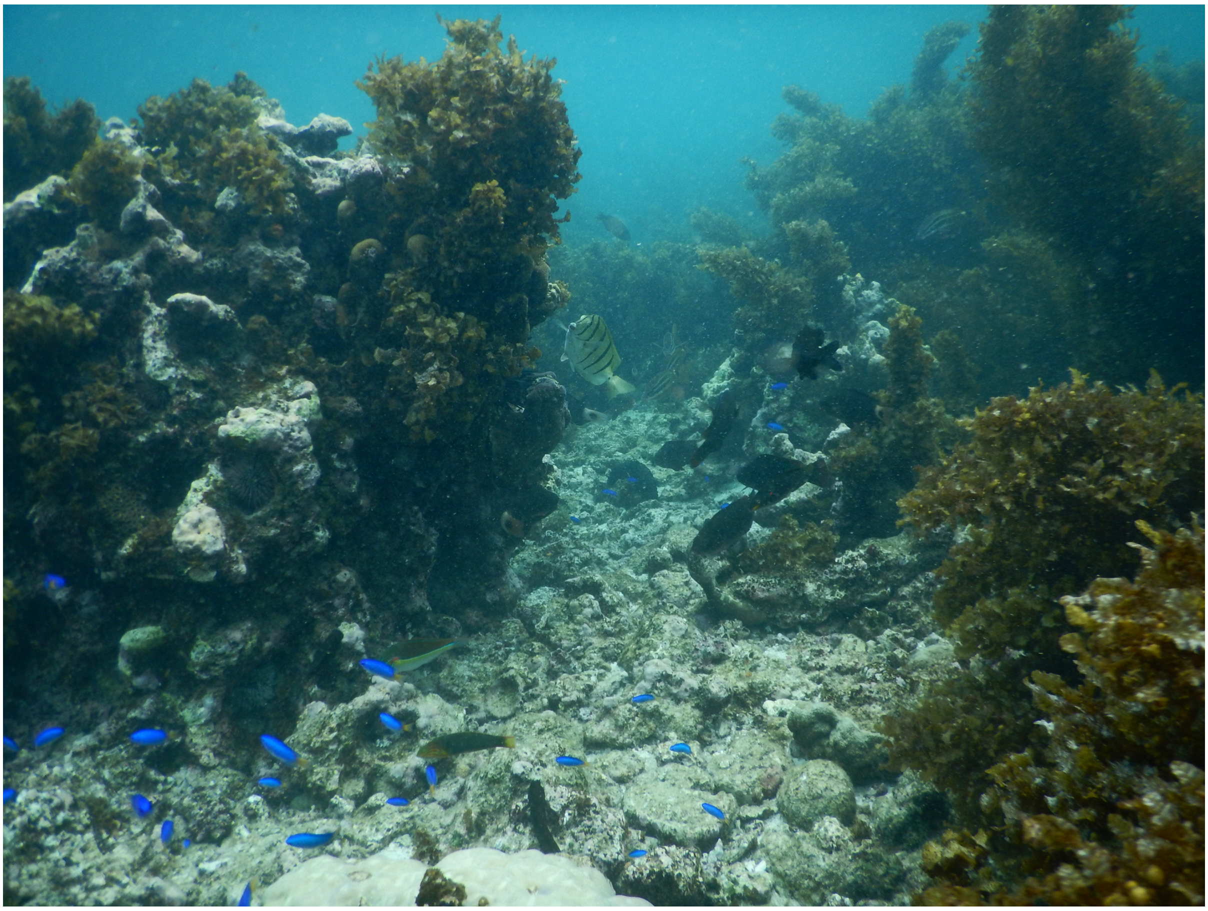
Right place, right height: habitat connectivity and condition underpin fish community structure across coastal seascapes



Joshua van Lier

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Declaration

This thesis is my original work. I am the lead author on all the data-based chapters presented within this thesis, which involved leading the conception, experimental design, data collection and analysis, and writing each chapter. All published chapters are co-authored with my principal supervisor Christopher Fulton, who contributed to study conception, experimental design, funding, data collection, assistance with data analysis and constructive comments on early drafts of each manuscript. David Harasti was a co-author on chapter 2, having provided funding and, along with Mae Noble and Roger Laird, also assisted in data collection and manuscript feedback. Lucy Wenger is a co-author on chapters 3 and 4 for providing assistance in data collection and manuscript feedback. Shaun Wilson and Martial Depczynski, the other members of my supervisory panel, are co-authors on chapters 3, 4 and 5 for contributing to experimental conception, design and manuscript feedback. Mae Noble, Paul Tinkler, Thomas Holmes and Maria Eggertsen are also co-authors on chapter 5 for contemporary and historic data collection. Given the collaborative nature of the data chapters, and that they were/are prepared for publication in peer-reviewed journals, I use the pronoun ‘we’ to represent all the co-authors. Of the chapters that are published, the text presented within this thesis is the pre-publication version of the manuscripts, with adjustments made as necessary for formatting from the published versions. Ethics approval was provided by the Australian National University Animal Ethics Committee, protocols A2016/03 and A2018/05. No part of this thesis has been submitted for a previous degree.

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Arohanui, whakawhetai ki a koe me kia ora.

Abstract

Community ecology seeks to understand the variety of factors that influence biodiversity. Early work has recognised that local habitat quality is important (e.g., niche theory), but so is spatial context (e.g., Island Biogeography Theory). In my PhD, I build upon these concepts in marine biomes by combining underwater surveys with Geographic Information Systems to explore how habitat quality and spatial context shapes fish community structure and function in a variety of soft-structure coastal habitats.

Local-scale aspects of habitat quality, like three-dimensional hard complexity, are recognised as key predictors of fish diversity. However, relatively little is known about the effects of soft-structure habitat complexity on fish diversity. Using a best-subsets modelling approach and data from three temperate mesohabitats, I assessed what aspects of soft structure best predicted differences in reef fish community composition. I found that high levels of canopy cover and height were key predictors in supporting a diverse fish community across mesohabitats. Thus, it is important that habitat quality in soft-structure environments account for variation across three dimensions.

In addition to local habitat quality, the spatial context of an area within the wider seascape mosaic can influence patterns of diversity. Using a patch network of tropical macroalgal meadows that varied in size and distance to a coral reef, I assessed the relative importance of local patch quality and spatial context for predicting the diversity and structure of the local fish community. Multivariate analysis showed the relative importance of these variables differed depending on a taxonomic or functional focus of fish diversity. Most importantly, when species identity was explicitly examined, the placement of macroalgal patches within 500m of a coral reef was among the key predictors, along with hard complexity and soft canopy height.

Many accounts of local habitat quality as a predictor of diversity are based on observational studies, such as the results I report on above. Therefore, I used an experimental unseasonal reduction of tropical macroalgal canopy height to explore the consequences of unseasonal canopy loss on resident fishes over short-to-long time-scales. Despite these meadows undergoing a similar, seasonal change in canopy structure, experimental sites, relative to nearby reference sites, had significant decreases in fish species richness and density within five days of canopy height reduction which was coupled with a short-term increase in the density of higher-order carnivores. Some of these effects were still evident two years later, despite an overall recovery in canopy structure.

Habitat variation across multiple-scales has often shown to influence patterns of diversity, but their effects on ecological processes are less well known. Predators, through regulation of prey populations, may structure ecological communities via top-down effects. Therefore, I explored the behavioural ecology of a common mesopredatory fish (*Thalassoma lunare*) to understand how local habitat quality and spatial context may influence patterns of predation. While *T. lunare* showed indications of habitat preference in early life history stages, adult fish were habitat generalists who varied their foraging behaviour according to spatial context. Specifically, individuals in isolated patches would forage across significantly smaller distances than those in well-connected patches, and may therefore contribute to differing local predation pressures under different spatial contexts.

My work shows that a holistic, multi-scale approach is needed to understand ecological patterns and processes in marine biomes. I discuss how these insights add to our understanding of marine ecology, and can inform management and design of marine reserves by identifying well connected and structurally complex areas of the seascape to facilitate movement between these high quality areas.

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Chapter 1

General Introduction

Community diversity and structure across multiple scales

Understanding what drives the diversity and structure of ecological communities over space and time is the fundamental goal of community ecology. Early attempts to unravel the complicated processes underpinning the presence or absence of species in a community invoked local-scale explanations, which was best epitomised by niche theory (Grinnell 1917; Hutchinson 1957). This suggested that a larger diversity of localised habitats across a number of size-scales should allow for a greater number of species to co-exist (Hutchinson 1957; Hardin 1960). While the amount of available habitat types play a key role in the diversity and structure of ecological communities (Anderson and Millar 2004; Cromsigt et al. 2009), the variations in habitat through space and time are also important for regulating key processes. The three-dimensional structure of a habitat being particularly important in opening up niche space by providing variation in environmental conditions (e.g., light and moisture regimes; Kerry and Bellwood 2015; Cárdenas et al. 2016) or augmenting biotic interactions (e.g., locations for predatory ambush or prey refugia; Almany 2004; Horinouchi et al. 2009; Hempson et al. 2017). Such structural variation may therefore lead to differences in the local habitat condition with which species may respond to in a variety of ways, resulting in fundamentally different local communities expressed in the same broad habitat type. While insightful on a local-scale, these approaches are limited in that they do not account for broad-scale, spatially explicit complex life-history processes that connect observed local-scale events in a heterogeneous environment, such as dispersal, diel movements and migration (Nathan 2006; Green et al. 2015). Thus, recognizing local scale patterns and processes in a spatial context is critical for understanding community assembly and the effective conservation of species and ecosystems.

One of the first attempts to formally theorise spatial mechanisms underpinning the diversity of species in heterogeneous patch-habitats was put forward by Island Biogeography Theory (IBT; MacArthur and Wilson 1963; Simberloff and Wilson 1970). Based on theory and empirical evidence of terrestrial insects colonising mangrove islands, IBT posits that climax levels of species richness within an ecological 'island' are a direct consequence of island size and isolation. Applied to existing patchy habitats, and contiguous habitats subject to fragmentation, this concept was utilised in early design of conservation reserves and other spatial management approaches (Diamond 1975). However, while conceptually useful, IBT is limited in applicability as it did not consider aspects such as local habitat condition, or the influence of surrounding landscape mosaic-factors on a local patch, which have emerged as important to the dynamics of meta-communities occupying patchy environments (Connell 1978; Fahrig and Jonsen 1998; Lim et al. 2016). Accordingly, the debate on patch-habitat effects has advanced on IBT, such as the more recent Habitat Amount Hypothesis, which suggests that the collective habitat area within a region (i.e. habitat summed across one or more connected patches) may be the driving factor in community structure (Fahrig 2013).

The conceptual framework provided by IBT has provided the basis for paradigm shifts in our understanding of community assembly and ecological processes (e.g., landscape ecology, metacommunity theory; Turner 1989; Leibold et al. 2004; Turner 2005), that combines these disparately scaled aspects to gain a fuller understanding of community patterns and processes. Indeed, recent studies that have been able to explain a high level of community variation are those that have included both aspects of local habitat condition and broader habitat context (Olds et al. 2012; Hanski et al. 2017; Michael et al. 2017). For example, Thomas et al. (2001) showed that local habitat condition, determined by variation in flora height, along with the configuration of desirable patch-habitats in the landscape, was critical for the continued persistence of several butterfly species. It is evident then, that habitat should be viewed holistically across multiple scales in time and space. Improved knowledge of species' multi-scale responses to variations in habitat condition and context can help us predict their responses to changing conditions, plan effective conservation strategies, and, given the goals of community ecology, further ecological theory.

The rise of seascape ecology

Recognition is growing among marine ecologists that the arrangement and condition of patch-habitats can influence patterns of diversity, distribution and abundance in marine species. Fishes often use a variety of mesohabitats in the course of their diel activities (e.g., foraging; Davis et al. 2014), and throughout their life-cycle (e.g., ontogenetic shifts out of nursery habitats; Nagelkerken et al. 2000). Historically, marine ecologists have often focused on finer-scale microhabitat characteristics (e.g., habitat complexity) when exploring habitat influences on patterns of biodiversity (e.g., Öhman and Rajasuriya 1998, Gratwicke and Speight 2005, Rogers et al. 2014). However, emerging research into the effects of broader-scale characteristics such as patch shape or connectivity is also highlighting these as potentially important predictors of marine community structure and function (Boström et al. 2011; Hitt et al. 2011; Olds et al. 2012; Hensgen et al. 2014; Sawayama et al. 2015). Such awareness has come from applying the spatially explicit approaches of landscape ecology to marine biomes.

Theoretical frameworks provided by landscape ecology applications in terrestrial systems (e.g., Turner 1989, 2005, Dunning et al. 1992, Leibold et al. 2004), can provide key insights into the causes and consequences of heterogeneity in marine seascapes (Bartlett and Carter 1991; Robbins and Bell 1994). These approaches examine how patch-level spatial traits (e.g., shape, area etc.), inter-patch arrangement (e.g., proximity, isolation etc.) and biotic dispersal potential influence the assembly of individuals and species throughout a patch-habitat network (Boström et al. 2011; Heino et al. 2015). How these spatially contextual theories and approaches, developed in terrestrial settings, extend to the patterns and processes in fundamentally different marine biomes (e.g., common bi-partite life history of organisms, absolute three-dimensional nature of the environment and stronger influence of physical forces) is an emerging field.

Multi-scale fish-habitat associations

Coastal marine environments are often comprised of a mosaic of mesohabitat types, such as hard coral, seagrass and macroalgae-dominated patches embedded within a low-complexity background of soft-sediment habitat. Fishes tend to occur within each mesohabitat type, often according to their habitat preferences and level of specialisation as adults (Wilson et al. 2010; Fitzpatrick et al. 2012; Brooker et al. 2014), and/or juveniles (Nagelkerken et al. 2000; Kimirei et al. 2013). Other fishes who are more habitat generalists can occupy several different mesohabitats types and/or roam through the seascape (Morton and Gladstone 2011; Davis et al. 2014). As such, habitat selectivity can be a key mechanism in shaping and maintaining differences in fish community structure within and between patch mesohabitats.

While relatively nascent, the field of seascape ecology has started to change our understanding of how spatial context can influence patterns of marine community structure and function (Boström et al. 2011). For example, the size of patch area has previously been an effective predictor of coral-associated fish diversity and abundance (Acosta and Robertson

2002; Chittaro 2002), yet recent analyses that include metrics of patch context (e.g., connectivity to other habitats) have found an area effect to be negligible (Grober-Dunsmore et al. 2007). Additionally, the ubiquity of patch area as a predictor of fish diversity appears to be mesohabitat-specific, with Boström et al. (2011) highlighting patch area is generally insignificant for predicting fish diversity in soft-structure seagrass mesohabitats. Furthermore, traditional drivers of coral-associated fish community structure, such as live coral cover and complexity (Pratchett et al. 2008; Graham and Nash 2013) may be augmented or overridden by the proximity of nearby mangrove and seagrass mesohabitats in the surrounding seascape (Olds et al. 2012). Results such as these highlight the need for studies that account for variation in habitat across multiple scales, taxa and ecosystems (Boström et al. 2011; Fisher et al. 2011a; Fisher et al. 2011b).

To understand how these local-scale variables combine with broader-scale spatial aspects to influence fish diversity and community structure across the seascape mosaic, a greater understanding is also needed about local habitat quality in under-studied systems. While marine ecology has had a strong focus on local-scale fish-habitat interactions, such studies have disproportionately favoured certain mesohabitats (Fig. 1.1), with their broad applicability being called into question (Fisher et al. 2011b). This means that while we may have a solid understanding of the mechanisms that underpin fish diversity and community structure in ecosystems such as coral reefs (Pratchett et al. 2008; Graham and Nash 2013), our knowledge in other prominent coastal systems is more rudimentary (Fig. 1.1). Soft structure mesohabitats, those formed by less-rigid habitat forming organisms (e.g., macroalgae, soft coral etc.), are ubiquitous to polar, temperate and tropical systems that cover proportionately vast areas of coastlines (e.g., Kobryn et al. 2013). There is strong evidence to suggest that they provide a range of ecosystem functions and services, such as

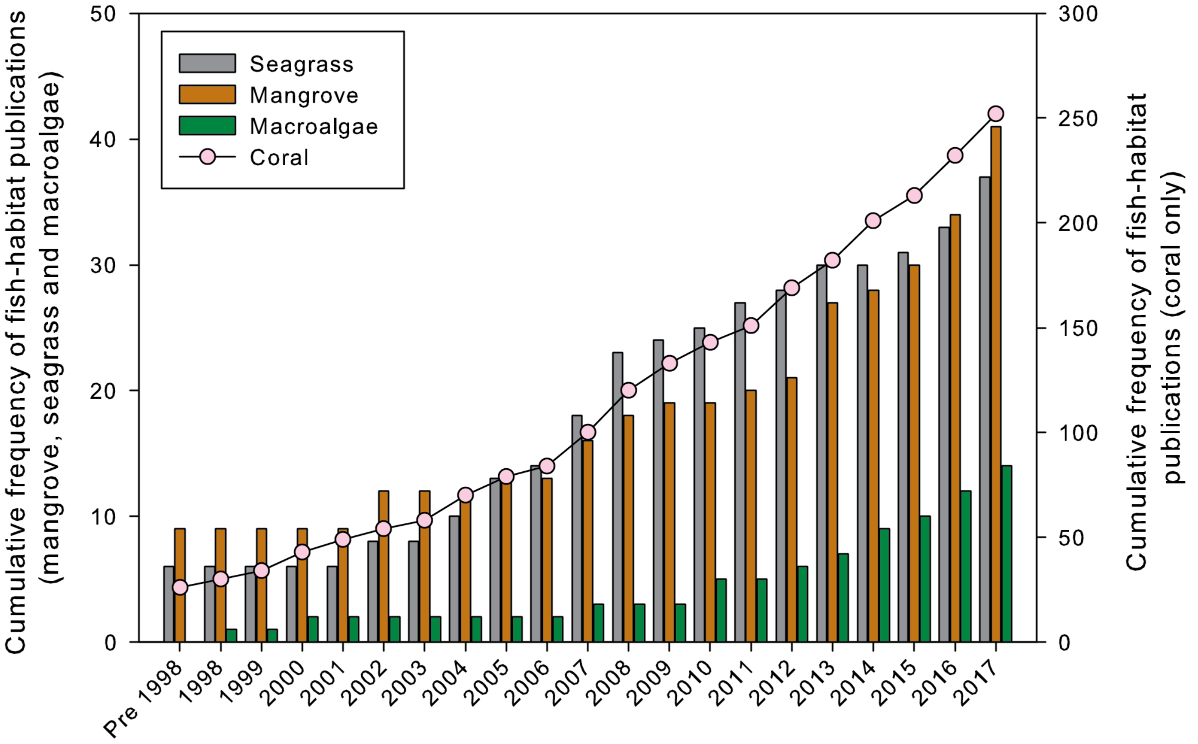

Figure 1.1. Cumulative number of original research papers on fish-habitat interactions across four major tropical mesohabitats. Literature search was conducted in Scopus and results were evaluated for relevance.

nursery habitat (Heck Jr et al. 2003; Tano et al. 2017), food resources (Tano et al. 2016; Corry et al. 2018), and sediment stabilisation (Fonseca 1989; Bell 2008). Therefore, how three-dimensional structure in these soft-structure environments, set amongst different spatial contexts, affects fish diversity is a current knowledge gap that needs to be addressed. Furthermore, information on these topics may be helpful in guiding the success of ecosystem-level approaches to the conservation and management of coastal systems.

Thesis outline

In this thesis, I used *in situ* survey techniques combined with Geographic Information Systems (GIS) to investigate the community structure and behaviour of reef fishes relative to habitat quality at a range of spatial scales. I explored these trends and mechanisms in several under-represented biomes - sponge gardens, soft coral beds and macroalgal meadows. By combining traditional surveys of local-habitat condition with novel explorations of broad-scale spatial aspects, my thesis aims to provide a more holistic understanding of the complex processes underlying coastal fish diversity and community structure. Below, I outline the four different components of my PhD research, divided into four self-contained data chapters.

Local-scale aspects of habitat condition have historically provided science with strong predictors to explain patterns in fish abundance diversity (e.g., Horinouchi 2007; Wilson et al. 2014; Harasti 2016) so understanding relationships at this scale is vital to a broader, multi-scale comprehension of community structure. However, such studies have often disproportionately targeted a narrow range of tropical mesohabitat types (e.g., coral reefs) and not always accounted for the full three-dimensional structure present (i.e., tending to focus on a two-dimensional view of habitat cover/composition). In **Chapter 2**, "*Importance of soft canopy structure for labrid fishes in estuarine mesohabitats*", I investigate differences in community structure across three under-studied, but ecologically important, temperate mesohabitats (sponge, soft coral and macroalgae) that typically occur in a patchy estuarine mosaic. In doing so, I also quantify the importance of different values of three-dimensional structure, seeking to identify metrics common across mesohabitat type.

Recent studies in tropical macroalgae have identified several important aspects of local-scale habitat condition useful in predicting patterns of fish diversity and abundance (Wilson et al. 2014; Lim et al. 2016). However, such studies are yet to incorporate the multi-scale framework of seascape ecology. In **Chapter 3**, "*Habitat connectivity and complexity underpin fish community structure across a tropical seascape*", I provide the first spatially-explicit examination of variation in tropical macroalgae-associated fishes to explore whether improved connectivity between mesohabitat types changes patterns in local fish diversity. Furthermore, by using a best-subsets model selection process I investigate the relative importance of these multi-scale variables across different levels of taxonomic, functional and ontogenetic resolution. Such analysis allows for a more nuanced understanding of when and where to best apply these multi-scale variables in predicting patterns of fish diversity.

The majority of local-scale fish-habitat interaction studies are based on observational work. However, these studies are often confounded by local environmental conditions and there is a need for manipulative experiments to help tease apart the underlying drivers of abundance and diversity. For example, results in chapters 2 and 3, along with previous field surveys at Ningaloo (Lim et al. 2016; Wenger et al. 2018), indicate fish abundance correlates positively with canopy height. In **Chapter 4**, "*Unseasonal reductions in macroalgal canopy height have lasting effects on tropical fish communities*", I experimentally investigate the influence of macroalgae canopy height as a direct driver while holding other potential predictors constant. In doing so, I am able to quantify the response of fish diversity, abundance and community structure to an acute disturbance over short-to-long time-scales- which provides critical knowledge for conservation and management of this climatically sensitive mesohabitat.

While there have been a number of studies exploring patterns of species distribution and community structure moderated by habitat across multiple spatial scales, relatively few have examined ecological processes and behaviour in this context. Predation is an important ecological process that underpins community structure in coastal marine environments (Hixon 2015), with some indication that this can be altered by differences in local habitat composition (Almany 2004; Horinouchi et al. 2009). In **Chapter 5**, "*Foraging across seascapes: shifting patterns of habitat association and foraging behaviour in a mesopredatory reef fish*" I use the fish *Thalassoma lunare* as a model species to explore the variation in these multi-scale aspects of habitat and their consequences on its distribution and foraging patterns through space and time in a tropical macroalgae meadow. Overall, and exemplified by this final data chapter, my thesis demonstrates the importance of taking a holistic view to understand ecological pattern and process; that, in understanding what comprises a quality habitat for a community, one must account for variation across multiple spatial and temporal scales.

Chapter 2

Importance of soft canopy structure for labrid fish communities in estuarine mesohabitats

Photo credit: David Harasti

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Abstract

Hard structural complexity is widely recognised as important for assessing fish habitat quality, but our understanding of the importance of soft habitat microstructure for temperate marine fishes is less developed. We used best-subsets modelling of underwater surveys in sponge, soft coral and macroalgae mesohabitats within a temperate estuary to assess what measures of soft habitat structure best predicted differences in wrasse (family: Labridae) fish community composition. We found significant differences in the labrid fish community among and within mesohabitat types were best explained by a combination of percent canopy cover and soft canopy height, with increased canopy height being correlated with increased fish abundance and species richness. Sponge and macroalgae mesohabitats emerged as particularly important, but vulnerable habitats for a diversity of fishes unique to these mesohabitat types. Ultimately, mesohabitats with high percent canopy cover and height appear to be particularly valuable for supporting estuarine fish communities. Due to this importance, and the potential for decadal-scale recovery times of sponge canopies, we believe patches with complex canopy structure should warrant special protection from documented local threats such as anchor and fishing damage.

Introduction

Habitat availability plays a key role in shaping the diversity and abundance of fishes across a range of spatial and temporal scales (Anderson and Millar 2004; Morton and Gladstone 2011; Wilson et al. 2006). At relatively coarse scales, mesohabitats (which we define here as habitat patches of similar benthic composition embeded within a sand matrix) often have an overarching role in structuring the fish communtiy, such as the distinct fish species that occur within macroalgae versus coral-dominated mesohabitats, or kelp forests versus rocky barrens (Holbrook et al. 1990b; Wilson et al. 2010). Microhabitat structure within mesohabitats is also of key importance, particularly for habitat specialists like coral reef fishes who utilise a small suite of preferred coral species (e.g., Munday et al. 1997; Pratchett et al. 2012). Close fish-habitat relationships, such as these, mean that habitat loss can precipitate profound shifts in fish abundance and diversity (Munday 2004; Wilson et al. 2008). Consequently, we must identify the key aspects of habitat structure that underpin fish communities if we are to understand and manage fish responses to habitat change.

In addition to habitat availability, structural complexity and variation is seen as a key factor in the capacity for habitats to sustain large and/or diverse fish populations (Gratwicke and Speight 2005; Graham and Nash 2013). Indeed, niche theory suggests that a complexity and abundance of habitat types should allow for coexistince of a greater number of individuals and species within a given area via niche partitioning (Hardin 1960; Hortal et al. 2009). Structural complexity in fish habitats can be captured in a number of ways, and is typically characterised as percentage cover of different functional habitat-forming groups, and/or a measure of vertical relief (e.g. Wilson et al. 2007). However, these measures are often of hard complexity, and may overlook the importance of soft structure as a measure of habitat quality (Nash et al. 2012). Indeed, a recent study of macroalgae-dependent parrotfishes found that a vertical measure of soft seaweed canopy height provided a key predictor for seasonal shifts in fish abundance over both small and large spatial scales (Lim et al. 2016). However, there is a paucity of evidence for the relevance of soft habitat strutucture in ecologically important temperate marine habitats, such as estuarine sponge (Bell 2008), macroalgae (Fulton et al. 2016) and soft coral (Poulos et al. 2013). In one of the few examples, Harasti et al. (2014) found that individuals of the seahorse *Hippocampus whitei* showed a significant preference for soft coral colonies greater than 40 centimetres in height, while displaying direct avoidance of colonies under 20 centimetres. With the exception of seagrass habitats (Horinouchi 2007), temperate marine studies to date have largely illustrated links between three-dimensional hard complexity, especially vertical relief, and patterns of reef fish diversity and abundance (Wellenreuther et al. 2008; Kutti et al. 2015).

Using wrasses (family Labridae) as a model study group, we aimed to determine: (1) whether distinct labrid communities are associated with each of three common mesohabitat types within a temperate estuary, and (2) what measures of soft habitat structure best predict the differences in fish community composition among and within these mesohabitat types. Wrasses were chosen as a model study group because of their status as one of the most speciose fish families which can provide an effective surrogate for temperate reef fish communities due to their wide diversity of trophic groups, body sizes and movement patterns (Fulton and Bellwood 2002; Kulbicki et al. 2005; Malcolm and Smith 2010; Kramer et al. 2015). Our focal habitats were the three common marine mesohabitat types of (1) sponge, (2) soft coral, and (3) canopy-forming macroalgae, which are found along temperate coastlines around the world.

2. Material and Methods

2.1. Study sites & underwater surveys

Surveys were conducted during March 2015 within the Port Stephens estuary located within the Port Stephens-Great Lakes Marine Park, New South Wales, Australia (32° 42' 52.20" S, 152° 09' 06.96" E). Our survey sites were balanced across Sanctuary (no-take) and Habitat Protection (fishing allowed) Zones, and encompassed three prominent mesohabitat types within the estuary that are most abundant and diverse along the southern shoreline of the Port Stephens estuary, as this is where tidal current and water depths are greatest (Davis et al. 2015; Poulos et al. 2015).

