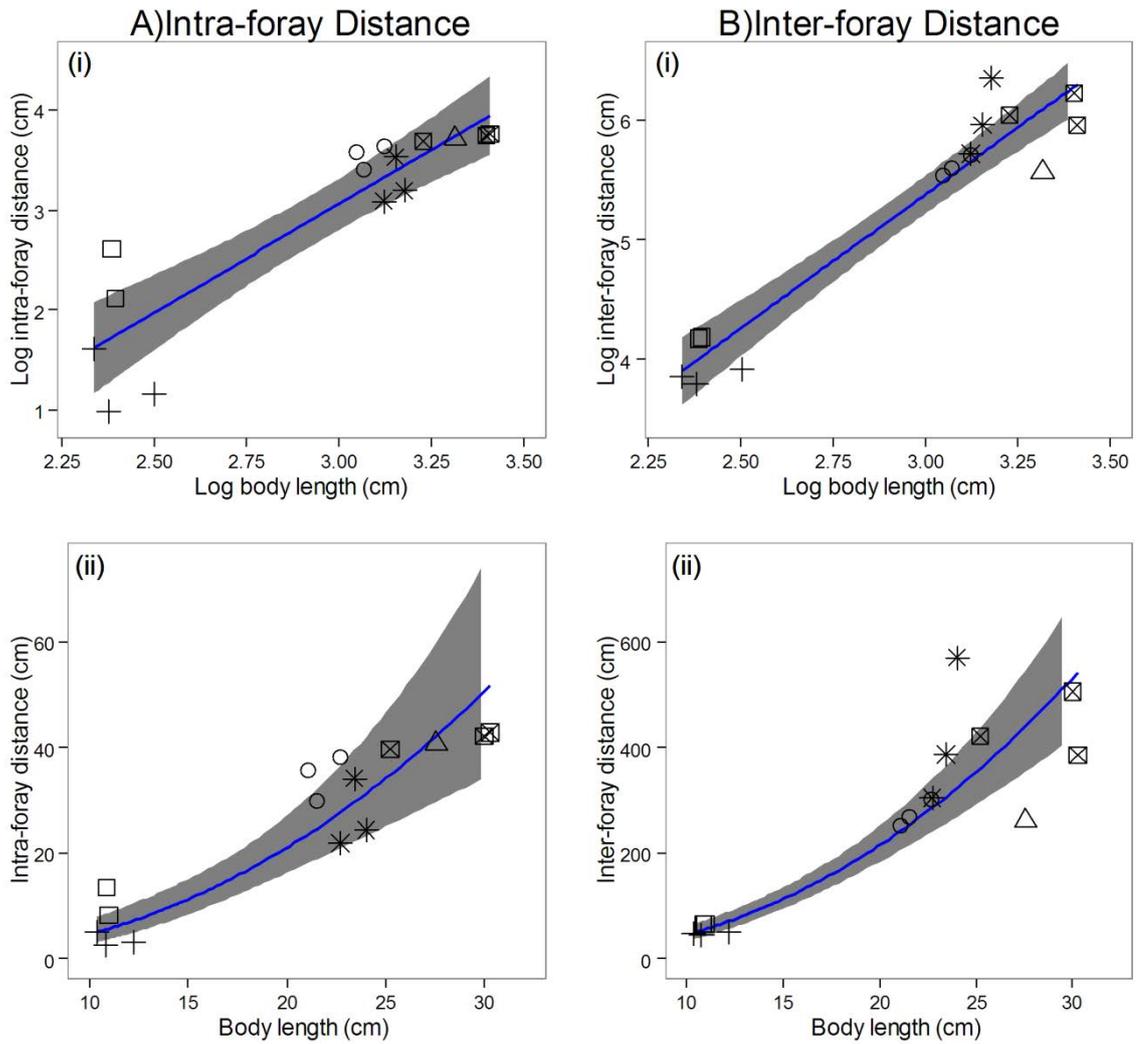


Figure S1: Relationship between body length and A) Intra-foray distance or B) Inter-foray distance for herbivorous reef fish at the family level, presented in i) log-log scales and ii) back-transformed to arithmetic scales. Lines represent significant relationships ($\pm 95\%$ CI) based on OLS regression, showing common slope and intercept among sites for both variables. Symbols indicate family: circle-Acanthuridae, triangle-Kyphosidae, square-Pomacanthidae, cross-Pomacentridae, star-Siganidae, crossed square-Scaridae.

Appendix C: Supplemental information for Chapter 4

Text S1: Estimation of Flight Initiation Distance (FID)

FID was measured for at least 3 individuals of both target species prior to starting foraging range measurements. To estimate FID, individual fish which were feeding or moving slowly across the reef, were approached along the bottom at a slow speed, perpendicular to their direction of travel. At the moment the fish fled from the diver (flight was defined an increase in speed or change in direction), a marker was dropped in line with the diver's head, and a second marker dropped at the location of the fish at the moment of flight (following Januchowski-Hartley et al. 2011). The distance between these two markers was measured.

References:

Januchowski-Hartley FA, Graham NAJ, Feary DA, Morove T, Cinner JE (2011) Fear of fishers: human predation explains behavioral changes in coral reef fishes. PLoS ONE 6:e22761

Table S1: Lifeforms of coral driving coral cover as a predictor of inter-foray distance for a) *Scarus niger* and b) *Scarus frenatus* in best-fit GAMM and GLMM models. Significant predictors are in bold, alpha values were corrected for multiple comparisons ($\alpha = 0.002$).

a) <i>Scarus niger</i>	
Model	Adj. R^2
Branching & Submassive coral cover	0.72
Massive & Encrusting coral cover	0.12
Plate coral cover	0.07
b) <i>Scarus frenatus</i>	
Model	Adj. R^2
Branching & Submassive coral cover	0.07
Plate coral cover	0.03
Massive & Encrusting coral cover	0.02

Table S2: Best-fit models for predicting area of short-term foraging range of a) *Scarus niger* and b) *Scarus frenatus*. Models presented are those with lowest AICc values from GLMM that evaluate the influence of reef, exposure, structural complexity, coral cover, EAM cover, parrotfish abundance and large piscivore abundance. Significant predictors are in bold ($\alpha = 0.01$).

a) <i>Scarus niger</i>				
Model	AICc	ΔAICc	wAICc	Adj. R^2
In Parrotfish abundance	741.13	0.00	0.67	0.17
In Parrotfish abundance, Structural complexity	743.09	1.96	0.25	0.17
In Parrotfish abundance, Structural complexity, Exposure	745.92	4.78	0.06	0.15
b) <i>Scarus frenatus</i>				
Model	AICc	ΔAICc	wAICc	Adj. R^2
In Parrotfish abundance	648.69	0.00	0.72	0.03
In Parrotfish abundance, Exposure	651.02	2.33	0.22	0.05
In Parrotfish abundance Exposure, Structural complexity	653.94	5.25	0.05	0.15

Table S3: Lifeforms of coral driving coral cover as a predictor of shape of foraging range of a) *Scarus niger* and b) *Scarus frenatus* in best-fit GAMM and GLMM models. Significant predictors are in bold, alpha values were corrected for multiple comparisons ($\alpha = 0.002$).

a) <i>Scarus niger</i>	
Model	Adj. R^2
Branching & Submassive coral cover, ln(Parrotfish abundance)	0.61
Massive & Encrusting coral cover, ln(Parrotfish abundance)	0.45
Plate coral cover, ln(Parrotfish abundance)	0.36
b) <i>Scarus frenatus</i>	
Model	Adj. R^2
Branching & Submassive coral cover	0.48
Massive & Encrusting coral cover	0.07
Plate coral cover	0.04

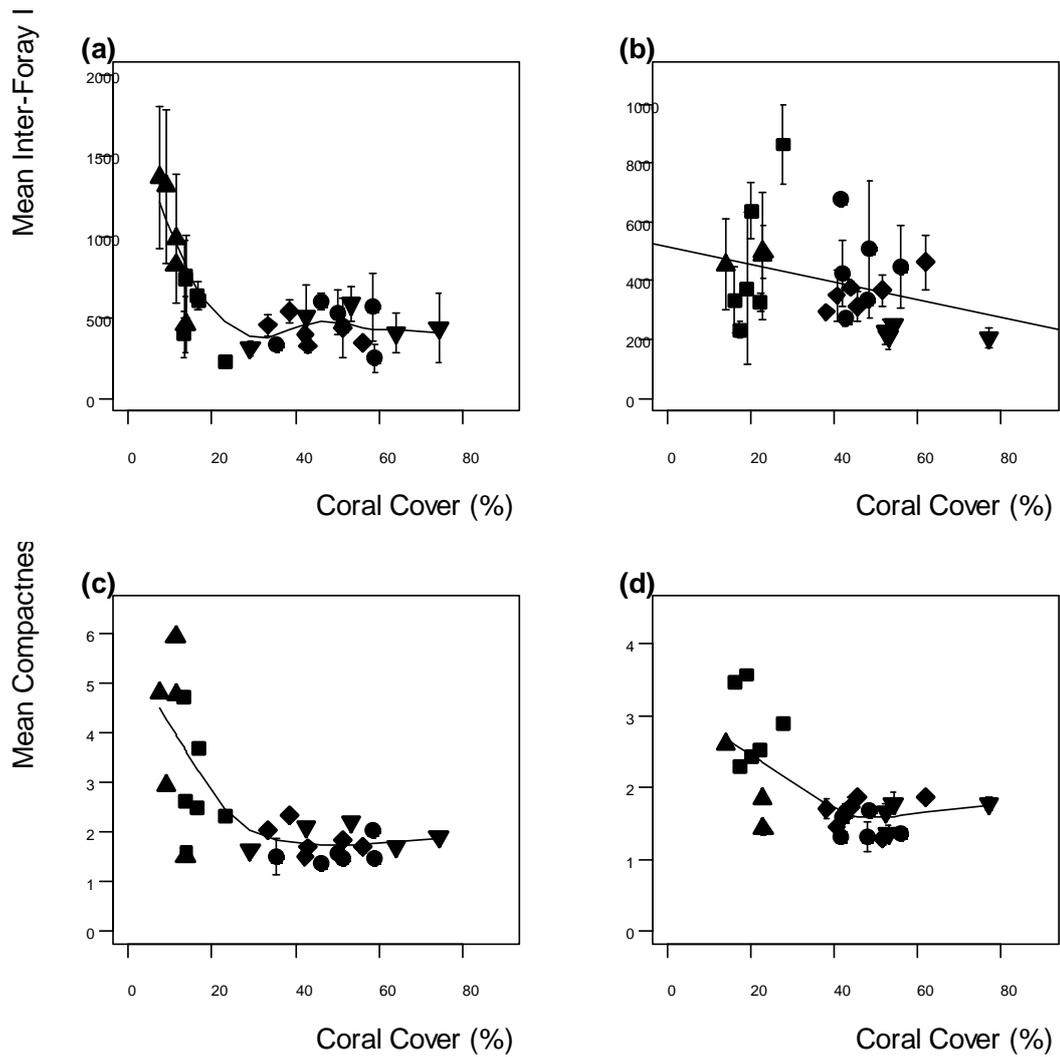


Fig. S1: Raw data used to produce GAMS. Relationship between coral cover (%) and inter-foray distance for a) *Scarus niger* and b) *Scarus frenatus*, and between coral cover and shape of foraging range (compactness ratio) for c) *Scarus niger* and d) *Scarus frenatus*. Solid curves represent linear and nonlinear relationships used in GAMM and GLMM models. Error bars represent \pm SE. Locations are distinguished as follows: squares - John Brewer; diamonds - Rib; upward pointing triangles - Trunk; downward pointing triangles - Wheeler. Note different scales on the y axes.

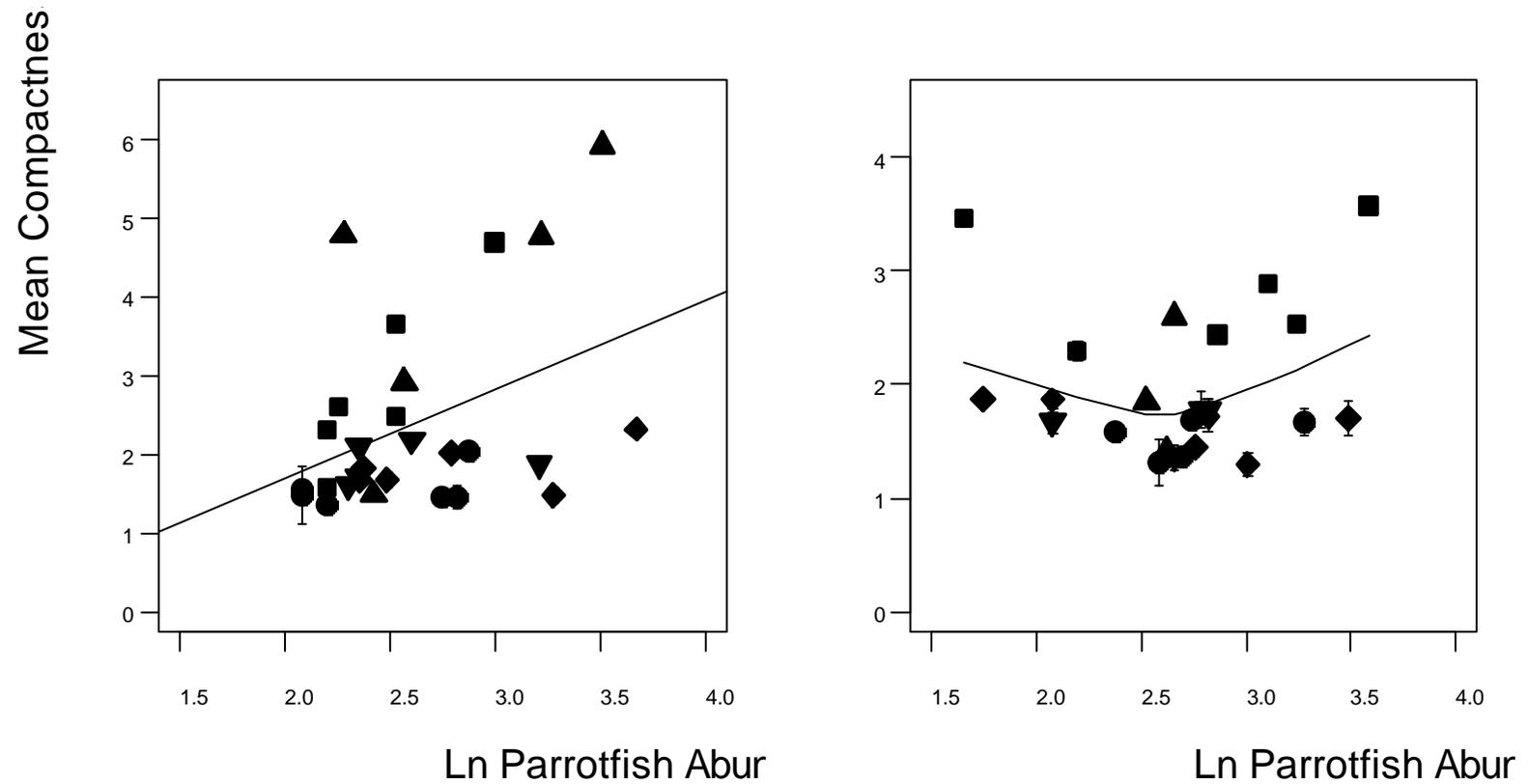


Fig. S2: Raw data used to produce GAMS. Relationship between Ln parrotfish abundance and shape of foraging range (compactness ratio) for a) *Scarus niger* and b) *Scarus frenatus*. Solid curves represent linear and nonlinear relationships used in GAMM and GLMM models. Error bars represent \pm SE. Locations are distinguished as follows: squares - John Brewer; diamonds - Rib; upward pointing triangles - Trunk; downward pointing triangles - Wheeler. Note different scales on the y axes.

Appendix D: Supplemental information for Chapter 6

Table S1. Hierarchy theory, panarchy theory, scale domains and power laws. The co-dependency of pattern, process and scale in ecosystems necessitates models that are sensitive to the specific system context (Levick and Rogers 2011). Over the last thirty years, the development of a number of models has helped to simplify the inherent complexity of ecosystems. Each is an attempt at dissecting systems into manageable units for meaningful inference of pattern and process, by using the scale of observation as a reference. Despite this underlying commonality they retain subtle differences.

Model	Description
Hierarchy theory	Describes ecosystems as a hierarchical structure, with smaller scale pattern and process nested within the constraints imposed by larger patterns and processes (Allen and Starr 1982, O'Neill et al. 1989). For example, in forest ecosystems, small and fast scales are dominated by biophysical processes that control plant morphology and function. At larger and slower scales, interspecific plant competition for nutrients, light, and water interacts with climate and affects local species composition and regeneration. At the scale of forest stands, mesoscale processes of fire, storm, insect outbreak, plant diseases and large mammal herbivores determine structure and succession dynamics from tens of meters to kilometres, and years to decades. The largest landscape scales have geomorphological and evolutionary processes that affect structure and dynamics over hundreds of kilometres and millennia, and constrain lower levels in the hierarchy (Holling 1992, Sankaran et al 2005). Hierarchy theory has provided the foundation for further predictive, ecosystem models that rely on scale-space-pattern relationships, for example <i>panarchy theory</i> , <i>scale domains</i> , the <i>discontinuity hypothesis</i> , and may be contrasted to the <i>power law</i> model.
Panarchy theory	Provides a dynamic interpretation of hierarchy theory. A panarchy is a nested set of adaptive cycles operating at discrete scales. Discontinuities are thresholds between the dynamic levels, i.e., adaptive cycles, of a panarchy. Unlike the top-down control envisioned in hierarchy theory, connectivity between adaptive cycles in a panarchy can be from levels above or below. In a hierarchy, lower-level patterns and processes are dominated by higher levels in the hierarchy. Panarchy differs from this characterization of nesting, in that conditions can arise that trigger “bottom-up” (i.e., cross-scale cascading) change in the system. The multiple but distinct scales of self-organization and the distribution of function within and across the scales create resilient systems. This model of social-ecological systems captures the “surprise” or uncertainty inherent in such systems (Gunderson and Holling 2002, Garmestani et al. 2009).
Scale domains	Hierarchically structured ecosystems possess a high degree of co-dependency between components with similar process rates and overlapping

spatial scales (O'Neill et al. 1989, Levin 1992). This concept was formalized as the scale domain (Wiens 1989). Scale domains define a section of the scale spectrum where process-pattern relationships are consistent, i.e. they are homogeneous or change monotonically, and persist over the timescale of interest (Stallins 2006). Also termed 'intrinsic' scales (Figure 6-1). A domain is separated from neighbouring domains by scale breaks, which are zones of variability where there is a change in the dominant processes. The discontinuity hypothesis builds on the idea of scale domains by highlighting the discontinuous cross-scale pattern provided by scale domains and breaks, linking aggregations and discontinuities in body mass distributions or vegetative pattern to scale domains and breaks, respectively.

Power laws

In contrast to hierarchy theory, panarchy theory and scale domains, power law relationships emphasize self-similar patterns across a range of scales and have been used as evidence of self-organization within a system (Scanlon et al. 2007). For example, small scale processes such as local level facilitation, combined with resource competition such as competition for water in semi-arid savannah systems, drive scale invariant behaviour (Kefi et al. 2007). Power laws focus on the importance of patterns at larger scales being indicative of smaller scale processes, whereas, hierarchy theory and its derivatives emphasize that processes are dominant over a particular range of scales, although effects may percolate up or down through the hierarchy. This distinction is largely semantic, however, as there may be a power law relationship within a scale domain (Wiens 1989), and power laws observed in ecosystems are bounded, constrained by larger scale processes such as substrate availability or climate (Brown et al. 2002, Kefi et al. 2007, Scanlon et al. 2007).

Table S2. Different methods used to examine the shape of body size distributions. To date, discontinuity analyses have primarily targeted body size as the variable of interest (but see Gunderson 2008, Angeler et al. 2012). Studies of body size distributions are widespread in ecology because the links between organism size and individual, population and community characteristics provide powerful ways of evaluating ecosystem dynamics at a range of organizational levels (Brown et al. 2004, Marquet et al. 2005, Woodward et al. 2005). However, confounding approaches, particularly along a marine-terrestrial divide, result in body size distributions that are subject to different drivers (White et al. 2007, Webb 2012). This has resulted in a lack of clarity regarding the shape of these distributions (White et al. 2007).

Terrestrial	Aquatic
1. Studies largely use size-density relationships, where size is aggregated at the species level.	1. Studies predominantly use size spectra, where abundance of different size classes are calculated regardless of taxonomic affinity.
2. Greater relative weight is given to taxonomic identity versus individual size.	2. Greater relative weight is given to individual size versus taxonomic identity.
3. Species level size-density relationships have received attention due to interest in energetic equivalence, i.e. invariant energy requirements across body sizes (Brown et al. 2004).	3. Size spectra have been used to study the dynamics of aquatic communities (Marquet et al. 2005) and to evaluate the impacts of fishing pressure (Edwards et al. 2012).
4. Discontinuity studies using this approach include Holling (1992) and Fischer et al. (2008).	4. Discontinuity studies using this approach include Thibault et al. (2011) and Nash et al. (2013).



References:

- Allen, T. F. H. and Starr, T. B. (eds.). 1982. *Hierarchy: perspectives for ecological complexity*. - University of Chicago Press.
- Angeler, D. G., et al. 2012. Insight on invasions and resilience derived from spatiotemporal discontinuities of biomass at local and regional scales. - *Ecology and Society* 17: 32.
- Brown, J. H., et al. 2004. Toward a metabolic theory of ecology. - *Ecol.* 85: 1771-1789.
- Brown, J. H., et al. 2002. The fractal nature of nature: power laws, ecological complexity and biodiversity. - *Philos. Trans. Royal Soc. B* 357: 619-626.

- Edwards, C. T. T., et al. 2012. Fisheries assessment and management: a synthesis of common approaches with special reference to deepwater and data-poor stocks. - *Reviews in Fisheries Science* 20: 136-153.
- Fischer, J., et al. 2008. The role of landscape texture in conservation biogeography: a case study on birds in south-eastern Australia. - *Diversity and Distributions* 14: 38-46.
- Garmestani, A. S., et al. 2009. Panarchy: discontinuities reveal similarities in the dynamic system structure of ecological and social systems. - *Ecology and Society* 14: 15.
- Gunderson, L. H. 2008. Biophysical discontinuities in the Everglades system. - In: Allen, C. R. and Holling, C. S. (eds.), *Discontinuities in ecosystems and other complex systems*. Columbia University Press, pp. 83-100.
- Gunderson, L. H. and Holling, C. S. 2002. *Panarchy: understanding transformations in human and natural systems*. - Island Press.
- Holling, C. S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. - *Ecological Monographs* 62: 447-502.
- Kefi, S., et al. 2007. Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. - *Nature* 449: 213-217.
- Levick, S. and Rogers, K. 2011. Context-dependent vegetation dynamics in an African savannah. - *Landscape Ecol.* 26: 515-528.
- Levin, S. A. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur Award lecture. - *Ecol.* 73: 1943-1967.
- Marquet, P. A., et al. 2005. Scaling and power-laws in ecological systems. - *J. Exp. Biol.* 208: 1749-1769.
- Nash, K. L., et al. 2013. Cross-scale habitat structure drives fish body size distributions on coral reefs. - *Ecosyst.* 16: 478-490.
- O'Neill, R. V., et al. 1986. *A hierarchical concept of ecosystems*. - Princeton University Press.
- Sankaran, M., et al. 2005. Determinants of woody cover in African savannas. - *Nature* 438: 846-849.
- Scanlon, T. M., et al. 2007. Positive feedbacks promote power-law clustering of Kalahari vegetation. - *Nature* 449: 209-212.
- Stallins, J. A. 2006. Geomorphology and ecology: unifying themes for complex systems in biogeomorphology. - *Geomorphology* 77: 207-216.
- Thibault, K. M., et al. 2011. Multimodality in the individual size distributions of bird communities. - *Global Ecology and Biogeography* 20: 145-153.
- Webb, T. J. 2012. Marine and terrestrial ecology: unifying concepts, revealing differences. - *Trends Ecol. Evol.* 27: 535-541.
- White, E. P., et al. 2007. Relationships between body size and abundance in ecology. - *Trends Ecol. Evol.* 22: 323-330.
- Wiens, J. A. 1989. Spatial scaling in ecology. - *Func. Ecol.* 3: 385-397.
- Woodward, G., et al. 2005. Body size in ecological networks. - *Trends Ecol. Evol.* 20: 402-409.