Fourteen patch-habitat sites separated by a minimum of 180 metres were surveyed, with each dominated by either sponge (n = 6, mean depth ± SE = 11.8 ± 0.6m), soft coral (n = 4, mean depth = 12.1 ± 0.8m) or macroalgae (n = 4, mean depth = 6.4 ± 0.2m) that was embedded within a low-relief abiotic matrix of <2 centimetre deep sand over rocky substrate (Fig. 2.1). Within each site, a team of four divers working at a minimum of 10 metres apart employed the stationary cylinder survey method of Noble et al. (2013), with replicate survey cylinders haphazardly placed within each patch so that they were a minimum of 10 metres apart and at least 5 metres from the patch edge. For each replicate, the diver ran out a 5 metre transect tape that both indicated the diameter of the survey area and provided the line transect for the habitat assessment. Following a 3-minute wait for the fish to recover from the tape laying, the diver then recorded all conspicuous labrid fishes within the bounds of the cylinder by scanning for large mobile fishes first, followed by a detailed crawl survey for benthic labrid fishes located within the habitat matrix. Habitat surveys were then conducted along the 5 metre line transect to record the distance occupied by each microhabitat category

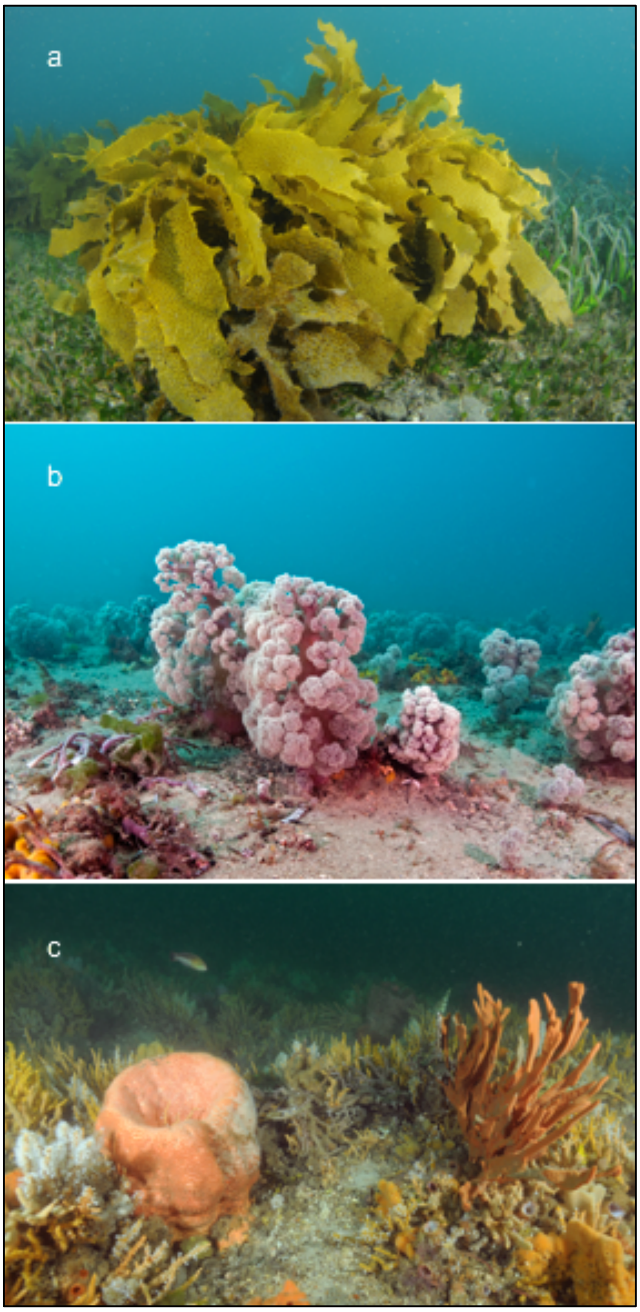

Figure 2.1 Examples of canopy structure within (a) sponge, (b) soft coral and (c) macroalgae mesohabitats within the Port Stephens estuary, New South Wales. Photos: D. Harasti.

and the undisturbed vertical height of the soft canopy at 1 metre intervals (starting from 0 metres, n = 6 per transect), both to the nearest centimetre. Microhabitat categories included genera of canopy-forming macroalgae (*Ecklonia*, *Sargassum*), pyurids, soft coral (*Dendronephthya*, *Carijoa*), seagrass (*Halophila*, *Posidonia*) and echinoderms, sponge morphological groups (following Boury-Esnault and Rutzler 1997), as well as foliose and turfing groups of macroalgae (5 - 30 cm high and <5 cm high, respectively), bryozoans, and sand. Two sets of these surveys were made by each diver in non-overlapping cylinders (separated by a minimum of 10 metres) to yield a total of 8 replicate surveys per site. Pre-survey dives were used to ensure that all four survey divers were familiar with the labrid species in the mesohabitats, and that they were all conducting the fish and habitat surveys in the same systematic fashion.

2.2. Data analysis

Raw habitat data were collated into eight measures that included percentage cover (converted from distances recorded on 5 metre line transects) of the three canopy-forming groups (all sponges, all soft coral, all *Ecklonia* + *Sargassum*), understory macroalgae, other understory components (seagrass, echinoderms, pyurids, bryozoans), vertical canopy height, habitat richness, and habitat evenness. Habitat richness was calculated as the total number of different habitat types (including all the separate genera and sponge growth forms) present in a given replicate. Habitat evenness, which is a measure of equitability in the amount of different habitat components present, was calculated using a modified version of the Shannon-Weaver Index (H’) as

$$\mathrm{Habitat\ Evenness} = \frac{-\Sigma_{\mathrm{i}=1}^{\mathrm{R}} \mathrm{p_i} \ln{(\mathrm{p_i})}}{\ln \mathrm{R}}$$

where R is the number of habitat components in a given replicate, and p_i is the proportional cover of the *i*th habitat component (Mulder et al. 2004). This provides a proportion in which values closer to 1 are considered to be more evenly distributed in their benthic composition, while values closer to 0 are mostly dominated by a single benthic component. All eight habitat components were then normalised to bring variables of differing metrics to a notionally common scale, and assembled into a resemblance matrix using Euclidean distance, upon which a one-way analysis of similarity (ANOSIM) was used to test for differences in benthic composition among the *a priori* mesohabitat types (Clarke & Gorley 2006).

From a total of 20 labrid species encountered in the surveys, four species (*Choerodon cephalotes*, *Hologymnosus annulatus*, *Labroides dimidiatus* and *Stethojulis strigiventer*) had fewer than three occurrences across the 112 replicates, and so were excluded from further analysis (following Anderson et al. 2008). Raw fish densities for the remaining species across all replicate surveys were then assembled into a resemblance matrix using the zero-modified Bray-Curtis measure of similarity (Clarke and Gorley et al. 2006), upon which a two-way ANOSIM was used to test for differences in fish community composition for the random factor of site (n = 14) which was nested within the fixed factor of mesohabitat (3 levels). A Canonical Analysis of Principal Coordinates (CAP) and leave-one-out procedure was then used in combination with a similarity percentages test (SIMPER) to explore key species that underpinned differences in fish community structure among mesohabitat types (Anderson et al. 2008). Best-subsets model selection was used to explore which combination of habitat variables may best predict variations in fish community composition (Burnham and Anderson 2002). In the first instance, we explored this for the entire dataset of all mesohabitat types to explore cross-biome predictors. We used multivariate distance-based linear models (DistLM) and the Akaike Information Criterion corrected for finite samples (AICc) to consider all possible combinations of habitat predictor variables (Anderson et al. 2008). The most parsimonious model was chosen as that which had the fewest predictor variables within 2 AICc units of the top model (lowest AICc value), following Burnham and Anderson (2002). The relative importance of each habitat predictor was further explored using the sum of weighted AICc scores for all models in which that variable occurred (Burnham and Anderson 2002). This procedure was then repeated separately for each of the three mesohabitat types. Given the prominence of canopy height in the outcomes of these analyses, we explored bivariate relationships between canopy height and both fish species richness and density across all replicates. All multivariate analyses were conducted in PRIMER (version 6.1.12) with PERMANOVA+ (Anderson et al. 2008). Bivariate model fitting was made in SigmaPlot (version 11).

Results

Habitat structure among and within mesohabitats

Significant variations in multivariate habitat structure were apparent among mesohabitat types (Global R = 0.715, $p < 0.01$) and sites (Global R = 0.118, $p < 0.05$). While canopy-forming organisms were the dominant biogenic microhabitat in terms of percent cover in the respective mesohabitat types, this dominance ranged from over half (canopy macroalgae) to around a quarter (sponge) of the total benthic cover (Fig. 2.2a); the abiotic sand matrix was the other major component (Fig. 2.2a). Macroalgae and soft coral had higher canopies than sponge (Fig. 2.2b), while habitat richness and evenness was higher in sponge than in either soft coral or macroalgae (Fig. 2.2c,d).

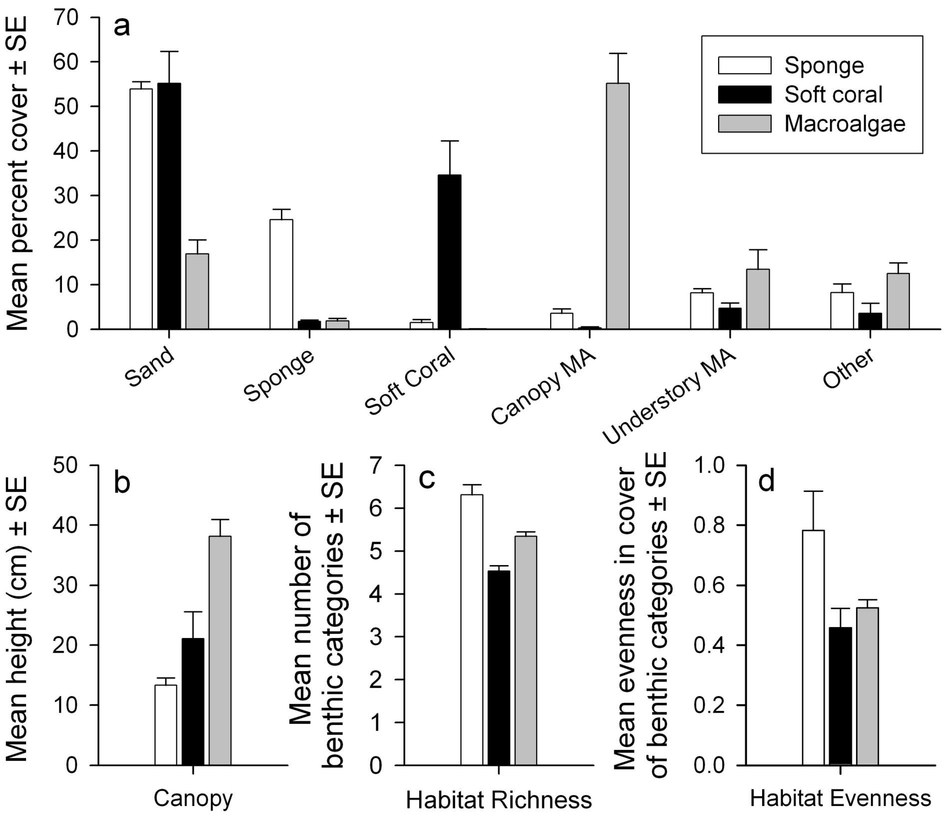

Figure 2.2. Habitat structure within sponge, soft coral and macroalgae mesohabitats within the Port Stephens estuary, New South Wales in terms of (a) percent cover and (b) vertical canopy height, as well as (c) richness, and (d) evenness of different benthic habitat categories. MA = macroalgae; SE = standard error of the mean.

Fish community composition

From a total of 20 labrid species recorded across all replicates, species richness was highest in sponge and macroalgae mesohabitats with 16 species each (Fig 2.3). Of these, 12 were shared between the two mesohabitats with 2 being unique to sponge and 4 being unique to macroalgae. Soft coral had the lowest species richness with only 10 species recorded and no unique species (Fig. 2.3). Significant differences were apparent in fish community composition among sites (Global R = 0.284, $p < 0.05$) and mesohabitats (Global R = 0.338, $p < 0.05$), with pairwise differences evident for sponge-macroalgae (R = 0.333, $p < 0.05$) and macroalgae-soft coral (R = 0.799, $p < 0.05$), but not sponge-soft coral (R = 0.042, p = 0.24). Labrid species

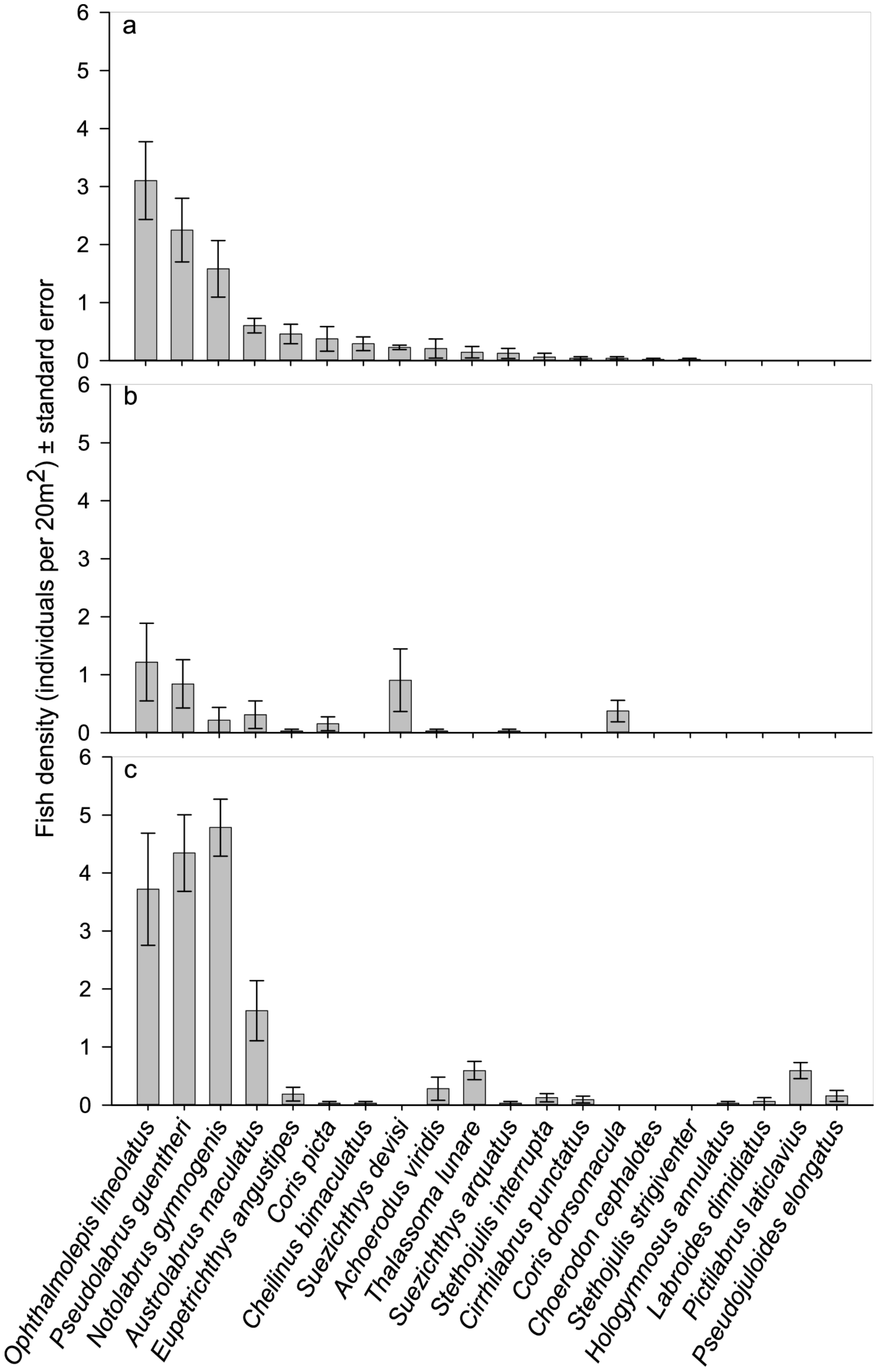

Figure 2.3. Mean density of labrid species encountered within (a) sponge, (b) soft coral and (c) macroalgae mesohabitats at Port Stephens, New South Wales.

associated with soft coral were a smaller subset of the sponge fish community. There was also some overlap in fish community composition among sponge and macroalgae mesohabitats, but a clear distinction between macroalgal- and soft coral-associated labrid communities (Fig. 2.4, Table 2.1). SIMPER revealed that *Ophthalmolepis lineolatus* (sponge = 48.%, macroalgae 24.6%), *Pseudolabrus guentheri* (sponge = 24.7%, macroalgae = 34.6%) and *Notolabrus gymnogenis* (sponge = 17.3%, macroalgae = 31.1%) were the most influential in the sponge-associated and macroalgae-associated fish communities, while *O. lineolatus* (42.1%), *Suezichthys devisi* (28.4%) and *P. guentheri* (22.6%) characterised the soft coral fish community. Aside from the three fish species that were particularly common across all mesohabitat types (*O. lineolatus, P. guentheri* and *N. gymnogenis*), other species tended to show a strong abundance bias towards one mesohabitat type. For example, *P. laticlavius* and *Pseudojuloides elongatus* occurred exclusively within macroalgae, while *S. devisi* occurred exclusively within soft coral (Fig. 2.3).

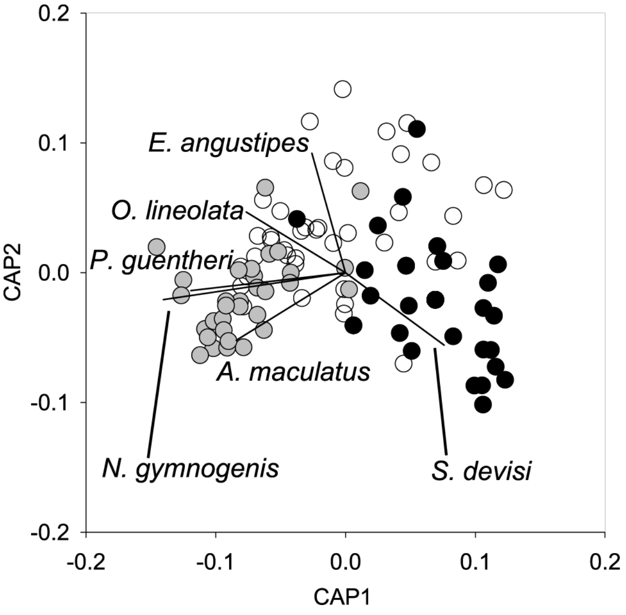

Figure 2.4. Canonical analysis of principal (CAP) coordinates for the all fishes recorded in sponge (white circles), soft coral (black), and macroalgae (grey) mesohabitats. Vectors indicate species most strongly correlated (Pearson's r > 0.5) with the ordination structure.

Table 2.1. Results of leave-one-out allocation (m = 8) of replicate fish surveys to each mesohabitat types by a canonical analysis of principal (CAP) coordinates of the labrid fish communities of Port Stephens estuary. Rows indicate *a priori* grouping of mesohabitat type in which a survey was known to be taken, while columns indicate mesohabitat placement by the CAP analysis, and the percentage that were correctly allocated (Fig. 3). Note the extent to which sponge surveys were interchangeably classified to other mesohabitat types.

	Sponge	Soft Coral	Macroalgae	Total	Percent Correct
Sponge	19	15	14	48	40
Soft Coral	9	23	0	32	72
Macroalgae	4	0	28	32	88

Habitat-based predictors of fish community composition

Best-subsets model selection highlighted percent cover of the main canopy-forming habitat component and/or canopy height as the key predictors for fish community structure, although there were some exceptions (Fig. 2.5, S2.1). In an analysis of all mesohabitat types together, the most parsimonious model combined canopy height with sponge, canopy macroalgae and other habitat components percentage cover (Table 2.2; Table S2.1), which was supported by the examination of the sum of AICc weights for these variables across all models examined (Fig. 2.5). Within each mesohabitat type, canopy height also emerged as a key predictor for fish community structure in both sponges and soft coral (Fig. S2.2a-d, Table S2.2, S2.3), but not macroalgae, where percent cover of understory macroalgae and soft coral were the best predictors (Fig. S2.2e, f; Table S2.4). Further exploration revealed significant positive correlations between habitat canopy height and both fish species richness and fish density (Fig. 2.6).

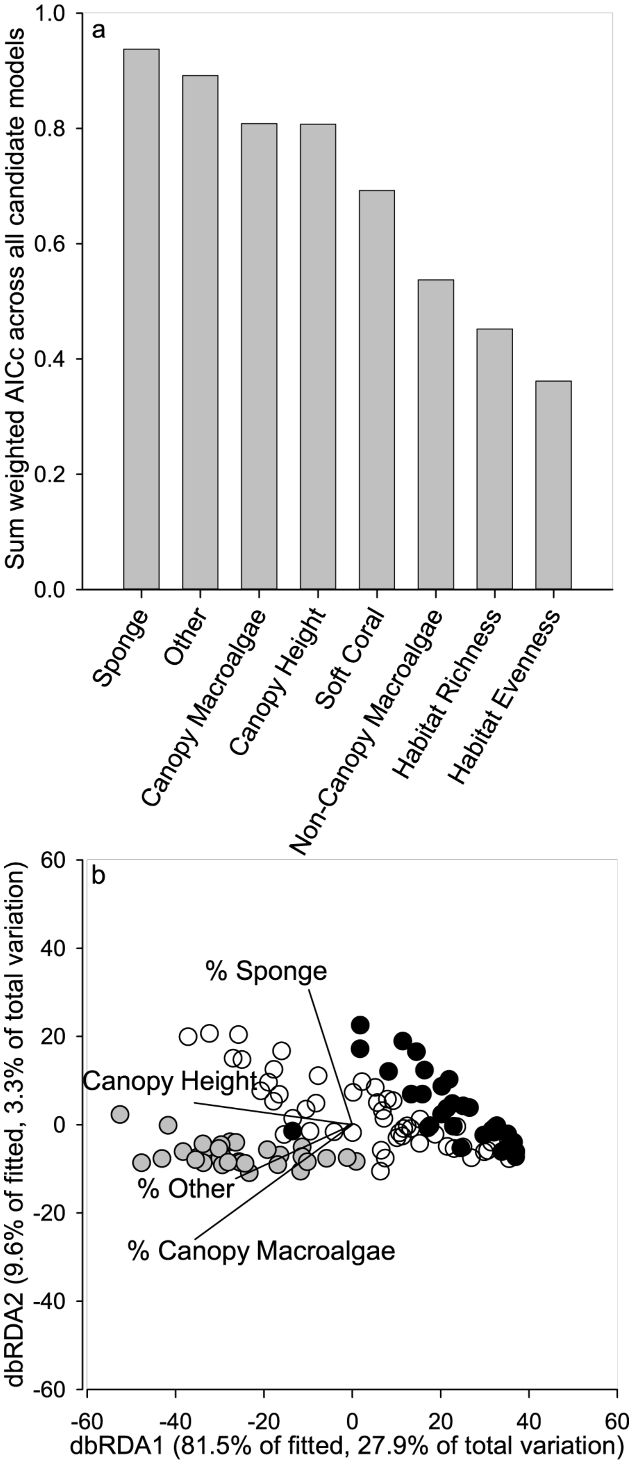

Figure 2.5. Summary of the best-subsets model selection indicating (a) model weights for all predictor variables considered, and (b) distance-based redundancy analysis (dbRDA) ordination of the most parsimonious model explaining fish community composition across three mesohabitat types (sponge - white circles, soft coral - black, macroalgae - grey) according to the key predictors of canopy height and percentage cover of sponge, canopy macroalgae and other that were identified in the best-subsets model selection (Table 2.2a).

Table 2.2. Top and most parsimonious (bolded) models from best-subsets model selection of habitat variables to explain variation in fish community structure within Port Stephens for (a) all mesohabitats, and separately for (b) sponge, (c) soft coral, and (d) macroalgae. Full results for the top models are provided in Supplementary Materials (Tables S2.1-S2.4).

Model	AICc	r^2
(a) All mesohabitats		
Canopy Height, % Canopy Macroalgae, % Sponge, % Soft Coral, % Other	818.5	0.34
Canopy Height, % Canopy Macroalgae, % Sponge, % Other	**819.4**	**0.32**
(b) Sponges		
Canopy Height, % Other	354.1	0.23
Canopy Height	**354.3**	**0.19**
(c) Soft corals		
% Soft Coral, % Understory Macroalgae, % Other	238.7	0.30
% Soft Coral	**239.4**	**0.16**
Canopy Height	**239.7**	**0.15**
(d) Macroalgae		
%Understory Macroalgae, % Soft Coral	215.1	0.19
%Understory Macroalgae	**215.7**	**0.11**
% Soft Coral	**216.4**	**0.09**

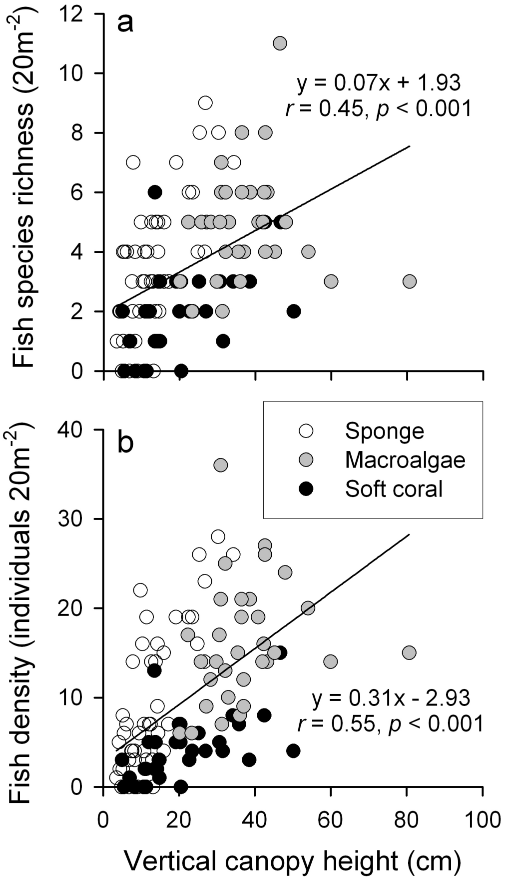

Figure 2.6. Least-squares linear regressions between vertical habitat canopy height and (a) fish species richness and (b) fish density across all mesohabitat types. Mesohabitat-specific relationships are provided in Supplementary Materials (Figure S2.2).

Discussion

Differences in labrid community structure among and within three temperate marine mesohabitat types were aligned with key aspects of soft microhabitat structure. In accordance with past temperate fish community studies (e.g., Anderson and Millar 2004; La Mesa et al. 2011; Morton and Gladstone 2011; Poulos et al. 2013), we found some fish species were unique to sponge or macroalgae mesohabitats. However, sponge-dominated habitats were home to many of the fish species found elsewhere, with strong overlap among sponge and macroalgae habitats, and all labrid species found within soft coral also present within the sponge mesohabitat. Alongside the traditional measure of soft microhabitat structure (percent cover), we found canopy height was often one of the key habitat-based predictors for fish community structure.

Compositional differences in temperate fish assemblages among mesohabitat types can arise from specificity in the habitat-associations of species, particularly specialists that may only occupy certain microhabitat niches (La Mesa et al. 2011; Morton and Gladstone 2011). Habitat generalists tend to have broader fundamental habitat niches, which means they can occupy a broad suite of different mesohabitats, and often at high abundances (e.g., *O. lineolatus*; Morton and Gladstone 2011; this study). However, habitat specialists (e.g., *P. laticlavius*) that have more specific resource requirements will only occur in mesohabitats that contain their required resource niche. Consequently, mesohabitats with the most diverse and evenly available array of microhabitats could be expected to attract the largest number of fish species. Here, we found that sponge mesohabitats, which had the equal highest species richness of fishes, also had the highest mean habitat richness and evenness. This is supported by other studies that have included other pairwise mesohabitat comparisons between sponges and either seagrass (Poulos et al. 2013), algal fringe, and/or urchin barrens (Curley et al. 2002; Morton and Gladstone 2011). Sponge communities provide a high structural complexity that is analogous to tropical coral reefs (e.g., range of functional growth forms; Boury-Esnault and Rutzler, 1997), as well as a broad mix of sponge, soft coral and understory macroalgae. Nonetheless, we also found that both sponge- and macroalgae-dominated habitats can harbour unique fish species, which could be due to certain microhabitat-specific matching with fish morphology (e.g. green-brown colour of *P. laticlavius* and *P. elongatus*), and/or their preferred prey are epibionts found on kelp or sponges (Taylor 1998; Poore et al. 2000; Morton et al. 2008). Habitat-specificity can also arise through ontogeny, whereby reef fishes preferentially use a variety of habitat types from settlement to juvenile and adult life history stages (Nagelkerken et al. 2002; Lecchini and Galzin 2005; Wilson et al. 2010; Fulton et al. 2016). Habitat specificity has been documented for labrid fishes in temperate seas (Choat and Ayling 1987; Gillanders and Kingsford 1998), which in some cases, can be much greater than that seen among adults of the same species (Morton and Gladstone 2011; Fulton et al. 2016). While we are unable to comment on the role of ontogeny in our current assessments, we suggest future work should explore the potential for nursery habitat quality to vary among and within these estuarine mesohabitats.