Appendix E: Supplemental information for Chapter 7

Text S1: Details of Datasets

Bird Communities - Mount Lofty Ranges

Data were sourced from The Mount Lofty Ranges Bird Survey website (www.ecology.uq.edu.au). Bird surveys were conducted at sites within two habitat types: stringybark and gum forests of the Mount Lofty Ranges between November and December 2000. The stringybark forest was characterised by two main levels of habitat structure: a canopy of *Eucalyptus baxteri* and *E. oblique*, with a thick understory of sclerophyllous vegetation such as acacias and banksias (Possingham et al. 2004). In contrast, the gum habitat consisted of three main levels of habitat structure a canopy primarily composed of *E. leucoxylon* and *E. fasciculosa*, a sparse but mixed species (e.g. *E. cosmophylla* and *Bursaria spinosa*) mid-storey, and low level shrubs and grasses (Possingham and Possingham 2008). Bird species and abundances were recorded at 48 stringybark and 61 gum woodland sites. Birds were surveyed in a 2 ha area for three 20 min intervals over three one hr sessions. All individuals visually or aurally identified and considered to be occupying the site (i.e. not transiting the area overhead) were recorded (see Possingham et al. 2004, Possingham et al. 2006, Possingham and Possingham 2008 for full details).

Bird Communities - Borneo Upland Forest

Data were sourced from Cleary et al. (2007). Bird surveys were conducted in upland forests within the Central Kalimantan province of Indonesia between June and October 1997, and July and October 1998. Sites were located in three different habitat types: unlogged primary forest, forest logged between 1989 and 1990, and forest logged between 1993 and 1994 (termed unlogged, logged_89, and logged_93 habitats, respectively). The areas subject to logging were selectively harvested with extraction primarily targeting dipterocarp tree species. The unlogged primary forest was characterised by greater canopy height, higher density of tall saplings and dead wood. In contrast, the recently logged sites were composed of greater densities of smaller saplings, understory fern cover and small lianas. The older logged sites presented a transitional state between the primary forest and recently logged forest. Bird species and abundances were recorded at 14 unlogged sites, 10 sites in logged_89 areas, and 13 sites in logged_93 areas. Birds were surveyed along two 300m transects, and surveys were repeated twice at each site (see Cleary et al. 2007 for full details).

Fish Communities - Seychelles Reef

Fish and benthic surveys were conducted on reefs of the inner granitic islands of the Seychelles in April 2011. Sites were located in three different habitat types: coral-dominated carbonate reefs, algal-dominated carbonate reefs and granitic reefs (termed coral, algae, and granite habitats, respectively). The coral-dominated reefs were characterised by high coral and low algal cover, and non-living substrata was dominated by sand and rubble. The algal-dominated reefs had been coral-dominated prior to the 1998 bleaching event, but in 2011 were composed of high macroalgal cover and little hard coral cover. The granitic sites had high coral and low algal cover, but non-living substrate was dominated by large smooth granite boulders. The three habitat types were characterised by different patterns of cross-scale habitat structure (Nash et al. 2013). Fish surveys were performed at 7 coral sites, 3 algae sites, and 5 granite sites. Fish abundance and individual body length were estimated at each site, using UVC in eight 7 m radius point counts located on the reef slope. The same observer conducted all fish counts (N.A.J.G.), and the accuracy of fish body length estimations were assessed daily using lengths of PVC pipe, prior to the start of data collection, with estimates consistently within 9% of actual lengths (see Graham et al. 2006 for full details).

Fish Communities - Great Barrier Reef

Fish and benthic surveys were conducted at five mid-shelf reefs on the central Great Barrier Reef (GBR) between November 2010 and January 2011. Sites were located in three different habitat types: two reefs that had been largely un-impacted by major pulse disturbances since the 1980s and had relatively high coral cover, two reefs that had very low coral cover having experienced multiple, large-scale disturbances (crown-of-thorns starfish *Acanthaster planci* outbreaks and coral bleaching) since the early 1980s, and 1 reef that had been severely impacted by crown-of-thorns outbreaks, but has been showing signs of recovery with coral cover increasing (AIMS 2011) (termed undisturbed, disturbed, and recovering habitats, respectively). Fish abundance and individual body length were estimated at each site using instantaneous underwater visual census (UVC) along four 50m transects located on the reef slope. The same observer conducted all fish counts (N.A.J.G.), and the accuracy of fish body length estimations were assessed daily using lengths of PVC pipe, prior to the start of data collection, with estimates consistently within 8% of actual lengths (see Nash et al. 2012 for full details).

Text S2: Measuring habitat structure, and biases in survey data and construction of size distributions

Measurement of habitat structure

The measures of habitat structure used in this study were qualitative in nature. However, the datasets were specifically selected because of their inclusion of sites with contrasting cross-scale habitat structure (see descriptions in Text S1). These differences have been quantified for the Borneo (Cleary et al. 2007) and Seychelles (Nash et al. 2013) datasets and have been described for the Lofty Ranges (Possingham et al. 2004) and Great Barrier Reef sites (Graham et al. 2014). Consistency in the findings across multiple replicate sites of each habitat type within the four datasets, and multiple datasets within terrestrial and aquatic communities, lends support to the discontinuity hypothesis (Webb et al. 2011, Ernest 2013), which predicts that habitat structure influences the size of species within associated communities. Nevertheless, where detailed data is available on habitat structure at different scales, my approach should be extended to produce a rigorous quantitative evaluation. For example, constrained ordination methods such as Redundancy Analysis would allow habitat variables to be directly related to body size distributions (Legendre and Legendre 1998). Such predictions are critical for forecasting the future impacts of habitat fragmentation and degradation.

Biases inherent in survey data and construction of size distributions

There are a number of potential biases inherent in the collection and analysis of community abundance and size data. For example, the lower end of the size distribution is likely to be influenced by size-related under-sampling (Blackburn and Gaston 1994). In addition, the shape of body size distributions may change across scales, with different patterns found at local, regional and continental scales (Bakker and Kelt 2000), due to cross-scale patterns of individual drivers such as habitat structure or as a result of different scale-specific drivers (Allen et al. 2006). To ensure comparability, care was taken in this study to use datasets that were collected over local scales and were compared using the same analyses and bin widths. In-water size estimation of fish, and generation of individual-level size data for the bird surveys using published mean and variance data, both provide potential for introducing further biases (Blackburn and Gaston 1994). Measurement error was calculated for the size estimates in the fish datasets (see Text S1). Similar calculations are not possible for the simulated bird data, which likely contain different biases (as discussed earlier), and errors may have masked some of the differences between habitat types for the bird ISDRs.

Once the data has been collected, size-distribution relationships may be constructed in a number of ways, regardless of the index chosen. An early step is the choice of bin width and the location of class breaks in size-based analyses. This can influence the shape of distributions, and thus need to be selected with care (Silverman 1986). I constructed log size classes that were 0.001 units in width. This allowed differentiation between individuals that were 10g difference in weight when those individuals were >1kg in size (due to the log scale).

Size distributions were analysed in two ways: evaluating discontinuities and abundance patterns. The discontinuity approach contrasts with the way in which marine communities, in particular, have traditionally been studied. Specifically, linear relationships (such as pareto functions; e.g. Quintana et al. 2002) are often fitted to fish size-abundance or size-biomass distributions based on logged data. This latter approach has been shown to be useful when evaluating the distribution of biomass across size classes in aquatic taxa (e.g. Cattaneo 1993), or as a metric of the change in abundance between small and large individuals due to fishing pressure (e.g. Graham et al. 2005). However, multi-modal body size distributions have been found in an increasing array of aquatic environments (e.g. Havlicek and Carpenter 2001, Dornelas et al. 2006). My abundance analyses, particularly using individual level data, make no assumption about the form of the relationship between abundance and body mass and as such could be used to analyse size distributions that are either multi-modal or linear in form.

Table S1: Analysis of Similarities (ANOSIM) comparing the size distributions of communities for sites of different habitat type for A) Lofty Ranges bird, B) Borneo bird, C) Seychelles fish, and D) Great Barrier Reef fish communities, where size distributions are based on either maximum mass recorded in the literature (Birds: Dunning Jr. 2008; Fish: FishBase) or maximum observed mass, for each species. Analysis 1: Comparison of discontinuities in species size relationships (SSRs). Analysis 2: Comparison of abundance in species size-density distributions (SSDRs). The resemblance matrices were calculated using Euclidean distances for Analyses 1 and chord distances for Analyses 2.

Factor	Analysis 1 - Maximum Mass from Literature		Analysis 2- Maximum Mass from Literature		Analysis 1 - Maximum Observed Mass		Analysis 2 - Maximum Observed Mass	
	R	Significance	R	Significance	R	Significance	R	Significance
A) Bird - Lofty								
Habitat	0.116	0.001	0.217	0.001				
B) Bird - Borneo								
Habitat								
C) Fish - Seychelles								
Habitat	-0.099	0.801	0.454	0.001	0.203	0.055	0.337	0.006
Algae, Granite			0.846	0.018			0.508	0.018
Algae, Coral			0.647	0.008			0.397	0.042
Granite, Coral			0.242	0.040			0.259	0.035
D) Fish - GBR								
Habitat	0.077	0.006	0.085	0.003	0.086	0.007	0.079	0.001
Undisturbed, Disturbed	0.097	0.001	0.092	0.002	0.150	0.001	0.081	0.002
Undisturbed, Recovering	0.001	0.344	0.119	0.010	0.069	0.97	0.124	0.014
Disturbed, Recovering	0.116	0.043	0.043	0.186	-0.023	0.601	0.015	0.355

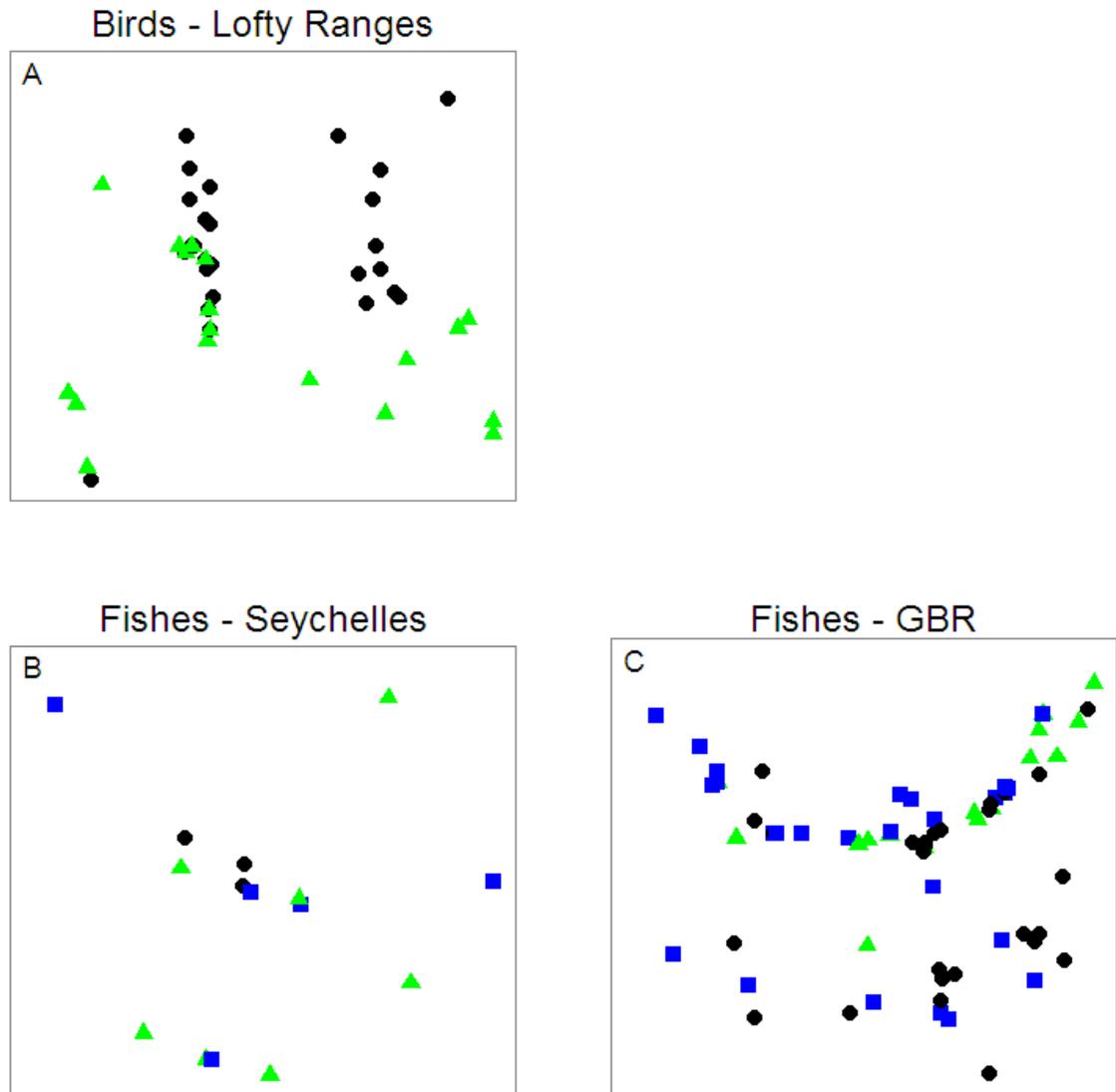


Figure S1: Non-metric multi-dimensional scaling (nMDS) comparing size distributions of communities for sites of different habitat type. Comparison of discontinuities in species size relationships based on maximum mass recorded in the literature (SSRs; Analysis 1; Birds: Dunning Jr.,2008; Fish: FishBase) for A) Lofty Ranges bird, B) Seychelles fish, and C) Great Barrier Reef fish communities. The resemblance matrices were calculated using Euclidean distances. Symbols in A: black circles – gum woodland, green triangles – stringybark woodland; symbols in B: black circles – algal-dominated carbonate reef, green triangles – coral-dominated carbonate reef, blue squares – granitic reef; symbols in C: black circles – disturbed reef, green triangles – recovering reef, blue squares – undisturbed reef.

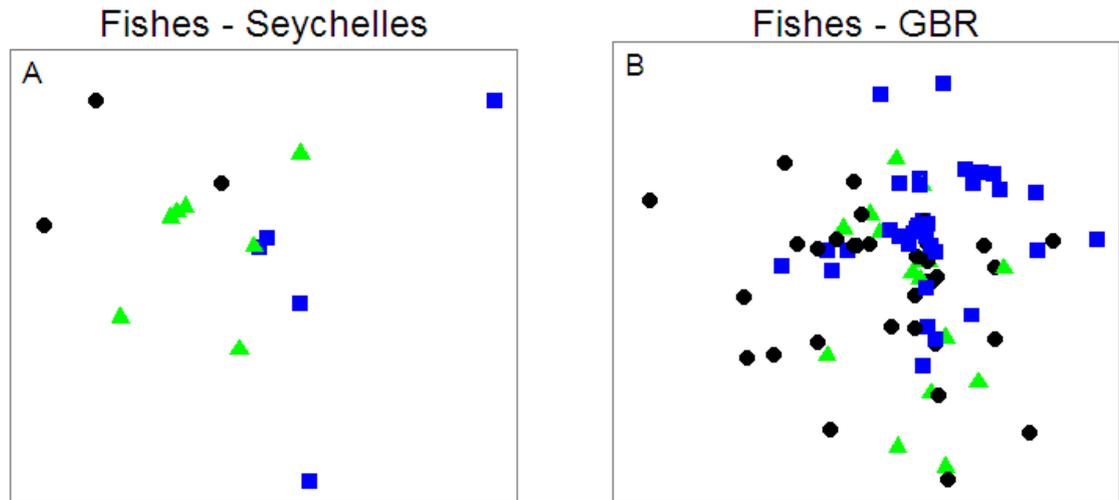


Figure S2: Non-metric multi-dimensional scaling (nMDS) comparing size distributions of communities for sites of different habitat type. Comparison of discontinuities in species size relationships based on maximum observed mass (SSRs; Analysis 1) for A) Seychelles fish, and B) Great Barrier Reef fish communities. The resemblance matrices were calculated using Euclidean distances. Symbols in A: black circles – algal-dominated carbonate reef, green triangles – coral-dominated carbonate reef, blue squares – granitic reef; symbols in B: black circles – disturbed reef, green triangles – recovering reef, blue squares – undisturbed reef.

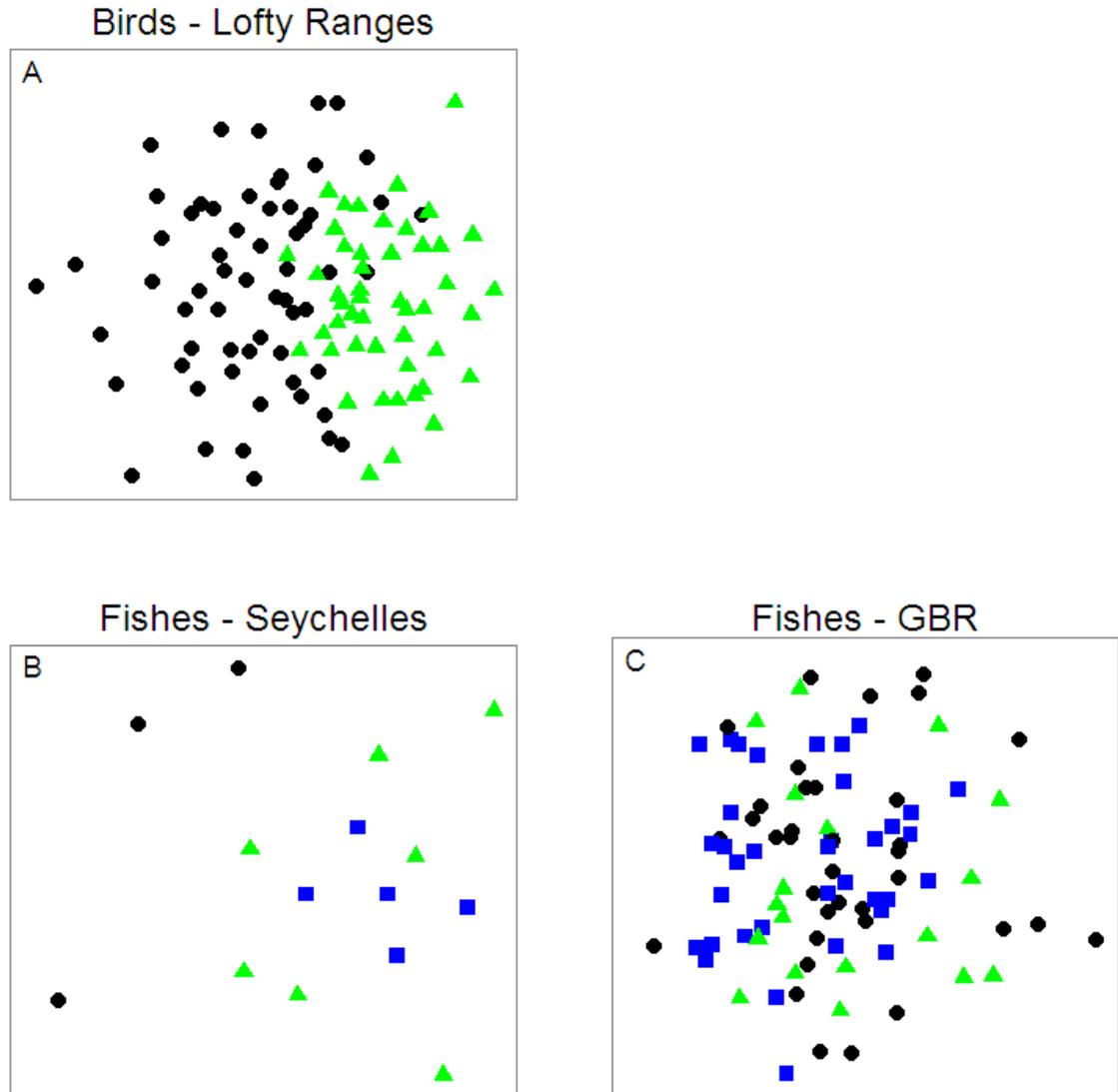


Figure S3: Non-metric multi-dimensional scaling (nMDS) comparing size distributions of communities for sites of different habitat type. Comparison of abundance patterns in species size-density relationships based on maximum mass recorded in the literature (SSDRs; Analysis 2; Birds: Dunning Jr.,2008; Fish: FishBase) for A) Lofty Ranges bird, B) Seychelles fish, and C) Great Barrier Reef fish communities. The resemblance matrices were calculated using chord distances. Symbols in A: black circles – gum woodland, green triangles – stringybark woodland; symbols in B: black circles – algal-dominated carbonate reef, green triangles – coral-dominated carbonate reef, blue squares – granitic reef; symbols in C: black circles – disturbed reef, green triangles – recovering reef, blue squares – undisturbed reef.

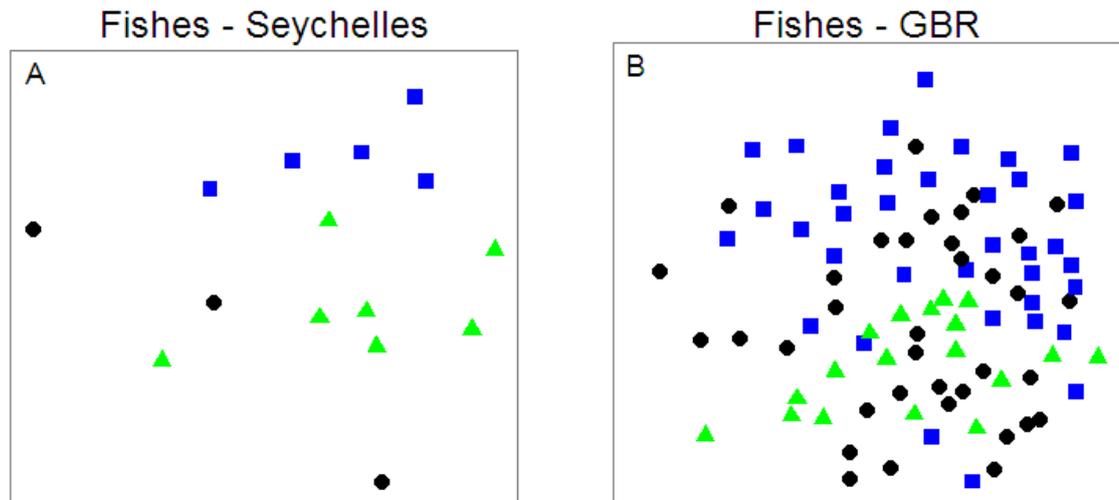


Figure S4: Non-metric multi-dimensional scaling (nMDS) comparing size distributions of communities for sites of different habitat type. Comparison of abundance patterns in species size-density relationships based on maximum observed mass (SSDRs; Analysis 2) for A) Seychelles fish, and B) Great Barrier Reef fish communities. The resemblance matrices were calculated using chord distances. Symbols in A: black circles – algal-dominated carbonate reef, green triangles – coral-dominated carbonate reef, blue squares – granitic reef; symbols in B: black circles – disturbed reef, green triangles – recovering reef, blue squares – undisturbed reef.

References:

- AIMS. 2011. Reef monitoring.
- Allen, C. R., et al. 2006. Patterns in body mass distributions: sifting among alternative hypotheses. - *Ecol. Lett.* 9: 630-643.
- Bakker, V. J. and Kelt, D. A. 2000. Scale-dependent patterns in body size distributions of neotropical mammals. - *Ecol.* 81: 3530-3547.
- Blackburn, T. M. and Gaston, K. J. 1994. Animal body size distributions: patterns, mechanisms and implications. - *Trends in Ecology and Evolution* 9: 471-474.
- Cattaneo, A. 1993. Size spectra of benthic communities in Laurentian streams. - *Can. J. Fish. Aq. Sci.* 50: 2659-2666.
- Cleary, D. F. R., et al. 2007. Bird species and traits associated with logged and unlogged forest in Borneo. - *Ecol. Appl.* 17: 1184-1197.
- Dornelas, M., et al. 2006. Coral reef diversity refutes the neutral theory of biodiversity. - *Nature* 440: 80-82.
- Dunning Jr., J. B. (ed.). 2008. *CRC Handbook of Avian Body Masses*. - CRC Press.
- Ernest, S. K. M. 2013. Using size distributions to understand the role of body size in mammalian community assembly. - In: Smith, F. A. and Lyons, S. K. (eds.), *Animal body size*. The University of Chicago Press.
- Graham, N. A. J., et al. 2014. Coral reef community composition in the context of disturbance history on the Great Barrier Reef, Australia. - *PLoS ONE* 9: e101204.
- Graham, N. A. J., et al. 2005. Size-spectra as indicators of the effects of fishing on coral reef fish assemblages. - *Coral Reefs* 24: 118-124.

- Graham, N. A. J., et al. 2006. Dynamic fragility of oceanic coral reef ecosystems. - *Proceedings of the National Academy of Sciences of the United States of America* 103: 8425-8429.
- Havlicek, T. D. and Carpenter, S. R. 2001. Pelagic species size distributions in lakes: are they discontinuous? - *Limnology and Oceanography* 46: 1021-1033.
- Legendre, P. and Legendre, L. 1998. *Numerical Ecology*. - Elsevier Science.
- Nash, K. L., et al. 2012. Influence of habitat condition and competition on foraging behaviour of parrotfishes. - *Mar. Ecol. Prog. Ser.* 457: 113-124.
- Nash, K. L., et al. 2013. Cross-scale habitat structure drives fish body size distributions on coral reefs. - *Ecosyst.* 16: 478-490.
- Possingham, M. L., et al. 2004. Species richness and abundance of birds in Mt Lofty Ranges stringybark habitat: 1999-2000 survey. - *South Australian Ornithologist* 34: 153-169.
- Possingham, M. L., et al. 2006. Species richness and abundance of birds in Mt Lofty Ranges stringybark habitat: year 2000 survey. - *South Australian Ornithologist* 34: 228-241.
- Possingham, M. L. and Possingham, H. P. 2008. Species richness and abundance of birds in Mt Lofty Ranges gum woodland habitat: year 2000 survey. - *South Australian Ornithologist* 35: 69-85.
- Quintana, X. D., et al. 2002. Biomass-size spectra in aquatic communities in shallow fluctuating Mediterranean salt marshes (Empordà wetlands, NE Spain). - *Journal of Plankton Research* 24: 1149-1161.
- Silverman, B. W. 1986. *Density estimation for statistics and data analysis*. - Chapman & Hall/CRC Press.
- Webb, T. J., et al. 2011. The birds and the seas: body size reconciles differences in the abundance–occupancy relationship across marine and terrestrial vertebrates. - *Oikos* 120: 537-549.

Appendix F: Supplemental information for Chapter 8

Table S1: Results of power analysis to evaluate the need for 16 versus 8 replicates for the field surveys. Mean percent change ($\pm 95\%$ CI) detectable across sites from 1994 to 2005 in A) coral cover and B) fish biomass are presented. Analysis used observed pooled standard deviations of sites in 1994 and 2005, a power of 0.8 and an alpha level of 0.05.

	Coral Cover		Fish Biomass	
	N=8	N=16	N=8	N=16
Mean % Change Detectable	53.2 \pm 10.1	41.5 \pm 7.4	77.11 \pm 12.20	60.36 \pm 7.36

Table S2: Matrix setup for the metrics incorporating functional group information, using example data. A) Trait matrix where row labels are species, column titles are traits, and entries are trait attributes; B) Biomass matrix where row labels are sites by year, column titles are species and entries are biomass. FG is functional group, BR is browser, DG is detritivore/grazer, SE is scraper/excavator.

A		B							
FG			<i>Acanthurus leucosternon</i>	<i>Acanthurus lineatus</i>	<i>Chlorurus gibbus</i>	<i>Leptoscarus vaigiensis</i>	⋮	<i>Siganus sutor</i>	<i>Zebrasoma scopas</i>
<i>Acanthurus leucosternon</i>	DG	S1_94	944	693	1835	0		139	62
<i>Acanthurus lineatus</i>	DG	S2_94	245	1105	741	254		502	383
<i>Chlorurus gibbus</i>	SE	S3_94	667	1857	1104	150		583	197
<i>Leptoscarus vaigiensis</i>	BR	S4_94	187	436	564	0		183	0
⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮
<i>Scarus frenatus</i>	SE	S20_11	1030	552	487	951		615	503
<i>Scarus tricolor</i>	SE	S21_11	0	274	1311	771		154	139
<i>Siganus sutor</i>	DG								
<i>Zebrasoma scopas</i>	DG								

Table S3: Matrix setup for the metrics incorporating functional group and size information, using example data. A) Trait matrix where row labels are species-size groupings, column titles are traits, and entries are trait attributes; B) Biomass matrix where row labels are sites by year, column titles are species-size groupings and entries are biomass. Size is body size in cm, averaged over all individuals within the species-size grouping. FG is functional group, BR is browser, DG is detritivore/grazer, SE is scraper/excavator.

A)			B)													
	Size	FG		Acanthurus leucosternon 10-15	Acanthurus leucosternon 15-20	Acanthurus leucosternon 20-25	Acanthurus lineatus 15-20	Acanthurus lineatus 20-25	Chlorurus gibbus 30-35	Chlorurus gibbus 35-40	Leptoscarus vaigiensis 20-25	:	Siganus sutor 10-15	Siganus sutor 15-20	Siganus sutor 20-25	Zebrasoma scopas15-20
Acanthurus leucosternon 10-15	13	DG	S1_94	91	188	665	693	0	964	871	0		0	139	0	62
Acanthurus leucosternon 15-20	16	DG	S2_94	75	0	170	973	132	405	336	254		82	420	0	383
Acanthurus leucosternon 20-25	22	DG	S3_94		667	0	902	955	415	689	150		0	239	344	197
Acanthurus lineatus 15-20	19	DG	S4_94	187	0	0	0	436	251	313	0		0	183	0	0
Acanthurus lineatus 20-25	24	DG	:	:	:	:	:	:	:	:	:	:	:	:	:	:
Chlorurus gibbus 30-35	32	SE	S20_11	50	0	980	0	552	66	421	951		136	0	479	503
Chlorurus gibbus 35-40	37	SE	S21_11	0	0	0	154	120	782	529	771		480	491	782	139
Leptoscarus vaigiensis 20-25	21	BR														
:	:	:														
Siganus sutor 10-15	14	DG														

Signanus sutor 15-20	18	DG
Signanus sutor 20-25	23	DG
Zebrasoma scopas15-20	16	DG

Table S4. Model selection comparing the utility of the different redundancy metrics in 1994 as predictors of reef benthic trajectories from 2005 to 2011, where fishing pressure was incorporated into the models. A) Step 1 evaluated the performance of the metrics from the functional group and the functional & size approaches, and B) Step 2 evaluated the performance of models combining different metrics arising from the functional & size approach.

Model	K	AICc	Δ AICc	AICc Wt
A				
Functional group & size dispersion + Functional group & size evenness + Fishing pressure	5	64.4	0.00	0.55
Null	2	64.9	0.56	0.41
Functional group dispersion + Functional group evenness + Fishing pressure	5	69.5	5.18	0.04
B				
Functional group & size dispersion + Functional group & size evenness	4	62.2	0.00	0.41
Functional group & size dispersion + Functional group & size evenness + Fishing pressure	5	64.4	2.13	0.14
Null	2	64.9	2.70	0.11
Functional group & size dispersion	3	65.2	2.96	0.09
Fishing pressure	3	65.4	3.20	0.08
Functional group & size evenness	3	65.6	3.42	0.07
Functional group & size evenness + Fishing pressure	4	65.9	3.66	0.07
Functional group & size dispersion + Fishing pressure	4	67.0	4.75	0.04

Table S5: Models of relationships between A) function & size dispersion, and B) function & size evenness in the different years.

Model	F	P value	Adj. R²
A) Functional group & size dispersion			
2005 ~ 1994	0.09	0.77	-0.05
2011 ~ 2005	0.06	0.29	0.01
2011 ~ 1994	0.00	0.95	-0.05
B) Functional group & size evenness			
2005 ~ 1994	0.04	0.38	-0.01
2011 ~ 2005	2.92	0.10	0.09
2011 ~ 1994	3.44	0.08	0.11

Appendix G: Publications arising during candidature

Publications derived from thesis chapters

Chapter 2: Nash, K. L., et al. *in press*. Home range allometry in coral reef fishes: comparison to other vertebrates, methodological issues and management implications. *Oecologia*.

Chapter 3: Nash, K. L., et al. 2013. Fish foraging patterns, vulnerability to fishing and implications for the management of ecosystem function across scales. *Ecological Applications* 23: 1632-1644.

Chapter 4: Nash, K. L., et al. 2012. Influence of habitat condition and competition on foraging behaviour of parrotfishes. *Marine Ecology Progress Series* 457: 113-124.

Chapter 5: Nash, K. L., et al. 2013. Cross-scale habitat structure drives fish body size distributions on coral reefs. *Ecosystems* 16: 478-490.

Chapter 6: Nash, K. L., et al. 2014. Discontinuities, cross-scale patterns and the organization of ecosystems. *Ecology* 95: 654-667.

Chapter 7: Nash, K. L., et al. 2014. Habitat structure and body size distributions: cross-ecosystem comparison for taxa with determinate and indeterminate growth. *Oikos* 123: 971-983.

Other peer-reviewed articles published during PhD candidature

Spanbauer, T. L., Allen, C. R., Angeler, D. G., Eason, T., **Nash, K. L.**, Fritz, S. C., Stone, J. R., Garmestani, A. S. *in press*. A shift in time: statistical evidence of a slow regime shift from paleoecological data. - PLoS ONE.

Graham, N. A. J., Chong-Seng, K. M., Huchery, C., Januchowski-Hartley, F. A., **Nash, K. L.** 2014. Coral reef community composition in the context of disturbance history on the Great Barrier Reef, Australia. *PLoS ONE* 9: e101204.

Chong-Seng, K. M., **Nash K. L.**, Bellwood, D. R., Graham, N. A. J. 2014. Macroalgal herbivory on recovering versus degrading coral reefs. *Coral Reefs* 33: 409-419.

- Zhang, S. Y., Speare, K. E., Long, Z.T., McKeever, K. A., Cyorkoe, M., Ramus, A. P., Mohorn, Z., Akins, K. L., Hambridge, S. M., Graham, N. A. J., **Nash, K.L.**, Selig, E. R., Bruno, J. F. 2014. Is coral richness related to community resistance to and recovery from disturbance? *PeerJ* 2: e308.
- Graham, N. A. J. and **Nash, K. L.** 2013. The importance of structural complexity in coral reef ecosystems. *Coral Reefs* 32: 315-326.
- Januchowski-Hartley, F., **Nash, K. L.**, Lawton, R. J. 2012. Influence of spear guns, dive gear and observers on estimating fish flight initiation distance on coral reefs. *Marine Ecology Progress Series* 469: 113-119.
- Wilson, S. K., Graham, N. A. J., Fisher, R., Jennings, S., Robinson, J., **Nash, K. L.**, Chong-Seng, K., Polunin, N. V. C., Aumeeruddy, R., Quatre, R. 2012. Effect of Macroalgal Expansion and Marine Protected Areas on Coral Recovery Following a Climatic Disturbance. *Conservation Biology* 26: 995-1004.
- Graham, N., **Nash, K. L.**, Kool, J. T. 2011. Coral reef recovery dynamics in a changing world. *Coral Reefs* 30: 283-294.

Fish foraging patterns, vulnerability to fishing, and implications for the management of ecosystem function across scales

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Abstract. The function of species has been recognized as critical for the maintenance of ecosystems within desired states. However, there are still considerable gaps in our knowledge of interspecific differences in the functional roles of organisms, particularly with regard to the spatial scales over which functional impact is exerted. This has implications for the delivery of function and the maintenance of ecosystem processes. In this study we assessed the allometric relationship between foraging movements and fish body length at three sites, for 20 species of herbivorous reef fishes within four different functional groups: browsers, farmers, grazer/detritivores, and scraper/excavators. The relationship between vulnerability of species to fishing and their scale of foraging was also examined. We present empirical evidence of the strong, positive, log-linear relationship between the scale of foraging movement and fish body length. This relationship was consistent among sites and between the two different movement metrics used. Phylogeny did not affect these results. Functional groups foraged over contrasting ranges of spatial scales; for example, scraper/excavators performed their role over a wide range of scales, whereas browsers were represented by few species and operated over a narrow range of scales. Overfishing is likely not only to remove species operating at large scales, but also to remove the browser group as a whole. Large fishes typically have a significant role in removing algae on reefs, and browsers are key to controlling macroalgae and reversing shifts to macroalgal-dominated states. This vulnerability to exploitation has serious consequences for the ability of fish assemblages to deliver their functional role in the face of anthropogenic impacts. However, identification of the scales at which herbivorous fish assemblages are susceptible to fishing provides managers with critical knowledge to design management strategies to support coral-dominated reefs by maintaining function at the spatial scales at which vulnerable species operate.

Key words: allometry; coral reef; ecosystem processes; fisheries; functional group; Great Barrier Reef, Australia; herbivore; redundancy; resilience.

INTRODUCTION

Species of different body sizes perceive and interact with their environment over different spatial and temporal scales (Holling 1992). These relationships have been explored thoroughly in many terrestrial systems, particularly for birds and mammals, with respect to length of stride (Calder 1984), home range area (Peters 1983, Harestad and Bunnell 1979), and aggregation of resources (Laca et al. 2010). In contrast, such relationships have not been adequately investigated in aquatic systems, with many studies of movement limited to one or a few species (e.g., Nanami and Yamada 2008, Freiwald 2012), and few reviews aimed at consolidating this information with respect to body size (but see Kramer and Chapman 1999). Aquatic organisms are subject to different processes and constraints than

terrestrial species (White et al. 2007), and as such may show contrasting allometric patterns, driving a need for further studies in this area.

The role or function organisms play within a particular environment, such as pollination, grazing, and nitrogen fixation has attracted considerable attention in recent years (Folke et al. 2004). There is an increasing awareness that management may support a system within a desired state by maintaining the core ecosystem processes provided by different functional groups (e.g., Christensen et al. 1996, Bellwood et al. 2004, Pikitch et al. 2004). In response, there have been calls for new ways to evaluate the delivery of function to provide the knowledge needed by managers to effectively implement appropriate mitigation strategies to support important ecosystem processes (Hughes et al. 2010). One avenue of research has examined the significance of multiple species performing a similar role within an ecosystem, providing redundancy or a degree of “insurance” in the face of anthropogenic pressures that drive species declines and, in turn, may reduce

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functional impact (Walker et al. 1999, Elmqvist et al. 2003, Cheal et al. 2010). The benefits of this redundancy are reliant on the members of a functional group responding to a disturbance differently, with some species maintaining or increasing their functional impact to compensate for the loss or decline of other members of their functional group (Walker et al. 1999, Elmqvist et al. 2003). Species performing similar functions at different spatial and/or temporal scales are likely to exhibit a range of responses to disturbances impacting at specific scales, thus providing effective redundancy (Peterson et al. 1998, Elmqvist et al. 2003). As a result, characterizing the scales at which species within a functional group operate and provide their role is fundamental knowledge needed to inform management actions aimed at supporting: (1) redundancy of function across scales (termed cross-scale redundancy), and (2) delivery of function at specific scales.

The temporal and spatial characteristics of movement may be assessed at a number of levels, from the large scales of dispersal, through mid-scales of home range use, down to small scales of patch and food selection (Holling 1992). Movements at these various scales have a range of implications for the ecology of communities and populations, and a species' impact on the ecosystems they inhabit. For example, dispersal will influence community assembly (Chase 2003), whereas more localized movements may affect the function of a species within a system (e.g., Vaughn and Hakenkamp 2008). Movement is often investigated at the scale of home range (Börger et al. 2008). However, these types of studies may not effectively describe the spatial dimensions of a species' functional impact. Home range encompasses the area occupied by an organism while performing a range of activities such as feeding, sleeping and breeding (Samuel et al. 1985, Börger et al. 2008). The location of these activities may not overlap (Lazenby-Cohen and Cockburn 1991); as a result, the home range will incorporate areas in which an individual is exerting critical functional impact, and areas where this impact may not be as significant (Welsh and Bellwood 2012). Furthermore, differences in home range size among species may not correlate with differences in functional range size among species, as distinct drivers influence decision-making and movements at different scales (Senft et al. 1987). For example, decisions regarding reproductive opportunities within the broader home range will be driven by different factors than those regarding movements in relation to food choice (Senft et al. 1987). As a result, although there is evidence from a range of systems that species' body size is positively related to home range (e.g., Harestad and Bunnell 1979), it cannot be assumed that the relationship between body size and movement at the home range scale is representative of movements at other scales. To gain a comprehensive understanding of the functional impact of a species, there is a need to examine the allometry of

movement at a scale relevant to the use of space while individuals are actively performing their functional role.

Herbivorous reef fishes drive a key ecosystem process on coral reefs by mediating competition between coral and algae, removing algae, and creating space for coral recruits (Hughes et al. 2007). However, there is growing evidence that herbivorous fish functions on reefs are more complex than simple classifications such as "herbivore" suggest, with important differences both within and among species. For example, ontogenetic changes and growth within species may influence diet (e.g., Buckle and Booth 2009), grazing rate, and bite size, with larger individuals providing greater functional impact through higher rates of grazing and larger bite areas (Ferreira et al. 1998, Paddack et al. 2006, Lokrantz et al. 2008). Similarly, interspecific differences in foraging behavior have been shown to influence finer scale functional classifications within broad diet groups. Herbivorous fish species may be split into farmers, grazer/detritivores, scraper/excavators, and browsers (Green and Bellwood 2009). Farmers are site-attached species that actively tend and defend algal resources within their territory (Ceccarelli et al. 2001). Grazer/detritivores feed on the epilithic algal matrix (EAM), which is composed of algal turf, detritus, microbes, sediment, and invertebrates (Wilson and Bellwood 1997), and scraper/excavators remove both components of the EAM and underlying substrate, and therefore, are also important for the process of bioerosion (Green and Bellwood 2009). These groups help reduce colonization by macroalgae and so assist in maintaining reefs within a coral-dominated state. In contrast, browsers feed on mature macroalgae and as such are critical for reversing shifts from coral to macroalgal dominance (Bellwood et al. 2006). Despite this growing literature on the role of herbivores on reefs, very little work has examined the scale of foraging by fish species.

One of the greatest potential threats to herbivore redundancy on coral reefs is fishing. Fishing is exerting significant pressure on marine systems worldwide (Jackson et al. 2001), influencing the delivery of ecosystem processes (Hughes 1994). For example, in areas subject to heavy fishing pressure, 95% of parrotfish may be <25 cm in length, with significant consequences for sediment removal and bioerosion (Bellwood et al. 2012). Currently, however, we have no understanding of how fishing is likely to impact the scale at which ecosystem functions are delivered. In light of the degree of overfishing in certain areas, there is potential for significant modifications to cross-scale patterns of redundancy within functional groups, with serious implications for the stability of ecosystem processes. For managers to be able to address these pressures effectively, detailed knowledge of the spatial scales of functional impact is needed.

In examining the scales over which herbivorous reef fishes forage, this study evaluated interspecific patterns in functionally important space use by herbivorous

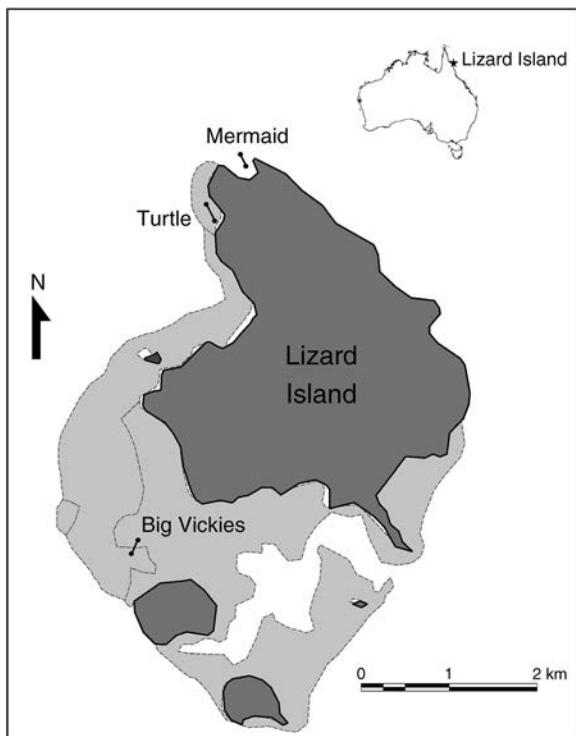


FIG. 1. Map of study sites at Lizard Island on the Great Barrier Reef, Australia. Light gray areas represent reef and lagoon. Prevailing winds are from the southeast.

species. The outcomes indicate the potential for cross-scale redundancy within reef ecosystems, and reveal the influence of fishing pressure on these patterns, neither of which has been assessed to date. The aims of this study, therefore, were to use assessments of foraging movements to: (1) determine the interspecific relationship between body size and space use at scales pertinent to functional impact, (2) examine if the scales of operation of species within herbivorous functional groups are distributed across spatial scales (i.e., assess the potential for functional redundancy), and (3) determine the relationship between vulnerability to fishing and foraging scale. This will provide fundamental knowledge needed to understand patterns of cross-scale redundancy of function on reefs. Furthermore, it will indicate how fishing impacts may modify the delivery of ecosystem processes, and thus highlight the scales at which targeted mitigation measures are needed to support reefs within a coral-dominated state.

METHODS

Study sites and species

This study was undertaken in July and August 2012 on the sheltered, western side of Lizard Island (14°40' S, 145°28' E; Fig. 1) on the Great Barrier Reef, Australia. Observations of foraging behavior were made at three sites (Mermaid, Turtle Beach, and Big Vickies; Fig. 1) to

determine whether foraging behavior varied consistently with body size across sites. Mermaid and Turtle Beach are southwest-facing fringing reefs with a narrow reef flat and shallow slope down to a maximum depth of ~10 m. Big Vickies is a large patch reef and observations were made on the southeast side, where the reef structure meets the sand at a depth of 5–7 m. All three sites are in a marine park, designated as a no-take area since 2003, and subject to fishing restrictions since 1983.

Fish and benthic censuses

Fish abundance of diurnally active non-cryptic herbivorous species were estimated at each site using instantaneous underwater visual census (UVC) along eight 50-m transects; four transects were located on the reef slope and four on the reef crest. All species (≥ 5 cm) were recorded in a 5-m swath as the transect was laid, with the exception of Pomacentrids, which were recorded on the return swim along the transect in a 2-m swath. Replicates were haphazardly arranged along the reef, with a minimum of 15 m separating neighboring transects. The percent cover of different benthic types, such as coral genera and life-form, algae, sponges, and so on, were calculated from observations taken every 50 cm along each transect using the point intercept method. Structural complexity was estimated for each transect, using a six-point visual scale (Wilson et al. 2007).

Study species

Herbivorous species were chosen as the focus for this study for two reasons: (1) they drive a critical ecosystem function on reefs (Bellwood et al. 2004), and (2) by feeding on the substrate, it is possible to clearly delineate and mark where feeding occurs and to observe multiple feeding events, thus ensuring high levels of replication. Twenty nominally herbivorous reef fish species (Appendix A) were selected for study at each site, including representatives from browser, farmer, grazer/detritivore, and scraper/excavator functional groups (Green and Bellwood 2009). The exact composition of species differed between sites due to localized relative abundance. The species ranged in length from 6 cm to 55 cm total length (TL), and at least a 36-cm body size range was maintained at all sites. The focus of the study was interspecific differences in foraging and space use by adult herbivorous reef fishes. Fish species may exhibit ontogenetic shifts in diet (e.g., from herbivore as a juvenile to planktivore as an adult; Green and Bellwood 2009), and foraging behavior (Lokrantz et al. 2008). Therefore, to remove the influence of ontogenetic changes within species (Bonaldo and Bellwood 2008), and allow comparability among species of different adult body sizes, a single 5–6 cm size class was selected for each species up to 35 cm, and a 5–10 cm size class for the larger species (Appendix A). These size classes were based on the most abundant adult body lengths.

Behavioral studies

All behavioral data were collected between 09:30 hours and 14:30 hours, and distributed approximately evenly to minimize the effect of time of day on feeding (Zemke-White et al. 2002). Fine-scale foraging mobility of target individuals was estimated using two metrics: (1) intra-foray distance and (2) inter-foray distance, where a foray was defined as a cluster of feeding bites separated from the previous cluster of bites by elevation of the fish's head greater than 45 degrees from the substratum and a period of active swimming (following Nash et al. 2012). A focal individual was identified and followed until it commenced feeding. To estimate inter-foray distance, markers were dropped at the last bite of the first foray taken by the fish, and the first bite of the next foray. To estimate intra-foray distance, markers were placed at the location of the two most distant bites within the second foray. The distance between markers was measured. Inter-foray distance is therefore an integration of all movements between successive forays, whereas intra-foray distance is the maximum linear dimension covered by all movements within a foray. The benthos on which the fish fed (e.g., EAM, macroalgae, soft coral) identified by each marker, was recorded. A single observation of intra- and inter-foray distance was recorded for each individual, and where possible, these observations were repeated for 30 individuals of each species at each site (Appendix A). Two strategies were used to minimize the chance of sampling the same individual more than once: (1) after each observation, observers moved linearly along the reef away from the area used by individuals that had already been sampled; and (2) where members of the same species were targeted sequentially, fish of different body sizes were chosen. Where the population size of a species was too small to allow the desired degree of replication without resampling individuals, smaller sample sizes were used (Appendix A).