Hard habitat complexity (e.g., rugosity, growth form or vertical relief) is now widely accepted to be a major predictor and driver of fish diversity and abundance in both tropical and temperate biomes (Gratwicke and Speight 2005; Kutti et al. 2015; Syms and Jones 2000; Wilson et al. 2006). For example, tabular corals have been recently established as a keystone coral reef canopy microhabitat, which is directly linked to the abundance and diversity of large predatory reef fishes that use the corals as shelters from solar irradiance (Kerry and Bellwood 2015a, b). When such tabular components of the coral canopy are missing, so too are the large predatory fishes, with broader consequences for fish community structure. Our current study highlights the finding that measures of soft habitat complexity, including both canopy cover and height, are also key measures of fish habitat quality in a range of temperate mesohabitats. In terms of soft canopy height, a recent study by Kutti et al. (2015) suggested that vertical relief of deep water sponges had a large positive effect on the abundance of two fish species, *Brosme brome* and *Sebastes viviparus*. Here, we show increased fish species richness and density are associated with increased canopy heights within sponge and soft coral mesohabitats. Similarly, positive correlations between soft canopy height and the population and community structure of fishes have been identified in a range of marine macrophyte habitats, including seagrass beds, tropical *Sargassum* meadows and temperate kelp forests (Horinouchi 2007; Tuya et al. 2009; Lim et al. 2016). However, this strong influence of canopy height did not hold for the estuarine kelp forests examined in our study. Notably, the height of the *Ecklonia* canopy in our surveys was at the upper end of the mean soft canopy heights across our three mesohabitat type. This suggests that once the soft canopy matures and reaches a certain height, other measures of structural complexity, such as hard complexity and understory composition (this study; Tuya et al. 2009), or holdfast density (Wilson et al. 2014) may be more influential on fish community composition. In our study, hard complexity was unlikely to be influential, given the pervasive sand matrix that infilled interstices in the rocky substratum.

Canopy cover and height were highly variable among and within mesohabitat types and sites, which suggests important spatial and temporal dynamics in these canopy-forming organisms may underpin the quality of fish habitat in this temperate estuary. For instance, there is potential for widely different rates of temporal change in canopy cover and height among mesohabitat types. At one extreme, the soft coral *Dendronephthya australis* can exhibit up to a 360% change in vertical canopy height (and corresponding percent cover) over a six hour tidal cycle, in response to rising and falling water velocities (Davis et al. 2015). Conversely, sponges are likely to have a much slower rate of temporal change in canopy cover and height. Given canopy height and cover can be important predictors of fish richness and abundance (present study; Harasti et al. 2014; Lim et al. 2016), such canopy instability may be a key reason for the relatively low number of species, particularly unique taxa, that were recorded in soft coral relative to the more stable sponge and macroalgae mesohabitats. Canopy-forming macroalgae can also undergo relatively large shifts in canopy structure over seasonal to decadal scales, due to processes of canopy growth and decay over seasonal, annual or semi-decadal cycles (Larkum 1986; Ettinger-Epstein and Kingsford 2008; Mabin et al. 2013; Fulton et al. 2014). For example, seasonal shifts in the canopy of *Sargassum* can provide a high cover of structurally complex macroalgae habitat for fishes during summer, followed by major reductions (in most cases more than 50% of canopy cover and height lost) a few months later in the winter of the same year (Fulton et al. 2014; Lim et al. 2016). Sponges, however, tend to exhibit a relatively slow and steady canopy increase over longer timescales than either soft coral or macroalgae. For instance, Ayling (1983) found a low-stature sponge to grow at a rate of 0.23 mm^2 day^{-1}, which would mean this sponge would take approximately 10 years to obtain 15 cm in diameter. Another study of vertical linear growth rates in sponges found an average of 1.98 cm $year^{-1}$ (Leys and Lauzon 1998), which, when compared to the sponge canopy heights measured in our study, would equate to a mean canopy age of approximately seven years, and some of the tallest samples taking approximately 20 years to reach such heights. As sponge mesohabitats provide a range of important ecosystem services (Bell 2008), and harbour a diverse assemblage of fishes (Curley et al. 2002; Morton and Gladstone, 2011; Poulos et al. 2013; this study) that change with canopy cover and height, there is a need to monitor and protect established sponge mesohabitats.

Similarly, macroalgae mesohabitats formed by both laminarian and fucoid taxa should be a priority for monitoring and protection as key fish habitat. Growth rates and longevity of *Ecklonia radiata* vary with temperature, location and depth, but for the south-eastern region of Australia estimates show growth can reach 19.6 mm day^{-1} in times of high productivity, with full adult size of the canopy being reached in 6-10 months, and remaining relatively constant for up to 5 years or more within a given site (Larkum 1986; Ettinger-Epstein and Kingsford 2008; Shepard and Edgar 2013). Accordingly, measures of macroalgae canopy cover have been found to provide a good indicator of fish abundance and recruitment over local to regional scales in multiple locations around the world (e.g., Holbrook et al. 1990a; Perez-Matus and Shima 2010; Fulton et al. 2016). Macroalgae-associated fishes are essentially responding to the canopy directly for shelter and/or food (Morton et al. 2008; Fulton et al. 2016) or key understory components (this study) that are supported by shading from kelp (Cárdenas et al. 2016). There are multiple threats to kelp canopy cover arising from thermal stress, tropicalization and acidification (Vergés et al. 2014; Wernberg et al. 2016a, b), which is cause for concern and raises the question of what measures we can put in place to protect macroalgae-associated endemic fishes by mitigating local stressors (e.g. fishing, anchoring) on kelp forest habitat.

Habitat loss from sediment smothering, pollution, anchor damage, fishing gear, and climate change are all key threats to these common mesohabitats in temperate estuaries, which in turn threaten their capacity to support an abundance and diversity of fishes. Canopy cover and height provide key measures by which we can assess and monitor the ongoing quality and change in these habitats by professionals and citizen scientists alike. By those metrics, both published and anecdotal evidence suggests that serious degradation is already occurring in the temperate estuarine habitats (Freese et al. 1999; Coleman et al. 2008;

Demers et al. 2013; Poulos et al. 2015; Harasti 2016). We observed many instances of severe damage (uprooting, cleaving, mechanical fragmentation) to sponges via fishing (indicated by discarded fishing line wrapped around damaged sponges; Chiappone et al., 2005) and anchoring activities (based on large cleaving damage to massive sponges along a linear trajectory). Indeed, Poulos et al. (2015) and Harasti (2016) noted damage to soft coral habitats caused by anchor and chain drag damage was a major source of the uprooting and death of *D. australis* soft coral colonies. Given the slow growth and long-term recovery trajectory of sponge canopy cover and height (likely to be decadal scale), and the rarity of soft corals (Poulos et al. 2013), more effective habitat protection measures are needed, which could include provision for no-anchoring areas, and/or the installation and mandated use of environmentally friendly boat moorings (Demers et al. 2013). Concurrently, spatial conservation planning and protection should evaluate whether high quality canopy states of each mesohabitat type are being maintained in sanctuary/no-fishing zones. For sponge mesohabitats, we suggest the focus should be on preferentially protecting patches with higher canopy cover and height as areas with greater potential for housing an abundance and diversity of fishes, and the decadal scale of recovery times for damaged sponge canopy structure.

Supplementary Material

Table S2.1. Summary of the best-subsets selection models explaining variation in labrid fish community structure within three common mesohabitat types of the Port Stephens estuary. Models shown are within 2 AICc of the top model, with the most parsimonious in bold having the fewest explanatory variables.

Model	AICc	Δ AICc	r^2
Canopy Height, % Canopy Macroalgae, % Sponge, % Soft Coral, % Other	818.53	0	0.34
Canopy Height, % Canopy Macroalgae, % Sponge, % Soft Coral, % Other, Habitat Richness	818.81	0.28	0.35
Canopy Height, % Canopy Macroalgae, % Understory Macroalgae, % Sponge, % Soft Coral, % Other	818.91	0.38	0.35
Canopy Height, % Canopy Macroalgae, % Understory Macroalgae, % Sponge, % Other	819.16	0.63	0.33
Canopy Height, % Canopy Macroalgae, % Sponge, % Soft Coral, % Other, Habitat Evenness	819.2	0.67	0.35
Canopy Height, % Canopy Macroalgae, % Understory Macroalgae, % Sponge, % Soft Coral, % Other, Habitat Richness	819.26	0.73	0.37
Canopy Height, % Understory Macroalgae, % Sponge, % Soft Coral, % Other	819.41	0.88	0.34
Canopy Height, % Canopy Macroalgae, % Sponge, % Other	819.44	0.91	0.32
Canopy Height, % Canopy Macroalgae, % Understory Macroalgae, % Sponge, % Other, Habitat Richness	819.5	0.97	0.35
% Canopy Macroalgae, % Understory Macroalgae, % Sponge, %Soft Coral, % Other	819.67	1.14	0.34
Canopy Height, % Canopy Macroalgae, % Sponge, % Other, Habitat Richness	819.77	1.24	0.34
% Canopy Macroalgae, % Understory Macroalgae, % Sponge, % Soft Coral, % Other, Habitat Richness	819.79	1.26	0.35
Canopy Height, % Understory Macroalgae, % Sponge, % Soft Coral, % Other, Habitat Richness	819.86	1.33	0.35
Canopy Height, % Canopy Macroalgae, % Understory Macroalgae, % Sponge, % Soft Coral, % Other, Habitat Evenness	820.06	1.53	0.36
Canopy Height, % Canopy Macroalgae, % Sponge, % Soft Coral, % Other, Habitat Evenness, Habitat Richness	820.24	1.71	0.36
Canopy Height, % Canopy Macroalgae, % Understory Macroalgae, % Sponge, % Other, Habitat Evenness	820.37	1.84	0.35
Canopy Macroalgae, % Sponge, % Soft Coral, % Other	820.38	1.85	0.32

Table S2.2. Summary of the best-subsets selection models explaining variation in Port Stephen fish community within sponge mesohabitat. Models shown are within 2 AICc of the top model, with the most parsimonious in bold having the fewest explanatory variables.

Model	**AICc**	**Δ AICc**	**r^2**
Canopy Height, % Other	354.09	0	0.23
Canopy Height	**354.28**	**0.19**	**0.19**
Canopy Height, % Sponge, % Other	354.78	0.69	0.27
% Sponge, % Other, Habitat Richness	354.95	0.86	0.25
Canopy Height, Habitat Richness	355	0.91	0.21
Canopy Height, % Understory Macroalgae, % Other	355.16	1.07	0.25
Canopy Height, % Other, Habitat Richness	355.25	1.16	0.25
Canopy Height, % Canopy Macroalgae, % Other	355.25	1.16	0.25
Canopy Height, % Understory Macroalgae	355.31	1.22	0.21
Canopy Height, % Canopy Macroalgae	355.34	1.25	0.21
Canopy Height, % Sponge	355.62	1.53	0.20
% Sponge, % Other	355.67	1.58	0.20
Canopy Height, % Sponge, % Other, Habitat Richness	355.76	1.67	0.28
% Sponge, Habitat Richness	355.87	1.78	0.20
Canopy Height, Habitat Evenness	355.88	1.79	0.20
Canopy Height, % Other, Habitat Evenness	355.97	1.88	0.24
Canopy Height, % Understory Macroalgae, % Sponge, % Other	355.97	1.88	0.28
Canopy Height, % Understory Macroalgae, Habitat Richness	356.05	1.96	0.24
%Understory Macroalgae, % Sponge, % Other, Habitat Richness	356.06	1.97	0.28

Table S2.3. Summary of the best-subsets selection models explaining variation in Port Stephen fish community within soft coral mesohabitat. Models shown are within 2 AICc of the top model, with the most parsimonious in bold having the fewest explanatory variables.

Model	**AICc**	**Δ AICc**	**r^2**
% Understory Macroalgae, %Soft Coral, % Other	238.67	0	0.30
% Soft Coral, % Other	239.15	0.48	0.23
% Soft Coral, Habitat Evenness	239.17	0.5	0.23
Canopy Height, % Understory Macroalgae, % Other	239.31	0.64	0.28
% Soft Coral	**239.39**	**0.72**	**0.16**
Canopy Height, % Other	239.6	0.93	0.21
Canopy Height	**239.71**	**1.04**	**0.15**
% Understory Macroalgae, % Soft Coral	239.75	1.08	0.21
% Canopy Macroalgae, % Understory Macroalgae, % Soft Coral, % Other	239.79	1.12	0.33
% Soft Coral, % Other, Habitat Evenness	239.92	1.25	0.27
% Sponge, % Soft Coral, Habitat Evenness	240.1	1.43	0.27
% Canopy Macroalgae, % Soft Coral, % Other	240.12	1.45	0.26
Canopy Height, % Understory Macroalgae	240.14	1.47	0.20
Canopy Height, % Canopy Macroalgae, % Understory Macroalgae, % Other	240.19	1.52	0.33
% Understory Macroalgae, % Sponge, % Soft Coral, % Other	240.41	1.74	0.32
% Soft Coral, % Other, Habitat Richness	240.58	1.91	0.25
% Canopy Macroalgae, % Soft Coral	240.65	1.98	0.19

Table S2.4. Summary of the best-subsets selection models explaining variation in Port Stephen fish community within macroalgae mesohabitat. Models shown are within 2 AICc of the top model, with the most parsimonious in bold having the fewest explanatory variables.

Model	**AICc**	**Δ AICc**	**r^2**
% Understory Macroalgae, % Soft Coral	215.05	0	0.19
Canopy Height, % Understory Macroalgae, % Soft Coral	215.19	0.14	0.25
% Understory Macroalgae, % Sponge, % Soft Coral	215.64	0.59	0.24
% Understory Macroalgae	**215.65**	**0.6**	**0.11**
& Understory Macroalgae, % Sponge	215.76	0.71	0.17
Canopy Height, % Understory Macroalgae	215.86	0.81	0.17
Canopy Height, % Understory Macroalgae, % Sponge, % Soft Coral	216.09	1.04	0.30
% Understory Macroalgae, % Soft Coral, % Other	216.22	1.17	0.22
Canopy Height, % Understory Macroalgae, % Sponge	216.26	1.21	0.22
% Understory Macroalgae, %Soft Coral, Habitat Evenness	216.32	1.27	0.22
% Canopy Macroalgae, % Understory Macroalgae, % Soft Coral	216.37	1.32	0.22
%Soft Coral	**216.42**	**1.37**	**0.09**
Canopy Height, % Soft Coral	216.59	1.54	0.15
% Understory Macroalgae, % Other	216.62	1.57	0.15
Canopy Height, % Understory Macroalgae, % Soft Coral, % Other	216.82	1.77	0.28
Canopy Height, % Understory Macroalgae, % Soft Coral, Habitat Evenness	217.04	1.99	0.27
%Understory Macroalgae, Habitat Richness	217.04	1.99	0.14

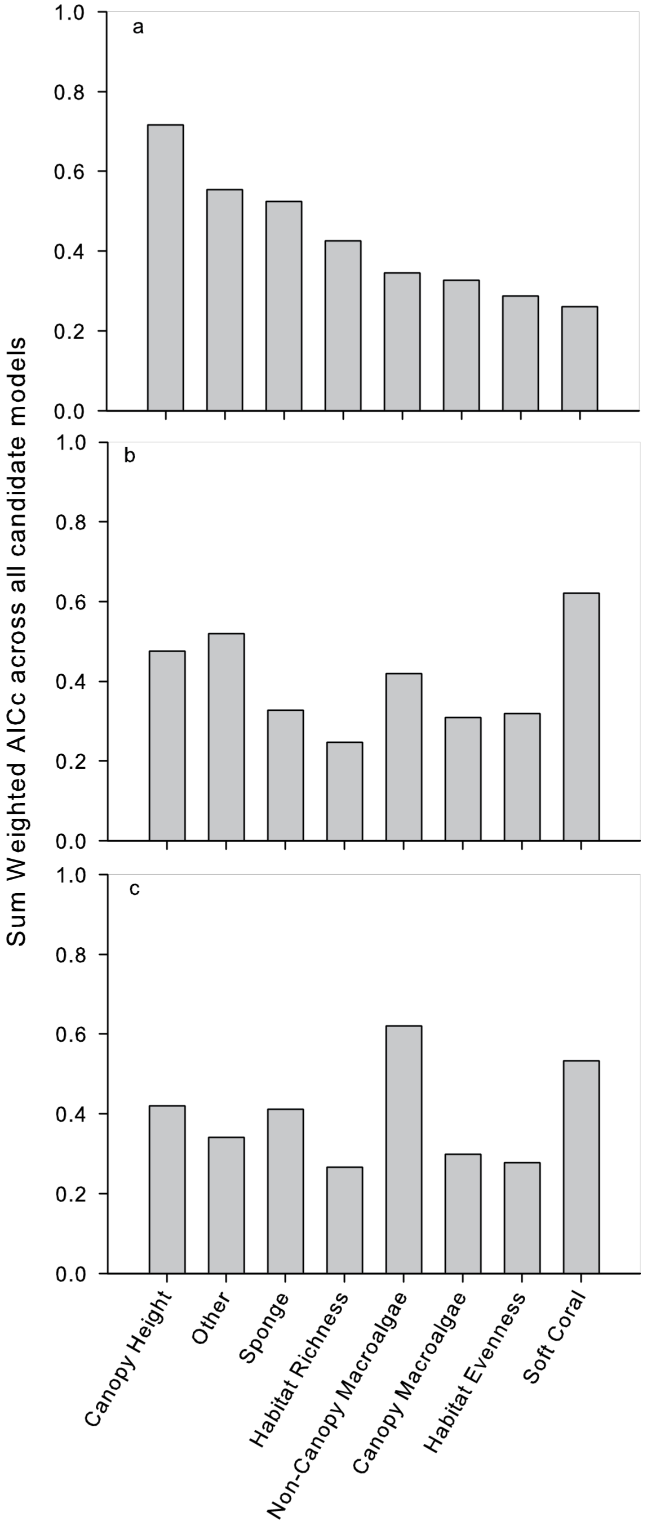

Figure S2.1. Results from the best-subsets model selection showing the AICc summed weights for all candidate models of all predictor variables considered within each mesohabitat type of (a) sponge, (b) soft coral and (c) macroalgae mesohabitats. Apart from canopy height, habitat richness and evenness, all other variables are percent cover of that habitat type.

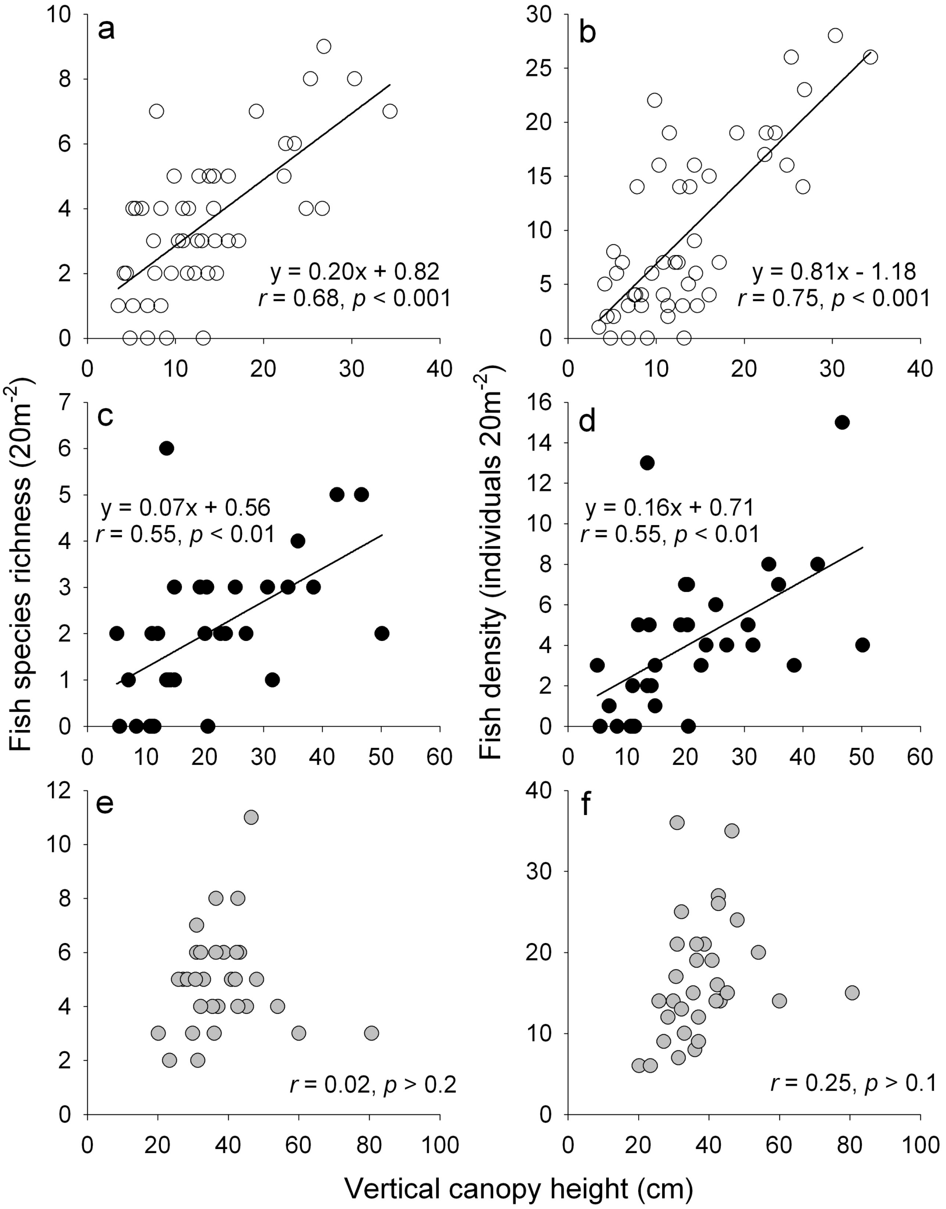

Figure S2.2. Relationships between vertical habitat canopy height and labrid fish species richness (a, c, e) and fish density (b, d, f) within, sponge (a, b), soft coral (c, d), and macroalgae (e, f). Least-squares regressions are fitted only for significant relationships.

Chapter 3

Habitat connectivity and complexity underpin fish community structure across a seascape of tropical macroalgae meadows

Photo credit: David Ellis

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Abstract

In heterogeneous landscapes, local patterns of community structure are a product of the habitat size and condition within a patch interacting with adjacent habitat patches of varying composition and quantity. While evidence for local versus landscape factors have been found in terrestrial biomes, support for such multi-scale effects shaping marine ecological communities is equivocal. We investigated whether within-patch habitat condition can override seascape context to explain the community structure of macroalgae-associated reef fishes across a tropical seascape. We mapped the distribution and abundance of a diverse family of reef fishes (Labridae) occupying macroalgae meadows within a tropical reef ecosystem, and using best-subsets model selection, investigated the potential for habitat structural connectivity and/or local habitat quality for predicting variations in fish community structure across the seascape. Local habitat quality (canopy structure, hard habitat complexity) and area of coral-dominated habitat within 500m of a macroalgal meadow provided the best predictors of fish community structure. However, the specific importance of a given predictor varied with fish life history stage and functional trophic group. Interestingly, macroalgae meadow area was among the least important predictors. Given the complex interplay between local habitat quality and spatial context effects on fish biodiversity, our study reveals the multi-scale predictors that should be used in spatial conservation and management approaches for tropical fish diversity. Moreover, our findings question the ubiquity of habitat area effects in patchy landscapes, and cautions against a sole reliance on habitat quantity in spatial management.

Introduction

Early attempts to unravel the mechanisms shaping the structure of communities in patch-habitats highlighted the importance of both patch size and isolation for species richness patterns (MacArthur and Wilson 1963; Simberloff and Wilson 1970). Since then, increasing evidence has shown patterns of landscape configuration (e.g., connectivity) and composition (e.g., number and area of different mesohabitat types) to be key predictors of community structure across a range of taxa, biomes and geographic locations (Turner 1989, 2005; Boström et al. 2011). Indeed, the recently developed Habitat Amount Hypothesis posits that species richness within a single delineated patch should be a function of the total suitable habitat available across a given area of landscape, rather than the area of the respective patch (Fahrig 2013). However, much of the empirical evidence to support these hypotheses have been based on terrestrial systems; the extent to which these processes apply in aquatic ecosystems has yet to be confirmed.

A general assumption in spatial ecology is that species of varying mobility may need to access different resources throughout their life-history, which may require traversing a heterogeneous landscape to reach food, breeding/nursery grounds or shelter (Berkström et al. 2012; Hanski et al. 2017). As such, within-patch conditions and landscape structural connectivity (i.e., proximity and area of similar and/or different mesohabitat types; Calabrese and Fagan 2004) can influence patch-level diversity, size and abundance of species within a particular mesohabitat type (e.g., Garden et al. 2010; Hanski et al. 2017; Michael et al. 2017). For example, Michael et al. (2017) demonstrated how reptile patch-occupancy could be better explained by considering topographic variables alongside within-patch habitat complexity. Such results highlight the importance of considering a multi-scale approach when assessing patterns of community structure.

While relatively nascent, the field of seascape ecology has started to reshape our awareness of how spatial context can influence patterns of marine community structure and function (Boström et al. 2011). For instance, traditional habitat metrics that can influence fish community structure, such as coral cover and complexity (Pratchett et al. 2011; Darling et al. 2017), have shown to be augmented or overridden by the structure of the surrounding seascape (Olds et al. 2012) and/or presence of piscivores (Hixon 2015). For example, Olds et al. (2012) found differences in coral reef fish community structure could be primarily attributed to levels of habitat connectivity with mangrove and seagrass mesohabitats; within-patch variables like hard substratum complexity were only useful in distinguishing patterns among highly connected patches. Additionally, the importance of patch habitat area for patterns of fish community structure is also coming into question. Although coral reef patch area has been found to be an effective predictor of fish species richness and relative abundance (Acosta and Robertson 2002; Chittaro 2002), more recent analyses found patch area to have a negligible effect in models containing structural connectivity measures (Grober-Dunsmore et al. 2007). Furthermore, evidence for patch area as a predictor of marine diversity in soft-structure habitats like seagrass has been equivocal (Boström et al. 2011). Consequently, structural connectivity among different mesohabitat types has emerged as a key predictor for tropical fish communities in seagrass beds, mangrove forests and coral reefs (Pittman et al. 2007; Berkström et al. 2013; Henderson et al. 2017). Nonetheless, we still have a rudimentary understanding of these effects for fish communities occupying the broad range of marine patch-habitat types that contribute to the tropical seascape mosaic (Berkström et al. 2012).

Macroalgae meadows are an important part of coastal ecosystems where they are major primary producers (Fulton et al. 2014), and support a unique and diverse assemblage of adult and juvenile fishes (Chaves et al. 2013; Wilson et al. 2014; Eggertsen et al. 2017; Tano et al. 2017). As seasonally dynamic habitats, there is often a mosaic of local macroalgal habitat conditions present across a tropical seascape, with differences in fish community structure often strongly correlated to such local variation in habitat structure. For instance, spatial and temporal changes to within-patch macroalgal canopy height and cover have been linked to major shifts in the taxonomic composition and abundance of macroalgal-associated tropical fishes (Wilson et al. 2014; Lim et al. 2016; Wilson et al. 2017; Wenger et al. 2018). While within-patch habitat condition can have a strong influence on fish community structure, in many cases there has been a large amount of unexplained variation that may be attributable to seascape context. Indeed, there is evidence that distance to coral reef may be significant, with some herbivorous fishes occurring in macroalgal meadows at varying densities according to their proximity to coral reef habitat (Vergés et al. 2011)

Here, we used field surveys of reef fish distribution and abundance across a tropical seascape of macroalgal and coral mesohabitats to answer the question: Does within-patch habitat condition override seascape context (e.g., patch size, connectivity) to explain the community structure of reef fishes across a mosaic of patch habitats? Fishes from the family Labridae (wrasses, parrotfishes) were used as a focal group. Labrids are readily detectable by underwater visual census, and as one of the most speciose conspicuous reef fish families, they encompass a diversity of trophic groups and movement patterns to make them an effective surrogate for reef fish diversity (Fulton and Bellwood 2002; Kulbicki et al. 2005; Malcolm and Smith 2010).

Methods

Study area and seascape mapping

Our study region encompassed a $6km^2$ section of shallow (<6m) fringing reef lagoon within the Ningaloo Marine Park, Western Australia (23.1447° S, 113.7764° E). In terms of shallow-water habitat area available to fish, the Ningaloo lagoon encompasses two prominent mesohabitats: 1. a seasonally dynamic network of macroalgae-dominated (principally *Sargassum*) patches set within a matrix of ancient reef pavement and soft sediment and 2. the landward side of a relatively stable coral-dominated fringing reef (Kobryn et al. 2013; Fulton et al. 2014). We surveyed 28 macroalgal patch sites that were spaced 15-1150m apart (nearest-neighbour edge-to-edge linear distance) across the study region; 24 within the lagoon and 4 embedded within the fringing coral back reef (Fig. 3.1). Four coral-dominated sites were also surveyed to provide a reference for comparing coral- and macroalgal-affiliated fish taxa and to interpret whether increased structural connectivity of macroalgal patches to the coral fringing reef supported fish communities similar in structure to a coral-dominated habitat. All macroalgal patches were $>600m^2$ in area to allow for six replicate fish surveys to be conducted within each site (see fish survey details below).

Fish and habitat surveys

Fish surveys were carried out during February-March 2016, when annual abundance of juvenile fish and macroalgal biomass is high (McIlwain 2003; Fulton et al. 2014). Fish and habitat assemblages were quantified within six haphazardly placed 5m diameter cylinders following the method of Noble et al. (2013). Each survey cylinder was spaced at least 5m from all other replicates, and 5m from the edge of the habitat at each site. For each replicate, the diver scanned for all mobile labrids and putative piscivores (Lim et al. 2016) present from the

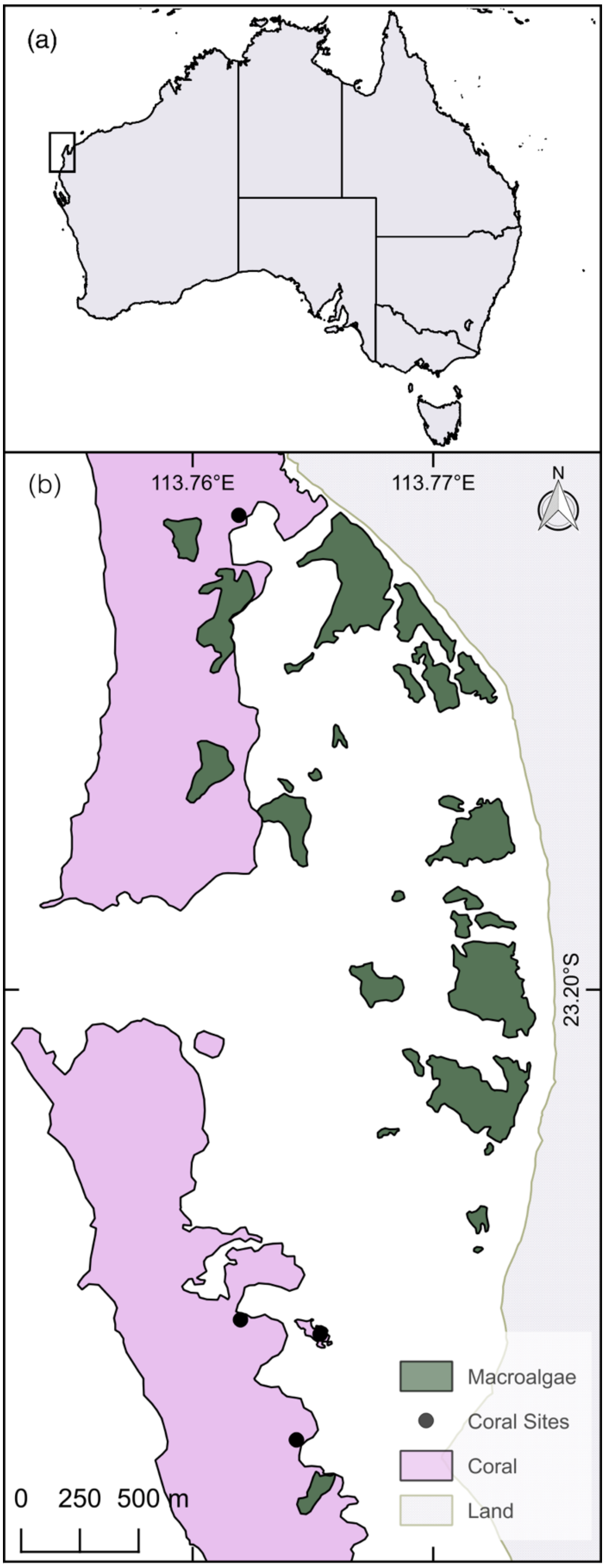

Figure 3.1. Map of the study region within the Ningaloo Marine Park near Coral Bay, Western Australia.

edge of the survey cylinder, and then systematically moved through the survey cylinder to look for more crypto-benthic fishes within the reef/macroalgae matrix. Habitat was assessed along a 5m line intercept transect, run across the same cylinder, which was used to record the distance occupied under the tape by each microhabitat category (genera of canopy and understory macroalgae, hard coral to growth form, seagrass, other invertebrates, as well as the abiotic components of sand, rubble and reef pavement). At each 1m interval, the undisturbed vertical height of canopy-forming macroalgae and the density (0.25m^2) of canopy-forming macroalgae holdfasts was also recorded. Finally, the three-dimensional complexity of the hard substratum within the cylinder was estimated on a scale of zero to five, following Polunin and Roberts (1993), where: 0 = no vertical relief, 1 = low vertical relief (<10cm), 2 = some vertical relief (11-30 cm), 3 = moderate vertical relief (31-60cm), 4 = high vertical relief (61-100cm), and 5 = very high vertical relief (>100cm). Site-level values for these local habitat conditions are shown in Figure S3.1 and S3.2. These paired surveys of fish and habitat were undertaken by two divers working underwater in the same site, with each diver completing three non-overlapping cylinders to yield a total of six replicates per survey site. Pre-survey training dives were used to ensure all divers were familiar with the target fish species and habitat categories, and were conducting replicate surveys in the same systematic fashion.

Spatial metrics

Macroalgal patch sites and fringing coral reef outlines for the entire study region were imported into QGIS (Version 2.18.2) to create a map of patch sites from which seascape variables were calculated (Table 3.1). Centroids for each patch were designated and used as a centre point from which to extend radii that defined our buffer zone for each site. Three

Table 3.1. List of possible predictors for macroalgae patch fish community structure included in best-subsets model selection.

Metric	**Description**
Seascape variables	
Coral Connectivity	Total area of coral habitat within a 50m, 150m or 500m radius (m^2).
Number of Patches	Total number of patches partially or completely within a 50m, 150m or 500m radius (m^2).
Reef Distance	Shortest linear edge-to-edge distance from a patch to the backreef (m).
Patch Isolation	Shortest linear edge-to-edge distance to nearest patch neighbour (m).
Patch Area	Total area of a patch (m^2).
Patch Edge	Total perimeter of a patch (m).
Within-patch variables	
Canopy Height	Mean height of free-standing canopy (cm).
Holdfast Density	Mean density of holdfasts of canopy forming macroalgae ($0.25m^{-2}$).
%Canopy Macroalgae	Mean percentage cover of canopy forming macroalgae.
%Understory Brown Algae	Mean percentage cover of understory brown macroalgae.
Hard Complexity	Mean index of variation in vertical relief of the hard substratum.
%Coral	Mean percentage cover of live hard coral.
%Other	Combined mean percentage cover of understory red and green algae, seagrass and other sedentary invertebrates.
Biotic variables	
Piscivore Density	Mean density of piscivorous fish ($20m^{-2}$).
Adult Density	Mean density of mature fish ($20m^{-2}$).

different radii were used: 50m, 150m and 500m. These radii were based on estimates of the likely home range of the largest individuals of each surveyed fish species (Nash et al. 2015; Table S3.1). Over 70% of fish taxa were found to have a max diel range of less than 8,000m^2, which equates to a circle with a radius of approximately 50m. The 150m radius incorporated the home range of the largest individual of each species across all taxa observed. The 500m radius is based on Green et al. (2015), which found that the largest labrid fishes can move linear distances of 1km or more, which equates to a minimum radius of 500m. These radii link spatial scale to the taxa of interest (Kendall et al. 2011), and are consistent with other measures used in the seascape ecology literature (e.g., Grober-Dunsmore et al. 2007; Olds et al. 2012; Berkström et al. 2013).Once overlayed, these three buffer zones were used to calculate further spatial metrics. The total number of macroalgae patches that lay completely or partially within a buffer zone were counted to provide a measure of total number of neighbourhood patches. Total area of coral habitat within a buffer zone were calculated as a measure of cross-habitat structural connectivity (Pittman and Olds 2015). Linear edge-to-edge distances between macroalgal patch sites and the coral fringing reef were also measured to provide a further measure of structural connectivity. Finally, patch isolation for each site was measured by taking the linear edge-to-edge distance to the nearest neighbouring patch.

Statistical analyses

Emergent properties of labrid fish community structure were calculated in terms of alpha and beta diversity, and Pielou's Evenness (J'), which emphasises the numerical equality of species within a community. Alpha diversity was the total number of unique species encountered within a site, while beta diversity was calculated for each site using a distance-based test for homogeneity of multivariate dispersions (using the PERMDISP routine; see Anderson et al. 2006 for details surrounding beta diversity calculations). These diversity measures were then placed into an interval map to reveal how these metrics differed spatially.

Habitat data was collated into eight variables: vertical canopy height, holdfast density, hard habitat complexity, percentage cover of canopy macroalgae (*Sargassum* + *Sargassopsis*), live coral, understory brown macroalgae, abiotic substratum (sand + pavement) and other understory organisms (red and green macroalgae + sessile invertebrates). The abiotic component was subsequently excluded from all analyses due to high correlation with macroalgae canopy cover. All habitat variables were normalised to account for the disparate measurement scales, and a resemblance matrix constructed using Euclidean distances. Expected differences in local habitat condition among macroalgal patch sites were confirmed using a nested Permutational Multivariate Analysis of Variance (PERMANOVA), with patch area included as a covariate and mesohabitat as fixed factor, and site as a random factor (Table S3.2).

Spatial differences in labrid assemblage structure were then examined using a PERMANOVA of the same design as the habitat condition analysis. Prior to this, fish densities for all species were square root transformed before a resemblance matrix was constructed using the Modified Gower (base 2) measure of similarity. This similarity measure considers both compositional and numerical change in a fish community whereby a doubling in species abundance will be given the same weight as the presence of a new species (Anderson et al. 2006). A similarity percentages test (SIMPER) was used to identify which fish species were most influential in the community-level differences among macroalgae and coral-dominated habitat types.

Fish species were then categorised by their affinity to coral or macroalgae-dominated habitat types, based upon their mean density within each. A species was considered affiliated with a particular mesohabitat type when they had a mean density that was an order of magnitude higher in one mesohabitat over the other; mesohabitat generalists were present in both mesohabitats with no order of magnitude difference between densities. A Euclidean distance resemblance matrix, constructed from untransformed means of species richness or density of differing fish-habitat association categories, was then examined in a PERMANOVA with the fixed factor of patch proximity group. Patch proximity groups were based on different linear distances from the landward edge of the fringing coral reef: distant (>750m), intermediate (250-750m), proximate (<250m), embedded (macroalgae patches that were set within the coral reef mesohabitat), and coral (sites that were of coral mesohabitat). Coral sites were excluded from the PERMANOVA, as were coral exclusive species, as the emphasis here is on macroalgae patch habitats, but values for these were reported alongside the macroalgae sites for interpretation. These proximity categories encompassed at least four patch sites at each level (Fig. S3.1). A Principal Coordinates Ordination (PCO), based on site level means, was used to illustrate the spatial variables and the 12 most abundant species that were correlated (Pearson's R) with multivariate variation in fish community structure.

Best-subsets model selection (DistLM) and distance based redundancy analysis (dbRDA) were used to explore which variables of within-patch habitat condition, seascape context, and piscivore abundance (and conspecific adults for juvenile analysis due to potential for gregarious settlement; Table 3.1) may best predict variations in fish community structure across the macroalgal patch sites. For this analysis, site-level fish densities and habitat structure metrics were analysed, with the fish data collated into two life-history (juvenile, adult) and nine functional trophic groups. The distinction between juvenile and adult stages was based on our length estimates and species-specific size-at-age data obtained from the literature (Table S3.1). The functional trophic group assigned to each species was based on evidence from the literature (Table S3.1), and included: piscivore, general zoobenthivore, macro-zoobenthivore, micro-zoobenthivore, corallivore, ectoparasitivore, browsing herbivore, excavating herbivore and scraping herbivore. Fish densities were assembled into a resemblance matrix using the Modified Gower (Base 2) measure of similarity. The model selection process considered all possible combinations (max of three variables) of the local habitat condition, seascape, and piscivore (alongside conspecific adult abundances for the juvenile analysis) predictors, using multivariate distance-based linear models and the Akaike

Information Criterion corrected for finite samples (AICc). The most parsimonious model was chosen as that which had the fewest predictors within 2 AICc units of the overall top model (lowest AICc value). Goodness-of-fit for each model was interpreted by calculation of r^2 values. This process was repeated using a combination of alpha and beta diversity, and evenness as the dependent variables, which were normalised before a resemblance matrix was constructed using Euclidean distance. The relative importance of each predictor was explored using the sum of weighted AICc scores for all candidate models which included that predictor (Burnham and Anderson 2002). All multivariate analyses and diversity calculations were performed in PRIMER (version 7.1.1) with PERMANOVA+ (Anderson et al. 2008).

Results

Reef fish community structure

A total of 46 labrid fish species were observed across both coral and macroalgae sites (Table S1), with strong variation in alpha diversity (max = 32, min = 8), species evenness (max = 0.91, min = 0.69), and beta diversity (max = 0.92, min = 0.55) apparent among the macroalgae-dominated sites (Fig. 3.2).

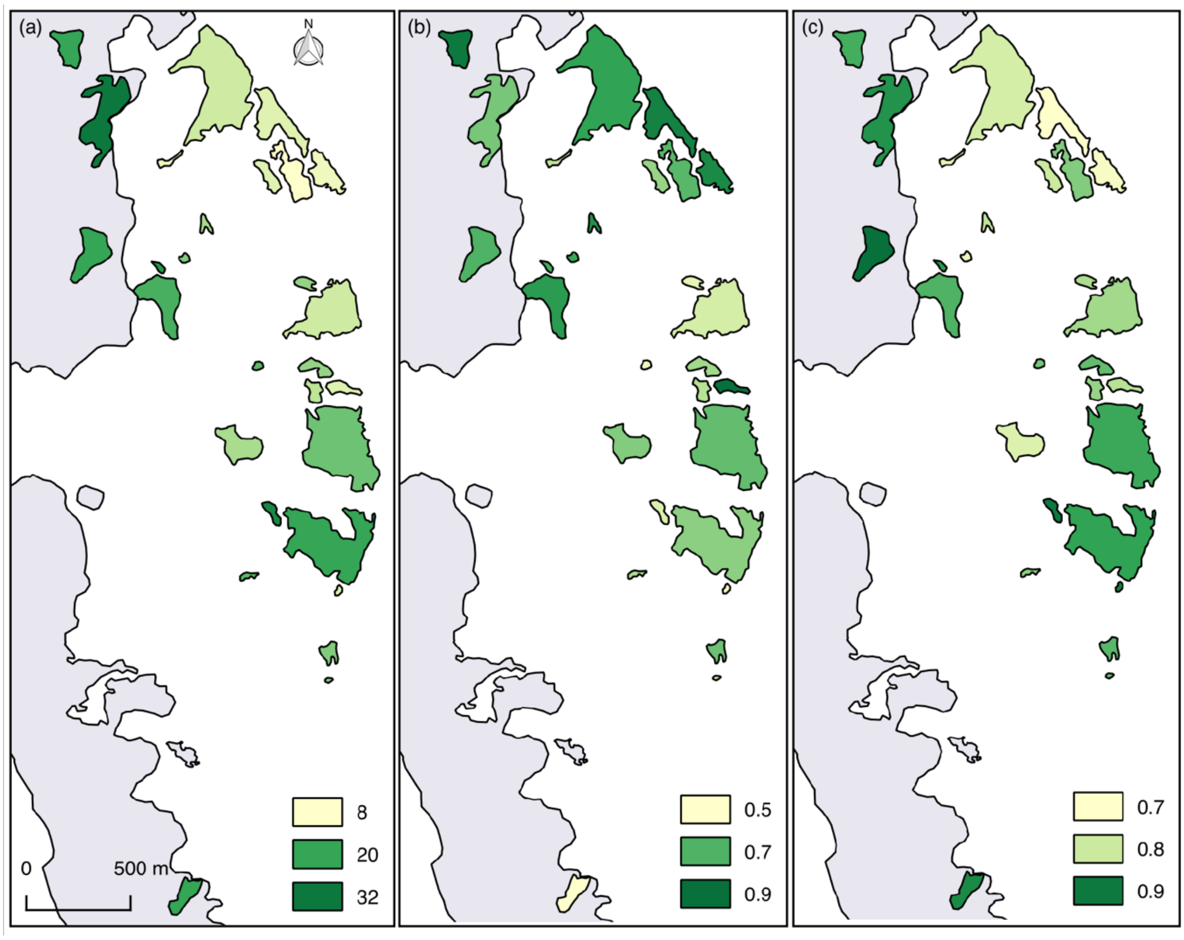

Figure 3.2. Interval maps indicating the alpha (a) and beta diversity (b), and evenness (c) of fish communities within each macroalgae patch site. Legends illustrate colour map for high, intermediate and low values of each variable

Labrid community structure showed significant differences between the coral and macroalgae-dominated mesohabitats ($F_1 = 6.84$, $p < 0.01$) and among macroalgae-dominated sites ($F_{26} = 4.55$, $p < 0.01$), with the two mesohabitats being characterised by distinct groups of fish species (Table S3.3, Fig. 3.3). Interestingly, fish species that characterised coral sites also tended to be abundant in macroalgal sites closest to the back reef, indicating increased overlap in community composition with structural connectivity (Fig. 3.3). Further evidence of this overlap could be seen by the significant difference in generalist labrid species among macroalgal patch sites ($F_3 = 5.22$, $p < 0.01$), with the highest densities occurring at patches embedded in the back reef (Fig. 4). However, there was no significant difference in the mean richness of generalist labrids among sites with different levels of reef connectivity ($F_3 = 1.67$,

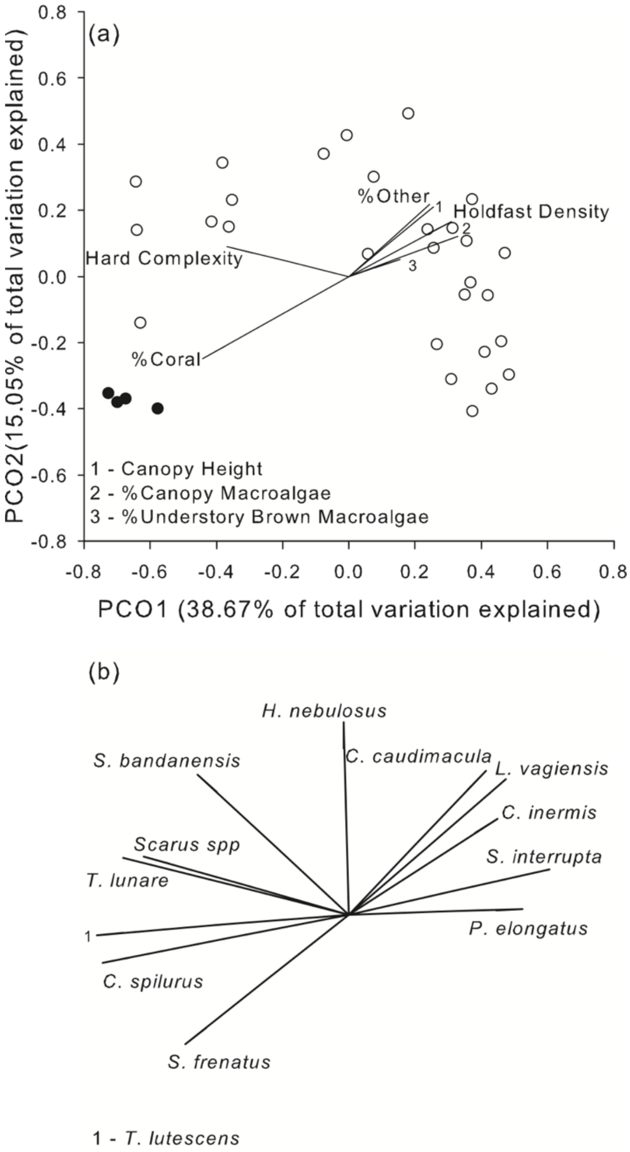

Figure 3.3 Principal Coordinates Ordination (a) of macroalgae sites (white) and coral sites (black). Vector overlays indicate the habitat condition variables (a) and 12 most abundant fish species (b) most strongly correlated (r > 0.5) with the ordination structure.

p = 0.19). Furthermore, significant declines in mean species richness (F_3 = 5.22, p = 0.01) and density (F_3 = 6.48, p < 0.01) of coral-affiliated fish with increasing distance from the fringing coral reef was observed (Fig. 3.4). No significant difference was found in the mean richness of generalist fishes among macroalgae-dominated sites at different levels of reef proximity. However, there was a significant difference in generalist fish densities among macroalgae patch sites, with the highest densities occurring at patches embedded in the backreef; Fig.

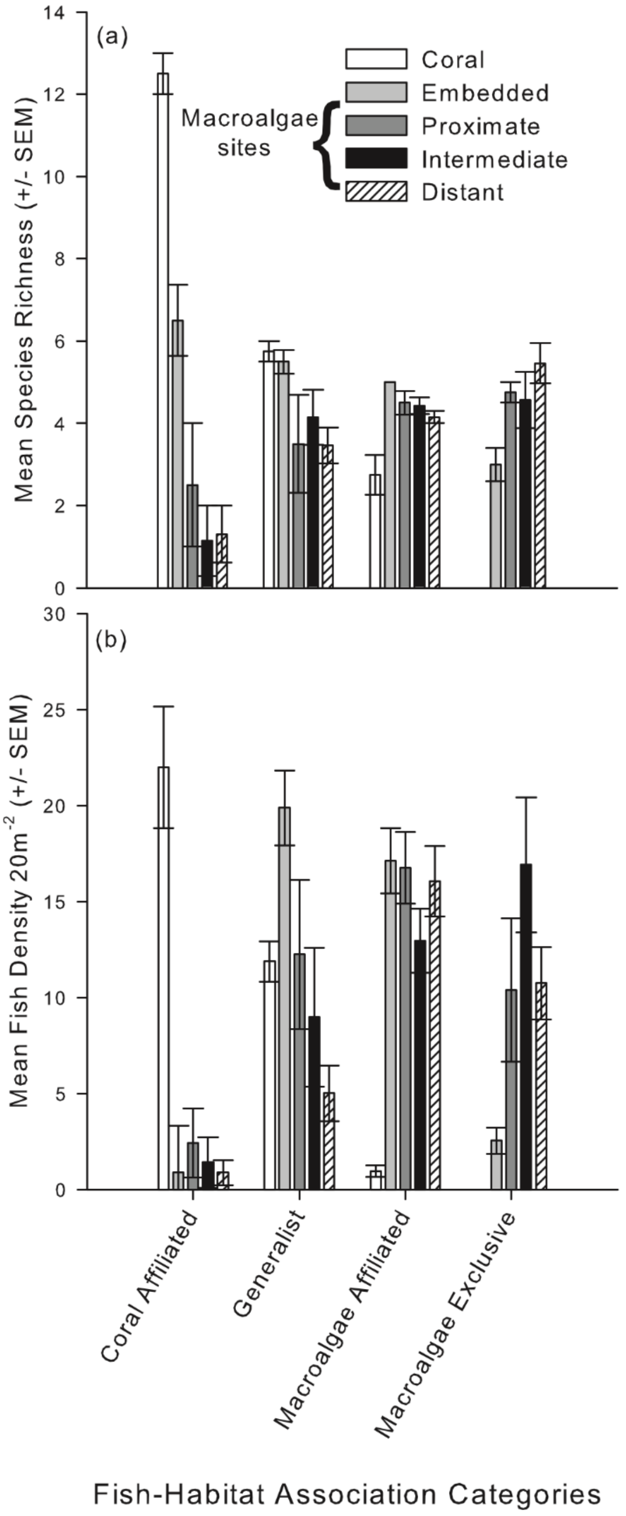

Figure 3.4. Mean fish species richness (a) and density (b) with standard error (SEM) for each fish-habitat association category. Means are presented for coral-dominated sites (white bars) and then macroalgae-dominated patches at five different proximities to the fringing coral reef (Embedded: macroalgae patch surrounded by fringing coral reef, Proximate: <250m, Intermediate: 250-750m, Distant: >750m).

3.4b). No significant differences in mean richness with distance from the reef were evident for macroalgae-affiliated (F_3 = 2.84, p = 0.07) and macroalgae exclusive (F_3 = 2.54, p = 0.08) reef fish, nor in terms of mean densities for macroalgae-affiliated fish (F_3 = 0.74, p = 0.54). However, macroalgae-exclusive fish densities were significantly greater on lagoonal macroalgae patches than embedded patches (F_3 = 3.43, p = 0.03; Fig. 4b).

Key predictors of macroalgae-associated fish community structure

The relative importance of seascape variables was dependent on whether species identity was taken into account when predicting labrid fish community structure. For emergent properties of community structure, and functional group structure, seascape variables were consistently overridden by within-patch variables, both in terms of the overall best models and the summed model weights (Table 3.2a, b, Fig. 3.5a, b). However, a combination of both seascape and within-patch variables were found to be important predictors of assemblage structure across life-history stages (Table 2c, d, Fig. 5c, d). Notably, patch area was among the poorest predictors of labrid diversity and assemblage structure in terms of AICc sum weights (Fig. 3.5).

Variation in the emergent properties of fish community structure were best predicted by a combination of three within-patch variables: canopy macroalgae cover, live coral cover and hard complexity (Table 3.2a, S3.4). Both alpha diversity and species evenness showed a strong positive correlation with these variables, while beta diversity showed a weak negative correlation (Fig. 3.6). When taking a functional approach and arranging the fish community into trophic groups, we found that the most parsimonious model showed macroalgae canopy height and live coral cover best predicted functional group assemblage structure (Table 3.2b, S3.5). Here, increases in live coral cover were positively correlated with increased densities of

Table 3.2. Top and most parsimonious (bolded) models of multi-scale predictors for fish community structure within the macroalgal patch network at Ningaloo Reef in terms of (a) fish diversity and evenness, (b) functional trophic groups, and (c) adult and (d) juvenile life-history stages.

Model	∆AICc	r^2
a) Diversity Metrics		
%Canopy macroalgae, %live coral	**0.00**	**0.40**
%Canopy macroalgae, hard complexity	**1.31**	**0.37**
b) Functional Groups		
Hard complexity, canopy height, coral connectivity (500m)	0.00	0.52
Canopy height, %coral	**0.98**	**0.45**
c) Adults		
Canopy height, hard complexity, coral connectivity (500m)	0.00	0.40
Hard complexity, coral connectivity (500m)	**0.27**	**0.34**
Hard Complexity, reef distance	**1.57**	**0.30**
Hard complexity, coral connectivity (150m)	**1.63**	**0.30**
%Coral, coral connectivity (500m)	**1.68**	**0.30**
d) Juveniles		
Adult density, hard complexity, coral connectivity (500m)	0.00	0.38
%Coral	**1.53**	**0.22**

scraping/excavating herbivores, piscivores and ectoparasitivores, while canopy height was negatively correlated with densities of browsing herbivores (Fig. S3.3a, b). Other within-patch variables such as percent cover of canopy-forming macroalgae, and hard complexity also had high summed model weights (Fig. 3.5b).

Key predictors for taxonomic (species-level) fish community structure included local-scale, seascape-scale and biotic variables, which differed according to life-history stage. For adult fishes, we found a number of competing models best explained variation among

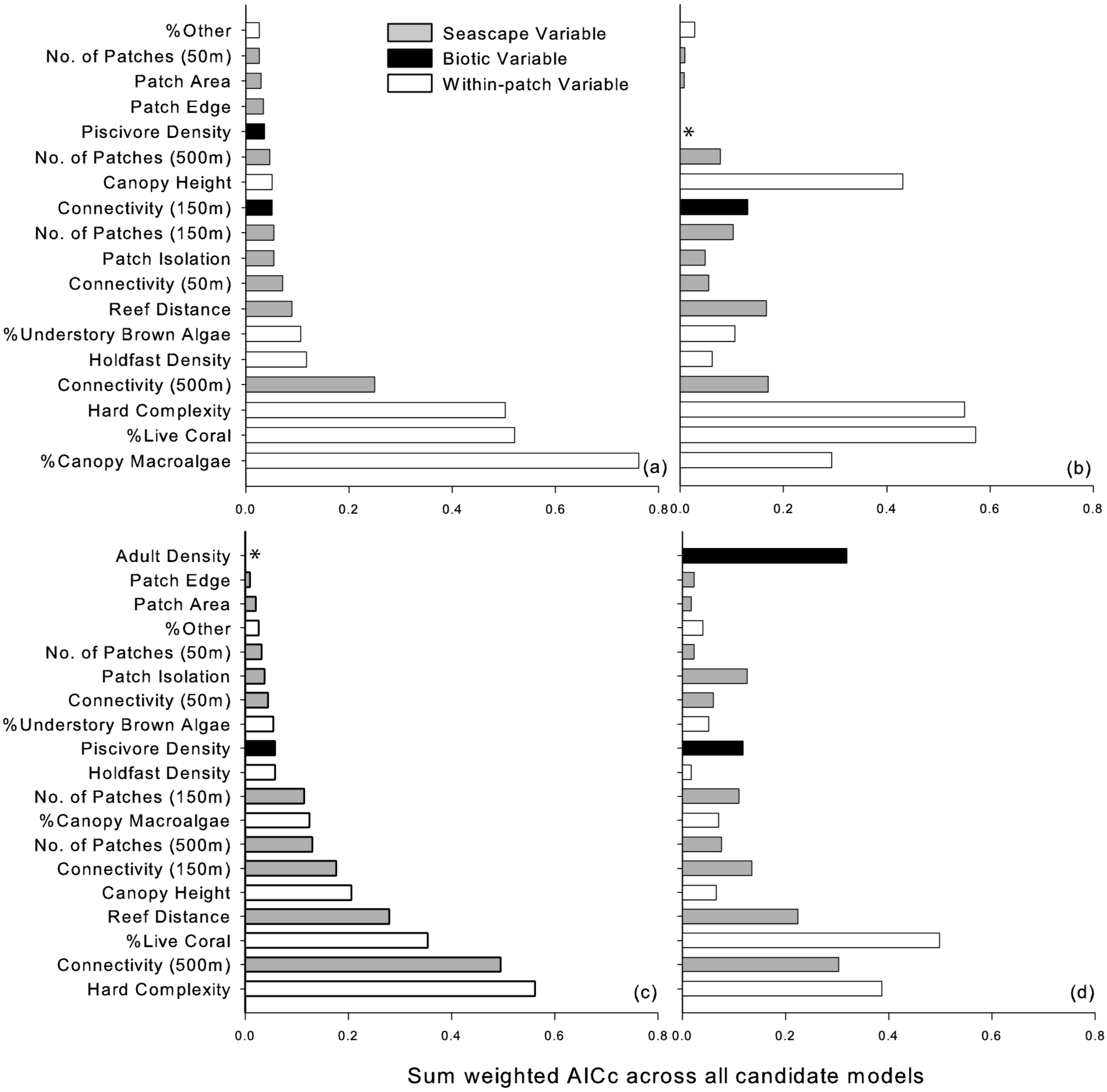

Figure 3.5. Summed model weights for all variables considered as predictors in best-subsets model selection for fish (a) diversity metrics, (b) functional group structure, (c) adult community structure, and (d) juvenile community structure. The ‘*’ indicates variables that were not included in that particular model selection.

macroalgal-dominated sites, which included the predictors of hard complexity, coral connectivity (at both 500m and 150m scales), linear distance to coral reef, and percentage cover of live coral (Table 3.2c, S3.6). Hard complexity and coral connectivity at the 500m scale had the highest summed model weights (Fig. 3.5c). All of these predictors were correlated with the main axis of variation in fish community structure across dbRDA1 (Fig. S3.3c, d). For juveniles, the most parsimonious model included the single predictor of live coral cover (Table

3.2d, S3.7) which had a strong positive correlation with the densities of many coral-affiliated juvenile labrids (Fig. S3.3e, f). However, densities of adult fish, hard complexity and coral connectivity (at the 500m scale) were of broad importance, each having a higher summed model weight than live coral cover (Fig. 3.5d).