When estimating the foraging range metrics, a distance of at least 2.5 m was maintained from all fish, although this distance was increased to 5 m for some of the larger, more mobile species due to increased flight initiation distances for larger individuals (Januchowski-Hartley et al. 2011). Data were discarded where fish showed signs of disturbance by the observer or where a constant visual fix on the individual could not be maintained. Accuracy of observer estimations of fish body length were tested daily using lengths of polyvinyl chloride (PVC) pipe, prior to the start of data collection, with estimates consistently within 10% of actual lengths.

Data analysis

The relationship between body size and the two foraging metrics (intra- and inter-foray distance) were analyzed using ordinary least squares regression as this approach is more suitable when: (1) there is a clear predictor and dependent variable in the relationship, and (2) residuals will be used for further analysis

(Warton et al. 2006, Smith 2009). The error structure of the data was determined using the guidelines provided by Xiao et al. (2011); likelihood analysis indicated that the data showed log-normal error and was therefore suitable for analysis using regression on log-transformed data (Xiao et al. 2011). Analysis of covariance (ANCOVA) and log-likelihood ratio tests were used to compare the slopes and elevations of relationships among sites (Warton et al. 2012). Data were back-transformed to allow presentation of the relationship between foraging metrics and body size on the arithmetic scale. Residuals were calculated for each species. To assess the influence of functional-group membership on the relationship between body size and the foraging metrics, the analysis was repeated with function as a categorical variable for those groups which had sufficient species (farmers, grazer/detritivores, and scraper/excavators). Phylogenetic relationships may confound interspecific relationships due to nonindependence of data points; therefore, the analysis was repeated at the family level (Martin et al. 2005), and the results compared to the species-level analysis.

To evaluate the potential effects of fishing on scales of functional impact provided by herbivorous fishes, the relationship between scales of foraging movements and vulnerability to fishing were analyzed using correlations. Data on the vulnerability of each species to fishing pressure were extracted from FishBase (*available online*),⁴ and are based on an index developed by Cheung et al. (2005) using a fuzzy logic expert system. This index combines information on eight life-history traits of fish species that affect susceptibility to fishing. It has been shown to provide sound predictions for species from a range of marine systems (Reynolds et al. 2005). Spearman rank correlations between both intra- and inter-foray distance, and fishing vulnerability were calculated.

RESULTS

Benthic cover and herbivore abundance

Benthic cover was primarily composed of live hard coral and epilithic algal matrix (EAM) at all of the three sites. However, the structural complexity and coral cover were slightly higher, and the EAM cover lower at the lagoonal Big Vickies (complexity 3.7 ± 0.2 [all values shown are mean \pm SE]; coral 36.2% \pm 4.9%; EAM 34.3% \pm 2.5%) compared to the fringing reefs at Mermaid (complexity 2.9 ± 0.1 ; coral 24.6% \pm 3.0%; EAM 52.9% \pm 5.3%) and Turtle (complexity 2.8 ± 0.2 ; coral 26.6% \pm 6.9; EAM 46.0% \pm 5.3%). Macroalgal cover was <1% at each of the three sites. The density of herbivorous fishes varied between 21.1 fish/100 m² at Turtle, to 33.5 fish/100 m² at Mermaid, but at all sites, grazer/detritivores were the most common herbivores (over 10 fish/100 m²), and browsers the least common

⁴ <http://www.fishbase.org/>

TABLE 1. Density of fish (mean \pm SE) within the four herbivorous functional groups and the proportion of functional group abundance represented by species assessed for foraging metrics and included in Fig. 2, at each site at Lizard Island on the Great Barrier Reef, Australia.

Functional group	Density (fish/100 m ²)			Proportion of functional group		
	Big Vickies	Mermaid	Turtle	Big Vickies	Mermaid	Turtle
Browser	0.4 \pm 0.1	1.6 \pm 0.4	1.2 \pm 0.4	42.9	46.4	69.6
Farmer	5.9 \pm 1.1	7.3 \pm 1.5	4.5 \pm 1.1	63.6	73.4	65.2
Grazer/detritivore	12.6 \pm 1.4	16.2 \pm 2.7	10.6 \pm 2.1	86.1	96.1	94.3
Scraper/excavator	10.2 \pm 1.6	8.4 \pm 1.0	4.9 \pm 0.5	79.3	84.4	84.7
Total herbivores	29.0 \pm 3.2	33.5 \pm 2.9	21.1 \pm 2.7	78.6	85.8	84.6

Note: Data are based on underwater visual census (UVC) counts, pooled to site level, and incorporating all size classes.

(under 2.0 fish/100 m²; Table 1A). The species studied in the behavioral observations accounted for over 75% of all herbivore individuals at each site, although this proportion was lower for browsers (over 40% of individuals) than for the other three herbivorous functional groups (Table 1B).

Behavioral metrics

Both log(intra-foray distance) and log(inter-foray distance) were positively, linearly related to log(fish body length) at all three sites (Fig. 2A, B; Table 2); therefore, as body size increases among species, the fine-scale movements made by foraging fish increase exponentially in length (Fig. 2C, D). The slope and elevation of the linear relationship between log(foraging metric) and log(body size) was not significantly different between sites (Table 2), giving common parameters of $\alpha = 0.03$ and $\beta = 2.19$ for intra-foray distance, and $\alpha = 0.34$ and $\beta = 2.12$ for inter-foray distance, where parameters represent $y = \alpha x^\beta$ in the back-transformed data (Fig. 2ii). The four herbivorous functional groups were not evenly spread across the scales of movement for either metric (Fig. 2C, D); farming species had small intra- and inter-foray distances, grazer/detritivores species exhibited mid-size foraging movements, while scraper/excavators and browsers showed mid- to large-size foraging movements.

The residuals for these relationships varied among functional groups (Fig. 3). Residuals were predominantly negative for farmers with respect to both intra- and inter-foray distance (mean of -0.28 and -0.14 , respectively), and for scraper/excavators with respect to intra-foray distance (-0.05), indicating these groups were generally moving shorter distances than predicted by the regressions. In contrast, predominantly positive residuals were recorded for both foraging metrics for grazer/detritivores (mean of 0.12 and 0.06 , respectively), and for browsers with respect to intra-foray distance (0.08), indicating generally larger movements than predicted. Members of all the four herbivorous functional groups fed primarily on EAM (over 85% of bites; Appendix B). No browsers were observed feeding on macroalgae; those species that did feed on macroalgae were primarily farmers or scraper/excavators.

When analyzed at the functional-group level, the relationship between body size and the two foraging metrics was nonsignificant for farmers, but was strongly positive for both the grazer/detritivores and the scraper/excavators (Appendix C). However, the intercepts varied among groups for intra-foray distance, and the slopes varied for inter-foray distance (Appendix C). There was insufficient data on browsing species to incorporate this group into the analysis. The results produced from the family-level analysis were both qualitatively and quantitatively similar to those at the species level, for both α and β (Appendices D and E), therefore, the species-level data were used for the remaining analyses.

There was a strong positive correlation between vulnerability to fishing and both intra- and inter-foray distance (Spearman $\rho = 0.69$, $P < 0.001$ and $\rho = 0.62$, $P < 0.001$, respectively); therefore, those species that moved further while foraging were also more vulnerable to fishing (Fig. 4). Members of grazer/detritivores and scraper/excavator functional groups showed a range of vulnerabilities to fishing, and foraged over a range of spatial scales. Farmers showed low vulnerability to fishing and low-movement distances, in contrast the browser species targeted in the foraging observations were highly vulnerable to fishing, and travelled mid-range distances while foraging.

DISCUSSION

This study empirically tests the allometric relationships between foraging movements and the body length of herbivorous reef fishes, indicating that body size is a good proxy for scale of functional impact in these species. Large species operate and deliver their functional role over larger areas than small herbivorous fish species. This finding has important ramifications for the redundancy of function in reef fishes. Analysis of different herbivorous functional groups suggests that although there is cross-scale redundancy for herbivorous fishes as a whole, there is the lack of redundancy in some of the more narrowly defined functional groups within the herbivore classification such as macroalgae browsers. Furthermore, vulnerability of certain species to fishing indicates that fish assemblages may lose function at certain scales in the face of overfishing, and this loss is

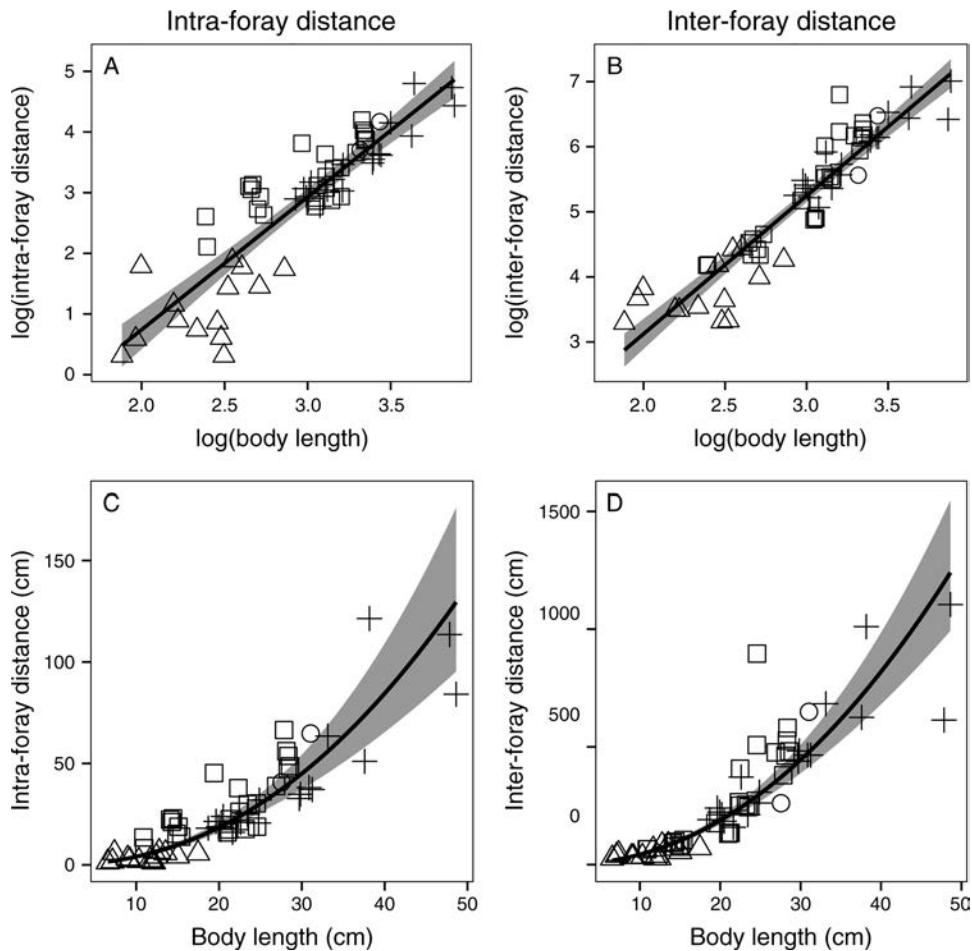


FIG. 2. Relationship between body length and (A, C) intra-foray distance or (B, D) inter-foray distance for herbivorous reef fish, presented in (A, B) log–log scales (intra- and inter-foray distances, and body length originally measured in centimeters) and (C, D) back-transformed to arithmetic scales. Lines represent significant relationships (with 95% CI) based on ordinary least-squares (OLS) regression, showing common slope and intercept among sites for both variables. Symbols indicate the functional group: triangles for farmers; squares for grazers/detritivores; circles for browsers; and crosses for scrapers/excavators. See *Methods: Behavioral studies* for clarification of intra- and inter-foray distance.

not limited to the function provided by large species. This highlights the need for management actions that support functions at scales used by relatively few, or vulnerable, herbivore species.

Allometric relationships

The positive relationships between body size and both metrics of foraging movement indicate that small species forage over smaller scales than large species. This pattern may be expected as swimming speed and cost of transport decreases with increasing body size in fish (McMahon and Bonner 1983), suggesting that large fish are more able to exploit resources at larger scales. In addition, large individuals require more resources and therefore are likely to forage over greater distances to meet energy requirements (Harestad and Bunnell 1979).

The allometric relationships were exponential in form, indicating that larger species not only feed at larger scales than smaller species, but they are also feeding over

a wider range of scales, suggesting that they have broader functional roles than smaller species with regards to space use. The importance of large herbivorous fish species for delivering function is mirrored by terrestrial herbivore species, where grazing by large species has been shown to drive habitat structure and functioning (Gordon et al. 2004). Species experience ontogenetic changes in function, and there is evidence that larger individuals may exhibit exponentially higher grazing rates (Lokrantz et al. 2008) and remove greater volumes of algae (Bonaldo and Bellwood 2008) than small individuals. Our study specifically focused on interspecific allometric patterns of space use while foraging. Further work is needed to look at intraspecific patterns of function and space use to understand if these mirror the positive relationships found between body size and grazing rates or bite volume within herbivorous species (Bonaldo and Bellwood 2008, Lokrantz et al. 2008).

TABLE 2. Summary of scaling parameters for the relationship between body length and (A) intra-foray distance and (B) inter-foray distance, where parameters represent $y = \alpha x^\beta$ in the back-transformed data.

Site	α (95% CI)	β (95% CI)	R^2	P
A) Intra-foray distance				
Big Vickies	0.01 (0.00–0.06)	2.35 (1.89–2.83)	0.86	<0.001
Mermaid	0.01 (0.00–0.08)	2.48 (1.81–3.14)	0.77	<0.001
Turtle	0.10 (0.03–0.34)	1.81 (1.40–2.21)	0.83	<0.001
Common parameters	0.03 (0.01–0.06)	2.19 (1.89–2.49)	0.79	<0.001
B) Inter-foray distance				
Big Vickies	0.44 (0.15–1.31)	1.99 (1.63–2.35)	0.88	<0.001
Mermaid	0.18 (0.05–0.70)	2.35 (1.89–2.80)	0.87	<0.001
Turtle	0.36 (0.12–1.10)	2.09 (1.72–2.46)	0.89	<0.001
Common parameters	0.34 (0.17–0.62)	2.12 (1.91–2.34)	0.87	<0.001

Notes: For panel A, the common-slope likelihood-ratio statistic was 4.54, $df = 2$, $P = 0.10$; and the common-elevation Wald statistic was 5.75, $df = 2$, $P = 0.06$. For panel B, the common-slope likelihood-ratio statistic was 2.53, $df = 2$, $P = 0.37$; and the common-elevation, Wald statistic was 2.41, $df = 2$, $P = 0.30$.

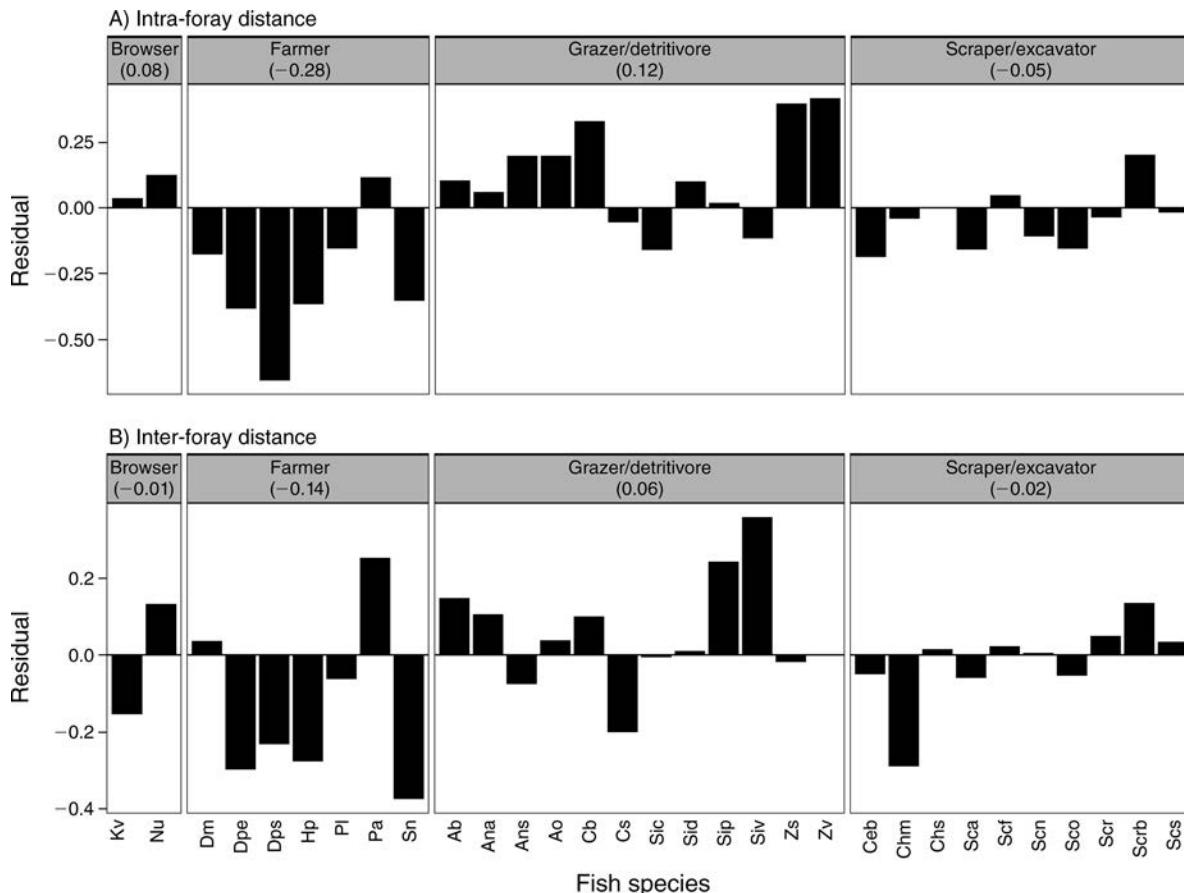


FIG. 3. Residuals for the relationship between body length and (A) intra-foray distance or (B) inter-foray distance for species of herbivorous reef fish. Bars represent the mean value across sites where a species was observed at multiple sites. Numbers in parentheses provide the mean residual for that functional group. Species abbreviations are as follows: Kv, *Kyphosus vaigiensis*; Nu, *Naso unicornis*; Dm, *Dischistodus melanotus*; Dpe, *Dischistodus perspicillatus*; Dps, *Dischistodus psuedochrysopeculus*; Hp, *Hemiglyphidodon plagiometopon*; Pl, *Plectroglyphidodon lacrymatus*; Pa, *Pomacentrus adelus*; Sn, *Stegastes nigricans*; Ab, *Acanthurus blochii*; Ana, *Acanthurus nigricauda*; Ans, *Acanthurus nigrofuscus*; Ao, *Acanthurus olivaceus*; Cb, *Centropyge bicolor*; Cs, *Ctenochaetus striatus*; Sic, *Siganus corallinus*; Sid, *Siganus doliatus*; Sip, *Siganus punctatus*; Siv, *Siganus vulpinus*; Zs, *Zebrasoma scopas*; Zv, *Zebrasoma veliferum*; Ceb, *Cetoscarus bicolor*; Chm, *Chlorurus microrhinus*; Chs, *Chlorurus sordidus*; Sca, *Scarus altipinnis*; Scf, *Scarus flavipectoralis*; Scn, *Scarus niger*; Sco, *Scarus oviceps*; Scr, *Scarus rivulatus*; Scrb, *Scarus rubroviolaceus*; and Scs, *Scarus schlegeli*.

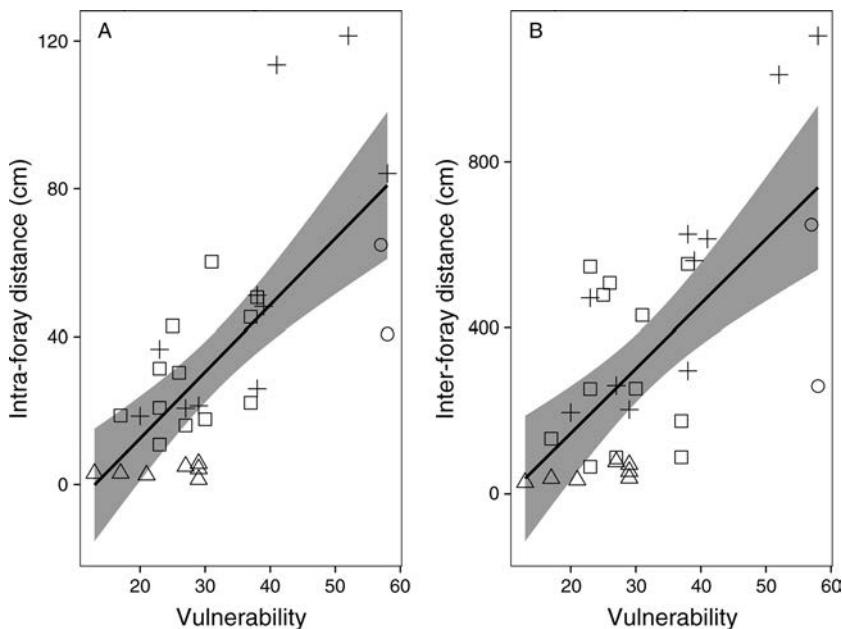


FIG. 4. Correlation between vulnerability to fishing pressure (based on an index by Cheung et al. [2005], where increasing numbers indicate increasing vulnerability) and (A) intra-foray distance (Spearman $\rho = 0.69$, $P < 0.001$) or (B) inter-foray distance (Spearman $\rho = 0.62$, $P < 0.001$). Intra-foray and inter-foray data for each species were pooled across sites. Symbols indicate the functional group: triangles for farmers; squares for grazers/detritivores; circles for browses; and crosses for scrapers/excavators.

The slopes of the relationships between body size and both intra- and inter-foray distance were similar, indicating that interspecific patterns may be comparable at different levels of the foraging decision hierarchy; for example, for within- or between-patch movements. Furthermore, the results mirror those found for the relationship between body size and home range (Kramer and Chapman 1999), suggesting that these comparisons may be made among levels of movement relating to foraging and other activities. The slopes and intercepts of the allometric relationships were not significantly different among sites, although the intercept was only slightly nonsignificant among sites for intra-foray distance. The three sites were chosen due to their similar benthic composition and geographic location. Changing habitat condition, and therefore resource availability and distribution, is likely to result in changes to both the intercept and slope of these relationships; Nash et al. (2012) reported reduced inter-foray distances of parrotfishes in response to increasing coral cover, but the shape of this decrease differed among species. Further work is needed to analyze whether these variations among species result in stronger or weaker allometric foraging relationships in the face of habitat degradation. Additionally, the effect of school size on foraging range was not assessed. Group size has been shown to be positively related to home range in mammal species (e.g., Dias and Strier 2003). Research is needed to analyze the effect of school size on the allometry of function and space use in herbivorous reef fishes.

Foraging decisions, at the scale relating to choice of specific EAM components, were not explicitly studied. However, consistency in the positive or negative nature of residuals within functional groups suggests that, although all species fed primarily on the EAM, different components of the algal matrix may have been selected for by species within the four functional groups (Crossman et al. 2005, Nash et al. 2012). The quality and composition of EAM varies over space (Purcell and Bellwood 2001), therefore differences in the distribution of constituents has the potential to influence the variation around the predicted allometric relationships for members of each functional group (Holling 1992). Farming species exhibited large, primarily negative residuals, signifying that these species cover smaller distances than expected based on body size. This is likely due to their ability to manipulate resource availability, concentrating food resources into a small patch through farming activities (Ceccarelli 2007); therefore, they are less reliant on existing resource distributions. This supposition is further supported by the pattern of large negative residuals recorded for farming species that are known to have a greater influence on benthic composition (intensive/extensive farmers; detailed in Appendix A), compared with the positive residuals of *Pomacentrus adelus* which exerts less influence on the benthos (an indeterminate farmer; Emslie et al. 2012).

The relationships between body size and the foraging metrics estimated for all species were qualitatively similar to those calculated for the separate functional groups, although these relationships were not significant

for farming species, suggesting body size is less critical within this group. Farmers are territorial and as such, space use may be limited by the costs arising from defending a territory (Brown 1964). The relationships between body size and the foraging metrics were quantitatively similar between species-level, and family-level analyses suggesting these patterns hold at a number of taxonomic levels, and is not an artifact of phylogenetic relationships. Therefore, the scale of functional impact of herbivorous reef fishes is positively and exponentially related to body size, although the rate of increase in spatial scale across body sizes depends on functional-group membership.