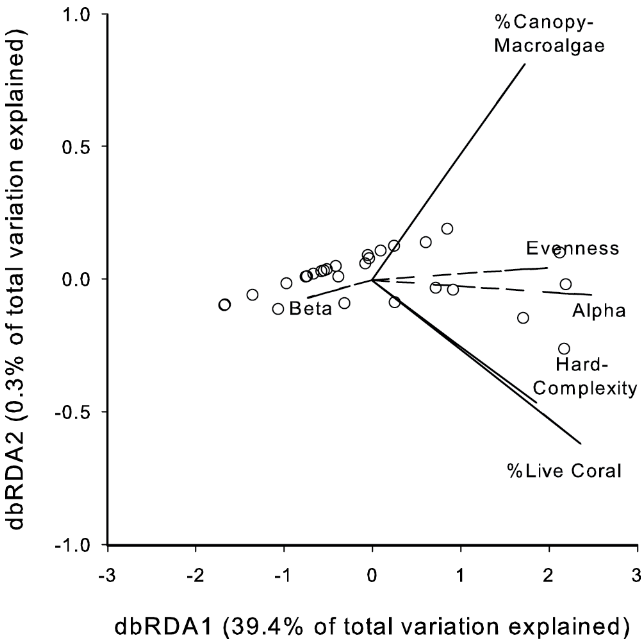

Figure 3.6. Distance-based redundancy analysis (dbRDA) from the best-subsets model for explaining emergent fish community structure across macroalgal patch sites. Dashed-line vectors emergent community properties, while solid-line vectors indicate strength and direction of variables from the most parsimonious models (Table 3.2).

Discussion

Heterogeneous landscapes are a feature of both terrestrial and aquatic systems, where habitats of varying quality and proximity are available for animals to utilise throughout their life-history. Here, we found the proximity of a patch to other macroalgal or coral patches was important for some aspects of fish community structure. However, local (within-patch) habitat condition appeared to be the main predictor(s) for emergent patterns of fish community structure across a tropical seascape. While confirming the importance of structural habitat connectivity (Grober-Dunsmore et al. 2007; Olds et al. 2012; Henderson et al. 2017), our findings also indicate the primary influence of local habitat conditions on a diverse tropical fish community. Despite this, we found no support for local patch area being a key predictor, which lends support to the notion that it is habitat quality, not quantity, that underpins fish community structure and stability (Fahrig 2013). Given the temporally dynamic nature of these macroalgae patch habitats and their sensitivity to climatic forcing by sea surface temperature (Fulton et al. 2014), these findings have important ramifications for how we monitor and adaptively manage our tropical coastal ecosystems.

Soft canopy complexity at the local scale (e.g., canopy cover, height and holdfast density) is now recognised to be a key habitat feature that underpins patterns of fish abundance, biomass and diversity in a range of marine biomes (Levin and Hay 1996; Wilson et al. 2014; van Lier et al. 2017). Our findings reinforce the value of canopy structure, and highlight the added importance of the underlying hard substratum complexity for fish. Indeed, the combination of underlying hard complexity and soft canopy structure can increase the abundance of microhabitat types in a local area to allow for the coexistence of a greater number of species via niche partitioning (Hardin 1960; Hortal et al. 2009). In this context, biogenic habitat created by canopy-forming macroalgae, corals and other organisms creates complex physical space for both fish and their prey to occupy within a patch (Tano et al. 2016), such that increases in canopy extent (area + height) have been closely correlated with changes in the abundance of reef fishes over space and time (Lim et al. 2016; Wenger et al. 2018). Similarly, complex structure in the underlying substratum can also provide niche spaces for other species that do not utilise the biogenic canopy (Tuya et al. 2009). Indeed, hard complexity addition experiments have found rapid and significant increases in abundance and/or richness of fishes in other macrophyte habitats such as seagrass beds (Cheminée et al. 2016; Cuadros et al. 2017). When these two elements of microhabitat complexity are maximised, then high levels of species packing can occur within a patch habitat, regardless of whether it may be one of the largest or smallest patches within a seascape. Future studies in soft-structure environments should therefore include some measure of hard complexity, as it appears to be another important component of local habitat quality.

At the seascape scale, our findings emphasise the importance of mesohabitat connectivity and proximity for increased fish community diversity and abundance within a patch habitat, which is consistent with studies in both marine and terrestrial systems (Grober-Dunsmore et al. 2007; Shanahan et al. 2011; Berkström et al. 2013; Michael et al. 2017). High levels of connectivity should facilitate the active movement of fishes at different life history stages, as well as transient adult fishes that may move between patches to exploit a range of resources. Davis et al. (2014) found several coral-associated fishes would access mangrove and seagrass mesohabitats to augment their diet (up to 44-78% depending on the species), with higher contributions being correlated with the proximity of these mesohabitats. We extend these effects to macroalgae patches within a coral reef setting, where habitat generalists (fishes able to exploit a wider range of niche space) exhibit significantly higher densities in macroalgae-dominated patches with the most structural connectivity to coral-dominated reef. Indeed, two of the more abundant fishes observed in our study (*Thalassoma lunare* and *Thalassoma lutescens*) were highly correlated with sites that had greater structural connectivity. Notably, this genera of fishes combine efficient swimming with trophic versatility (Fulton et al. 2017), which allows them to range between mesohabitats in order to exploit a diverse prey set (Kramer et al. 2015). These two species are exemplars of the many labrid fishes that are generalist feeders (Kramer et al. 2015) who respond positively to well connected, complex seascapes (Staveley et al. 2016).

Both coral and macroalgae-dominated patches are important fish nursery habitats (Wilson et al. 2010; Evans et al. 2014; Eggertsen et al. 2017), with some juvenile fishes (e.g., *Cheilio inermis, T. lunare*) showing strong or exclusive preference to one mesohabitat before ontogenetic shifts in habitat use occur (Wilson et al. 2010). Given that self-replenishment and retention of larvae from adjacent reefs is common (Green et al. 2015; Brown et al. 2016), it follows that structural connectivity was also an important predictor of juvenile community structure. Increased structural connectivity is likely to facilitate short-range dispersal by simultaneously reducing the amount of time exposed to predators, and increasing the likelihood of encountering suitable habitat for settlement.

Patch area had emerged from studies into Island Biogeography Theory (MacArthur and Wilson 1963) as key predictor of community structure and recovery from disturbance. However, in this tropical seascape, we found patch area to be one of the poorest predictors of fish diversity and community structure, regardless of life history stage or trophic group. In stark contrast to a number of terrestrial studies that find patch area to be an important predictor of diversity (Garden et al. 2010; Shanahan et al. 2011), the significance of patch size for patterns of diversity appears to be largely dependent on the focal mesohabitat. In a recent review on reef fish communities, Boström et al. (2011) found a largely positive relationship between the area of a coral reef and fish diversity, as opposed to 75% of insignificant effects of patch size on seagrass-associated communities. Our examination of macroalgae patch size and fish diversity seems to align with other soft complexity habitats in there being no demonstrable effect of patch size across the ranges examined here (>700 m^2. Instead, our findings lend support to the recent Habitat Amount Hypothesis (Fahrig 2013), which predicts that species richness increases as a function of total available mesohabitat within a given area, rather than as a function of the area of the local patch. Empirical studies testing this hypothesis have been equivocal, with support both for (Melo et al. 2017; Rabelo et al. 2017) and against (Haddad et al. 2017). Given this hypothesis' importance to the study of landscape ecology, and the potential to overturn existing paradigms which influence how conservation reserves are structured (e.g., Single Large Or Several Small debate), we think this is an important avenue for future research.

In looking across biomes, we find commonality in the interplay of structural connectivity among patch habitat types and local habitat conditions for shaping the spatial structure of motile animal communities. In tropical ecosystems, where there are often exceptionally high levels of diversity and specialisation, the overlap of sources (i.e. other patches of similar or different habitats) with high microhabitat complexity appear to underpin areas of high abundance and diversity. As such, we suggest moving towards a more nuanced consideration of patch habitats in spatial management and conservation designs – one that does not simply consider the broad type and area, but the combination of within-patch and landscape contexts that best meet management goals. If the objective is to maximise local richness, then patches with high structural connectivity, hard complexity and canopy cover should be given priority. However, to maximise regional diversity a range of appropriate patches need to be identified that will be suitable for different groups of fish (e.g., macroalgae exclusive fish reliant on quality soft-structure variables, less so on connectivity or hard complexity). Given the dynamic nature of habitats formed by climatically-sensitive macrophytes, such as macroalgae, there is plenty of scope to explore the various landscape and within-patch factors that may underpin the resistance and resilience of these ecological communities. Moreover, there is a need for landscape studies to start exploring how ecological processes that underpin ecosystem function, such as herbivory and piscivory, respond to these heterogeneous habitat mosaics.

Supplementary Materials

Table S3.1. List of labrid species observed in the study, with corresponding functional role, estimated juvenile size limits, and estimated (based on Nash et al. 2015) maximum home range size for the largest individual encountered in our study region.

Species	Functional Group	Juvenile Length (mm)	Home Range (m)
Anampses caeruleopunctatus	General Zoobenthivore[11]	110□	1407.95
Anampses geographicus	General Zoobenthivore[11]	70□	436.06
Anampses meleagrides	General Zoobenthivore[11]	70□	91.65
Cheilinus bimaculatus	Macrozoobenthivore[11]	50□	0.15
Cheilinus chlorourus	Macrozoobenthivore[11]	110□	255.28
Cheilinus trilobatus	Macrozoobenthivore[11]	130□	3831.84
Cheilio inermis	Piscivore[5]	160□	72997.9
Chlorurus microrhinos	Excavating Herbivore[4]	160□	31.8
Chlorurus spilurus	Excavating Herbivore*[6]	160□	10694.8
Choerodon rubescens	General Zoobenthivore[11]	270[8]	27.03
Choerodon schoenleinii	General Zoobenthivore[11]	260[9]	1191811.32
Coris auricularis	General Zoobenthivore[11]	100□	55.32
Coris aygula	General Zoobenthivore[11]	150□	32390.61
Coris caudimacula	General Zoobenthivore[11]	53[12]	322.08
Epibulus insidiator	Macrozoobenthivore[11]	90□	2144.78
Gomphosus varius	Macrozoobenthivore[11]	65[2]	1389.38
Halichoeres brownfieldi	Microzoobenthivore[11]	65□	16.86
Halichoeres margaritaceus	Microzoobenthivore[11]	40□	16.86
Halichoeres nebulosus	Microzoobenthivore[11]	40□	36.89
Halichoeres trimaculatus	Microzoobenthivore[11]	30□	21.28
Hemigymnus fasciatus	General Zoobenthivore[11]	160□	2085.87
Hemigymnus melapterus	General Zoobenthivore[11]	150□	9091.7
Hipposcarus longiceps	Scraping Herbivore[3]	200□	3902.02
Hologymnosus annulatus	Piscivore[5]	60□	91649.54
Labrichthys unilineatus	Corallivore[7]	45[7]	29.54
Labroides bicolour	Ectoparasitivore[1]	25[13]	1.76
Labroides dimidiatus	Ectoparasitivore[10]	40[13]	3.19
Leptoscarus vaigiensis	Browsing Herbivore[4]	60[14]	4721.17
Macropharyngodon ornatus	Microzoobenthivore[17]	40□	24.64
Pseudojuloides elongatus	Microzoobenthivore[1]	40□	6.12
Pteragogus flagellifera	Microzoobenthivore	40□	132.18
Scarus chameleon	Scraping Herbivore[4]	100□	5292.43
Scarus frenatus	Scraping Herbivore[16]	150□	15304.51
Scarus ghobban	Scraping Herbivore*[16]	253[16]	2137.38
Scarus prasiognathus	Scraping Herbivore[3]	230□	1661.71
Scarus psittacus	Scraping Herbivore[16]	100□	79.95
Scarus rivulatus	Scraping Herbivore[4]	130□	10192.32

Scarus rubroviolaceus	Scraping Herbivore[4]	230[□]	3902.53
Scarus schlegeli	Scraping Herbivore*[6]	70[□]	7469.06
Stethojulis bandanensis	Microzoobenthivore[11]	55[15]	31.93
Stethojulis interrupta	Microzoobenthivore[11]	45[□]	13.49
Stethojulis strigiventer	Microzoobenthivore[11]	40[□]	42.45
Thalassoma hardwicke	General Zoobenthivore[11]	65[□]	42.47
Thalassoma lunare	General Zoobenthivore[11]	80[15]	12423.38
Thalassoma lutescens	Macrozoobenthivore*[11]	65[2]	270.04
Xenojulis margaritaceus	Macrozoobenthivore[17]	40[□]	25.32

*Denotes species that undergo substantial ontogenetic shifts in their trophic category. Adult grouping shown.

[□] Denotes species where juvenile length was unavailable and so was estimated at a third their max body size (Nagelkerken and van der Velde 2002).

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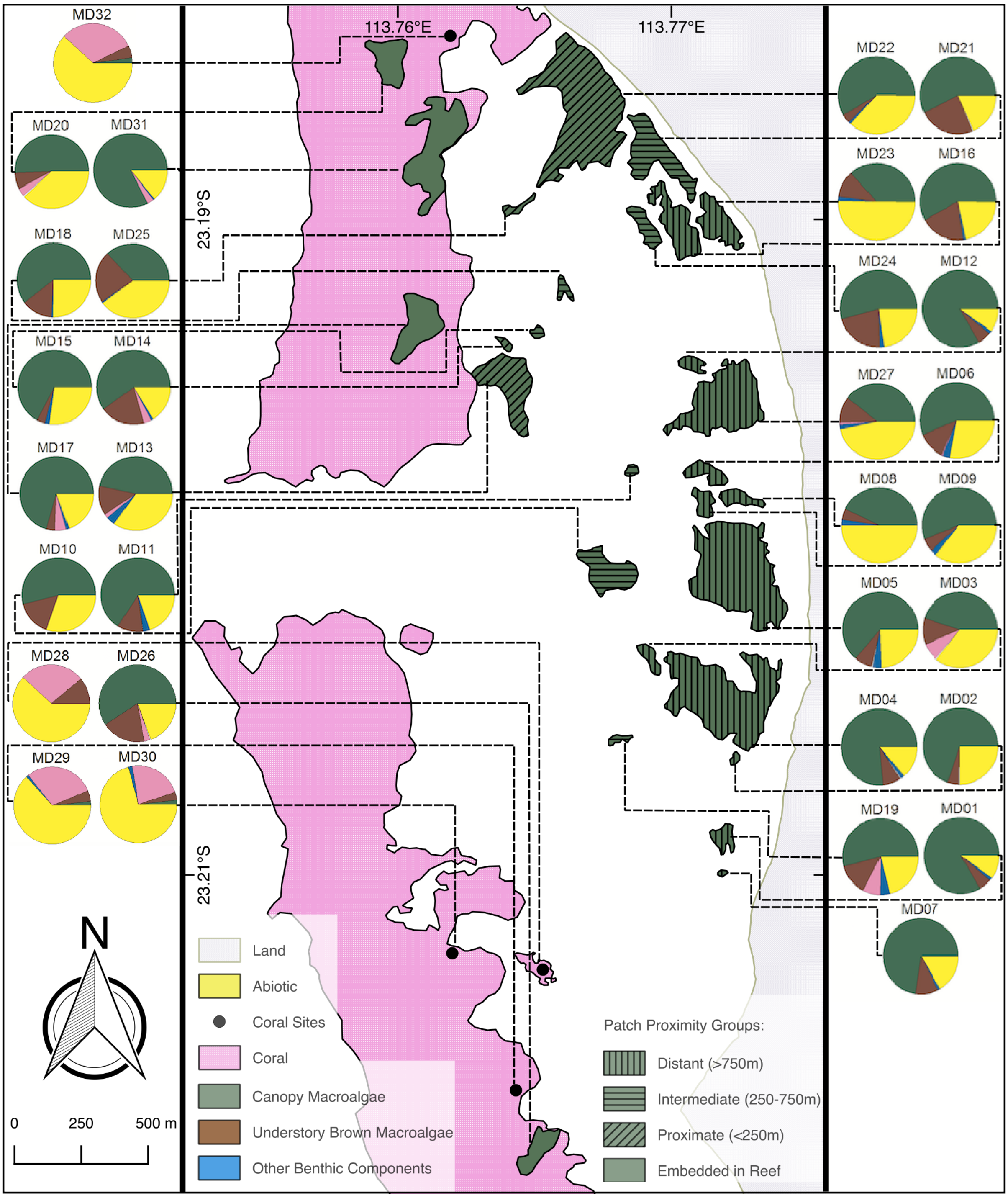

Figure S3.1. Map of the study region within the Ningaloo Marine Park near Coral Bay, Western Australia, with mean percent cover of benthic microhabitat categories and fringing reef-distance indicated for each macroalgal patch site

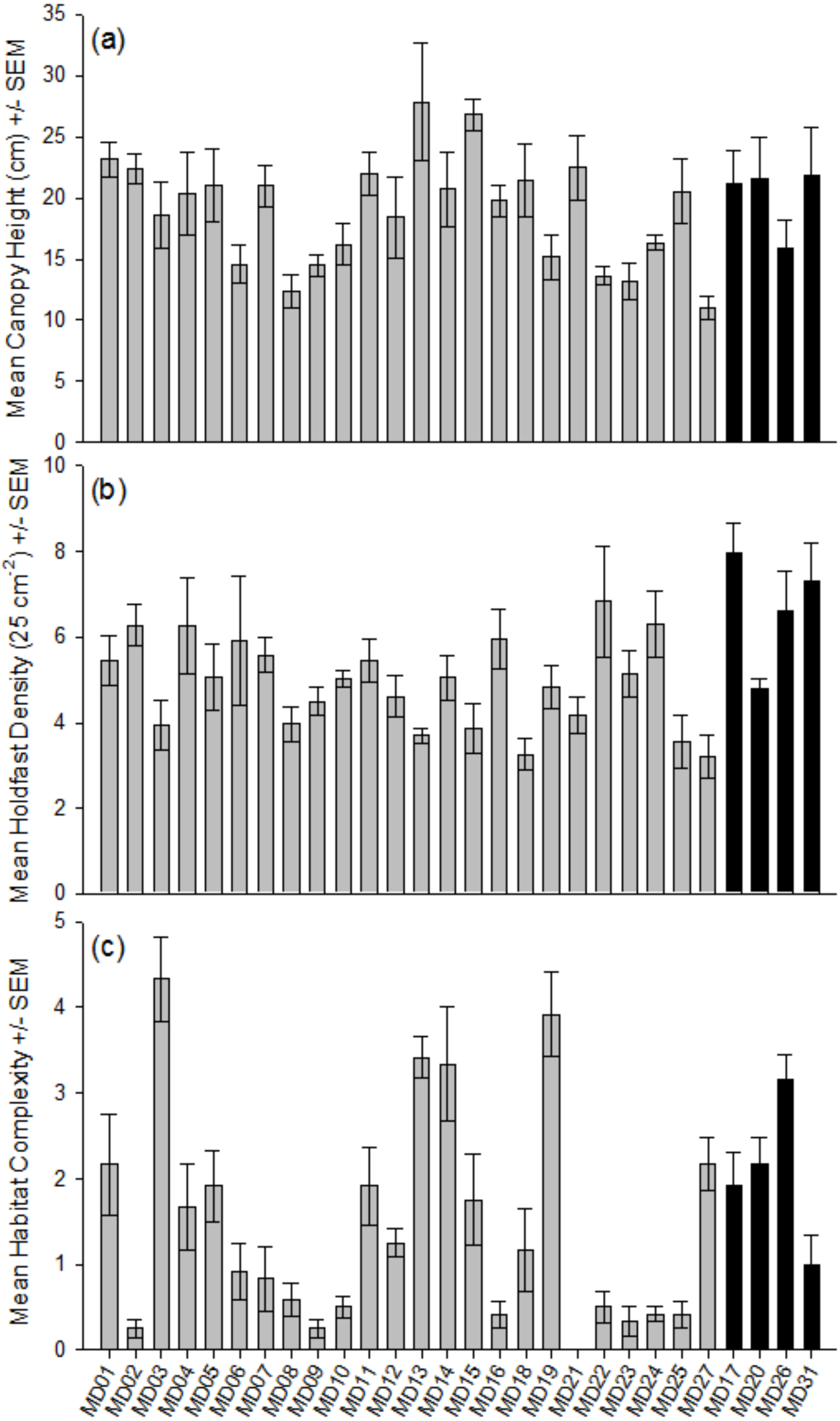

Figure S3.2. Mean canopy-forming macroalgae heights (a), holdfast densities (b) and hard substratum habitat complexity (c) across 28 macroalgae patch sites near Coral Bay, Ningaloo Marine Park. Grey bars indicate sites in the lagoon, while black indicates macroalgae patch sites embedded within the fringing coral-dominated reef.

Table S3.2. Summary of nested PERMANOVA comparing habitat structure between mesohabitats, and among patch sites within each mesohabitat.

Source	df	SS	MS	Pseudo-F	p-value
Mesohabitat	1	488.22	488.22	35.11	<0.01
Site(Mesohabitat)	30	417.22	13.91	3.57	<0.01
Residual	160	622.56	3.89		
Total	191	1528			

Table S3.3. Results from the Similarity Percentages (SIMPER) analysis for both (a) macroalgae and (b) coral mesohabitats. Average similarity based on Bray-Curtis similarity and the percentage of contribution for each species (up to 70% of the overall community).

Mesohabitat	Species	Average Similarity	Percentage of Contribution
a) Macroalgae	*Coris caudimacula*	7.50	16.93
	Pseudojuloides elongatus	6.91	15.59
	Stethojulis interrupta	5.41	12.20
	Halichoeres nebulosus	5.40	12.19
	Chelio inermis	4.39	9.90
	Leptoscarus vaigiensis	4.13	9.32
b) Coral	*Chlorurus spilurus*	18.77	27.59
	Thalassoma lutescens	9.08	13.35
	Stethojulis bandanensis	7.20	10.58
	Thalassoma lunare	6.75	9.93
	Scarus frenatus	4.16	6.11
	Scarus spp.	2.70	3.97

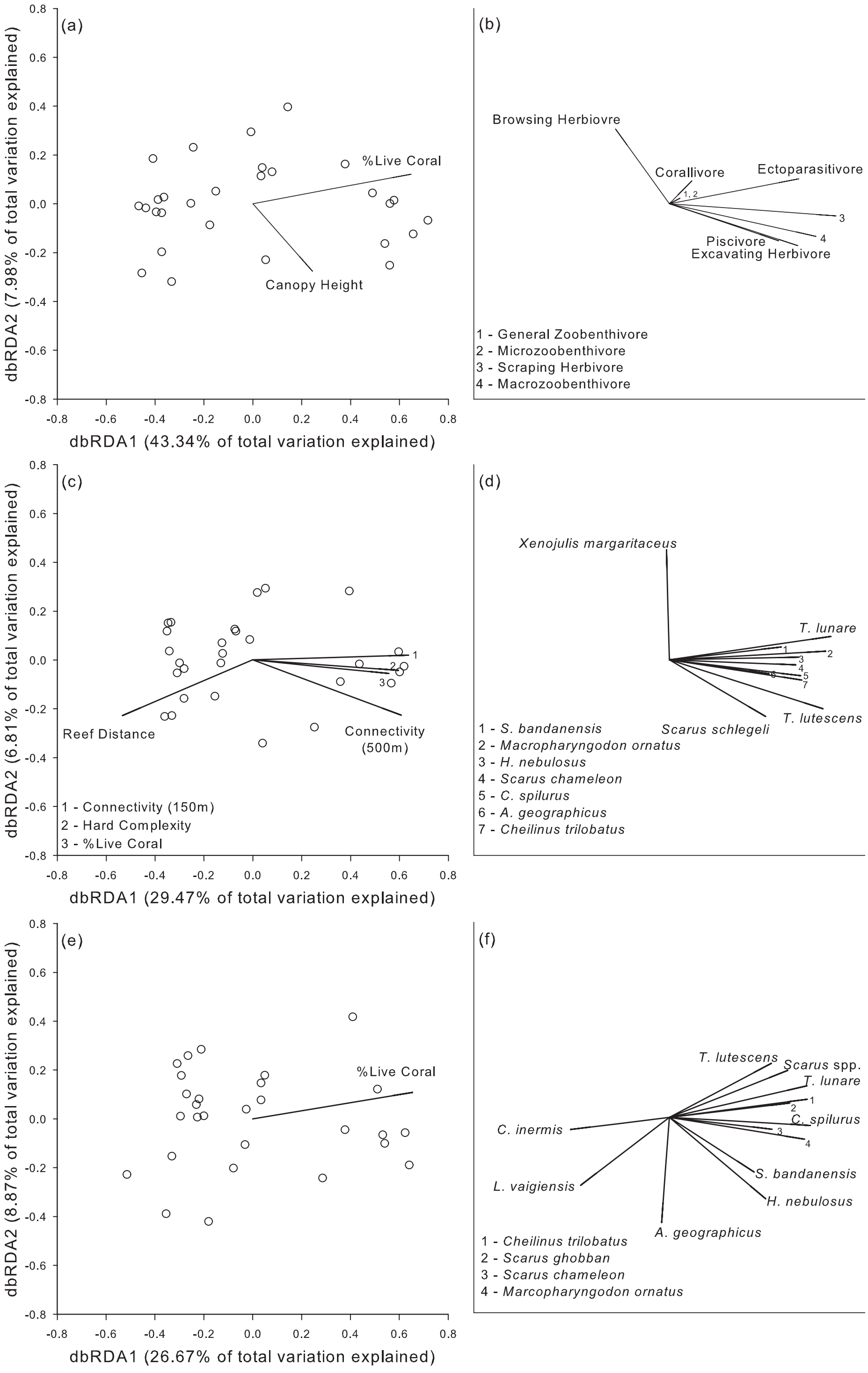

Figure S3.3. Distance-based redundancy analysis (dbRDA) ordination of the most parsimonious models (left column) and vector plots (right colum) for species using Pearson's R. Functional groups (a, b), adult fish community (c, d), juvenile fish community (e, f).

Table S3.4. Summary of the best-subsets selection models explaining variation in diversity metrics within macroalgal habitat type in Ningaloo Lagoon. Models shown are within 2 AICc of the top model, with the most parsimonious in bold having the fewest explanatory variables.