Cross-scale patterns

Foraging movements of herbivores, and scraper/excavators in particular, cover a wide range of scales, suggesting the potential for redundancy in the face of disturbances occurring at a given scale (Peterson et al. 1998, Elmquist et al. 2003), i.e., impacts deriving from the disturbance may be ameliorated by herbivores that are foraging at scales that do not coincide with the scale of the disturbance. The scraper/excavator group is composed of parrotfish species, therefore, this finding supports the well-described importance of parrotfishes for providing herbivory on coral reefs (Choat et al. 2004, Mumby 2006, Adam et al. 2011). Grazer/detritivores and farmers were somewhat more constrained in the scales of their movements, being restricted to mid and small scales, respectively. Siganids appear to extend the range of grazer/detritivores somewhat, as indicated by the large positive residual of *Siganus vulpinus*, a pattern that appears to be widespread in siganids (Fox and Bellwood 2012). In contrast, the range of scales over which farmers move is likely constrained by the costs associated with defending territories at larger scales (Brown 1964). Most surprisingly, browsers were limited to mid-scale movements. This finding may be a function of the low numbers of browsers studied (two species); however, individuals of these two species represented between 42% and 70% of browser abundance at the three sites. A maximum of five browsing species were observed at any one site, and mean density was <1.6 fish/100 m² at all sites; therefore, both cross-scale redundancy and abundance of this functional group appears to be low. This suggests that in the face of disturbances, which affect species operating at mid scales, there may be ecologically significant declines in the delivery of the browsing function. Demarcation of the scales across which the four functional groups operate highlight the relative potential for redundancy in each group. Similar multi-scale foraging patterns have been modeled in terrestrial herbivore communities, driven by interspecific body size variation (Illius and Gordon 1987, Ritchie and Olff 1999, Cumming and Cumming 2003), suggesting corresponding potential for cross-scale redundancy in certain taxa (Peterson et al. 1998, Cromsigt and Olff 2006, Laca et al. 2010).

Eighty-five percent of forays by members of each functional group were observed targeting the EAM, including 100% of forays by browsers. Browsers are defined as species which primarily target macroalgae and are therefore important for reversing shifts to a macroalgal-dominated state (Bellwood et al. 2006a). Browsers targeting EAM, rather than macroalgae, is likely a consequence of the limited cover of macroalgae at the study sites (<1%), and supports the contention that herbivores exhibit feeding versatility in response to changing availability of resources (Bellwood et al. 2006b). This has positive implications for control of EAM cover, but doesn't necessarily infer the same positive consequences for control of macroalgae, unless members of other functional groups switch to feeding on macroalgae when it is abundant, e.g., *Platax pinnatus* (Bellwood et al. 2006a).

Although certain functional groups appear to show low levels of redundancy across scales, this is not necessarily due to past disturbances, or impacts such as overfishing, occurring over ecological time scales. The study sites at Lizard Island have been closed to all fishing for eight years, prior to which there were restrictions on fishing for over 25 years. The presence of low redundancy and a high number of specialized functions within the herbivores is likely driven by relatively low variation in abiotic factors over evolutionary timescales (Walker et al. 1999), rather than due to recent impacts reducing cross-scale redundancy. If this is the case, then the distributions of functional groups observed in this study may be representative of relatively unexploited reefs, and therefore present a best case scenario for managers of reef systems. Reefs subject to high fishing pressure are likely to have experienced erosion of redundancy within functional groups and thus be characterized by a more depauperate cross-scale herbivore assemblage.

A number of caveats apply to the interpretation of cross-scale patterns of foraging movements by functional groups: (1) Assignment of functional groups necessarily results in relatively coarse classifications. As a result, feeding behaviors specific to individual species (e.g., Fox and Bellwood 2012) are not accounted for, potentially overestimating redundancy across scales. (2) The predominant role a species plays may change over time. This may have both negative consequences (e.g., herbivorous urchins driving significant bioerosion with increasing population abundance [McClanahan and Shafir 1990]), or positive impacts (e.g., the invertivore *Platax pinnatus* removing macroalgae in experimental phase-shifts [Bellwood et al. 2006a]). Nevertheless, the future delivery of a particular function is not guaranteed (Nyström 2006).

The spatial patterns of foraging by herbivores suggest that the four functional groups exhibit different degrees of cross-scale redundancy. The next step is to assess how foraging areas overlap among members of a functional group operating at different scales to provide this

redundancy. In boreal forests, birds foraging over a wide range of scales help control spruce budworm outbreak. Different sized species of bird forage for budworm at different scales during an outbreak, with larger species switching to this prey item as budworm becomes more aggregated over larger scales (Peterson et al. 1998). Similar research, examining the effect of broad vs. narrow ranges of foraging scales provided by members of herbivorous functional groups is needed to understand the importance of redundancy mechanisms on coral reefs and how this redundancy interacts with environmental factors (Cheal et al. 2013).

Vulnerability of cross-scale patterns to fishing

The positive relationship between vulnerability to fishing and the scale of foraging movements indicates that overfishing has the potential to reduce the range of scales over which herbivores are providing function by removing species operating at larger spatial scales. Although there is a strong correlation between species size and vulnerability to fishing (Jackson et al. 2001, Friedlander and DeMartini 2002), some species were more vulnerable than their body size alone would suggest, e.g., browsers. This is perhaps not surprising considering that the vulnerability metric used incorporates size as just one of eight traits (Cheung et al. 2005). Characteristics of a species, other than size, contribute to their relative susceptibility to being caught and the likelihood of populations rebounding from a given fishing pressure, both of which contribute to fishing vulnerability. Variability in the influence of different traits on hunting risk has been explored in terrestrial systems; large body size has been shown to be positively correlated with hunting risk in Australian mammal species (e.g., Cardillo and Bromham 2001), whereas work on African bushmeat exploitation has emphasized the importance of large population sizes and species' behavior (Fa et al. 2005). Indeed, behavioral changes in response to predation pressure add considerable complexity to assessments of species' vulnerability to exploitation. Predation risk may affect foraging behavior in communities subject to natural predators (e.g., in baboons [Cowlshaw 1997] and coral reef fishes [Randall 1965, Madin et al. 2011]), but there is also potential for behavioral modifications in response to hunting, which may affect vulnerability to being caught (Thiel et al. 2007). For example, recent work on coral reefs has demonstrated that herbivorous fishes flee from spearfishers earlier when they are in locations that experience greater fishing pressure (Januchowski-Hartley et al. 2011). An increased understanding of the vulnerability of herbivorous fishes to fishing, and how this is likely to vary under different fishing pressures and management contexts, should improve our understanding of how the delivery of herbivorous functions across spatial scales are likely to change over time.

Loss of function at specific scales may proceed unnoticed if metrics of function, such as herbivore

abundance, are used to monitor essential ecosystem processes (Bellwood et al. 2004). Where species are large and vulnerable to fishing, there are the compound issues of losing species operating over large scales and losing species that contribute most to functional impact via higher grazing rates and volumes (Bonaldo and Bellwood 2008, Lokrantz et al. 2008). These large species are primarily scraper/excavators and there is, therefore, the potential for losing a critical component of the herbivore assemblage responsible for algal control and bioerosion, even in areas subject to moderate fishing pressure (Bellwood et al. 2012). Where fishing reaches greater levels, we may see a subsequent reduction in grazer/detritivores, which are foraging at mid-scales. Cross-scale redundancy has the potential to counteract some of the impact of losing species operating at certain scales. For example, the positive effects of small individuals have been seen in Moorea, where large numbers of small parrotfishes controlled algal growth (Adam et al. 2011). However, there is evidence that species operating over small scales may be less effective at compensating for loss at larger scales than vice versa, particularly in the face of large scale disturbances. For example, assemblages of small-scale mammalian seed dispersers are unable to provide dispersal at scales sufficient to maintain tree populations when faced by large-scale disturbances, a problem that does not occur in assemblages with both large- and small-scale dispersers (Peterson et al. 1998). These contrasting findings suggest that caution needs to be taken when predicting the consequences of cross-scale redundancy for the continuation of ecosystem processes in the face of different disturbance regimes. There is a need to assess cross-scale patterns of function in concert with future levels of overfishing and the scale of disturbance regimes to make predictions about the usefulness of current cross-scale redundancy patterns for the ongoing maintenance of coral-dominated reefs.

Vulnerability to fishing is not limited to large species; the browsers exhibited significant susceptibility. When this vulnerability is considered in conjunction with (1) the low number of browsing species found at the three sites, (2) the low abundance of these species, and (3) the narrow range of spatial scales over which they operate, there is a clear need for concern regarding the redundancy of function within this group, and thus, the ongoing delivery of browsing function in the face of future change. However, in highlighting the susceptibilities of certain functional groups and spatial scales of function, this study provides managers with the fundamental knowledge needed to plan mitigation measures to counteract fishing pressure that undermines ecosystem processes at critical scales. There is an emerging body of work describing targeted mitigation strategies, such as gear-based management, which may minimize catches of important or susceptible species, including herbivores (Cinner et al. 2009, Johnson 2010). Our study provides the first step to enable managers to select from

these mitigation strategies appropriate tools to maintain function across scales. Due to the local to regional nature of fisheries management, there is the potential to implement such actions in a timely manner, resulting in relatively quick responses within the fish community (Graham et al., *in press*).

Conclusions

The small-scale movement metrics used in our study revealed the tight relationship between fish body size and space use at scales appropriate to the functional impact of herbivorous reef species. The results indicate that body size is a useful proxy for scale of foraging and functional impact among species, and that functional groups are not evenly distributed across scales. The influence of fishing pressure on cross-scale distributions of function is of significant concern for two key reasons: (1) Fishes operating over large scales (primarily scraper/excavators), and which likely exhibit greater grazing impacts, are particularly susceptible to exploitation; and (2) the few species that act as browsers, targeting mature macroalgae, provide their role over a narrow range of spatial scales and are extremely vulnerable to fishing. This study identifies the scales at which herbivorous function is at risk, and therefore provides critical information needed to inform management actions to support function at specific scales and the provision of the key ecosystem process of herbivory.

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LITERATURE CITED

- Adam, T. C., R. J. Schmitt, S. J. Holbrook, A. J. Brooks, P. J. Edmunds, R. C. Carpenter, and G. Bernardi. 2011. Herbivory, connectivity, and ecosystem resilience: response of a coral reef to a large-scale perturbation. *PLoS One* 6:e23717.
- Bellwood, D. R., A. S. Hoey, and T. P. Hughes. 2012. Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. *Proceedings of the Royal Society B* 279:1621–1629.
- Bellwood, D. R., T. P. Hughes, C. Folke, and M. Nyström. 2004. Confronting the coral reef crisis. *Nature* 429:827–833.
- Bellwood, D. R., T. P. Hughes, and A. S. Hoey. 2006a. Sleeping functional group drives coral-reef recovery. *Current Biology* 16:2434–2439.
- Bellwood, D. R., P. C. Wainwright, C. J. Fulton, and A. S. Hoey. 2006b. Functional versatility supports coral reef biodiversity. *Proceedings of the Royal Society B* 273:101–107.
- Bonaldo, R. M., and D. R. Bellwood. 2008. Size-dependent variation in the functional role of the parrotfish *Scarus rivulatus* on the Great Barrier Reef, Australia. *Marine Ecology Progress Series* 360:237–244.
- Börger, L., B. D. Dalziel, and J. M. Fryxell. 2008. Are there general mechanisms of animal home range behavior? A review and prospects for future research. *Ecology Letters* 11:637–650.
- Brown, J. L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bulletin* 76:160–169.
- Buckle, E. C., and D. J. Booth. 2009. Ontogeny of space use and diet of two temperate damselfish species, *Parma microlepis* and *Parma unifasciata*. *Marine Biology* 156:1497–1505.
- Calder, W. A. 1984. Size, function, and life history. Harvard University Press, Cambridge, Massachusetts, USA.
- Cardillo, M., and L. Bromham. 2001. Body size and risk of extinction in Australian mammals. *Conservation Biology* 15:1435–1440.
- Ceccarelli, D. 2007. Modification of benthic communities by territorial damselfish: a multi-species comparison. *Coral Reefs* 26:853–866.
- Ceccarelli, D., G. P. Jones, and L. J. McCook. 2001. Territorial damselfishes as determinants of benthic community structure on coral reefs. *Oceanography and Marine Biology: an annual review* 39:355–389.
- Chase, J. 2003. Community assembly: when should history matter? *Oecologia* 136:489–498.
- Cheal, A. J., M. Emslie, M. A. MacNeil, I. Miller, and H. Sweatman. 2013. Spatial variation in the functional characteristics of herbivorous fish communities and the resilience of coral reefs. *Ecological Applications* 23:174–188.
- Cheal, A. J., M. MacNeil, E. Cripps, M. Emslie, M. Jonker, B. Schaffelke, and H. Sweatman. 2010. Coral–macroalgal phase shifts or reef resilience: links with diversity and functional roles of herbivorous fishes on the Great Barrier Reef. *Coral Reefs* 29:1005–1015.
- Cheung, W. W. L., T. J. Pitcher, and D. Pauly. 2005. A fuzzy logic expert system to estimate intrinsic extinction vulnerabilities of marine fishes to fishing. *Biological Conservation* 124:97–111.
- Choat, J. H., W. D. Robbins, and K. D. Clements. 2004. The trophic status of herbivorous fishes on coral reefs. *Marine Biology* 145:445–454.
- Christensen, N. L., et al. 1996. The report of the Ecological Society of America Committee on the Scientific Basis for Ecosystem Management. *Ecological Applications* 6:665–691.
- Cinner, J. E., T. R. McClanahan, N. A. J. Graham, M. S. Pratchett, S. K. Wilson, and J.-B. Raina. 2009. Gear-based fisheries management as a potential adaptive response to climate change and coral mortality. *Journal of Applied Ecology* 46:724–732.
- Cowlishaw, G. U. Y. 1997. Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Animal Behaviour* 53:667–686.
- Cromsigt, J. P. G. M., and H. Olf. 2006. Resource partitioning among savanna grazers mediated by local heterogeneity: an experimental approach. *Ecology* 87:1532–1541.
- Crossman, D. J., J. H. Choat, and K. D. Clements. 2005. Nutritional ecology of nominally herbivorous fishes on coral reefs. *Marine Ecology Progress Series* 296:129–142.
- Cumming, D. H. M., and G. S. Cumming. 2003. Ungulate community structure and ecological processes: body size, hoof area and trampling in African savannas. *Oecologia* 134:560–568.
- Dias, L. G., and K. B. Strier. 2003. Effects of group size on ranging patterns in *Brachyteles arachnoides hypoxanthus*. *International Journal of Primatology* 24:209–221.
- Elmqvist, T., C. Folke, M. Nyström, G. Peterson, J. Bengtsson, B. Walker, and J. Norberg. 2003. Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment* 1:488–494.
- Emslie, M., M. Logan, D. Ceccarelli, A. Cheal, A. Hoey, I. Miller, and H. Sweatman. 2012. Regional-scale variation in the distribution and abundance of farming damselfishes on Australia's Great Barrier Reef. *Marine Biology* 159:1293–1304.

- Fa, J. E., S. F. Ryan, and D. J. Bell. 2005. Hunting vulnerability, ecological characteristics and harvest rates of bushmeat species in afro-tropical forests. *Biological Conservation* 121:167–176.
- Ferreira, D. E. L., A. C. Peret, and R. Coutinho. 1998. Seasonal grazing rates and food processing by tropical herbivorous fishes. *Journal of Fish Biology* 53:222–235.
- Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics* 35:557–581.
- Fox, R. J., and D. R. Bellwood. 2012. Niche partitioning of feeding microhabitats produce a unique function for herbivorous rabbitfishes (Perciformes, Siganidae) on coral reefs. *Coral Reefs* 32:13–23.
- Freiwald, J. 2012. Movement of adult temperate reef fishes off the west coast of North America. *Canadian Journal of Fisheries and Aquatic Sciences* 69:1362–1374.
- Friedlander, A. M., and E. E. DeMartini. 2002. Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian Islands: the effects of fishing down apex predators. *Marine Ecology Progress Series* 230:253–264.
- Gordon, I. J., A. J. Hester, and M. Festa-Bianchet. 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. *Journal of Applied Ecology* 41:1021–1031.
- Graham, N. A. J., D. R. Bellwood, J. E. Cinner, T. P. Hughes, A. V. Norstrom, and M. Nystrom. *In press*. Managing resilience to reverse phase shifts in coral reefs. *Frontiers in Ecology and the Environment*.
- Green, A. L., and D. R. Bellwood. 2009. Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience: a practical guide for coral reef managers in the Asia Pacific Region. IUCN, Gland, Switzerland.
- Harestad, A. S., and F. L. Bunnell. 1979. Home range and body weight: a reevaluation. *Ecology* 60:389–402.
- Holling, C. S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecological Monographs* 62:447–502.
- Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547–1551.
- Hughes, T. P., D. R. Bellwood, C. S. Folke, L. J. McCook, and J. M. Pandolfi. 2007. No-take areas, herbivory and coral reef resilience. *Trends in Ecology and Evolution* 22:1–3.
- Hughes, T. P., N. A. J. Graham, J. B. C. Jackson, P. J. Mumby, and R. S. Steneck. 2010. Rising to the challenge of sustaining coral reef resilience. *Trends in Ecology and Evolution* 25:633–642.
- Illiuss, A. W., and I. J. Gordon. 1987. The allometry of food intake in grazing ruminants. *Journal of Animal Ecology* 56:989–999.
- Jackson, J. B. C., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–637.
- Januchowski-Hartley, F. A., N. A. J. Graham, D. A. Feary, T. Morove, and J. E. Cinner. 2011. Fear of fishers: human predation explains behavioral changes in coral reef fishes. *PLoS ONE* 6:e22761.
- Johnson, A. 2010. Reducing bycatch in coral reef trap fisheries: escape gaps as a step towards sustainability. *Marine Ecology Progress Series* 415:201–209.
- Kramer, D. L., and M. R. Chapman. 1999. Implications of fish home range size and relocation for marine reserve function. *Environmental Biology of Fishes* 55:65–79.
- Laca, E. A., S. Sokolow, J. R. Galli, and C. A. Cangiano. 2010. Allometry and spatial scales of foraging in mammalian herbivores. *Ecology Letters* 13:311–320.
- Lazenby-Cohen, K. A., and A. Cockburn. 1991. Social and foraging components of the home range in *Antechinus stuartii* (Dasyuridae, Marsupialia). *Australian Journal of Ecology* 16:301–307.
- Lokrantz, J., M. Nystrom, M. Thyresson, and C. Johansson. 2008. The non-linear relationship between body size and function in parrotfishes. *Coral Reefs* 27:967–974.
- Madin, E. M. P., J. S. Madin, and D. J. Booth. 2011. Landscape of fear visible from space. *Science Reports* 1:14.
- Martin, R. D., M. Genoud, and C. K. Hemelrijk. 2005. Problems of allometric scaling analysis: examples from mammalian reproductive biology. *Journal of Experimental Biology* 208:1731–1747.
- McClanahan, T. R., and S. H. Shafir. 1990. Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. *Oecologia* 83:362–370.
- McMahon, T., and J. Bonner. 1983. *On size and life*. Scientific American Books, New York, New York, USA.
- Mumby, P. J. 2006. The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. *Ecological Applications* 16:747–769.
- Nanami, A., and H. Yamada. 2008. Size and spatial arrangement of home range of checkered snapper *Lutjanus decussatus* (Lutjanidae) in an Okinawan coral reef determined using a portable GPS receiver. *Marine Biology* 153:1103–1111.
- Nash, K. L., N. A. J. Graham, F. A. Januchowski-Hartley, and D. R. Bellwood. 2012. Influence of habitat condition and competition on foraging behaviour of parrotfishes. *Marine Ecology Progress Series* 457:113–124.
- Nyström, M. 2006. Redundancy and response diversity of functional groups: Implications for the resilience of coral reefs. *Ambio* 35:30–35.
- Paddack, M., R. Cowen, and S. Sponaugle. 2006. Grazing pressure of herbivorous coral reef fishes on low coral-cover reefs. *Coral Reefs* 25:461–472.
- Peters, R. H. 1983. *The ecological implications of body size*. Cambridge University Press, Cambridge, UK.
- Peterson, G. D., C. R. Allen, and C. S. Holling. 1998. Ecological resilience, biodiversity, and scale. *Ecosystems* 1:6–18.
- Pikitch, E. K., et al. 2004. Ecosystem-based fishery management. *Science* 305:346–347.
- Purcell, S. P., and D. B. Bellwood. 2001. Spatial patterns of epilithic algal and detrital resources on a windward coral reef. *Coral Reefs* 20:117–125.
- Randall, J. E. 1965. Grazing effect on sea grasses by herbivorous reef fishes in the West Indies. *Ecology* 46:255–260.
- Reynolds, J. D., N. K. Dulvy, N. B. Goodwin, and J. A. Hutchings. 2005. Biology of extinction risk in marine fishes. *Proceedings of the Royal Society B* 272:2337–2344.
- Ritchie, M. E., and H. Olff. 1999. Spatial scaling laws yield a synthetic theory of biodiversity. *Nature* 400:557–560.
- Samuel, M. D., D. J. Pierce, and E. O. Garton. 1985. Identifying areas of concentrated use within the home range. *Journal of Animal Ecology* 54:711–719.
- Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies. *Bioscience* 37:789–799.
- Smith, R. J. 2009. Use and misuse of the reduced major axis for line-fitting. *American Journal of Physical Anthropology* 140:476–486.
- Thiel, D., E. Menoni, J.-F. Brenot, and L. Jenni. 2007. Effects of recreation and hunting on flushing distance of capercaillie. *Journal of Wildlife Management* 71:1784–1792.
- Vaughn, C. C., and C. C. Hakenkamp. 2001. The functional role of burrowing bivalves in freshwater ecosystems. *Freshwater Biology* 46:1431–1446.
- Walker, B., A. Kinzig, and J. Langridge. 1999. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* 2:95–113.

- Warton, D. I., R. A. Duursma, D. S. Falster, and S. Taskinen. 2012. smatr 3: an R package for estimation and inference about allometric lines. *Methods in Ecology and Evolution* 3:257–259.
- Warton, D. I., I. J. Wright, D. S. Falster, and M. Westoby. 2006. Bivariate line-fitting methods for allometry. *Biological Reviews* 81:259–291.
- Welsh, J., and D. Bellwood. 2012. Spatial ecology of the steephead parrotfish (*Chlorurus microrhinos*): an evaluation using acoustic telemetry. *Coral Reefs* 31:55–65.
- White, E. P., S. K. M. Ernest, A. J. Kerkhoff, and B. J. Enquist. 2007. Relationships between body size and abundance in ecology. *Trends in Ecology and Evolution* 22:323–330.
- Wilson, S. K., and D. R. Bellwood. 1997. Cryptic dietary components of territorial damselfishes (Pomacentridae, Labroidae). *Marine Ecology Progress Series* 153:299–310.
- Wilson, S. K., N. Graham, and N. Polunin. 2007. Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Marine Biology* 151:1069–1076.
- Xiao, X., E. P. White, M. B. Hooten, and S. L. Durham. 2011. On the use of log-transformation vs. nonlinear regression for analyzing biological power laws. *Ecology* 92:1887–1894.
- Zemke-White, L., J. C. Choat, and K. C. Clements. 2002. A re-evaluation of the diel feeding hypothesis for marine herbivorous fishes. *Marine Biology* 141:571–579.

SUPPLEMENTARY MATERIAL

Appendix A

Table summarizing fish species and sizes used in behavioral observations ([Ecological Archives A023-084-A1](#)).

Appendix B

Table summarizing benthos targeted during forays by each functional group ([Ecological Archives A023-084-A2](#)).

Appendix C

Table summarizing relationships between foraging metrics and body size for each functional group ([Ecological Archives A023-084-A3](#)).

Appendix D

Table summarizing relationships between foraging metrics and body size at the family level ([Ecological Archives A023-084-A4](#)).

Appendix E

Figure showing relationships between foraging metrics and body size at the family level ([Ecological Archives A023-084-A5](#)).