Model	AICc	ΔAICc	r^2
%Canopy Macroalgae, %Live Coral	**22.55**	**0.00**	**0.40**
%Canopy Macroalgae, %Understory Brown Algae, %Live Coral	22.57	0.02	0.45
%Canopy Macroalgae, Hard Complexity, Coral Connectivity (500m)	22.64	0.09	0.45
%Canopy Macroalgae, Coral Connectivity (500m), %Live Coral	23.00	0.45	0.44
%Canopy Macroalgae, %Live Coral, Reef Distance	23.50	0.95	0.43
%Canopy Macroalgae, Hard Complexity	**23.86**	**1.31**	**0.37**
Hard Complexity, Coral Connectivity (500m), Holdfast Density	24.15	1.60	0.42
%Canopy Macroalgae, Hard Complexity, %Understory Brown Algae	24.18	1.63	0.42
%Canopy Macroalgae, %Live Coral, Number of Patches (500m)	24.20	1.65	0.42
%Canopy Macroalgae, Hard Complexity, %Live Coral	24.32	1.77	0.42
Hard Complexity, Coral Connectivity (500m), Reef Distance	24.36	1.81	0.42
%Canopy Macroalgae, Coral Connectivity (50m), %Live Coral	24.38	1.83	0.42
%Canopy Macroalgae, %Live Coral, Patch Isolation	24.38	1.83	0.42
%Canopy Macroalgae, Piscivore Density, %Live Coral	24.39	1.84	0.42
Canopy Height, %Canopy Macroalgae, %Live Coral	24.39	1.84	0.42
%Canopy Macroalgae, Coral Connectivity (150m), %Live Coral	24.40	1.85	0.42
%Canopy Macroalgae, %Live Coral, Number of Patches (150m)	24.43	1.88	0.42
%Canopy Macroalgae, %Live Coral, Patch Edge	24.47	1.92	0.42

Table S3.5. Summary of the best-subsets selection models explaining variation in functional community structure within macroalgal habitat type in Ningaloo Lagoon. Models shown are within 2 AICc of the top model, with the most parsimonious in bold having the fewest explanatory variables.

Model	AICc	ΔAICc	r^2
Canopy Height, Hard Complexity, Coral Connectivity (500m)	-40.32	0.00	0.52
Canopy Height, Hard Complexity, %Live Coral	-39.80	0.52	0.52
Canopy Height, %Canopy Macroalgae, %Live Coral	-39.34	0.87	0.51
Canopy Height, %Live Coral	**-39.34**	**0.98**	**0.45**
Canopy Height, Hard Complexity, Coral Connectivity (150m)	-39.33	0.99	0.50
Canopy Height, %Understory Brown Algae, %Live Coral	-39.27	1.05	0.50
Canopy Height, %Live Coral, Reef Distance	-39.26	1.06	0.50
Canopy Height, Hard Complexity, Reef Distance	-39.17	1.15	0.49
Canopy Height, Coral Connectivity (150m), %Live Coral	-38.89	1.43	0.49
Canopy Height, %Live Coral, Patch Isolation	-38.71	1.61	0.49
Canopy Height, %Live Coral, Number of Patches (150m)	-38.46	1.87	0.48
Canopy Height, %Live Coral, Number of Patches (500m)	-38.44	1.89	0.48
Canopy Height, Coral Connectivity (50m), %Live Coral	-38.38	1.95	0.48
Canopy Height, %Live Coral, %Other	-38.35	1.97	0.48
Canopy Height, Coral Connectivity (500m), %Live Coral	-38.35	1.97	0.48

Table S3.6. Summary of best-subsets models explaining variation in adult labrid fish community structure within macroalgal habitat type in Ningaloo Lagoon. Models shown are within 2 AICc of the top model, with the most parsimonious indicated in bold.

Model	AICc	ΔAICc	r^2
Canopy Height, Hard Complexity, Coral Connectivity (500m)	-32.10	0	0.40
%Canopy Macroalgae, Hard Complexity, Coral Connectivity (500m)	-32.07	0.03	0.40
Hard Complexity, Coral Connectivity (500m)	**-31.83**	**0.27**	**0.34**
Hard Complexity, Coral Connectivity (500m), Number of Patches (500m)	-31.82	0.28	0.39
Canopy Height, Hard Complexity, Reef Distance	-31.16	0.94	0.38
Hard Complexity, Coral Connectivity (500m), %Understory Brown Algae	-31.04	1.07	0.38
Canopy Height, %Live Coral, Reef Distance	-30.95	1.15	0.38
Hard Complexity, Coral Connectivity (500m), Number of Patches (150m)	-30.93	1.18	0.38
Hard Complexity, Coral Connectivity (500m), Holdfast Density	-30.83	1.27	0.38
Canopy Height, Coral Connectivity (500m), %Live Coral	-30.65	1.46	0.37
Canopy Height, Hard Complexity, Coral Connectivity (150m)	-30.64	1.47	0.37
Hard Complexity, Reef Distance	**-30.54**	**1.57**	**0.30**
%Live Coral, Reef Distance	**-30.48**	**1.63**	**0.30**
Hard Complexity, Coral Connectivity (150m)	**-30.43**	**1.68**	**0.30**
Hard Complexity, Coral Connectivity (500m), %Live Coral	-30.41	1.70	0.30
Coral Connectivity (500m), %Live Coral	-30.39	1.71	0.30
%Canopy Macroalgae, Coral Connectivity (500m), %Live Coral	-30.37	1.74	0.36
%Canopy Macroalgae, Hard Complexity, Reef Distance	-30.32	1.78	0.36
%Canopy Macroalgae, Hard Complexity, Coral Connectivity (150m)	-30.31	1.80	0.36
Hard Complexity, Reef Distance, Number of Patches (500m)	-30.26	1.85	0.36
%Canopy Macroalgae, %Live Coral, Reef Distance	-30.23	1.88	0.36
Hard Complexity, Coral Connectivity (500m), Reef Distance	-30.17	1.94	0.36
Hard Complexity, Coral Connectivity (500m), Piscivore Density	-30.12	1.98	0.36

Table S3.7. Summary of the best-subsets selection models explaining variation in juvenile labrid fish community structure within macroalgal habitat type in Ningaloo Lagoon. Models shown are within 2 AICc of the top model, with the most parsimonious in bold having the fewest explanatory variables.

Model	AICc	ΔAICc	r^2
Habitat Complexity, Coral Connectivity (500m), Adult Density	-27.38	0.00	0.38
Adult Density, %Live Coral, Reef Distance	-26.88	0.5	0.37
Coral Connectivity (500m), Adult Density, %Live Coral	-26.63	0.75	0.37
Adult Density, %Live Coral	-26.57	0.81	0.30
Hard Complexity, Coral Connectivity (500m)	-26.44	0.94	0.30
Hard Complexity, Coral Connectivity (500m), Reef Distance	-26.37	1.01	0.36
%Live Coral, Reef Distance	-26.28	1.10	0.29
Coral Connectivity (500m), %Live Coral	-26.11	1.27	0.29
Hard Complexity, Coral Connectivity (150m), Adult Density	-26.06	1.32	0.35
Adult Density, %Live Coral, Number of Patches (150m)	-25.98	1.40	0.35
Piscivore Density, Adult Density, %Live Coral	-25.98	1.40	0.35
Hard Complexity, Adult Density, Reef Distance	-25.95	1.44	0.35
Coral Connectivity (150m), Adult Density, %Live Coral	-25.90	1.48	0.35
%Live Coral	**-25.85**	**1.53**	**0.22**
Hard Complexity, Coral Connectivity (500m), Number of Patches (500m)	-25.81	1.57	0.35
Hard Complexity, Coral Connectivity (500m), Piscivore Density	-25.81	1.57	0.35
Canopy Height, Adult Density, %Live Coral	-25.74	1.64	0.35
%Canopy Macroalgae, Hard Complexity, Coral Connectivity (500m)	-25.74	1.64	0.35
%Canopy Macroalgae, Adult Density, %Live Coral	-25.71	1.67	0.35
Hard Complexity, Coral Connectivity (500m), Adult Density	-25.68	1.70	0.35
Canopy Height, Hard Complexity, Coral Connectivity (500m)	-25.63	1.75	0.34
%Live Coral, Reef Distance. Number of Patches (150m)	-25.59	1.79	0.34
Hard Complexity, Piscivore Density, Adult Density	-25.52	1.86	0.34
Adult Density, %Live Coral, Number of Patches (500m)	-25.52	1.86	0.34
Hard Complexity, Coral Connectivity (500m), Number of Patches (150m)	-25.51	1.87	0.34
Adult Density, %Understory Brown Algae, %Live Coral	-25.49	1.89	0.34
Coral Connectivity (50m), Adult Density, %Live Coral	-25.48	1.90	0.34
Coral Connectivity (500m). %Live Coral, Reef Distance	-25.47	1.91	0.34
%Live Coral, Number of Patches (150m)	-25.46	1.92	0.27
%Canopy Macroalgae, Hard Complexity, %Live Coral	-25.44	1.94	0.34
%Canopy Macroalgae, %Live Coral, Reef Distance	-25.43	1.95	0.34
Coral Connectivity (500m), %Live Coral, Number of Patches (150m)	-25.40	1.98	0.34
Hard Complexity, Adult Density, %Live Coral	-25.39	1.99	0.34
Coral Connectivity (150m), %Live Coral	-25.39	1.99	0.27

Chapter 4

Unseasonal decline in habitat quality has lasting effects on tropical macroalgal fish communities

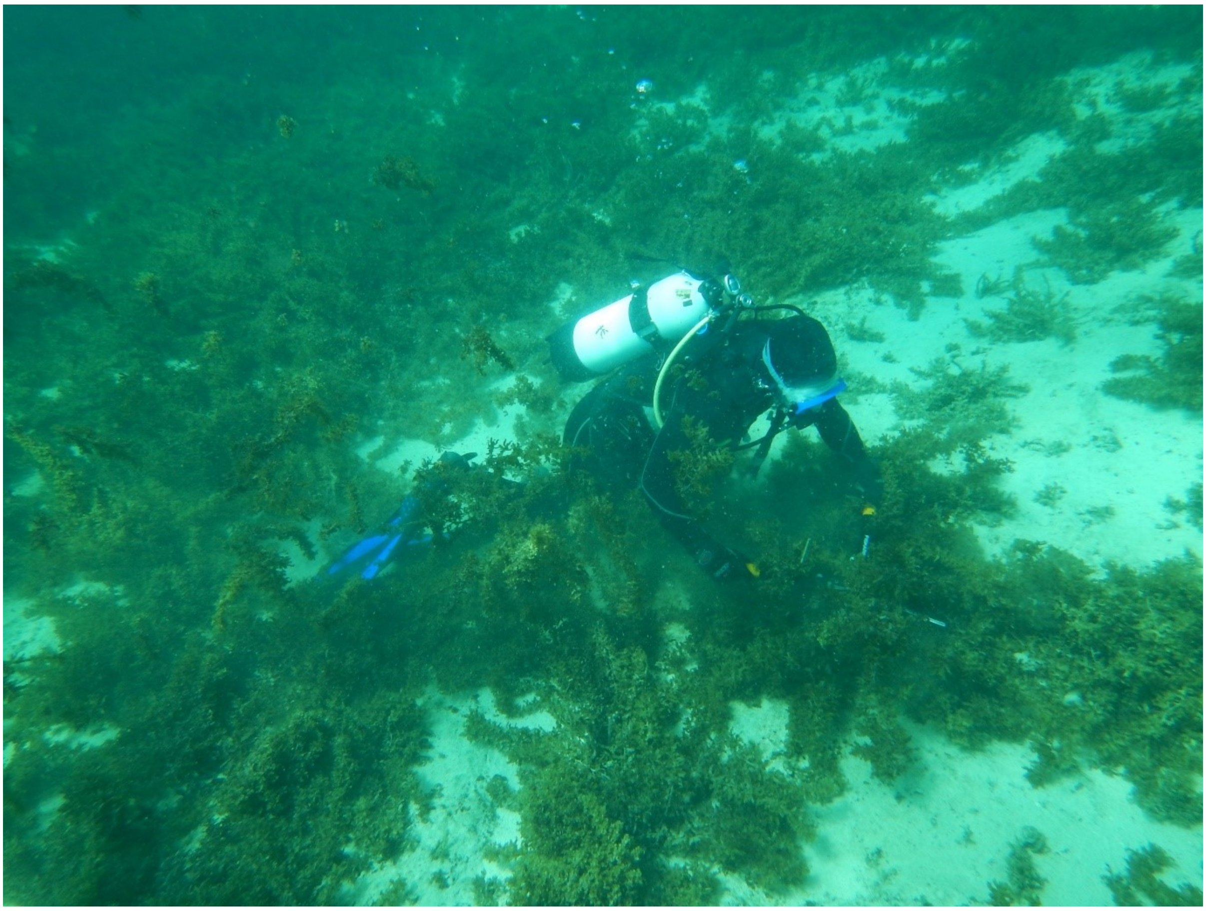

Photo credit: Lucy Wenger

Abstract: Coastal marine habitats are vulnerable to environmental and anthropogenic disturbances which affect their capacity to support reef fishes. Tropical macroalgal fields are important habitat for reef fish, with recent observational studies indicating canopy structure of *Sargassum* meadows is a strong predictor of fish abundance and diversity. However, the influence of disturbance on this habitat and associated fish community structure is poorly understood. Here, we experimentally halved the canopy height of *Sargassum* meadows within the Ningaloo Marine Park and investigate the impact on fish community composition and size-class structure. We assessed short- (days), medium- (months) and long-term (years) responses of labrid fish and their putative predators to this unseasonal loss of canopy height. Relative to nearby reference sites, the experimental meadows had significant reductions in fish species richness and abundance within five days of the experimental manipulation. Although the *Sargassum* canopy had fully recovered two years later, height of some macroalgal taxa (e.g., *Sargassopsis*) remained lower than expected, and some fish species continued to show reduced abundances in experimental meadows. Our results demonstrate that even a moderate macroalgal canopy height reduction can drive change in fish community structure of tropical seascapes, and that unseasonal disturbances can have lasting effects upon fish biodiversity.

Introduction: The severity and frequency of disturbance events are fundamental drivers of the structure and trajectory of natural ecological communities (Connell 1978; Sousa 1979). While all ecosystems experience disturbance events to varying degrees (Turner et al. 2003), it is important to understand a community's resilience to change in context with their disturbance regime. When a disturbance regime follows a predictable pattern (e.g., seasonal cycle), an associated community tends to show high resilience (Wilson et al. 2014; Bogan et al. 2015). However, increases in the frequency of severe climate-related disturbances (e.g., unseasonal cyclones, marine heatwaves; Knutson et al. 2010; Hughes et al. 2018; Oliver et al. 2018) may disrupt cycles of community succession in ways that compromise their capacity to fully recover from one disturbance before being faced with the next (Connell 1978; Sousa 1979).

In coastal marine habitats, one way in which disturbance events can affect an ecological community is by altering the physical structure of the local habitat. For example, coral bleaching events caused by thermal stress can lead to the rapid breakdown of coral skeletons decreasing three-dimensional hard complexity (Graham et al. 2006), while increased wave intensity from storms can cause the partial or total destruction of habitat-forming hard corals (Walsh 1983). The lack of hard complexity then reduces suitable refugia, altering the behaviour of fish predator-prey interactions (Beukers and Jones 1997), which can lead to declines in fish abundance and the local extinction of common fishes in the short-term (Pratchett et al. 2006; Darling et al. 2017; Boström-Einarsson et al. 2018). Worryingly, the long-term outlook in the mesohabitat can also be dire. Assessment of small-sized crypto-benthic fish communities following a mass bleaching event found that the community structure had undergone a fundamental shift which persisted over the ensuing years (Bellwood et al. 2006a; Bellwood et al. 2012). The three-dimensional complexity of soft-structure habitat, such as seagrass or macroalgae, may be equally susceptible to alteration following thermal and physical stress, but with likely impacts for associated fish communities. For instance, Wernberg et al. (2016) found an extensive collapse in temperate macroalgal canopy structure (following the 2011 extreme marine heatwave) drove wholesale changes in fish community structure along 100km of coastline. In contrast, however, Côté-Laurin et al. (2017) found significant loss in seagrass canopy cover and height after a powerful tropical cyclone did not have any apparent short-term effects on fish species richness or density. Given these differing examples of fish responses to climatic-related disturbances of local habitat structure across mesohabitat-types, it is critical we examine the short-to-long term consequences of likely disturbances in other mesohabitats that represent a substantial component of natural seascapes but have received relatively less attention.

Tropical *Sargassum*-dominated macroalgae meadows, which provide critical habitat for reef fish and are relatively understudied, are one such habitat that is likely sensitive to climatic disturbance through marine heatwaves and/or strong wave action during storms and cyclones. These meadows are known to house their own distinct fish and invertebrate communities (Tano et al. 2016; van Lier et al. 2018), and provide key habitats for juvenile fishes (Wilson et al. 2010; Evans et al. 2014; Eggertsen et al. 2017; Tano et al. 2017). Importantly, the *Sargassum* that constitutes the majority of these meadows is tightly coupled with sea surface temperature which can lead to substantial variation in canopy structure (cover, height and holdfast density) and biomass on a seasonal and inter-annual basis (Fulton et al. 2014; Wilson et al. 2014). Furthermore, recent observational studies have demonstrated that canopy structure is an important predictor of fish community structure, with reduced *Sargassum* height, density or cover leading to lower levels of fish richness and abundance (Wilson et al. 2014; Lim et al. 2016; Wenger et al. 2018).

Given the potential sensitivity of *Sargassum* canopy structure to intense wave action and changes in sea surface temperature, we must understand the impact of an unseasonal change in canopy structure on tropical macroalgae-associated fish communities. With such information, we would be able to more successfully manage or mitigate the impacts of unseasonal disturbance events, such as marine heatwaves, local anthropogenic impacts (e.g., dredging) and severe storms. In this study we experimentally manipulated an established predictor of the dominant habitat-forming *Sargassum* canopy structure: Canopy height. This was done with the aim to explore the short- (hours) to long-term (years) consequences of an acute and unseasonal macroalgal canopy reduction on the macroalgal-associated fish community. Fish from the family Labridae (wrasses + parrotfish) were chosen because of their status as one of the most speciose and conspicuous fish families on tropical reef systems. In addition, labrids span a range of body-sizes and trophic levels (Froese and Pauly 2018), which provides an excellent opportunity to investigate the ecological implications associated with changes in macroalgal height from an unseasonal disturbance over short- (days), medium- (months) and long-term (years) time-frames.

Methods

Study area and experimental design

The study took place in the shallow-water (<6m) fringing reef lagoon of Ningaloo Marine Park, Western Australia between 2016-2018. This area is comprised of a mosaic of *Sargassum*-dominated macroalgae patches growing on an underlying flat limestone pavement covered in a veneer of carbonate sediment (Kobryn et al. 2013; van Lier et al. 2018). Ningaloo macroalgae patches undergo significant seasonal fluctuations in biomass that correlate to sea-surface temperature (Fulton et al. 2014), with associated changes in canopy cover, height and holdfast density (Wilson et al 2014).

In order to better tease apart the effects of our canopy height reduction on associated fish communities, it was important to design the experiment in a way that accounted for established predictors of fish diversity, but still resembled a natural system within realistic sampling regime given the logistical constraints. Three macroalgae patches were selected as disturbed sites to undergo canopy height reduction, while another 3 sites (near each of the disturbed sites) were chosen as reference sites. Sites were all greater than 700m^2 in area to allow for a minimum of 6 5-metre underwater survey replicates to fit within 5m of their edges, but less than 2,000m^2 to allow divers to physically carry out the work of canopy height reduction within safe SCUBA dive limits. This is ensured some consistency in patch size (although this has found to be unrelated to fish community structure – see Chapter 3). The three reference sites were selected based on their similarity to a nearby disturbed site in terms of initial fish community structure and habitat condition (e.g., canopy height, macroalgae cover and holdfast density), as well as seascape position (e.g., proximity to coral reef/shoreline).

Within the disturbed sites. manual shears were use to reduce the canopy height of *Sargassum* (and, where it occurred, *Sargassopsis*) to 50% of their mean height by two SCUBA divers, during the late Austral summer (February-March) of 2016. Within the reference sites, divers swam through and physically disturbed the fish and macroalgal community structure in the same systematic fashion, but only mimicking the act of pruning without removing any macroalgae. Given the time and physiological constraints placed on divers, as well as the spatial limitations of a natural system, we were unable to establish a second control to determine whether diver presence without physical disturbance to the site (i.e., without pruning or mimicking pruning) could have had an effect.

Fish and habitat surveys

Surveys were carried out during the summers (February-March) of 2016 and 2018 when juvenile fish abundance and macroalgal height tends to be highest (McIlwain 2003; Wilson et al. 2014), and the winter (August) of 2016 when *Sargassum* canopies are typically low across the Ningaloo seascape (Fulton et al. 2014; Wilson et al. 2014). Surveys of fish and habitat were initially conducted 1-6 days before experimental reduction of canopy height. Following canopy reductions, habitat condition and fish community structure (details below) were (re)surveyed in both a disturbed site and the reference site initially most similar to it at two-hours, two-days, five-days, six-months (during the following winter), and two-years post-pruning.

Both the fish community and habitat conditions were quantified within six haphazardly placed 5m diameter cylinder replicates per site, following the methods of Noble et al. (2013). Each cylinder was spaced at least 5m apart from all other replicates, and a minimum of 5m from the edge of the site. For each replicate, a diver counted and estimated the total length (TL, to nearest cm) of all labrids and putative predators (see Lim et al. 2016) present within the bounds of the cylinder. Habitat was assessed along a 5m line intercept transect within the same cylinder. Under each transect, the distance occupied under the tape by each microhabitat category was recorded. Microhabitat categories included: canopy and understory macroalgae to genus, live coral growth form, seagrass, and the abiotic components of sand, rubble and reef pavement. At each 1m interval, the resting vertical height of canopy-forming macroalgae and density ($0.25m^{-2}$) of canopy-forming holdfasts were recorded. Pre-survey training dives were used to ensure divers were familiar with target species identification and size-class estimation, microhabitat categories, and were conducting the replicate surveys in the same systematic fashion.

Statistical Analysis

Within-site replicate level microhabitat data was collated into five distinct measures: mean vertical canopy height, mean holdfast density, understory genera richness and percentage cover (converted from distances recorded on the 5m line transect) of canopy macroalgae and understory macrophytes. Abiotic cover was excluded from the analysis due to high autocorrelation with canopy cover. Canopy macroalgae metrics were then normalized and assembled into a resemblance matrix using Euclidean distance due to it being environmental data measured on distinct scales. A repeated measures Permutational Multivariate Analysis of Variance (PERMANOVA), which included the fixed factors of time-step and treatment, with the random factor site nested in treatment, was then used to test for differences in habitat condition between treatments through time. Where sufficient unique permutations were unable to be run due to limited replication at the treatment level, Monte Carlo permutations were used to obtain a p-value (Anderson et al. 2008). Post-hoc pairwise PERMANOVA tests were then used to identify differences within the significant interaction terms, which were then illustrated through treatment-level means with 95% confidence intervals. Additionally, treatment-level means with 95% confidence intervals were calculated for both canopy forming genera, (*Sargassum* and *Sargassopsis*), two-years post-disturbance to explore differences in recovery rates from the known (pruned) baseline.

Spatial and temporal variation in fish community and size-class structure was explored in several ways. Square-root transformed densities and size-class frequencies for the 27 encountered labrid species across all replicate surveys were assembled into a resemblance matrix based on Modified Gower (base 10) similarities. Modified Gower was used as it considers both compositional and numerical changes in the fish community, whereby an order-of-magnitude change in species density is given a similar weight as the presence/absence of a novel species (Anderson et al. 2006). A repeated measures PERMANOVA of the same design as used for habitat analysis was then run on this matrix followed by post-hoc pairwise tests. Changes in labrid community and size-class structure were further illustrated by a metric multidimensional scaling plot (mMDS) on mean labrid densities. For ease of interpretation, a treatment-level mean (mean of site-level means) was calculated for reference sites, while disturbed sites were based on site-level mean densities. Differences in the temporal dynamics of within-treatment labrid assemblages were also explored by way of a cyclicity test using site-level mean densities in a Modified Gower (base 10) resemblance matrix for all sites in each treatment group. The cyclicity test works by comparing the observed community dynamics against a model resemblance matrix constructed out of a bounded time factor (for details see Clarke and Gorley 2015). For the model matrix, the start (predisturbance; designated value = 0) and end points (two-years post-disturbance; designated value = 1) of community structure are theoretically the same (one- year post-disturbance would also have had a designated value = 1, if we had collected data at this point). Time-steps between these bounded values are calculated as a proportion of time (in days) since disturbance, compared to the total number of days in a year. For example, the six-month time-step would be equal to 0.5 as it is halfway through an annual cycle. The cyclicity test then examines, via permutation, the degree to which the observed assemblage conform to what would be expected from a perfect cycle.

To provide finer resolution in patterns of fish community structure, mean differences between disturbance and reference sites was calculated at the treatment level (± 95% confidence intervals) for species richness, as well as overall, trophic-level and species-specific fish density across all time-steps. Trophic levels were defined as nominal herbivore (2-2.99), lower order carnivore (3-3.50) and higher order carnivore (>3.51) with values sourced from Froese and Pauly (2018). Changes in the size-class structure of the fish community were investigated by calculating the proportional abundance of each size-class in each time-step. Size-class data was pooled at the site-level, with a treatment-level mean (± 95% confidence intervals) being calculated for the reference sites for comparison. All multivariate analysis and diversity calculations were performed in PRIMER (version 7.1.1) with PERMANOVA+ (Anderson et al. 2008).

Results

Effects of canopy reduction on macroalgae structure

The overall canopy structure differed significantly at both the site and treatment level within time-steps (Table 4.1a). Pairwise tests using Monte Carlo methods indicated that this significant interaction between treatment and time-step was due to differences in canopy structure two hours ($t = 3.87$, $p < 0.01$), two days ($t = 3.07$, $p < 0.01$) and five days ($t = 3.88$, $p < 0.01$) post-disturbance. Exploration of mean differences between disturbance and reference sites highlighted that these differences were exclusively related to short-term reductions in canopy height (Fig. 4.1). No significant differences in canopy cover and holdfast density, understory cover and understory genera richness, were evident between treatments at any time-step (Fig. S4.1).

While mean canopy height showed no significant differences between treatments over the mid- (months), or long-term (2 years), we found evidence of genera specific responses in macroalgae. Mean height of the co-occurring canopy genera *Sargassopsis* was approximately 50% shorter in disturbed sites when compared with reference sites (21.75cm ± 2.97 and 40.89cm ± 6.59, respectively), while *Sargassum* heights were statistically similar between treatments (28.30cm ± 3.00 and 26.01cm ± 2.83). This difference in canopy height recovery was primarily evident between Disturbed Site 3 and its reference site, where *Sargassopsis* represented > 20% of canopy cover composition. Conversely, *Sargassopsis* cover at the other two disturbance-reference site pairs was <3%.

Table 4.1. Summary of repeated measures PERMANOVA comparing sites within treatment groups across different time-steps for (a) canopy structure, and (b) labrid community and (c) size-class structure.

Source	**df**	**SS**	**MS**	**Pseudo-F**	**P-Value**
a) Canopy habitat structure					
Treatment	1	26.811	26.81	1.18	0.3549
Time	5	155.71	31.14	10.66	0.0001
Site(Treatment)	4	91.20	22.80	14.67	0.0001
TreatmentxTime	5	33.08	6.62	2.26	0.0349
Site(Treatment)xTime	20	58.43	2.92	1.88	0.0004
Residuals	180	279.77	1.55		
Total	215	645			
b) Labrid community structure					
Treatment	1	3.09	3.09	1.45	0.2037
Time	5	5.51	1.10	4.20	0.0001
Site(Treatment)	4	8.54	2.13	11.32	0.0001
TreatmentxTime	5	1.95	0.39	1.49	0.0315
Site(Treatment)xTime	20	5.25	0.26	1.39	0.0007
Residual	180	33.94	0.18		
Total	215	58.29			
c) *Labrid size-class structure*					
Treatment	1	1.53	1.53	2.67	0.0815
Time	5	3.43	0.69	6.47	0.0001
Site(Treatment)	4	2.29	0.57	6.11	0.0001
TreatmentxTime	5	1.54	0.31	2.90	0.0015
Site(Treatment)xTime	20	2.12	0.11	1.13	0.2181
Residual	180	16.83	0.09		
Total	215	27.74			

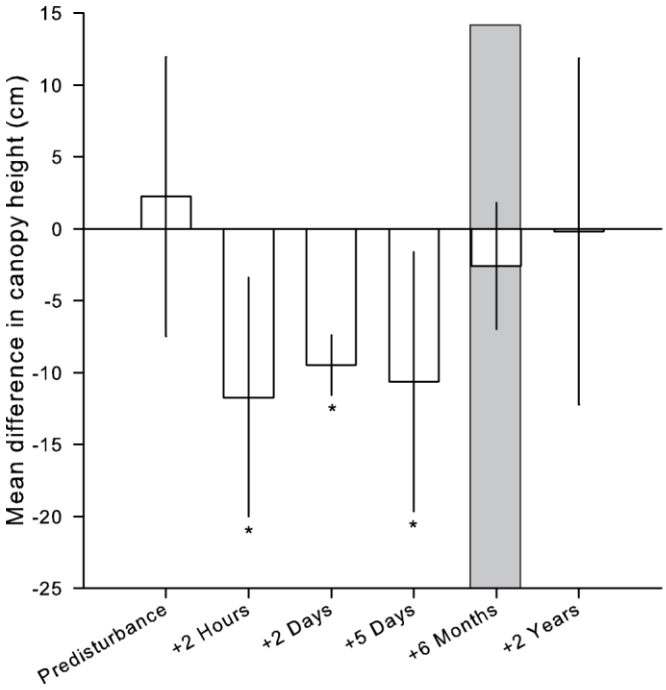

Figure 4.1. Changes in canopy macroalgae structure as a mean (± 95% confidence intervals) difference in canopy height among paired disturbance-reference sites for six different time-steps. Grey bar represents the winter period where reference sites inherently lose canopy height and we would expect disturbed and reference sites to be similar in their habitat structure.