Influence of habitat condition and competition on foraging behaviour of parrotfishes

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ABSTRACT: Metrics of foraging by herbivorous reef fishes have been shown to vary across space and time, and among species. However, little work has explicitly assessed how fish use space within their foraging ranges, or characterised relative foraging mobility in response to habitat condition. This knowledge is fundamental to understanding the functional impact of reef herbivores, and how spatially explicit functional roles may be modified by future reef degradation. In this study, we assessed the influence of among-site variation in habitat condition, competition and potential predation risk on the short-term foraging range of 2 species of parrotfish, *Scarus niger* and *S. frenatus*, on mid-shelf reefs of the Great Barrier Reef, Australia. Foraging ranges were evaluated using 3 metrics: (1) inter-foray distance and the (2) area and (3) shape of the short-term foraging range. The primary predictor of these metrics of foraging behaviour was coral cover. Inter-foray distance decreased with increasing coral cover for both *S. niger* and *S. frenatus*, and foraging ranges became more circular with increasing coral cover. Competitor abundance was a secondary driver of foraging behaviour, whereas potential predation had no detectable effect. This research provides a fine-scale understanding of how habitat condition and competition among herbivores shapes the spatial scales at which herbivores interact with their environment in the short term, and at which they perform functions essential for coral reef resilience. Critically, the study suggests that predicted changes in coral cover are likely to alter the way reef herbivores forage, and will shape the extent to which they can compensate for declining habitat condition through changes in their feeding behaviour.

KEY WORDS: Herbivory · Foraging range · Functional role · Ecosystem function · Mobility · Coral reef fish

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Cross-scale Habitat Structure Drives Fish Body Size Distributions on Coral Reefs

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ABSTRACT

Despite a large number of studies focusing on the complexity of coral reef habitats and the characteristics of associated fish assemblages, the relationship between reef structure and fish assemblages remains unclear. The textural discontinuity hypothesis, which proposes that multi-modal body size distributions of organisms are driven by discontinuous habitat structure, provides a theoretical basis that may explain the influence of habitat availability on associated organisms. In this study we use fractal techniques to characterize patterns of cross-scale habitat complexity, and examine how this relates to body-depth abundance distributions of associated fish assemblages over corresponding spatial scales. Our study demonstrates that: (1) Reefs formed from different underlying substrata exhibit distinct patterns of cross-scale habitat complexity; (2) The availability of potential refuges at different scales correlates with patterns in fish body depth

distributions, but habitat structure is more strongly related to the relative abundance of fish in the body depth modes, rather than to the number of modes; (3) As reefs change from coral- to algal-dominated states, the complexity of the underlying reef substratum may change, presenting a more homogeneous environment to associated assemblages; (4) Individual fish body depth distributions may be multi-modal, however, these distributions are not static characteristics of the fish assemblage and may change to uni-modal forms in response to changing habitat condition. In light of predicted anthropogenic changes, there is a clear need to improve our understanding of the scale of ecological relationships to anticipate future changes and vulnerabilities.

Key words: textural discontinuity hypothesis; structural complexity; rugosity; reef degradation; coral-dominated reef; algal-dominated reef.

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Discontinuities, cross-scale patterns, and the organization of ecosystems

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Abstract. Ecological structures and processes occur at specific spatiotemporal scales, and interactions that occur across multiple scales mediate scale-specific (e.g., individual, community, local, or regional) responses to disturbance. Despite the importance of scale, explicitly incorporating a multi-scale perspective into research and management actions remains a challenge. The discontinuity hypothesis provides a fertile avenue for addressing this problem by linking measurable proxies to inherent scales of structure within ecosystems. Here we outline the conceptual framework underlying discontinuities and review the evidence supporting the discontinuity hypothesis in ecological systems. Next we explore the utility of this approach for understanding cross-scale patterns and the organization of ecosystems by describing recent advances for examining nonlinear responses to disturbance and phenomena such as extinctions, invasions, and resilience. To stimulate new research, we present methods for performing discontinuity analysis, detail outstanding knowledge gaps, and discuss potential approaches for addressing these gaps.

Key words: *body mass; competition; discontinuity hypothesis; extinction; function; hierarchy theory; invasion; multiple-scale analysis; nonlinear responses; regime shift; resilience.*

INTRODUCTION

Toward the end of the 20th century, ecology underwent a conceptual shift from a linear, continuous view of ecosystem processes and structures to one that emphasized nonlinearity and the discontinuous nature of many variables and processes (Wiens 1989, Solé and Bascompte 2006). Ecosystems are strongly influenced by

biotic and abiotic processes that operate over different spatial and temporal scales (Levin 1992, Peterson et al. 1998, Peters et al. 2007). Therefore, although small-scale observations provide an important route to explore ecosystem dynamics, it is critical to understand how patterns and processes observed at finer scales represent those operating over broader spatiotemporal scales, and similarly, how large-scale processes correspond to small-scale phenomena (Levin 1992, Cooper et al. 1998, Scheffer and van Nes 2007). These multi-scale patterns will affect the manner in which ecosystems respond to disturbance operating over different scales (Peters et al.

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TABLE 1. Glossary of terms.

Term	Definition
Aggregation	Clusters of measurements in the distribution of a variable. In a body size distribution, an aggregation is a cluster of species that are of similar size. Synonymous with lump or mode in the distribution and driven by the underlying pattern of resource availability or habitat structure, although a focus on modality differs from one on discontinuity in that the expected mechanisms are different (see Discontinuous and Multi-modal distribution). An aggregation is separated from its neighbor by a discontinuity.
Discontinuity	Break in the distribution of a variable. In a body size distribution, this would be a region of the distribution with no species. Synonymous with gap and driven by an underlying break between “intrinsic” scales (see Appendix A for further details). Discontinuities separate aggregations in the distribution.
Discontinuous distribution	The distribution of a variable where measurements are clustered in groups along the axis, and clusters are separated from each other by gaps (cf. multi-modal distribution). For example, a body mass distribution, where species of similar size are clustered in aggregations separated from species of different size by gaps or discontinuities in body mass. Methods aimed at evaluating distributions for discontinuities look for gaps rather than aggregations.
Ecological resilience	A measure of the amount of change needed to transform an ecosystem from one set of processes and structures to a different set. An ecosystem with high resilience would require a substantial amount of energy to transform, whereas a low-resilience system would transform with a relatively small amount of energy.
Intrinsic scales	Sections of the scale spectrum where process–pattern relationships are consistent, i.e., they are homogeneous or change monotonically, and persist over the time scale of interest (Stallins 2006). Also termed scale domains (see Appendix A). A domain is separated from neighboring domains by breaks, which are zones of variability where there is a change in the dominant processes.
Multi-modal distribution	The distribution of a variable where measurements are clustered along the axis. Clusters may be separated from each other by troughs in the distribution (cf. discontinuous distribution). Methods aimed at evaluating modality of a distribution look for modes rather than gaps.
Process	In this context, process includes endogenous processes such as herbivory and exogenous drivers such as a storm. These processes and drivers operate over a discrete range of spatial and temporal scales, forming “intrinsic” scales within a system.

2007); therefore, knowledge of how pattern–process relationships are distributed across scales is crucial for a better understanding of the current state of ecosystems and to make predictions of their response to change.

Despite this interest in scale-specific patterns, effective implementation of a multi-scale approach in theoretical and empirical research remains elusive (Wheatley and Johnson 2009). This is primarily due to the difficulties of identifying appropriate scales and the logistics of targeting multiple scales during data collection (Addicott et al. 1987). Analysis of discontinuities (Table 1) found within a range of abiotic and biotic variables, such as habitat structure, body mass, and range size (e.g., Fischer et al. 2008, Gunderson 2008, Restrepo and Arango 2008), offers a fertile avenue for examining processes and interactions in a multi-scale context. This approach allows the identification of scale-specific relationships among ecosystem drivers and processes, habitat structure, resource availability, and organisms. Here, we outline and evaluate evidence for a conceptual framework that accounts for discontinuities within ecosystems and draw links to work in other ecological and biological fields such as hierarchy theory. Second, we provide and describe tools for evaluating discontinuities across a range of data types. Third, we explore the emerging literature incorporating discontinuity analysis. We illustrate how this approach may be used to address a range of ecological questions regarding cross-scale patterns in abundance, function, diversity, and organismal traits as they relate to that pattern, as

well as to emergent phenomena such as resilience. Finally, we highlight the potential limits of applying discontinuity theory and analyses to specific systems and the current gaps in knowledge, providing stimulus for new research.

DISCONTINUITIES: FRAMEWORK, EVIDENCE, AND EXTENSIONS

Conceptual framework

The discontinuity approach is derived from hierarchy theory (Appendix A). Growing evidence from nature and ecological modeling suggests that ecosystem structure and dynamics are dominated by the influence of a small set of plant, animal, and abiotic processes operating at specific temporal periodicities and spatial scales, forming a hierarchy (O’Neill et al. 1986, Holling 1992). Each level in this nested hierarchy of variables is controlled by processes sufficiently different in speed and size to introduce discontinuities in the distribution and pattern of ecosystem attributes such as habitat structure and resource availability (Fig. 1; see Allen and Starr 1982, O’Neill et al. 1986, Kolasa 1989). Thus ecological structure varies with scale and reflects the actions of the particular processes operating at a given scale. Such discontinuous hierarchical patterns of processes, structure, and resources were first proposed in systems theory over 50 years ago (Simon 1962). Some 30 years later, ecologists began applying these concepts to describe and understand a

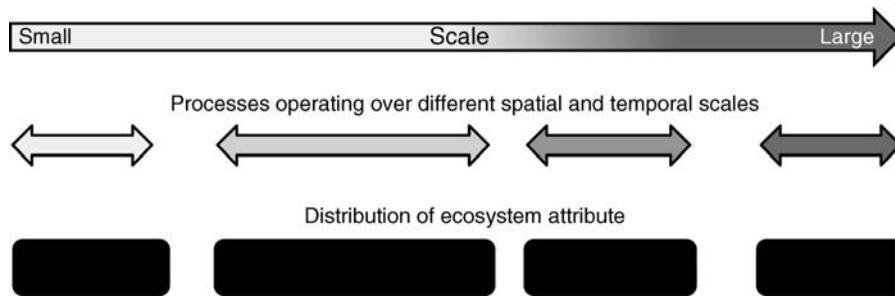


FIG. 1. Multi-scale relationship between processes occurring over different, discrete spatial and temporal scales, and the resulting discontinuous distribution of an ecosystem attribute, such as physical habitat structure. The distribution of processes over discrete scale ranges, and the landscape patterns they produce, represent the “intrinsic” scales (Table 1) of a system (adapted from Wiens 1989). Discontinuities, or zones of low or variable resource availability, lie between these “intrinsic” scales.

range of aquatic and terrestrial ecosystems (Levin 1992, Gillson 2004, Gunderson 2008). For example, the scales of food and shelter afforded by the physical structures of a coral reef ecosystem vary from individual coral branches up to multi-reef complexes, with implications for the abundance of associated organisms (Fig. 2a; see Nash et al. 2013). Discontinuous, hierarchical structure is being used to assess hydro-geomorphic processes in fluvial systems (Poole 2002), and the concept underpins considerable work in landscape ecology (e.g., Kolasa 1989, Pavlacky and Anderson 2007, Johnson 2009).

A number of theoretical frameworks have linked patterns in habitat structure to attributes of associated communities (e.g., MacArthur and Wilson 1967, Milne et al. 1992, Brown 1995, Ritchie 1998). The discontinuity hypothesis, as originally framed by Holling (1992), proposed that where ecosystem patterns are persistent over ecological time scales, biological processes unrelated to the original structuring processes will become entrained by and adapted to the pattern across scales. For example, life history, behavioral, and morphological attributes of animals may adapt to the discontinuous landscape pattern as this pattern reflects opportunities for shelter, food, and resources (Fauchald and Tveraa 2006). However, these opportunities are mediated by the scales at which individuals interact with the landscape and exploit resources (Holling 1992, Haskell et al. 2002), and the scales of these interactions are positively correlated with body size (Peters 1983).

Holling (1992) found a correlation between breaks in distributions of animal body masses and discontinuities in structures and processes in the boreal forest of Canada. At about the same time, similar hypotheses were presented in paleontology (Legendre 1986, Traouillon and Legendre 2009). Aggregations of species (or modes; Table 1) along body mass distributions indicate scales at which resources and structure are available to organisms and persist within a given landscape over ecological time scales (Fig. 2). In contrast, gaps (discontinuities or troughs) in the distribution reflect the transition to a new set of

structuring processes, and therefore few and highly variable resources (Wardwell and Allen 2009). Because animals themselves often strongly modify their environment, such interactions facilitate and reinforce the resources and structure at specific scales (e.g., Bozec et al. 2012).

Modeling and empirical evidence

Discontinuous and multi-modal body size distributions (Table 1) have been observed in numerous ecological systems, including both terrestrial and aquatic ecosystems. Studied taxa include birds (Fischer et al. 2008, Skillen and Maurer 2008, Thibault et al. 2011), reptiles and amphibians (Allen et al. 1999), fish and plankton (Havlicek and Carpenter 2001), and mammals (Lambert 2006, Rodríguez et al. 2008, Wardwell et al. 2008). Separate work looking at other species and community attributes, such as species' abundances and biomass (Angeler et al. 2011), richness (Warwick et al. 2006), range size (Restrepo and Arango 2008), and occupancy patterns (Hartley et al. 2004) across spatial and temporal scales, show similar discontinuous distributions (Table 1).

Similarities in body size distributions among different taxa within a single ecosystem (that are thus exposed to the same habitat structure), and body size distributions of a single taxa among structurally similar systems, have been presented as evidence of the influence of habitat on body size distributions (Holling 1992, Sendzimir 1998). However, the specific mechanisms driving the link between body size and hierarchical habitat structure need explicit exploration (Robson et al. 2005). Szabó and Meszéna (2006) modeled competitive interactions among species of different sizes and showed that the positive relationship between body size and the scale at which species perceive and use resources (Peters 1983, Laca et al. 2010) will produce discontinuous body size distributions where resources are heterogeneously distributed across scales. Empirical studies exploring the link between habitat structure and body size distributions provide further indications of the importance of scaling of the perception of resources with body size.

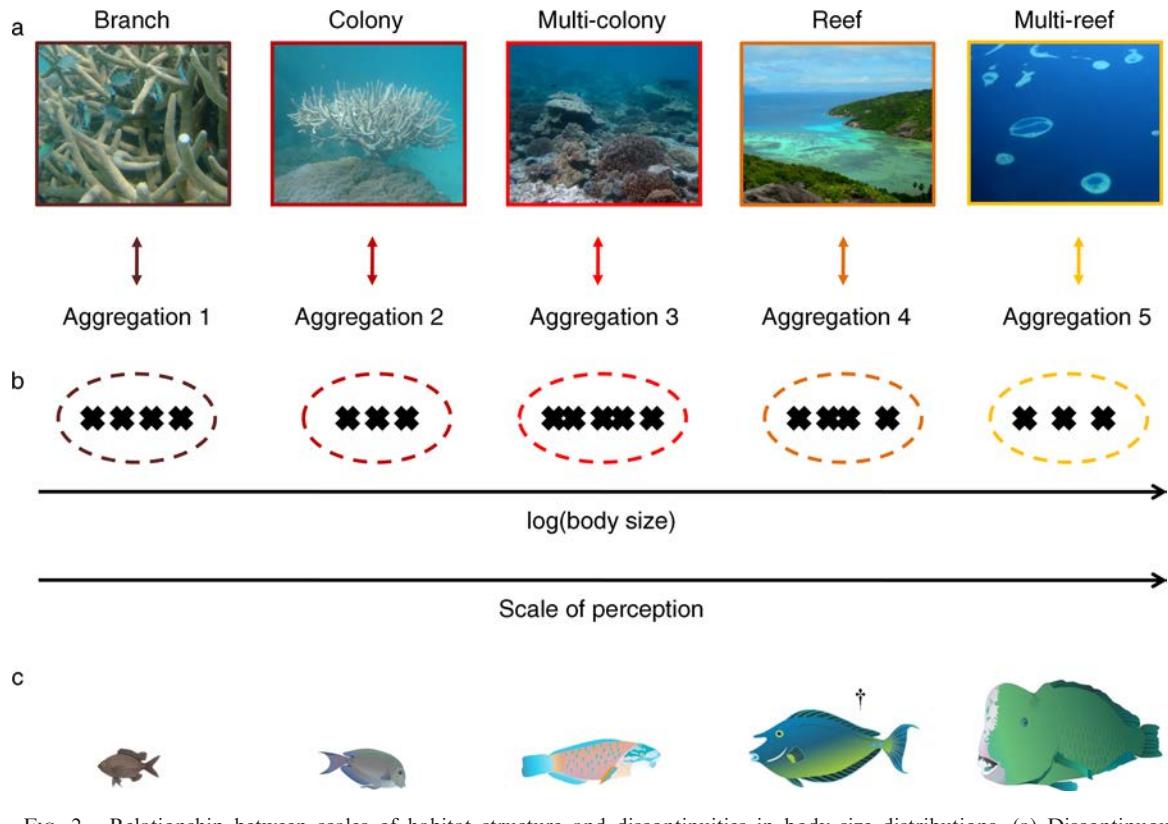


FIG. 2. Relationship between scales of habitat structure and discontinuities in body size distributions. (a) Discontinuous hierarchy of scale for structure and resources within a reef ecosystem, from the individual branches of coral colonies to multi-reef scales. (b) A discontinuous fish body size distribution. Crosses represent individual species; aggregations (dashed circles) of similarly sized species operate at similar scales, and are separated from neighboring aggregations by discontinuities. Body size correlates with scale of perception, such that larger species operate over larger scales. (c) Representative species from each of the five aggregations. For example, the blue spine unicornfish (with dagger symbol) is a member of aggregation 4, and perceives and interacts with its habitat at the reef scale. The multi-reef image is courtesy of James Oliver (<http://www.reefbase.org>); fish vector graphics are courtesy of, from right to left, Tracey Saxby, Joanna Woerner, Joanna Woerner, Christine Thurber, and Tracey Saxby (Integration and Application Network, <http://ian.umces.edu/imagelibrary/>).

For example, the distributions of food and habitat resources at different spatial and temporal scales have been shown to influence body size distributions in deserts (Borthagaray et al. 2012), forests (Fisher et al. 2011), and transition zones between rain forest and savannah habitats (Smith et al. 1997), and availability of shelter to different-sized fish has been linked to body depth distributions in reef ecosystems (Nash et al. 2013). Similarly, thinning of tree stands, reducing the fine-scale complexity of forest habitats, influences bird body size distributions, resulting in smaller mean body size (de la Montaña et al. 2006). In contrast, research investigating the influence of habitat structure on invertebrate body size distributions has produced mixed results (Gunnarsson 1992). Marine intertidal communities show evidence of distributions driven by sediment structure (Schwinghamer 1981), whereas seasonal and spatial changes in body size distributions are significant in freshwater sediment infaunal communities, suggesting that habitat structure is less important in this context (Stead et al. 2005).

The discontinuity hypothesis represents one of a number of proposed drivers of body size distributions (e.g., Brown et al. 1993, Hubbell 2001, Scheffer and van Nes 2006). However, these drivers are, by and large, complementary as they reflect multiple mechanisms operating at distinct scales. Hypotheses such as community interaction, biogeographical, phylogenetic, and discontinuity hypotheses explain pattern and allometry at distinctly different spatial and temporal scales (reviewed in Allen et al. 2006). The phylogenetic hypothesis, for example, is appropriate at continental scales (Cassey and Blackburn 2004), whereas the discontinuity hypothesis is relevant at regional scales (Allen et al. 2006).

There has been some debate regarding the relative importance of the discontinuity hypothesis vs. emergent neutrality in driving discontinuous distributions at similar scales. The latter hypothesis proposes that competitive interactions alone can generate a discontinuous body mass distribution, although the locations of the modes are the result of stochasticity and so differ from community to community (Scheffer and van Nes

2006). This is in contrast to the discontinuity hypothesis, which proposes that the location of modes is driven by biota interacting with habitat structure, and therefore would be similar among sites characterized by the same habitat. Thibault et al. (2011) examined biomass size spectra of breeding and overwintering birds at multiple scales and found strong consistency in the number and location of the modes, suggesting non-stochastic structuring processes at work. In contrast, Vergnon et al. (2012) found evidence supporting emergent neutrality in plankton communities, although their treatment of migrants may not be applicable to terrestrial systems, and their representation of the discontinuity hypothesis should be modified; the discontinuity hypothesis predicts weaker interactions among species operating at different scales compared with those operating at similar scales (Fig. 3); this is contrary to the idea of no interaction as suggested by Vergnon et al. (2012). These contrasting results may be a function of the relative complexity of the different ecosystems under study. More work is needed to understand the mechanisms responsible for body size distributions at defined scales and in a wider range of ecosystems to assess scale- and system-specific factors that may influence this relationship (Sendzimir et al. 2003, Robson et al. 2005, Yvon-Durocher et al. 2011).

Extensions to original framework

Coincident with the growing body of evidence for discontinuities in numerous ecological systems, a number of species' attributes have been shown to be associated with discontinuous body mass patterns. These include invasion, extinction, high population variability, migration, and nomadism (Allen et al. 1999, Allen and Holling 2002, Wardwell and Allen 2009). Additionally, the roles that species play and the distribution of the functional attributes of these species within and across scales may strengthen the resilience of ecological systems (Peterson et al. 1998, Walker et al. 1999). Peterson et al. (1998) expanded upon Holling's (1992) discontinuity hypothesis by proposing that functional diversity within body mass aggregations and redundancy of functional groups across body mass aggregations (i.e., scales) support system resilience (see *Applications* section). Despite these advances, much of the potential of evaluating discontinuities and their implications for addressing a broad range of ecological questions remains unexplored.

APPLICATIONS OF DISCONTINUITY ANALYSIS

Evaluating and analyzing data for discontinuous patterns (Table 2) has two primary uses. First, it is an independent method for identifying "intrinsic" scales (Table 1, Fig. 1) of pattern and process in ecosystems. Second, it provides a platform from which to assess the distribution of key traits or processes within and across the scales of any given system. As a result, it may be used to explain cross-scale patterns such as abundance,

functionality, diversity, and organismal traits as they relate to that pattern, as well as emergent phenomena such as resilience.

Identification of scales

Incorporating a multi-scaled perspective into empirical research remains a key issue, with choice of discrete scales often being arbitrary (Levin 1992, Wheatley and Johnson 2009). Such subjectivity introduces two problems. First, the scales chosen may be relevant for a subset of focal species or ecological processes, but may not be suitable for all species or processes of interest (Davidson et al. 2012). Second, the relevance of theoretical models to empirical results may be masked due to a scale mismatch (Addicott et al. 1987, Roubicek et al. 2010), with the inherent danger that findings are an artifact of ad hoc scale choices and effects (Wiens 1989, McGeoch and Gaston 2002, Halley et al. 2004, Lechner et al. 2012).

Selecting scales for investigation and analysis that are relevant to the particular individual, population, or community is, therefore, a goal of effective ecological research. This has resulted in the development of a range of multi-scale methods for identifying "intrinsic" scales in ecosystems, largely arising out of work on hierarchy theory in landscape ecology (Wu and Li 2006). However, the information needed to make such informed decisions is often considerable (Addicott et al. 1987). Discontinuity analysis provides a method for detecting underlying scales of process and structure in a system, which is not dependent on arbitrary methodological choices and is relatively data inexpensive, using simple proxies such as animal body size (Appendix B; Holling 1992, Wardwell and Allen 2009) or how patterns change across scales (Bradbury et al. 1984, Hartley et al. 2004).

Such analyses present a number of important opportunities, including the ability to: (1) differentiate between systems exhibiting scale invariance of variables and processes (i.e., consistent patterns across scales) vs. those with discrete, "intrinsic" scales (see "power laws" and "scale domains" in Appendix B; Wiens 1989, Kerkhoff and Enquist 2007); (2) reduce the arbitrariness of scale selection and increase the likelihood of designing effective multi-scale studies (Wheatley and Johnson 2009); (3) delimit the appropriate scales for ecological surrogates (Hartley et al. 2004, Januchowski-Hartley et al. 2011); (4) predict congruence in the response of species to disturbance or environmental drivers (Peterson et al. 1998, Chen et al. 2011); and (5) partition out variance associated with scale effects prior to running other analyses. An example of such an analytical integration is seen in tests for priority effects in Hawaiian avifauna (C. R. Allen, M. P. Moulton, and C. S. Holling, *unpublished data*). Inhibitory priority effects describe the negative influence of species already present at a site on the colonizing ability of new species (Belyea and Lancaster

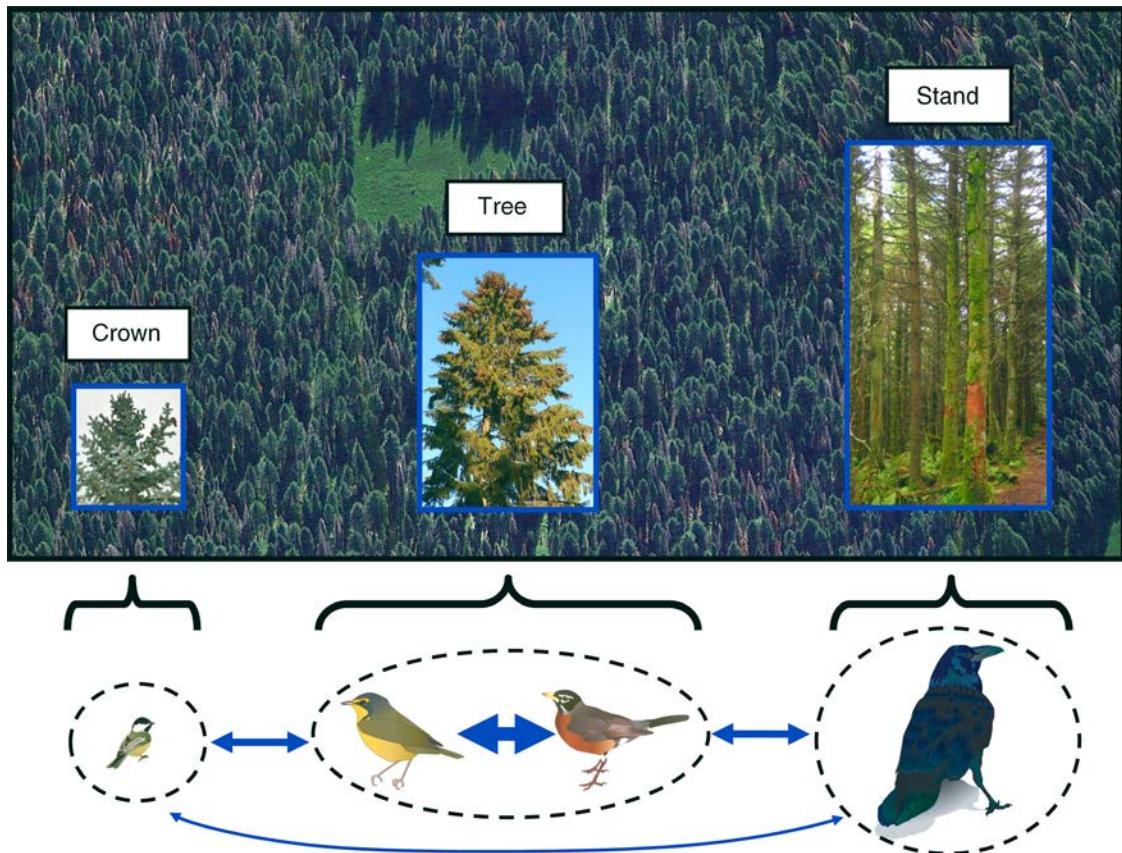


FIG. 3. Strength of competitive interactions among species using similar resources at different scales. The range of scales at which birds in different body size aggregations perceive and feed on spruce budworm extends from the crown of a fir to a stand of trees, and these sit within larger spatial scales (forest). Blue arrows represent the relative strength of competitive interactions among these species. When species are located within the same body size aggregation (dashed circles), they forage over similar scales and thus experience relatively strong competitive interactions (thick arrow) compared with species in different body size aggregations that are foraging at different scales (thinner arrows). The tree aerial photo is courtesy of Google Earth; the spruce tree image is courtesy of Rosendahl (<http://www.public-domain-image.com/>); chickadee, warbler, and robin graphics are courtesy of Tracey Saxby (Integration and Application Network, <http://ian.umces.edu/imagelibrary/>); the crow image is ©Can Stock Photo/ Birchside).

1999). The strength of the negative relationship between the number of species present in the Hawaiian bird community and the success of introduced species was strengthened when body size was accounted for, i.e., membership within a specific body size aggregation was used as a blocking factor in the analysis of variance. This outcome is linked to scale-specific competitive interactions; species within the same aggregation are predicted to experience greater interspecific competition than with species in other aggregations (Fig. 3; see Peterson et al. 1998). As a result, priority effects are stronger in aggregations containing greater numbers of species (C. R. Allen, M. P. Moulton, and C. S. Holling, *unpublished data*).

Evaluations of discontinuities in body size distributions are based on links between body size and patterns of habitat structure, driven by the scale at which species interact with their environment (Szabó and

Meszéna 2006, Fisher et al. 2011, Nash et al. 2013). The drivers of discontinuities in other traits or community characteristics, such as biomass, are less clear and need further exploration. Nevertheless, such investigations present the opportunity to identify the “intrinsic” scales within a system and to develop clear testable hypotheses regarding mechanisms driving these hierarchies.

Identification of nonlinearities and regime shifts

Interactions among processes operating at different temporal and spatial scales can generate nonlinear behavior (Burkett et al. 2005, Peters et al. 2007). To model these dynamics and minimize “ecological surprises” at local and system-wide scales, development of robust methods for detecting and evaluating nonlinearities is essential (Peters et al. 2004). Discontinuity analysis may be used to explicitly identify nonlinear

TABLE 2. Practical tools for detecting discontinuities.

Method	Discontinuities or multi-modality	Data	Platform	Description	Example references
Bayesian classification and regression trees (BCART)	discontinuities	mean values†	executable file: http://www.rob-mcculloch.org/code/CART/index.html	identifies groups using successive partitions of the data	Chipman et al. (1998), Stow et al. (2007)
Gap rarity index (GRI)	discontinuities	mean values†	BASIC; R code currently under development	observed distributions are compared with continuous null distribution and significant gaps are identified	Restrepo et al. (1997), Allen (2006)
Hierarchical cluster analysis	discontinuities	mean values†	R: hclust in stats library	identifies groups using successive partitions of the data	Fischer et al. (2007)
Multivariate time series modeling	discontinuities	species abundance	R: quickPCNM in PCNM library	identifies groups of species exhibiting different temporal trends	Angeler et al. (2009, 2012)
Fractal analysis	discontinuities	various	various	identifies groups based on changes in fractal dimension across scales	Krummel et al. (1987), Nash et al. (2013)
Kernel-density estimation	modality	mean values†,‡	R: density within stats library	estimates probability density function of a variable	Havlicek and Carpenter (2001)
Mixture models	modality	mean values†,§	R: OpenBUGS	uses MCMC estimation to model modality	Xu et al. (2010), Wang et al. (2012b)

Notes: Several methods have been described for identifying discontinuities and multi-modality within the distributions of variables such as body size or biomass. The suitability of these methods varies with respect to the type of data available and the research question (e.g., identifying discontinuities or multi-modality). All techniques have their biases (reviewed in Stow et al. 2007); therefore a combination of methods, followed by triangulation of their respective results, has been identified as the most robust approach (Stow et al. 2007). To date, mean body mass has been primarily used as a measure of body size, although for species with indeterminate growth, other metrics may be more appropriate (Robson et al. 2005). The list of platforms specified is not exhaustive.

† Other descriptive statistics, such as mode, median, or maximum value may be used, depending on the research question and data.

‡ May incorporate a measure of dispersion.

§ May be modified to incorporate abundance.

patterns within social and ecological systems. For example, these methods have highlighted nonlinearities in both city size and plankton biomass distributions (Garmestani et al. 2007, Angeler et al. 2012). This approach can be extended to characterize nonlinear temporal behavior at the system level, to detect impending regime shifts (Allen et al. 2014).

The capacity for leading indicators, such as recovery rate, rising variance, skewness, or “flickering,” to reveal approaching regime shifts has generated considerable interest (e.g., Scheffer et al. 2009, Wang et al. 2012a). Nonetheless, there is concern that proposed metrics may provide an inadequate warning period to allow policy changes in time to address and counteract forecasted shifts (Biggs et al. 2009). Discontinuity analysis may contribute to regime shift detection using existing indicators, by highlighting more sensitive variables that will provide earlier warning signals. For example, rising variance has been presented as a prospective leading indicator (Carpenter and Brock 2006). However, some populations, communities, and abiotic variables are likely to show greater variability than others; thus a method of selecting appropriate variables is needed to

inform the design of monitoring programs developed to highlight ecosystem changes (Carpenter and Brock 2006, Wardwell and Allen 2009). Wardwell and Allen (2009) found rising variance in bird population abundance close to discontinuities in body mass distributions (Fig. 4), and proposed that this type of analysis could be used to highlight which variables are likely to show increased variance prior to a regime shift (Wardwell and Allen 2009).

T. L. Spanbauer et al. (*unpublished manuscript*) present a novel regime shift indicator based on analysis of discontinuities in species abundances over time. Multivariate time series analysis (Angeler et al. 2011) was used to successfully delimit regime shifts in lakes using paleo-diatom data. Where large spatial and temporal data sets are not available (Biggs et al. 2009), other indicators based on discontinuity analysis that require comparatively little data are proposed. The cross-scale pattern of habitat structure and body size distributions is driven by dominant processes and drivers operating over specific spatial and temporal scales (Holling 1992). Therefore, changes in the number or location of discontinuities within habitat or body size

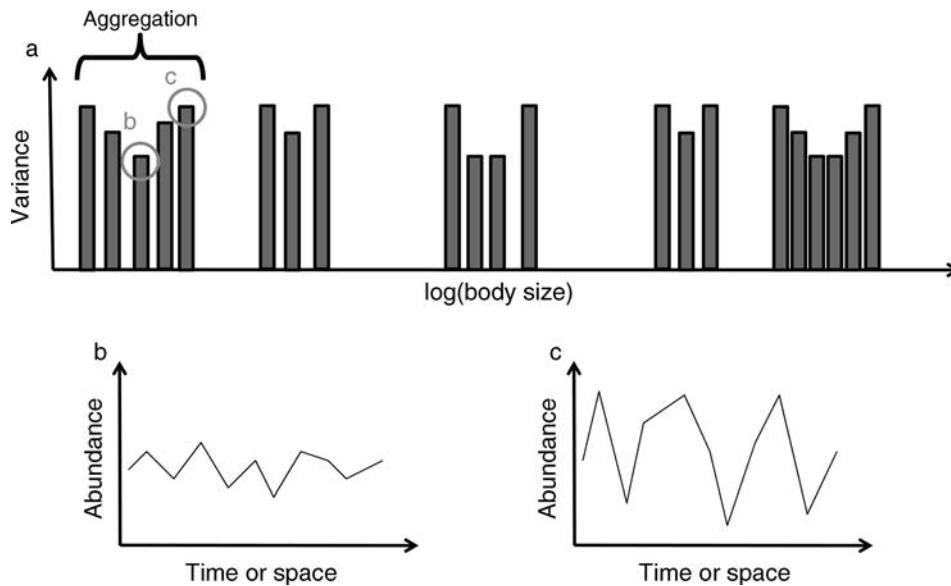


FIG. 4. (a) Patterns of variance in abundance of species located in body mass aggregations. Those species at the center of aggregations exhibit lower variance in abundance (b), than those at the edges of aggregations (c). Here body size and abundance are used as an example. Other variables may show similar patterns of aggregation and variability.

distributions over time would indicate changes in the dominant processes driving these discontinuous patterns; i.e., would provide evidence of a regime shift (Holling 2001). Such changes have been observed spatially in bird communities, among sites experiencing differing levels of landscape modification (Fischer et al. 2007). Temporal changes in the structure of body size distributions could be used to forewarn of reorganization within a system leading to a new regime. In light of research highlighting the need for robust multi-metric early warning frameworks (Lindgren et al. 2012), discontinuities present an innovative method with which existing metrics can be compared and combined.

Functional distributions, macroecology, and resilience

Species may be grouped according to the functional role that they play in the environment. Functions performed by vertebrate and invertebrate species include pollination, grazing, nitrogen fixation, seed dispersal, decomposition, soil nutrient generation, modification of water flows, opening up patches, and modifying environmental gradients within the landscape (Folke et al. 2004). Body size is a proxy for the scale at which species operate (Peters 1983); therefore, body size distributions can be combined with functional classifications to describe and enumerate the distribution of members of functional groups within and across scales, i.e., the range of scales over which each group delivers its functional role. This information is of direct interest to two fields of ecology: macroecology and resilience (Kerkhoff and Enquist 2007).

There has been an increasing recognition that competitive and other forms of intra- and interspecific interactions need to be incorporated into macroecolog-

ical studies (Araújo and Luoto 2007), but to date there has been a lack of clarity regarding the influence of competition on local assembly (Gotelli et al. 2010). Where studies have incorporated competition, the strength of interactions has been inferred from membership within species or functional groups (e.g., Gotelli et al. 2010). Peterson et al. (1998) predict that species using similar resources could minimize competitive interactions via differentiation of the scales at which they operate (Fig. 3). Therefore, members of a functional group are more likely to be distributed across scales (and thus body size aggregations) than expected by chance. This nonrandom pattern has been demonstrated in bird and mammal populations (Wardwell et al. 2008), suggesting that functionally similar species within the same body size aggregation are subject to stronger interactions than those operating at different scales (Peterson et al. 1998). As a result, macroecological studies that group species according to body size aggregation would provide a clearer picture of the likely strength of competitive interactions among species using similar resources, and may help to resolve some of the current uncertainties. The effectiveness of this approach was illustrated in the discussion on Hawaiian avifauna priority effects.

Redundancy of species within functional groups is thought to underpin ecological resilience, as it reflects the potential for each group to compensate for the loss of one or multiple species in the face of disturbance, and thus continue to drive ecological processes (Fig. 5a, b; see Walker et al. 1999, Sundstrom et al. 2012). But the value of this redundancy is misleading if each species responds to a disturbance in a similar manner. Species interacting with their environment at different scales are

likely to respond to disturbances differently (Fig. 5b, c; see Elmqvist et al. 2003); therefore, the scale-specific distribution of functions may be used to quantify the degree of cross- and within-scale redundancy of an assemblage (Allen et al. 2005). This approach, known as the cross-scale resilience model, has been tested on bird community data from southeastern Australia, providing promising results that indicate reduced resilience of modified landscapes (Fischer et al. 2007). However, there is a need to evaluate these metrics in a wider range of ecosystems and taxa. Furthermore, opportunities remain to examine the effects of abundance on functional redundancy (Walker et al. 1999) and to incorporate trait-based functional categorization that transcends the relatively coarse nature of some functional classifications (Fischer et al. 2007).

The distribution of functional groups in time and space may indicate the scales at which species are fulfilling their role. However, the relative impact of organisms of different body sizes is inextricably linked to individual abundance (White et al. 2007). Therefore decline in the abundance of common species, which may form habitat structure within an ecosystem and/or drive key processes (Gaston and Fuller 2008), has significant implications for functional impact at different spatial and temporal scales, which is not quantified by functional distributions alone. The role of species abundance in resilience is largely unexplored, except in the general sense that minor species can sometimes be functional substitutes for more dominant species whose populations are depressed after a disturbance (Walker et al. 1999). To date, the cross-scale resilience model and empirical evaluations of this model have not incorporated abundance and its influence on the functions that species perform (Peterson et al. 1998, Fischer et al. 2007). There is a clear need to address this gap through the addition of abundance into current models relating biological diversity to resilience.

A more detailed characterization of species roles, other than simple functional groups, is possible through the use of multidimensional functional space indices. This approach has been used to examine drivers of community assembly (Ackerly and Cornwell 2007), the delivery of ecosystem processes (Pakeman 2011), and has been proposed as a way of predicting the response of communities to specific disturbances (Mouillot et al. 2012). Mouillot et al. (2012) discuss body size as one of a number of possible traits that may vary in response to disturbance. Therefore, classifying species according to body mass aggregation in a functional trait-based analysis would explicitly group species operating at similar scales and thus incorporate scale-specific response to disturbance, increasing the sensitivity of such analyses.

The resilience of an ecosystem to specific disturbances may be related to connectivity among habitat patches. This connectivity may be passive (e.g., propagules) or due to mobile links, i.e., individuals moving between

areas (Nyström and Folke 2001). Characterizing distributions of function across scales will highlight the likely spatial extent of mobile links and identify vulnerabilities due to a narrowing of the range of scales over which an assemblage is functionally effective (Nyström 2006). For example, large reef fish are subject to extreme fishing pressure in certain areas, resulting in the removal of those species that operate over large scales and thus provide critical linkages among locations across the broader seascape (Jackson et al. 2001, McCauley et al. 2012). This loss has significant implications for the connectivity and spatial resilience of coral reefs, and limits the likelihood of mobile links connecting undamaged reefs with those impacted by disturbance (Fig. 5).

Extinctions and invasions

The rising number of invasions by nonindigenous species and extinctions in terrestrial and aquatic environments are of serious concern (Pimentel et al. 2005, Vié et al. 2009). These changes are often associated with significant modifications to habitats and food webs, with important ramifications for the delivery of ecosystem services and the maintenance of key ecosystem processes (Simberloff et al. 2013). For example, in New Zealand, functional extinction of some bird species has significantly reduced pollination of endemic plant species, leading to reduced plant density (Anderson et al. 2011). The cost associated with the impact of invasive species in the United States alone is estimated to exceed US\$100 billion per annum (Pimentel et al. 2005).

Predicting the likelihood of a species either becoming extinct or being introduced and then successfully establishing a breeding population, is critical for management and for mitigation efforts. However, such prediction is extremely difficult due to the range of species-, community-, and habitat-level factors influencing the decline of species and the success of invasions (Brook et al. 2008, Hayes and Barry 2008, Harnik et al. 2012). Nonetheless, proximity to the edge of body mass aggregations has been found to be a significant predictor of invasion success for both bird and mammal species, and of extinction risk among mammals (Allen et al. 1999, Allen 2006). Edges of body mass aggregations are associated with increased variability in abundance (Wardwell and Allen 2009), and are linked to less predictable resource availability (Fig. 4; see Wiens 1989). Consequently, these edges represent locations where species may be more susceptible to extinction or more able to exploit opportunities (Allen et al. 1999, Allen 2006). The strength of using proximity to a discontinuity in the body mass distribution as a predictor is that it incorporates both community- and habitat-level factors. Specifically it indicates the likely level of competition experienced by an invading species (Fig. 3) and the scales at which resources are available to species, because body mass distributions are thought to reflect underlying habitat structure. In ecosystems where body size aggregations are demonstrated to reflect the

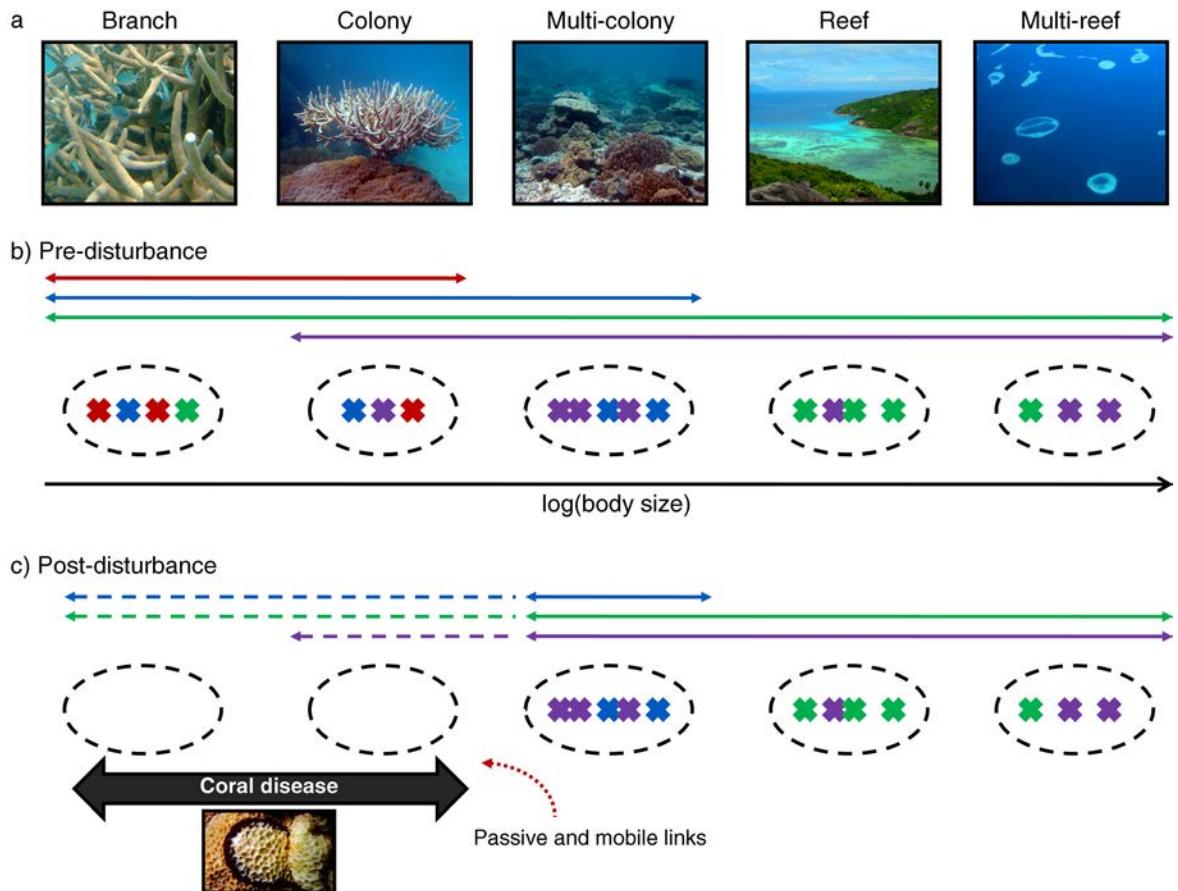


FIG. 5. Influence of disturbance on the distribution of functional groups across scales. (a) The range of scales at which fish perceive, interact with, and use resources on the reef, from the individual branches of coral colonies to multi-reef scales. (b) Pre-disturbance: discontinuous fish body size distribution, where crosses represent individual species and colors indicate functional group membership. Colored arrows indicate the range of scales over which each group operates and therefore provides its function: the green functional group operates over a wide range of scales, whereas the red functional group only operates over small scales. (c) Post-disturbance: coral disease provides a small-scale disturbance that affects fish species operating at the branch and colony scales (empty aggregations). Those functional groups with redundancy across spatial scales (blue, green, and purple groups) may compensate for loss of species at these small scales (dashed arrows), whereas those functional groups with low cross-scale redundancy (red group) are reliant on passive links (recruitment) or mobile links (adult fish) recolonizing from neighboring regions (red dotted arrow) for maintenance of function. The multi-reef image is courtesy of James Oliver (<http://www.reefbase.org>).

underlying scales of pattern–process relationships (Borthagaray et al. 2012), the distribution of extinctions and invasions across body mass distributions can also be used to identify scales particularly vulnerable to change and impact (Cardillo and Bromham 2001, Petchey and Gaston 2002, Woodward et al. 2005). In addition, proximity to discontinuities can be used to predict extinctions or the likely success of invasions of introduced species, prior to their occurrence or establishment, respectively. Considering the global threats that extinction and invasion present (for example, 56 species of amphibians and reptiles have successfully invaded and established breeding populations in Florida alone; Krysko et al. 2011), such a predictive ability is of considerable importance. There is however, a clear need to assess the relationship between discontinuities and

invasions or extinctions among taxa other than birds and mammals.

FUTURE DIRECTIONS

The discontinuity hypothesis provides a conceptual framework, arising from hierarchy theory, within which to examine the organization of ecosystems. However, much of the potential of this framework is unexploited and presents a fertile arena for original research in a wide range of ecological fields. To date, discontinuity research has primarily focused on adult body size as the variable of interest. Performing such studies on plants and modular organisms with no discrete body size, or in species that experience significant ontogenetic changes and indeterminate growth such as fish, remains a challenge that invites innovative approaches. For example, work by Angeler et al. (2013) used multivariate

time series modeling of invertebrate species abundance in subarctic lakes as a novel way to examine patterns of function and resilience at multiple scales, which did not rely on body size metrics. To broaden the utility of discontinuity analysis, similar efforts are needed to address this challenge across the range of potential applications. Furthermore, although there is an emerging literature on the mechanistic links between habitat and body size distributions, additional studies are needed to understand the mechanisms driving discontinuities in variables such as species biomass (Angeler et al. 2011), richness (Warwick et al. 2006), and occupancy (Hartley et al. 2004).

Our discussion of modeling and empirical evidence illustrates the range of studies providing support for the discontinuity hypothesis. However, to date there has been little exploration of those systems where discontinuities are less likely to be found. The discontinuity hypothesis links cross-scale habitat structure to community attributes, such as body size, over ecological time scales. In ecosystems where such structure is less consistent over time, e.g., pelagic systems with dynamic oceanographic conditions and boundaries, discontinuous signals may not be evident. Some work has looked at discontinuities in the body mass (Havlicek and Carpenter 2001), biomass (Angeler et al. 2012), and abundance (Angeler et al. 2011) distributions of lake system communities; however, little work has investigated discontinuities in marine pelagic systems (but see Vergnon et al. 2009). It therefore remains to be seen whether, in comparatively dynamic pelagic environments, discontinuities consistently arise and may be detected.