Effects of canopy reduction on macroalgal-associated fish communities and populations

Overall, we recorded 6,797 individual fishes and 27 species of labrids throughout the course of the experiment. Examination of mean differences between disturbed and reference sites indicated substantial and significant drops over the short- and long-term in both species richness and overall total density (Fig. 4.2a, b). Short-term decreases in density are related to decreases in the density of nominal herbivores and lower-order carnivores, which had significantly lower densities in disturbed sites between two- to five-days post-disturbance (Fig 4.2c, d).

Species-specific examination found significant decreases within two hours of pruning for the small-bodied invertivore *Halichoeres nebulosus* (x̅ = -0.28 ± 0.23) and *Xenojulis margaritaceus* (x̅ = -1.17 ± 1.10), while *Stethojulis interrupta* (x̅ = -0.72 ± 0.24) and the nominally herbivorous *Leptoscarus vaigiensis* (x̅ = -10.28 ± 10.26) also decreased significantly five-days post-disturbance (Table S4.1). Unseasonal canopy reduction also had negative

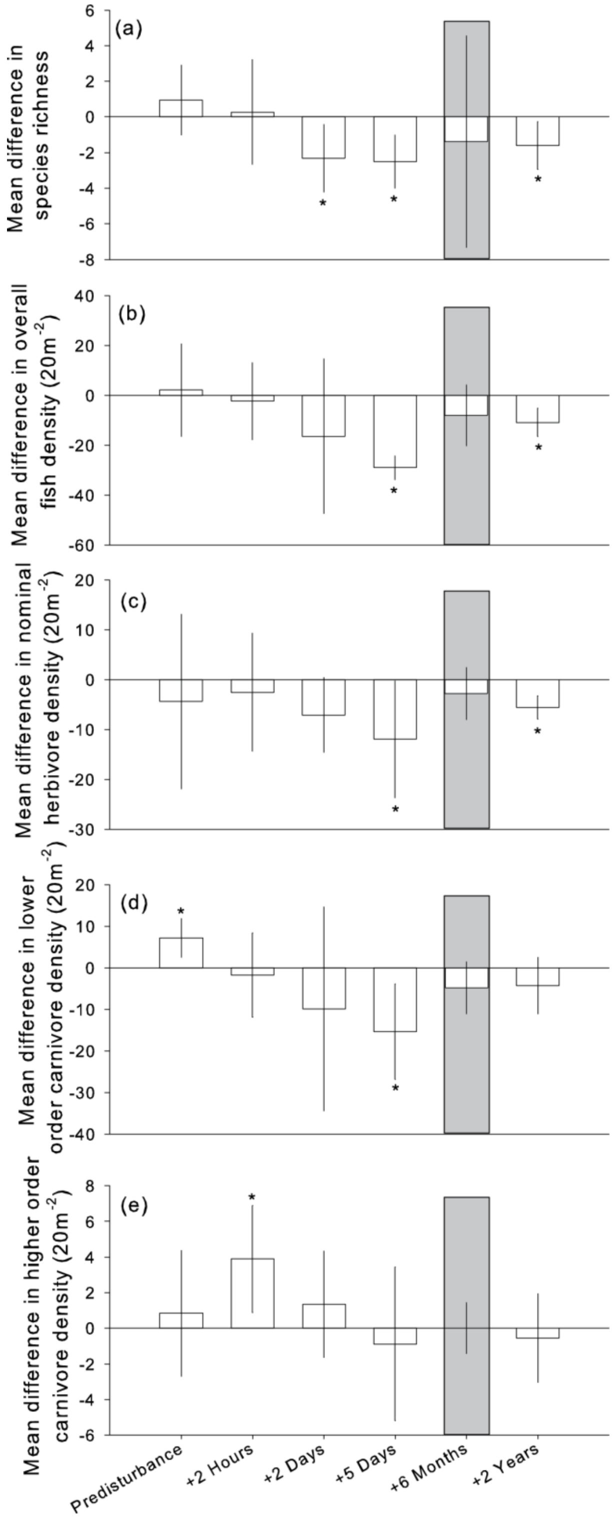

Figure 4.2. Mean differences among paired disturbance-reference sites in terms of (a) labrid species richness, (b) labrid fish density, (c) herbivore density, (d) invertivore density, and (e) piscivore density. Asterisks indicate where the mean difference and 95% confidence intervals did not intersect zero. Grey shading indicates winter when the *Sargassum* biomass naturally decreases. Error are 95% confidence intervals

effects on the long-term densities of herbivorous fishes, with decreases still evident two-years after the disturbance event (Fig. 4.2d). This was largely driven by significant reductions in *L. vaigiensis* (x̅ = -4.33 ± 2.48) and *Scarus* spp (x̅ = -0.72 ± 0.63). Significant changes in higher-order carnivore density were only evident at the two-hour post-disturbance time-step where it increased (Fig. 4.2e). This was largely driven by *Thalassoma lunare,* which showed significant increases at both the two-hour (x̅ = 2.22 ± 2.12) and two-day (x̅ = 0.83 ± 0.72) time-step.

The community structure of labrid fishes exhibited a major departure from reference sites (Fig. 4.3a). Labrid community structure showed a significant interaction between treatment and time-step (Table 4.1b), with post-hoc pairwise tests highlighting five-days post-disturbance as being significantly different (t = 1.68, p = 0.04). Short-term responses to both community and size-class structure were immediately apparent, with responses five-days post-disturbance rapidly approaching a composition similar to that seen during winter (where fish diversity is normally substantially reduced). In particular, Disturbed Site 3 can be seen to undergo the largest departure from pre-disturbance conditions. In contrast, patterns from the short-term reference sites show a tight clustering in the mMDS. Medium-term winter responses were mostly comparable to the change shown by reference sites, with the exception being a large change in Disturbed Site 3. Over the long-term, neither reference or disturbed sites return to initial conditions, indicating some inherent seasonal variation in the system, but this effect is certainly more pronounced in the disturbed sites; particularly in Disturbed Site 3. While most sites followed the same downwards direction on the mMDS biplot as their community structure changed through time, Disturbed Site 1 changed in a different direction, indicating assemblage structure was altered differently to other sites. Finally, results from the cyclicity test found both treatment groups to differ significantly from a theoretical cycle in terms of community structure, but that the degree of non-conformity was far greater in the disturbed treatment for fish community structure (disturbed: Rho value = 0.48, p < 0.01; reference: Rho value = 0.31, p < 0.01).

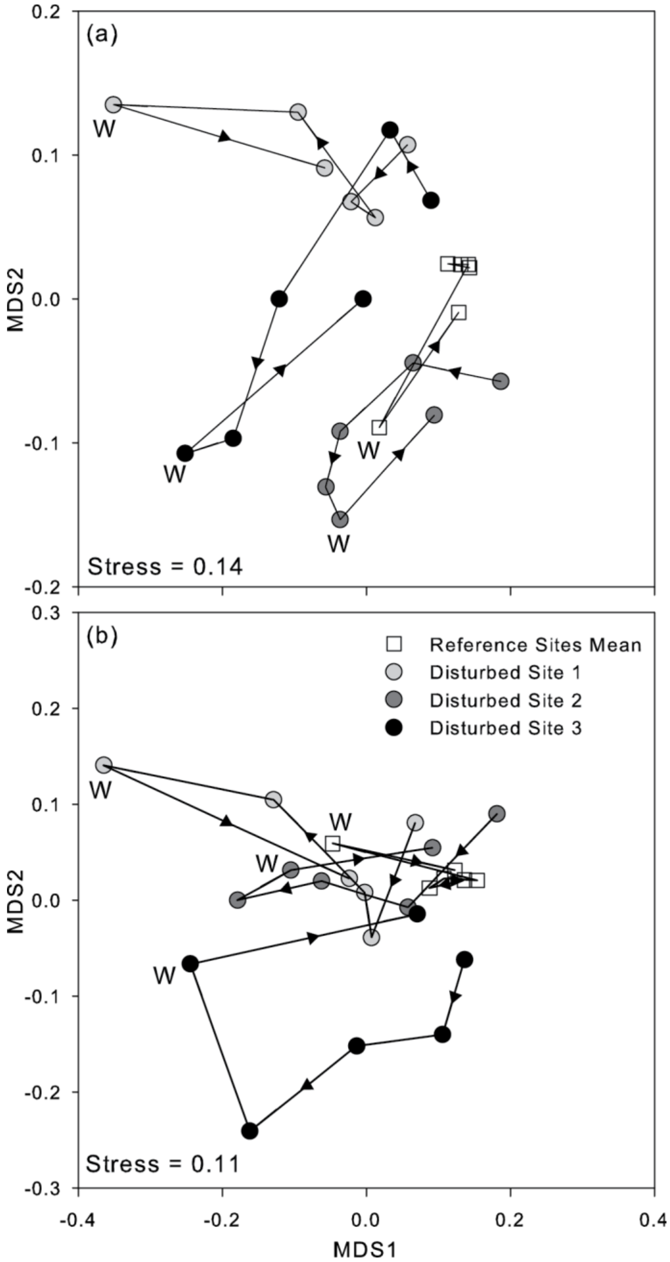

Figure 4.3. Metric multidimensional scaling plot (mMDS) with temporal overlays to indicate the trajectories of each canopy-disturbed site from the pre- to post-disturbance time periods, alongside the aggregate trajectory for the reference sites, in terms of labrid fish (a) community and (b) size-class structure. The winter season is indicated by ‘W’.

Labrid size-class structure also showed a significant interaction between treatment and time-step (Table 4.1c), with post-hoc testing identifying the five-days post-disturbance as the significant time-step ($t = 3.20$, $p < 0.01$). Closer examination of the size-class structure of the fish community highlights some interesting trends (Fig. 4.3b, 4.4). While no significant difference is evident between disturbance and reference sites for any size-class pre-disturbance, Disturbed Site 3 and the nearby reference site had a much higher proportion of fish <5cm, at both two-hours and two-days post-disturbance. Disturbed Site 1 exhibits a major increase in the proportion of these larger-bodied fish over the first two days, with a corresponding decrease in <5cm fish. A similar pattern can be seen in Disturbed Site 3 five-days post-disturbance, where a major increase in the proportion of larger-bodied fish corresponds with a substantive drop in the proportion of small fish <5 cm. Over the long-term however, the relative abundance of the different size-classes appears to return to predisturbance levels (Fig 4.3b, Fig. 4.4f).

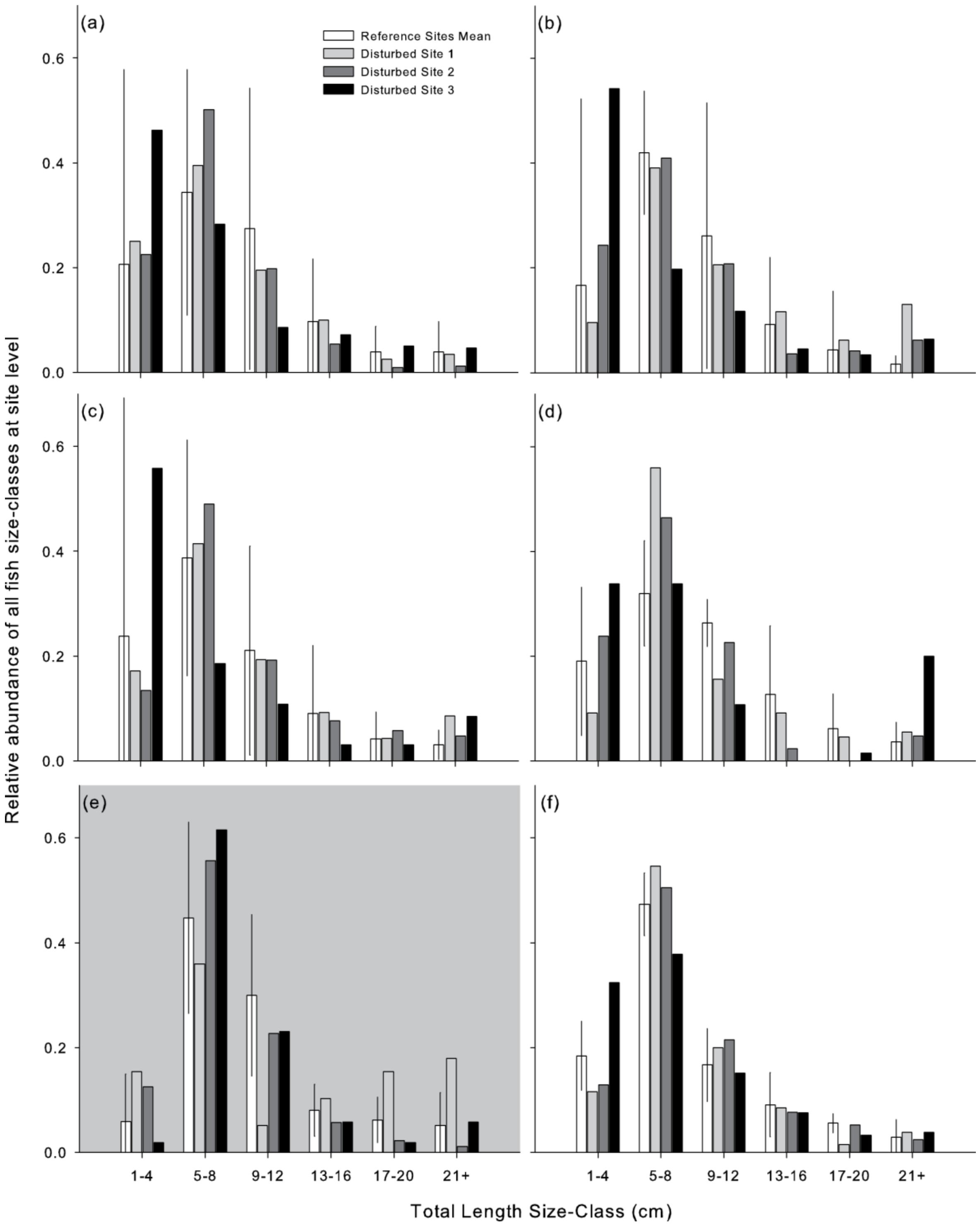

Figure 4. The relative abundance of fish in 4 cm TL size-classes at (a) pre-disturbance, and then (b) two hours (c) two days (d) five days (e) six months and (f) two years post-disturbance. Reference values are means calculated from the abundances of each size class across the three reference sites (± 95% confidence intervals), while values for each of the disturbance sites are presented. Grey shading indicates winter season.

Discussion

Through an unseasonal manipulation that targeted this aspect of macroalgal habitat structure, we provide some of the strongest evidence yet that changes in *Sargassum* canopy height drives significant change in fish community structure over the short to long term. Structural complexity in soft canopy habitats can be an effective predictor of fish diversity across a range of subtidal marine habitats (Levin and Hay 1996; Harasti et al. 2014; Wilson et al. 2014; van Lier et al. 2017). Among a range of measures, canopy height has often been found to be a key predictor for fish diversity and abundance in tropical macroalgal habitats (Lim et al. 2016; van Lier et al. 2018; Wenger et al. 2018). In our experiment, substantial changes were demonstrable within hours of the initial disturbance, indicating the rapid influence that habitat change can have on macroalgae-associated fishes. Furthermore, the negative consequences of canopy reduction on diversity and abundance were still evident two years later, which differs to the effects of experimental reduction of canopy structure in other marine macrophytes such as seagrass beds (Connolly 1994).

Changes to size-class structure were evident in the immediate aftermath of canopy height reduction, and relate to proportional decreases in the smallest-bodied, and increases in largest-bodied fish. In the summer months, small-bodied fish in Ningaloo’s macroalgae meadows include a large proportion of recruit and juvenile labrid fishes (Wilson et al. 2010; van Lier et al. 2018). Such small-bodied fish represent an important dietary component of many local piscivorous fish at Ningaloo (Holmes et al. 2012; Thillainath et al. 2016). Given the positive relationship between length and mobility (Green et al. 2015; Nash et al. 2015), small bodied prey fish are unlikely to move to more suitable refuge habitat post-disturbance, leading to increased susceptibility to predation. Conversely, larger-bodied fish, which are more likely to be of higher trophic levels (Romanuk et al. 2011), may readily move into a disturbed area of macroalgae to prey upon small-bodied fish. Accordingly, the rapid size-class response to canopy height reduction is associated with changes in the relative abundance of fish from different trophic levels. In particular, higher-order carnivores showed a short-term increase in density following canopy height reduction. The loss of canopy complexity has been shown to increase foraging efficiencies for active, search-and-attack style, piscivores (Horinouchi et al. 2009). This would allow mobile piscivores in the area (e.g., *T. lunare*; Holmes et al. 2012; Fulton et al. 2017) to take advantage of juvenile fishes suddenly exposed through reduced canopy structure and refugia. We suspect that this, possibly in conjunction with new fish recruits arriving (post-disturbance) preferentially avoiding areas with reduced canopy structure, could largely explain the changing dynamics in size-class and trophic distributions over the initial five day period in our study (Shima 2001; Evans et al. 2014; Wilson et al. 2014). Canopy height reduction therefore alters predator-prey dynamics, resulting in changes to size-class and trophic structure.

In contrast to higher-order carnivores, both nominal herbivores and lower-order carnivores decreased following a decrease in canopy height, a reaction likely due to reduction of both habitat structure and important trophic resources. Some large-scale disturbances on coral reefs (e.g., bleaching, crown-of-thorns outbreak) can leave complex habitat structure in place (albeit degraded), which means that many fish species persist or even increase in the near term providing they are not obligate corallivores (Wilson et al. 2006; Rogers et al. 2017). However, our manipulation removed habitat structure as well as the food base for many vertebrates and invertebrates in these biomes. Herbivores such as *L. vaigiensis* feed directly on *Sargassum* and have been shown to preferentially avoid areas in the seascape with lower canopy height (Lim et al. 2016). Macroalgae canopies also support a diversity of epifauna which is available for lower-order carnivores to consume (Edgar and Aoki 1993; Tano et al.

2016) so reductions to in canopy height are likely to reduce food resources for these species. For example, Wenger et al. (2018), found a positive relationship between the density of the carnivorous *X. margaritaceus* and macroalgal canopy height. Future work on the foraging preferences of macroalgae-associated fishes could explore specifically which parts of the canopy structure they are targeting (i.e., holdfasts or higher in the canopy) to better understand how a partial canopy loss can affect fishes to the extent demonstrated here.

The long-term responses to coral reef-associated fishes following habitat degradation have shown long-term declines in species reliant on the hard structure for food, and even wholesale changes to the community structure several years after an initial disturbance (Bellwood et al. 2006a; Pratchett et al. 2006; Emslie et al. 2011; Bellwood et al. 2012). We found that while the canopy structure of *Sargassum* showed a full long-term recovery, the labrid fish community did not; species richness, overall density and, specifically, the density of nominal herbivores were all significantly lower at our disturbed sites two years post-disturbance. In comparison to some coral reef communities that have shown a long-term switch to an alternate community structure (e.g., Bellwood et al. 2006; Bellwood et al. 2012), macroalgae-associated fish communities seemed to return to an approximate version of their predisturbance structure, albeit with a reduced density of herbivores. Lim et al. (2016) found that the browsing herbivorous fish, *L. vaigiensis*, preferentially selected for *Sargassum*-dominated patch habitats with taller canopies. Given the reduction in herbivorous fish observed over two years after canopy height reduction occurred, this may provide evidence that herbivorous fish may continually avoid an area they have known to be poor. Notably, the site that showed the largest disparity in fish structure between the first and last time-step had the highest coverage of *Sargassopsis* canopy, a macroalgae genera our results indicated did not recover well from canopy loss. Resilience of macroalgal meadows is therefore dependant on the canopy forming taxa and this will have consequences for habitat-associated fauna. The interactions of macroalgae-associated fishes with different canopy-forming taxa should be a focus for future research given the questions our results raise around the potential implications for resistance and resilience of different macroalgae patches within a seascape, and how the fish that use it respond over the long term.

Community structure may also follow a different recovery trajectory due to location within the seascape. Recent evidence highlights the importance of connectivity to adjacent habitats in structuring fish communities (van Lier et al. 2018), which may influence recovery after disturbance. Such findings highlight the importance of the overall marine estate to account for broad-scale spatial differences and microhabitat variation in fish response to disturbance, and the need to improve understanding of the relationship between these aspects and community structure.

Overall, we find that an acute, unseasonal reduction in canopy height has both rapid and lasting consequences for the associated fish community. Despite occupying a relatively dynamic habitat type that undergoes extensive change in habitat structure over both short (seasonal) and longer timescales (e.g., decadal ENSO cycles; Wilson et al. 2018), macroalgal-associated fishes still appear to be highly sensitive to habitat loss. Accordingly, we now have evidence that habitat loss in a whole suite of tropical subtidal biomes – from coral reefs, to seagrass beds and now macroalgal meadows – can drive the loss of fish biodiversity and erode recruitment success (Hyndes et al. 2003; Pratchett et al. 2006). This may be especially important for the many species that recruit to macroalgae patches, as loss of habitat structure could increase post-recruitment mortality, reducing the size of adult populations of species of both ecological and fisheries importance (Fulton et al. *In Review*). Given the vast extent of macroalgal patch habitats at Ningaloo – conservative estimates suggest at least 16,000ha

(Kobryn et al. 2013; Fulton et al. 2014) – a broad-scale unseasonal disturbance (e.g., marine heatwave; Wernberg et al. 2016) could have catastrophic effects on macroalgal-associated fishes. Understanding the specific responses of differing canopy forming species to disturbance events, such as increased temperature, and how seascape moderates this response, may help identify disturbance refugia for macroalgal meadows. Such information could identify a network of high resilience areas that could receive priority protection from other potentially harmful practices (e.g., fishing).

Supplementary Material

Table S4.1. Mean difference in species density (± 95% confidence intervals) and trophic level for all species observed in the experiment over six different time-steps.

Species by family	Predisturbance	+2 Hours	+2 Days	+5 Days	+6 Months	+2 Years	Trophic Level
Apogonidae							
Cheilodipterus macrodon	-0.11±0.48	-	-	-	-	-	4.00
Cheilodipterus quinquelineatus	0.72±3.11	0.17±0.72	-0.33±1.10	0.11±0.48	-	-0.11±0.72	3.89
Fistularidae							
Fistularia commersonii	0.11±0.63	0.61±0.86	0.11±0.24	-0.06±0.48	-0.11±0.48	-	4.26
Labridae							
Anampses geographicus	-0.33±4.88	-0.55±2.50	-0.39±3.32	-1.17±2.99	0.22±0.63	-1.72±2.66	3.50
Cheilinus bimaculatus	-	-	-	-	-	0.11±0.48	3.74
Cheilinus chlorourus	0.22±0.86	0.06±0.24	-	-	0.06±0.24	-	3.90
Cheilinus trilobatus	-	-	-	-	-0.06±0.24	-	3.88
Cheilio inermis	-1.61±5.95	-0.17±2.59	-0.11±2.63	-1.94±5.54	-0.78±1.96	-0.33±2.99	4.10
Chlorous sordidus	-	-	-	-	-	-0.11±0.48	2.00
Choerodon rubescens	-0.06±0.24	-0.06±0.24	-0.17±0.72	-0.11±0.48	-	0.06±0.24	3.50
Choerodon schoenleinii	-	-	-	-	-0.11±0.48	-	3.40
Coris auricularis	-0.33±2.59	-0.22±2.12	-0.17±2.07	-0.22±0.63	0.11±0.86	0.17±0.41	3.50
Coris caudimacula	1.89±2.12	0.83±2.15	-1.22±2.94	-2.17±4.88	-1.44±4.43	1.56±7.99	3.40
Halichoeres brownfieldi	0.11±0.86	-0.33±1.43	-0.33±1.43	-0.33±1.43	-	-	3.46
Halichoeres nebulosus	-1.17±2.15	**-0.28±0.24**	-3.00±4.88	-2.39±5.59	-2.17±3.95	-0.28±2.39	3.34
Labracinus lineatus	-0.06±0.24	-	-	-0.06±0.24	-	-	3.97
Labroides dimidiatus	0.94±1.86	0.33±0.83	0.28±0.63	0.06±0.48	0.22±1.45	-0.01±0.41	3.46
Leptoscarus vaigiensis	-4.22±22.23	-2.22±12.60	-5.72±8.62	**-10.27±10.26**	-2.83±5.17	**-4.33±2.48**	2.00
Macropharyngodon ornatus	-0.06±0.24	-	-	-	-	-0.11±0.48	3.09
Pseudojuloides elongatus	**7.33±6.47**	3.11±9.19	0.83±4.77	-4.55±9.19	0.61±9.71	-0.94±9.44	3.50
Pteragogus flagellifera	0.22±0.63	-0.06±1.33	-0.56±1.72	-0.72±0.96	-0.55±2.12	-0.17±1.24	3.50
Scarus chameleon	0.11±0.24	-0.22±0.96	-0.06±0.24	-	-	-0.39±0.63	2.00
Scarus ghobban	-	-	-0.06±0.24	-0.11±0.48	-	-0.06±0.24	2.00
Scarus spp	-0.28±5.01	-0.11±0.47	-1.28±2.76	-1.56±3.45	-	**-0.72±0.63**	2.00
Stethojulis bandanensis	-1.17±2.59	-3.44±11.36	-1.83±5.80	-1.50±3.54	-0.44±1.04	-0.28±1.20	3.21
Stethojulis interrupta	**0.83±0.72**	0.39±2.28	-2.06±4.83	**-0.72±0.24**	-0.39±1.33	**-1.67±0.83**	3.37
Stethojulis strigiventer	-0.56±2.43	-0.33±1.43	-0.61±1.26	-0.61±0.86	-0.33±0.41	0.06±0.24	3.14
Thalassoma lunare	0.72±3.62	**2.22±2.12**	**0.83±0.72**	0.39±1.33	0.44±1.33	-0.61	3.87
Thalassoma lutescens							3.72
Thalassoma septemfasciatum	**-**	-	-	0.06±0.24	-	**-**	3.66
Xenojulis margaritaceus	-0.56±2.12	**-1.17±1.10**	-0.72±1.27	-1.00±1.43	-0.56±0.96	-1.00±2.19	3.50
Lutjanidae							
Lutjanus fulviflamma	0.06±0.24	-	-	-	-	-	3.79
Serranidae							
Epinephelus bilobatus	0.06±0.24	0.11±0.48	0.11±0.48	0.06±0.24	0.06±0.24	-	3.86
Epinephelus rivulatus	0.56±1.33	0.83±1.49	0.72±1.33	0.61±0.96	0.39±1.33	0.06±0.24	3.60
Synodontidae							
Synodus variegatus	-	0.06±0.24	-	-	-	-0.06±0.24	4.20

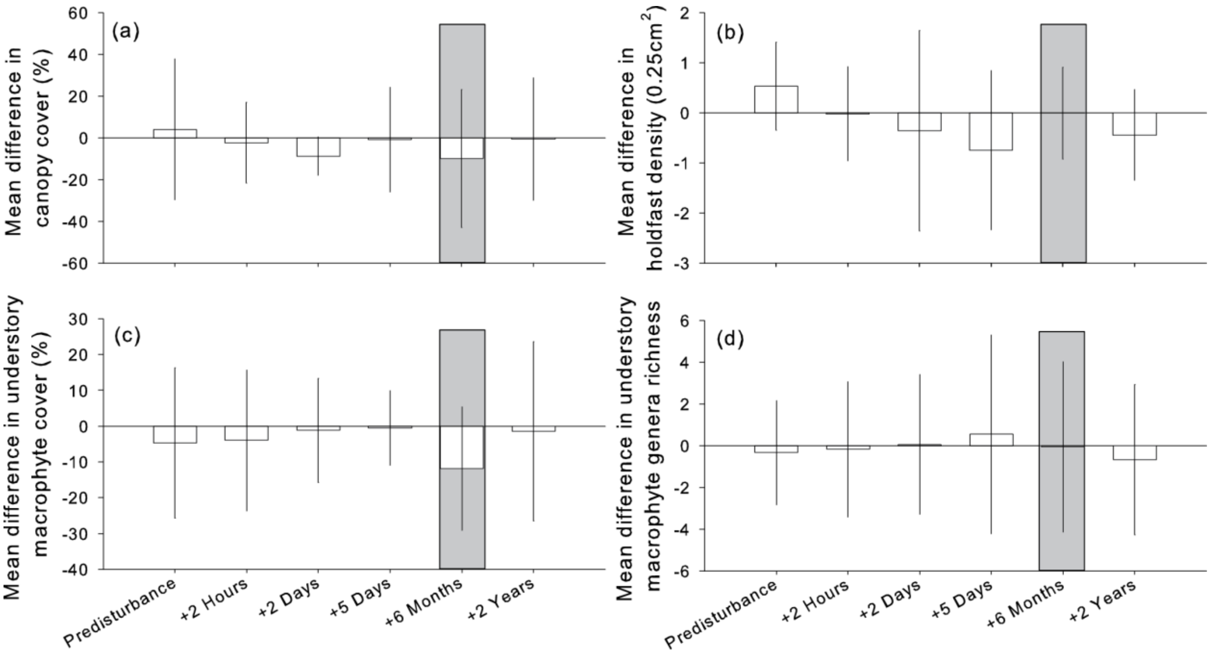

Figure S4.1. Mean changes to (a) canopy cover, (b) holdfast density, (c) understory macrophyte cover and (d) understory macrophyte genera richness showing mean difference between paired disturbance-reference sites for six different time-steps. Error bars are 95% confidence intervals. The grey bar represents the winter period where we would expect disturbed and reference sites to be similar in their habitat structure.