Discontinuity analysis offers a powerful tool for investigating cross-scale interactions, as it identifies scale-specific relationships between ecosystem drivers and processes, habitat structure, resource availability, and organisms. As a consequence, it provides a platform from which to assess the distribution of key traits or processes within and across the scales of any given ecosystem, e.g., the distribution of ecological function or invasive species. There is considerable scope to broaden the application of discontinuity analysis across ecosystems and taxa, and beyond its current focus on body size applications.

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LITERATURE CITED

- Ackerly, D. D., and W. K. Cornwell. 2007. A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. *Ecology Letters* 10:135–145.
- Addicott, J. F., J. M. Aho, M. F. Antolin, D. K. Padilla, J. S. Richardson, and D. A. Soluk. 1987. Ecological neighborhoods: scaling environmental patterns. *Oikos* 49:340–346.
- Allen, C. R. 2006. Predictors of introduction success in the South Florida avifauna. *Biological Invasions* 8:491–500.
- Allen, C. R., D. G. Angeler, A. S. Garmestani, L. H. Gunderson, and C. S. Holling. 2014. Panarchy: theory and application. *Ecosystems*, *in press*. <http://dx.doi.org/10.1007/s10021-013-9744-2>
- Allen, C. R., E. A. Forsy, and C. S. Holling. 1999. Body mass patterns predict invasions and extinctions in transforming landscapes. *Ecosystems* 2:114–121.
- Allen, C. R., A. S. Garmestani, T. D. Havlicek, P. A. Marquet, G. D. Peterson, C. Restrepo, C. A. Stow, and B. E. Weeks. 2006. Patterns in body mass distributions: sifting among alternative hypotheses. *Ecology Letters* 9:630–643.
- Allen, C. R., L. Gunderson, and A. R. Johnson. 2005. The use of discontinuities and functional groups to assess relative resilience in complex systems. *Ecosystems* 8:958–966.
- Allen, C. R., and C. S. Holling. 2002. Cross-scale morphology. Pages 450–452 in A. H. El-Shaarawi and W. W. Piegorsch, editors. *Encyclopedia of environmetrics*. John Wiley, Chichester, UK.
- Allen, T. F. H., and T. B. Starr, editors. 1982. *Hierarchy: perspectives for ecological complexity*. University of Chicago Press, Chicago, Illinois, USA.
- Anderson, S. H., D. Kelly, J. J. Ladley, S. Molloy, and J. Terry. 2011. Cascading effects of bird functional extinction reduce pollination and plant density. *Science* 331:1068–1071.
- Angeler, D. G., C. R. Allen, and R. K. Johnson. 2012. Insight on invasions and resilience derived from spatiotemporal discontinuities of biomass at local and regional scales. *Ecology and Society* 17:32.
- Angeler, D. G., C. R. Allen, and R. K. Johnson. 2013. Measuring the relative resilience of subarctic lakes to global change: redundancies of functions within and across temporal scales. *Journal of Applied Ecology* 50:572–584.
- Angeler, D. G., S. Drakare, and R. K. Johnson. 2011. Revealing the organization of complex adaptive systems through multivariate time series modeling. *Ecology and Society* 16:5.
- Angeler, D. G., O. Viedma, and J. Moreno. 2009. Statistical performance and information content of time lag analysis and redundancy analysis in time series modeling. *Ecology* 90:3245–3257.
- Araújo, M. B., and M. Luoto. 2007. The importance of biotic interactions for modeling species distributions under climate change. *Global Ecology and Biogeography* 16:743–753.
- Belyea, L. R., and J. Lancaster. 1999. Assembly rules within a contingent ecology. *Oikos* 86:402–416.
- Biggs, R., S. R. Carpenter, and W. A. Brock. 2009. Turning back from the brink: detecting an impending regime shift in time to avert it. *Proceedings of the National Academy of Sciences USA* 106:826–831.
- Borthagaray, A. I., M. Arim, and P. A. Marquet. 2012. Connecting landscape structure and patterns in body size distributions. *Oikos* 121:697–710.
- Bozec, Y.-M., L. Yakob, S. Bejarano, and P. J. Mumby. 2012. Reciprocal facilitation and non-linearity maintain habitat engineering on coral reefs. *Oikos* 122:428–440.
- Bradbury, R. H., R. E. Reichelt, and D. G. Green. 1984. Fractals in ecology: methods and interpretation. *Marine Ecology Progress Series* 14:295–296.

- Brook, B. W., N. S. Sodhi, and C. J. A. Bradshaw. 2008. Synergies among extinction drivers under global change. *Trends in Ecology and Evolution* 23:453–460.
- Brown, J. H. 1995. *Macroecology*. University of Chicago Press, Chicago, Illinois, USA.
- Brown, J. H., P. A. Marquet, and M. L. Taper. 1993. Evolution of body size: consequences of an energetic definition of fitness. *American Naturalist* 142:573–584.
- Burkett, V. R., et al. 2005. Nonlinear dynamics in ecosystem response to climatic change: case studies and policy implications. *Ecological Complexity* 2:357–394.
- Cardillo, M., and L. Bromham. 2001. Body size and risk of extinction in Australian mammals. *Conservation Biology* 15:1435–1440.
- Carpenter, S. R., and W. A. Brock. 2006. Rising variance: a leading indicator of ecological transition. *Ecology Letters* 9:311–318.
- Cassey, P., and T. M. Blackburn. 2004. Body size trends in a Holocene island bird assemblage. *Ecography* 27:59–67.
- Chen, I.-C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333:1024–1026.
- Chipman, H. A., E. I. George, and R. E. McCulloch. 1998. Bayesian CART model search. *Journal of the American Statistical Association* 93:935–948.
- Cooper, S. D., S. Diehl, K. Kratz, and O. Sarnelle. 1998. Implications of scale for patterns and processes in stream ecology. *Australian Journal of Ecology* 23:27–40.
- Davidson, Z., M. Valeix, A. J. Loveridge, J. E. Hunt, P. J. Johnson, H. Madzikanda, and D. W. Macdonald. 2012. Environmental determinants of habitat and kill site selection in a large carnivore: scale matters. *Journal of Mammalogy* 93:677–685.
- de la Montaña, E., J. M. Rey-Benayas, and L. M. Carrascal. 2006. Response of bird communities to silvicultural thinning of Mediterranean maquis. *Journal of Applied Ecology* 43:651–659.
- Elmqvist, T., C. Folke, M. Nyström, G. Peterson, J. Bengtsson, B. Walker, and J. Norberg. 2003. Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment* 1:488–494.
- Fauchald, P., and T. Tveraa. 2006. Hierarchical patch dynamics and animal movement pattern. *Oecologia* 149:383–395.
- Fischer, J., D. Lindenmayer, S. Blomberg, R. Montague-Drake, A. Felton, and J. Stein. 2007. Functional richness and relative resilience of bird communities in regions with different land use intensities. *Ecosystems* 10:964–974.
- Fischer, J., D. B. Lindenmayer, and R. Montague-Drake. 2008. The role of landscape texture in conservation biogeography: a case study on birds in south-eastern Australia. *Diversity and Distributions* 14:38–46.
- Fisher, J. T., B. Anholt, and J. P. Volpe. 2011. Body mass explains characteristic scales of habitat selection in terrestrial mammals. *Ecology and Evolution* 1:517–528.
- Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics* 35:557–581.
- Garmestani, A. S., C. R. Allen, C. M. Gallagher, and J. D. Mittelstaedt. 2007. Departures from Gibrat's Law, discontinuities and city size distributions. *Urban Studies* 44:1997–2007.
- Gaston, K. J., and R. A. Fuller. 2008. Commonness, population depletion and conservation biology. *Trends in Ecology and Evolution* 23:14–19.
- Gillson, L. 2004. Evidence of hierarchical patch dynamics in an east African savanna? *Landscape Ecology* 19:883–894.
- Gotelli, N. J., G. R. Graves, and C. Rahbek. 2010. Macroecological signals of species interactions in the Danish avifauna. *Proceedings of the National Academy of Sciences USA* 107:5030–5035.
- Gunderson, L. H. 2008. Biophysical discontinuities in the Everglades system. Pages 83–100 in C. R. Allen and C. S. Holling, editors. *Discontinuities in ecosystems and other complex systems*. Columbia University Press, New York, New York, USA.
- Gunnarsson, B. 1992. Fractal dimension of plants and body size distribution in spiders. *Functional Ecology* 6:636–641.
- Halley, J. M., S. Hartley, A. S. Kallimanis, W. E. Kunin, J. J. Lennon, and S. P. Sgardelis. 2004. Uses and abuses of fractal methodology in ecology. *Ecology Letters* 7:254–271.
- Harnik, P. G., et al. 2012. Extinctions in ancient and modern seas. *Trends in Ecology and Evolution* 27:608–617.
- Hartley, S., W. E. Kunin, J. J. Lennon, and M. J. O. Pocock. 2004. Coherence and discontinuity in the scaling of species' distribution patterns. *Proceedings of the Royal Society B* 271:81–88.
- Haskell, J. P., M. E. Ritchie, and H. Olf. 2002. Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. *Nature* 418:527–530.
- Havlicek, T. D., and S. R. Carpenter. 2001. Pelagic species size distributions in lakes: are they discontinuous? *Limnology and Oceanography* 46:1021–1033.
- Hayes, K., and S. Barry. 2008. Are there any consistent predictors of invasion success? *Biological Invasions* 10:483–506.
- Holling, C. S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecological Monographs* 62:447–502.
- Holling, C. S. 2001. Understanding the complexity of economic, ecological, and social systems. *Ecosystems* 4:390–405.
- Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Jackson, J. B. C., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–637.
- Januchowski-Hartley, S. R., V. Hermoso, R. L. Pressey, S. Linke, J. Kool, R. G. Pearson, B. J. Pusey, and J. VanDerWal. 2011. Coarse-filter surrogates do not represent freshwater fish diversity at a regional scale in Queensland, Australia. *Biological Conservation* 144:2499–2511.
- Johnson, C. R. 2009. Natural length scales of ecological systems: applications at community and ecosystem levels. *Ecology and Society* 14:7.
- Kerckhoff, A. J., and B. J. Enquist. 2007. The implications of scaling approaches for understanding resilience and reorganization in ecosystems. *BioScience* 57:489–499.
- Kolasa, J. 1989. Ecological systems in hierarchical perspective: breaks in community structure and other consequences. *Ecology* 70:36–47.
- Krummel, J. R., R. H. Gardner, G. Sugihara, R. V. O'Neill, and P. R. Coleman. 1987. Landscape patterns in a disturbed environment. *Oikos* 48:321–324.
- Krysko, K. L., et al. 2011. Verified non-indigenous amphibians and reptiles in Florida from 1863 through 2010: outlining the invasion process and identifying invasion pathways and stages. *Zootaxa* 3028:1–64.
- Laca, E. A., S. Sokolow, J. R. Galli, and C. A. Cangiano. 2010. Allometry and spatial scales of foraging in mammalian herbivores. *Ecology Letters* 13:311–320.
- Lambert, W. 2006. Functional convergence of ecosystems: evidence from body mass distributions of North American late Miocene mammal faunas. *Ecosystems* 9:97–118.
- Lechner, A. M., W. T. Langford, S. D. Jones, S. A. Bekessy, and A. Gordon. 2012. Investigating species–environment relationships at multiple scales: differentiating between intrinsic scale and the modifiable areal unit problem. *Ecological Complexity* 11:91–102.

- Legendre, S. 1986. Analysis of mammalian communities from the late Eocene and Oligocene of southern France. *Palaeo-vertebrata* 16:191–212.
- Levin, S. A. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur Award lecture. *Ecology* 73:1943–1967.
- Lindgren, M., V. Dakos, J. P. Gröger, A. Gårdmark, G. Kornilovs, S. A. Otto, and C. Möllmann. 2012. Early detection of ecosystem regime shifts: a multiple method evaluation for management application. *PLoS One* 7:e38410.
- MacArthur, R. H., and E. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- McCauley, D. J., H. S. Young, R. B. Dunbar, J. A. Estes, B. X. Semmens, and F. Micheli. 2012. Assessing the effects of large mobile predators on ecosystem connectivity. *Ecological Applications* 22:1711–1717.
- McGeoch, M. A., and K. J. Gaston. 2002. Occupancy frequency distributions: patterns, artefacts and mechanisms. *Biological Reviews* 77:311–331.
- Milne, B. T., M. G. Turner, J. A. Wiens, and A. R. Johnson. 1992. Interactions between the fractal geometry of landscapes and allometric herbivory. *Theoretical Population Biology* 41:337–353.
- Mouillot, D., N. A. J. Graham, S. Villéger, N. W. H. Mason, and D. R. Bellwood. 2012. A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution* 28:167–177.
- Nash, K. L., N. A. J. Graham, S. K. Wilson, and D. R. Bellwood. 2013. Cross-scale habitat structure drives fish body size distributions on coral reefs. *Ecosystems* 16:478–490.
- Nyström, M. 2006. Redundancy and response diversity of functional groups: implications for the resilience of coral reefs. *Ambio* 35:30–35.
- Nyström, M., and C. Folke. 2001. Spatial resilience of coral reefs. *Ecosystems* 4:406–417.
- O'Neill, R. V., D. L. DeAngelis, J. B. Waide, and T. F. H. Allen. 1986. *A hierarchical concept of ecosystems*. Princeton University Press, Princeton, New Jersey, USA.
- Pakeman, R. J. 2011. Multivariate identification of plant functional response and effect traits in an agricultural landscape. *Ecology* 92:1353–1365.
- Pavlacky, D. C., and S. H. Anderson. 2007. Does avian species richness in natural patch mosaics follow the forest fragmentation paradigm? *Animal Conservation* 10:57–68.
- Petchev, O. L., and K. J. Gaston. 2002. Extinction and the loss of functional diversity. *Proceedings of the Royal Society B* 269:1721–1727.
- Peters, D. P. C., B. T. Bestelmeyer, and M. G. Turner. 2007. Cross-scale interactions and changing pattern–process relationships: consequences for system dynamics. *Ecosystems* 10:790–796.
- Peters, D. P. C., R. A. Pielke, B. T. Bestelmeyer, C. D. Allen, S. Munson-McGee, and K. M. Havstad. 2004. Cross-scale interactions, nonlinearities, and forecasting catastrophic events. *Proceedings of the National Academy of Sciences USA* 101:15130–15135.
- Peters, R. H. 1983. *The ecological implications of body size*. Cambridge University Press, Cambridge, UK.
- Peterson, G. D., C. R. Allen, and C. S. Holling. 1998. Ecological resilience, biodiversity, and scale. *Ecosystems* 1:6–18.
- Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52:273–288.
- Poole, G. C. 2002. Fluvial landscape ecology: addressing uniqueness within the river discontinuum. *Freshwater Biology* 47:641–660.
- Restrepo, C., and N. Arango. 2008. Discontinuities in the geographical range size of North American birds and butterflies. Pages 101–135 in C. R. Allen and C. S. Holling, editors. *Discontinuities in ecosystems and other complex systems*. Columbia University Press, New York, New York, USA.
- Restrepo, C., L. M. Renjifo, and P. Marples. 1997. Frugivorous birds in fragmented Neotropical montane forests: Landscape pattern and body mass distribution. Pages 171–189 in W. F. Laurance and R. O. Bierregaard, Jr., editors. *Tropical forest remnants: ecology, management, and conservation of fragmented landscapes*. University of Chicago Press, Chicago, Illinois, USA.
- Ritchie, M. 1998. Scale-dependent foraging and patch choice in fractal environments. *Evolutionary Ecology* 12:309–330.
- Robson, B. J., L. A. Barmuta, and P. G. Fairweather. 2005. Methodological and conceptual issues in the search for a relationship between animal body-size distributions and benthic habitat architecture. *Marine and Freshwater Research* 56:1–11.
- Rodríguez, M. Á., M. Á. Olalla-Tárraga, and B. A. Hawkins. 2008. Bergmann's rule and the geography of mammal body size in the Western Hemisphere. *Global Ecology and Biogeography* 17:274–283.
- Roubicek, A. J., J. VanDerWal, L. J. Beaumont, A. J. Pitman, P. Wilson, and L. Hughes. 2010. Does the choice of climate baseline matter in ecological niche modeling? *Ecological Modelling* 221:2280–2286.
- Scheffer, M., J. Bascompte, W. A. Brock, V. Brovkin, S. R. Carpenter, V. Dakos, H. Held, E. H. van Nes, M. Rietkerk, and G. Sugihara. 2009. Early-warning signals for critical transitions. *Nature* 461:53–59.
- Scheffer, M., and E. H. van Nes. 2006. Self-organized similarity: the evolutionary emergence of groups of similar species. *Proceedings of the National Academy of Sciences USA* 103:6230–6235.
- Scheffer, M., and E. H. van Nes. 2007. Shallow lakes theory revisited: various alternative regimes driven by climate, nutrients, depth and lake size. *Hydrobiologia* 584:455–466.
- Schwinghamer, P. 1981. Characteristic size distributions of integral benthic communities. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1255–1263.
- Sendzimir, J. 1998. *Patterns of animal size and landscape complexity: correspondence within and across scales*. Dissertation. University of Florida, Gainesville, Florida, USA.
- Sendzimir, J., C. R. Allen, L. H. Gunderson, and C. A. Stow. 2003. Implications of body mass patterns: linking ecological structure and process to wildlife conservation and management. Pages 125–152 in J. Bissonette and I. Storch, editors. *Landscape ecology and resource management: linking theory with practice*. Island Press, Washington, D.C., USA.
- Simberloff, D., et al. 2013. Impacts of biological invasions: What's what and the way forward. *Trends in Ecology and Evolution* 28:58–66.
- Simon, H. A. 1962. The architecture of complexity. *Proceedings of the American Philosophical Society* 106:467–482.
- Skillen, J. J., and B. A. Maurer. 2008. The ecological significance of discontinuities in body-mass distributions. Pages 193–218 in C. R. Allen and C. S. Holling, editors. *Discontinuities in ecosystems and other complex systems*. Columbia University Press, New York, New York, USA.
- Smith, T. B., R. K. Wayne, D. J. Girman, and M. W. Bruford. 1997. A role for ecotones in generating rainforest biodiversity. *Science* 276:1855–1857.
- Solé, R. V., and J. Bascompte. 2006. *Self-organization in complex ecosystems*. Princeton University Press, Princeton, New Jersey, USA.
- Stallins, J. A. 2006. Geomorphology and ecology: unifying themes for complex systems in biogeomorphology. *Geomorphology* 77:207–216.

- Stead, T. K., J. M. Schmid-Araya, P. E. Schmid, and A. G. Hildrew. 2005. The distribution of body size in a stream community: one system, many patterns. *Journal of Animal Ecology* 74:475–487.
- Stow, C. A., C. R. Allen, and A. S. Garmestani. 2007. Evaluating discontinuities in complex systems: toward quantitative measures of resilience. *Ecology and Society* 12: 26.
- Sundstrom, S. M., C. R. Allen, and C. Barichievy. 2012. Species, functional groups, and thresholds in ecological resilience. *Conservation Biology* 26:305–314.
- Szabó, P., and G. Meszéna. 2006. Spatial ecological hierarchies: coexistence on heterogeneous landscapes via scale niche diversification. *Ecosystems* 9:1009–1016.
- Thibault, K. M., E. P. White, A. H. Hurlbert, and S. K. M. Ernest. 2011. Multimodality in the individual size distributions of bird communities. *Global Ecology and Biogeography* 20:145–153.
- Travouillon, K. J., and S. Legendre. 2009. Using cenograms to investigate gaps in mammalian body mass distributions in Australian mammals. *Palaeogeography, Palaeoclimatology, Palaeoecology* 272:69–84.
- Vergnon, R., N. K. Dulvy, and R. P. Freckleton. 2009. Niches versus neutrality: uncovering the drivers of diversity in a species-rich community. *Ecology Letters* 12:1079–1090.
- Vergnon, R., E. H. van Nes, and M. Scheffer. 2012. Emergent neutrality leads to multimodal species abundance distributions. *Nature Communications* 3:663.
- Vié, J.-C., C. Hilton-Taylor, and S. N. Stuart, editors. 2009. *Wildlife in a changing world—an analysis of the 2008 IUCN Red List of Threatened Species*. IUCN, Gland, Switzerland.
- Walker, B., A. Kinzig, and J. Langridge. 1999. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* 2: 95–113.
- Wang, R., J. A. Dearing, P. G. Langdon, E. Zhang, X. Yang, V. Dakos, and M. Scheffer. 2012a. Flickering gives early warning signals of a critical transition to a eutrophic lake state. *Nature* 492:419–422.
- Wang, S., J. Zhang, and A. B. Lawson. 2012b. A Bayesian normal mixture accelerated failure time spatial model and its application to prostate cancer. *Statistical Methods in Medical Research*. <http://dx.doi.org/10.1177/0962280212466189>
- Wardwell, D., and C. R. Allen. 2009. Variability in population abundance is associated with thresholds between scaling regimes. *Ecology and Society* 14:42.
- Wardwell, D. A., C. R. Allen, G. D. Peterson, and A. J. Tyre. 2008. A test of the cross-scale resilience model: functional richness in Mediterranean-climate ecosystems. *Ecological Complexity* 5:165–182.
- Warwick, R. M., S. L. Dashfield, and P. J. Somerfield. 2006. The integral structure of a benthic infaunal assemblage. *Journal of Experimental Marine Biology and Ecology* 330: 12–18.
- Wheatley, M., and C. Johnson. 2009. Factors limiting our understanding of ecological scale. *Ecological Complexity* 6: 150–159.
- White, E. P., S. K. M. Ernest, A. J. Kerkhoff, and B. J. Enquist. 2007. Relationships between body size and abundance in ecology. *Trends in Ecology and Evolution* 22:323–330.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385–397.
- Woodward, G., B. Ebenman, M. Emmerson, J. M. Montoya, J. M. Olesen, A. Valido, and P. H. Warren. 2005. Body size in ecological networks. *Trends in Ecology and Evolution* 20: 402–409.
- Wu, J., and H. Li. 2006. Perspectives and methods of scaling. Pages 17–44 in J. Wu, K. B. Jones, H. Li, and O. Loucks, editors. *Scaling and uncertainty analysis in ecology*. Springer, Dordrecht, The Netherlands.
- Xu, L., T. Hanson, E. Bedrick, and C. Restrepo. 2010. Hypothesis tests on mixture model components with applications in ecology and agriculture. *Journal of Agricultural, Biological, and Environmental Statistics* 15:308–326.
- Yvon-Durocher, G., J. Reiss, J. Blanchard, B. Ebenman, D. M. Perkins, D. C. Reuman, A. Thierry, G. Woodward, and O. L. Petchey. 2011. Across ecosystem comparisons of size structure: methods, approaches and prospects. *Oikos* 120: 550–563.

SUPPLEMENTAL MATERIAL

Appendix A

Table comparing hierarchy theory, panarchy theory, scale domains, and power laws (*Ecological Archives* E095-055-A1).

Appendix B

Table describing different methods used to examine the shape of body size distributions (*Ecological Archives* E095-055-A2).

Habitat structure and body size distributions: cross-ecosystem comparison for taxa with determinate and indeterminate growth

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Habitat structure across multiple spatial and temporal scales has been proposed as a key driver of body size distributions for associated communities. Thus, understanding the relationship between habitat and body size is fundamental to developing predictions regarding the influence of habitat change on animal communities. Much of the work assessing the relationship between habitat structure and body size distributions has focused on terrestrial taxa with determinate growth, and has primarily analysed discontinuities (gaps) in the distribution of species mean sizes (species size relationships or SSRs). The suitability of this approach for taxa with indeterminate growth has yet to be determined. We provide a cross-ecosystem comparison of bird (determinate growth) and fish (indeterminate growth) body mass distributions using four independent data sets. We evaluate three size distribution indices: SSRs, species size–density relationships (SSDRs) and individual size–density relationships (ISDRs), and two types of analysis: looking for either discontinuities or abundance patterns and multi-modality in the distributions. To assess the respective suitability of these three indices and two analytical approaches for understanding habitat–size relationships in different ecosystems, we compare their ability to differentiate bird or fish communities found within contrasting habitat conditions. All three indices of body size distribution are useful for examining the relationship between cross-scale patterns of habitat structure and size for species with determinate growth, such as birds. In contrast, for species with indeterminate growth such as fish, the relationship between habitat structure and body size may be masked when using mean summary metrics, and thus individual-level data (ISDRs) are more useful. Furthermore, ISDRs, which have traditionally been used to study aquatic systems, present a potentially useful common currency for comparing body size distributions across terrestrial and aquatic ecosystems.

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