Chapter 5

Foraging across seascapes: shifting patterns of habitat association and foraging behaviour in a mesopredatory reef fish

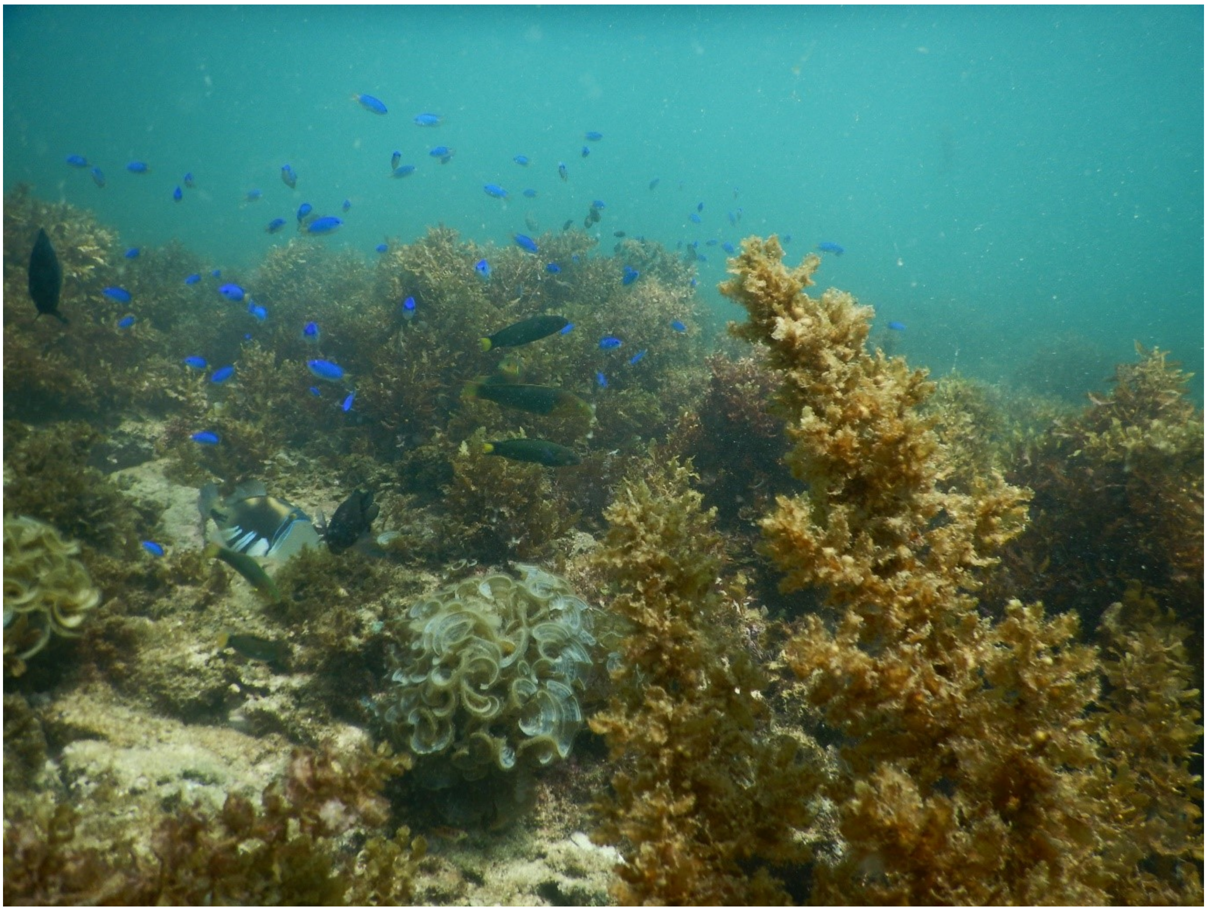

Photo credit: David Ellis

Abstract

Predators can regulate their prey populations in predictable ways, often with wider consequences for community structure through top-down effects. The multi-scale approach of seascape ecology has been useful in exploring how spatial context can affect patterns of abundance and diversity, but have rarely explored how this can augment behaviours important for ecological processes such as predation. Using a multivariate approach, I examined the behavioural ecology of a prominent mesopredatory fish (*Thalassoma lunare*) to explore how local habitat quality and spatial context may influence patterns of predation throughout its life history. We found multi-scale differences in habitat use, with indications of microhabitat specificity at early life history stages, while adult fishes were habitat generalists. Furthermore, we find that macroalgae-associated *T. lunare* vary their foraging behaviours according to structural connectivity of a nearby coral reef, with individuals distant from the reef exhibiting significantly reduced foraging distances. This study builds on a growing body of work in seascape ecology that seeks to understand ecological processes in a spatial context.

Introduction

The presence, foraging behaviour and success of predators regulates prey populations and is an important process in structuring ecological communities (Paine 1966; Savidge 1987; Hixon 2015). Predation may be especially important during the early life history stages, when individuals are naïve. In marine systems, both larger-bodied top predator and smaller-bodied mesopredator fish have been implicated as important predators of juvenile fishes (Connell 1998; Holmes et al. 2012), which can substantially reduce recruitment success (Almany 2004a). The presence of predatory fish may also improve recruitment success of specific species by generating a wider niche space. For example, Almany (2003) found that the presence of resident piscivores improved recruitment success of the wrasse (*Thalassoma bifasciatum*) by removing competitors for resources. Given a high degree of trophic connectedness, predators also act as an important energy conduit in coastal ecosystems (Thillainath et al. 2016) which can contribute to community stability. Understanding what underpins the distribution and behaviours of predators can therefore give better insights on how ecological communities are structured and function.

A well-studied facet of predator effects on communities is how the composition of the local area can influence foraging behaviour and efficiency. Prey species can utilise complex microhabitats in hard substrate (e.g., gaps, crevices, interstices etc.) as a refuge from predators thereby reducing predator efficiency (Beukers and Jones 1997; Hixon and Jones 2005). However, these findings may differ in soft habitat macrophyte-dominated areas or among predators. Horinouchi et al. (2009) demonstrated significant decreases in foraging efficiency for a transient predator within high density seagrass, yet this habitat improved foraging efficiency for an ambush style predator as increased density provided more locations from which attack was favourable while obstructing the view of prey species. Invertivorous fishes also exhibit differences in their foraging behaviours based on microhabitat availability and complexity. Almost all species of invertivores surveyed by Kramer et al. (2016) avoided complex live coral microhabitats, which are known to harbour a relatively high biomass of crustaceans (Kramer et al. 2014). Where they did show specific positive selection, fish tended to swim in a very direct manner, while fish exhibiting neutral preference for microhabitats exhibited more convoluted pathways (Fulton and Bellwood 2002; Kramer et al. 2016). These results indicate that spatially discrete resources are effectively foraged using directed search pathways, while spatially ubiquitous resources would be more optimally searched for following a convoluted search pattern. Predators may therefore forage based on the distribution of prey, rather than where prey is explicitly more abundant. Clearly predation is moderated by habitat complexity, but the extent to which this occurs varies with respect to the spatial scale at which complexity is measured, the type of environment it occurs in (i.e., soft macrophytes or hard coral), and the feeding strategy employed.

Broad-scale attributes of seascape configuration may also affect the distribution and foraging behaviours of fishes. Sambrook et al. (2016) highlighted how carnivorous and omnivorous fishes were significantly more abundant on the boundary of a coral reef, compared with the adjacent sand habitat or the reef interior, which is consistent with higher predation pressures on the boundary of marine ecotones (Hammerschlag et al. 2010). The proximity between habitats can also substantially influence foraging behaviour. For example, Davis et al. (2014) found that the herbivorous coral reef-associated fish *Siganus fuscescens* would regularly make daily foraging migrations to mangrove mesohabitats, with the overall contribution of mangrove-based resources made to its diet being a function of proximity.

Intraspecific differences in foraging behaviours can also drive shifts in habitat association and space use. Ontogenetic shifts in diet evident in many fish species (e.g., St John

1999) may be a consequence of shifts in habitat use that necessitate changes in foraging behaviours. Furthermore, reduction in the time and frequency of foraging behaviours (feeding, searching) has been demonstrated as fish develop (Layton and Fulton 2014). Predation risk and predation success can also significantly influence how long a fish will remain within a particular habitat patch (Devries et al. 1989; Holmes et al. 2012), while predation risk and distance between habitats alters how quickly and directly fish will move between patches of habitat (Turgeon et al. 2010; Ryan et al. 2012).

Recent studies have identified tropical macroalgae as important habitat for both juvenile and adult fish (Wilson et al. 2010; Evans et al. 2014; Wilson et al. 2014; Tano et al. 2017), and that predator abundance correlates positively with local abundance of juvenile fishes (Wilson et al 2017). Tropical macroalgal habitats also house a high richness, abundance and biomass of invertebrates, which likely provide a wealth of food resources for invertivorous fishes (Tano et al. 2016). However, the three-dimensional complexity of these canopies varies seasonally and spatially (Fulton et al. 2014; van Lier et al. 2018), which may alter the efficiency of predators. Furthermore, as habitat connectivity can augment predation, foraging behaviour is expected to vary at different levels of habitat connectedness (e.g., Fulton and Bellwood 2002; Kramer et al. 2016). Using the neighbouring coral- and macroalgae-dominated habitat at Ningaloo Reef, Western Australia (Kobryn et al. 2013), we examined how the distribution and foraging patterns of the ubiquitous predatory wrasse *Thalassoma lunare* vary over multiple spatial scales across different life history stages. Specifically, we tested the hypotheses that 1) there are ontogenetic-based differences in habitat use at local- and seascape-scales; and 2) foraging behaviours differ between size-classes and spatial contexts across coral and macroalgal dominated systems.

Methods

Study area and species

Field surveys of fish density, behaviour and habitat condition were conducted across the Ningaloo Marine Park in Western Australia (23.1447°S, 113.7764°E). This area comprises a fringing coral reef that encloses a shallow (<6m) lagoon that has a patchy network of *Sargassum*-dominated macroalgae meadows set within a matrix of sand-covered ancient reef pavement (Kobryn et al. 2013). These macroalgal meadows typically consist of between 20-80% *Sargassum* cover during the Austral summer months, which can reduce down to between 0-40% in periods of cooler sea temperatures during the winter (Fulton et al. 2014; Lim et al. 2016; van Lier et al. 2018). A range of understory macroalgae, principally from the genera *Lobophora*, *Dictyota* and *Dictyopteris* are also present and vary in percent cover according to levels of competing *Sargassum* canopy cover. The coral-dominated backreef enclosing the lagoon is typically dominated by live and dead coral set among sand, rubble and ancient reef pavement with the occasional embedded area of macroalgae (Lim et al. 2016; van Lier et al. 2018).

Thalassoma lunare (Family: Labridae) are common on temperate and tropical reefs with a wide ranging distribution throughout the Indo-Pacific, utilizing a range of coastal mesohabitats (Green 1996; Wilson et al. 2010; Berkström et al. 2012b; van Lier et al. 2018). *T. lunare* is an opportunistic mesopredator with a wide-ranging diet, which can include juvenile fish (Martin 1994; Holmes et al. 2012; Kramer et al. 2015). Shifts in diet have been apparent in this species, with changes largely corresponding to body-length thresholds indicative of key life-history stages in this protogynous hermaphrodite (recruit/juvenile = 1-6cm, initial phase = 7-15cm, terminal phase 16+ cm; Ackerman 2004; Holmes *et al.* 2012; Amalina *et al.* 2016).

Ontogenetic differences in habitat use at multiple scales

Broad-scale patterns of *T. lunare* population structure were recorded each February, between 2013-2018 at 32 sites (17 coral, 15 macroalgae) along the Ningaloo coast. At each site the number of *T. lunare* and their total length (TL) were recorded using underwater visual census (UVC) along nine haphazardly placed 30m transects. Adults were recorded along transects using a 5m wide belt, while recruits (<5cm) were recorded on a return run within a 1m wide belt. Percentage cover of the benthos was estimated within the 30x5 belt transect using the categories: Live coral, dead coral, macroalgae, abiotic (sand+pavement+rubble) and other biotic (sponge, ascidian, seagrass). This visual assessment of broad habitat categories correlates well with conventional methods of assessing habitat, such as line intercept transects (Wilson et al. 2007). Survey density of recruits were aligned to the 5m transect width (fish $150m^{-2}$) using the conversion Y = 1.278x, where x = density on 1m transects (Lim *et al.* (2016). Spatial and temporal variation in abundance of different life history stage *T. lunare* was examined using a three factor permutational multivariate analysis of variance (PERMANOVA), with the fixed factor of mesohabitat and random factors of year and site (nested within mesohabitat). Fish density was square-root transformed and arranged into a resemblance matrix using the Modified Gower (base 10) distance measure to weight an order-of-magnitude change in density within a life-history stage the same as the presence/absence of a different life-history stage. A dummy variable was included in the resemblance matrix construction to account for samples that had zero values. Significant interaction terms were examined using a metric multidimensional scaling ordination (mMDS) of the distance among group centroids for the combined factors.

Information on fine-scale habitat use by *T. lunare* individuals was obtained during February-March 2018 across 14 coral reef sites and 9 macroalgae sites using instantaneous focal surveys (Fulton et al. 2001). This involved an observer swimming a non-overlapping path throughout a site and recording data on a minimum of 50 individual fish. For each individual we obtained a measure of: total length (to the nearest cm), behaviour during the first three seconds of observations (travelling, sheltering, staiton-holding, searching, feeding; see Wenger *et al.* 2018 for behaviour descriptions) and the microhabitat condition (percentage cover and canopy height) within a 1m^2 area. A minimum of 60 haphazardly placed 1m^2 quadrats per site were also used to get a measure of site habitat condition against which *T. lunare* microhabitat preference could be compared. Differences in microhabitat use were assessed using the electivity indices of Vanderploeg and Scavia (1979), which were calculated as: $E_i^* = [W_i - (1/n)]/[W_i + (1/n)]$, where n is the number of microhabitat categories; Wi is the selectivity coefficient for microhabitat category i, calculated as $W_i = (r_i/p_i)/ (\Sigma_i r_i/p_i)$, where r_i is the proportional use and p_i the proportional availability of the microhabitat category i at each site. Values of 0 indicate use of a microhabitat at roughly equal to availability (neutral selection), while positive and negative values indicate preference and avoidance for a microhabitat type, respectively. Electivity indices were calculated at each site for each of the three *T. lunare* life-history categories, with mean values and associated 95% confidence intervals being calculated for microhabitat categories within each mesohabitat. A chi-square test was used to test the overarching null hypothesis that microhabitat use was proportional to availability for each life-history stage within the two mesohabitat types (Table S5.1).

Foraging patterns among different spatial contexts

Foraging data for 12 adults across nine macroalgal sites within three different spatial contexts was obtained via a 20-minute focal survey per individual (n = 108). The three different spatial contexts were based on a macroalgae site's spatial connectivity to the reef and were defined, following van Lier *et al.* (2018), as: 'embedded' – a macroalgae site set within the coral backreef, 'proximate' a macroalgae site within 500m of the backreef, and 'distant' a macroalgae site greater than 800m from the backreef. Foraging patterns were recorded by a diver haphazardly moving through a site until an adult *T. lunare* individual (>7cm; Ackerman 2004) was identified and then followed for 20 minutes. During this time, the diver recorded the number of foraging forays undertaken and the microhabitat where each foraging foray was observed (canopy or understory macroalgae, live/dead coral, abiotic matrix, water column, other biotic). Directly above the diver throughout the survey was a snorkeler that had a GPS unit to obtain movement pathway information. A 20-minute timed swim was selected based on maximum *T. lunare* swimming speeds (3.1 TL/s; Wainwright et al. 2002) which would allow an individual of 22 cm (their approximate upper length; Kuiter 2015) to travel up to 800m- the minimum distance between distant sites and the coral backreef. Once taken, tracking data was imported to QGIS 2.17 and the absolute distance measures of total path distance (D_T) and linear distance between start and finish (D_{SF}) were extracted, and used to calculate a tortuosity ratio (D_T/D_{SF}) following Secor (1994). Given the positive relationship between fish size and movement (Nash et al. 2015), our three foraging path metrics were tested against body size to check for allometry using a linear regression (Figure S5.1). Spatial variation in foraging forays was examined using a two-factor PERMANOVA with the random factor site nested in the fixed factor of spatial context. Given potential ontogenetic related differences in diet, we included body-size as a co-variable. Frequency of foraging forays on the different microhabitat categories was square-root transformed and arranged into a resemblance matrix using the Modified Gower (base 2) similarity measure. The calculation of site-level mean proportional values and associated 95% confidence intervals for microhabitat foraging target and availability at the spatial context level were used to explore potential differences in foraging microhabitat use relative to availability. Spatial variation in *T. lunare* foraging pathways was examined using a PERMANOVA of the same design as for the foraging forays above. Given some significant relationships between total length and foraging distances, total length was again included in the model as a covariate. Absolute distance (total distance + start-finish distance) measures were square-root transformed and arranged into a resemblance matrix using Euclidean distance measures, upon which the PERMANOVA was run. The tortuosity ratios underwent the same process upon which a univariate PERMANOVA was run. Qualitative differences in foraging pathways were also explored by comparing tracks typical of the differences between the spatial contexts.

Results

Ontogenetic differences in habitat use across spatial scales

The relative abundance of different *Thalassoma lunare* life history stages differed significantly among macroalgae and coral mesohabitats (Table 5.1). Ontogenetic differences in mesohabitat preference were evident with coral reefs possessing substantially higher densities of recruit and juvenile fish compared to macroalgae meadows where larger, terminal phase males were more dominant (Fig. 5.1).

In general, microhabitat use by *T. lunare* was not proportional to availability and differed between life-stages within mesohabitats (Chi- squared test; all p-values < 0.001 except terminal phase in coral reef mesohabitat where $p = 0.08$; Fig. 5.2). *T. lunare* showed preference for rarer microhabitat categories, highlighted by preferential use of macroalgae microhabitat in coral mesohabitats and live coral microhabitat in macroalgae mesohabitats. In coral mesohabitats, juvenile and initial phase fish showed significant avoidance for low complexity abiotic microhabitat, and exhibited neutrality for higher complexity dead corals, and, in regards to juvenile fish, live coral structure. In contrast, *T. lunare* had a high affinity for structurally complex live and dead coral microhabitat across life history stages in macroalgae mesohabitats.

Table 5.1. Summary of PERMANOVA exploring the variation in the density of three different life-history stages (juvenile, initial and terminal phase) among 32 sites in two different mesohabitats across six years. Significant effects highlighted in bold.

Source	df	SS	MS	Pseudo-F	P(perm)
Mesohabitat	**1**	**69.46**	**69.46**	**52.89**	**0.0001**
Year	**5**	**2.36**	**0.47**	**2.51**	**0.006**
Site(Mesohabitat)	**30**	**38.69**	**1.29**	**6.86**	**0.0001**
Mesohabitat x Year	5	1.02	0.20	1.08	0.37
Site(Mesohabitat) x Year	**133**	**25.01**	**0.19**	**1.60**	**0.0001**
Residuals	1400	164.74	0.11		
Total	1574	305.05			

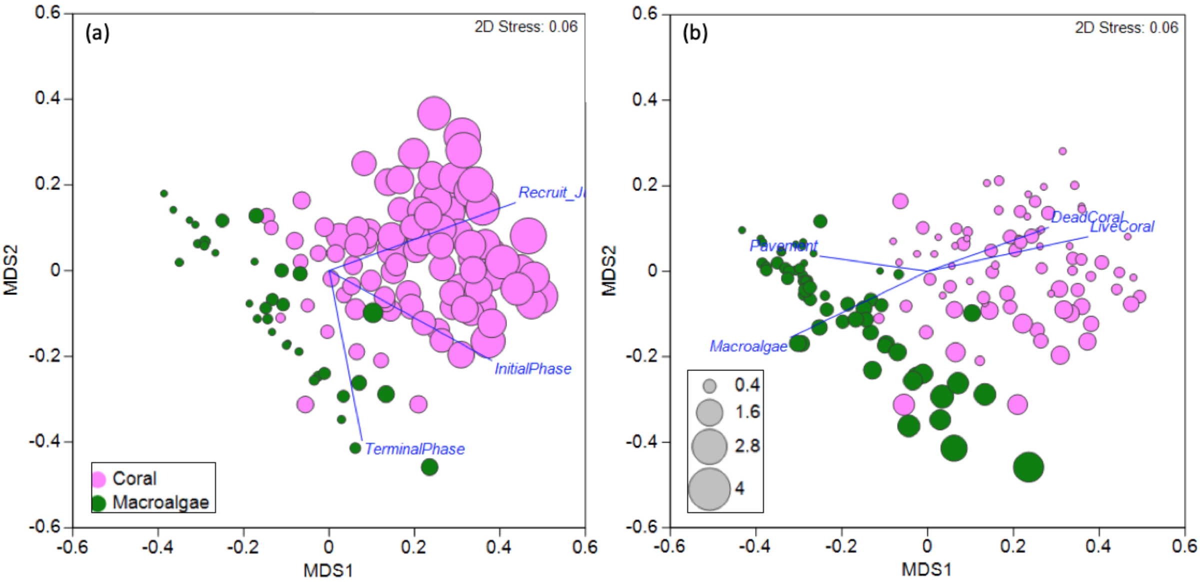

Figure 5.1. Metric multidimensional scaling ordination of *Thalassoma lunare* population densities at three different life-history stages (juveniles and adults at initial and terminal phases) across two tropical mesohabitat types at Ningaloo. Bubbles indicate (a) mean juvenile densities and (b) mean terminal phase densities (150m^{-2}) with each point representing a year specific site-mean calculated from nine survey replicates. Vectors show strength and direction of the different life-history stages (a) and cover of microhabitat category (b), with vectors shown having a Pearson's r value >0.5.

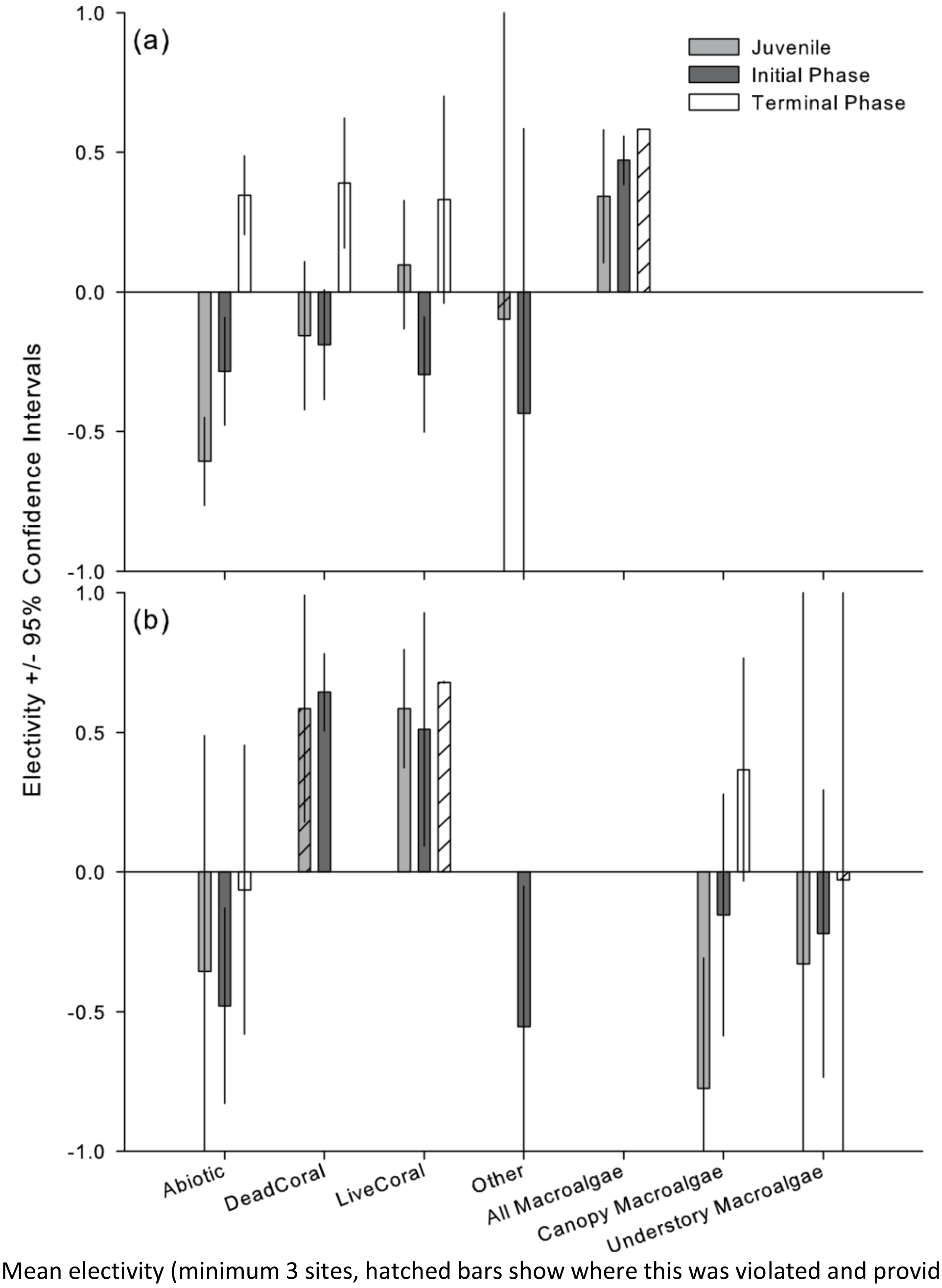

Figure 5.2. Mean electivity (minimum 3 sites, hatched bars show where this was violated and provide indicative values only) of *Thalassoma lunare* activity (all activities) towards different microhabitat categories within (a) coral-dominated and (b) macroalgae-dominated mesohabitats at Ningaloo. Values with errors that intersect zero indicate neutrality (no preference).

Variations in foraging patterns under different spatial contexts

Microhabitat targets for foraging forays differed significantly with respect to spatial context and size-class, with pairwise exploration revealing that forays varied among all three spatial contexts (Table 5.2a). In sites >800m from the backreef, we found that *T. lunare* were foraging

Table 5.2. Summary of PERMANOVAs exploring *Thalassoma lunare* (a) foraging behaviours, and movement pathways for (b) absolute distances and (c) tortuosity ratio, while accounting for body-size, between nine different sites within three different spatial contexts. Significant effects highlighted in bold.

Source	df	SS	MS	Pseudo-F	P(perm)
(a) Foraging Forays					
Body-size	**1**	**2.1109**	**2.1109**	**2.273**	**0.0456**
Spatial Context	**2**	**32.394**	**16.347**	**8.6133**	**0.0001**
Site(Spatial Context)	**6**	**11.574**	**1.929**	**2.3689**	**0.0004**
Residuals	98	79.801	0.81429		
Total	107	126.18			
(b) Absolute Distances					
Body-size	**1**	**436.22**	**436.22**	**17.904**	**0.0001**
Spatial Context	**2**	**337.47**	**168.74**	**6.1813**	**0.0096**
Site(Spatial Context)	6	164.35	27.392	1.1405	0.3279
Residuals	98	2353.8	24.01		
Total	107	3291.8			
(c) Tortuosity Ratio					
Body-size	1	0.0592	0.0592	0.0242	0.8768
Spatial Context	2	10.004	5.002	1.2984	0.3364
Site(Spatial Context)	6	23.385	3.8975	1.709	0.1266
Residuals	98	223.49	2.2806		
Total	107	256.94			

in canopy macroalgae at a lower proportion than its availability, while foraging in understory macroalgae was greater than its availability (Fig. 5.3). In both the proximate and embedded sites microhabitats were targeted approximately equal to their availability, but we did find significant differences in the proportion of foraging undertaken on canopy macroalgae between initial and terminal phase fishes (Fig. 5.3). While we were unable to quantify availability of ‘water column’, fish across both life history stages and all spatial contexts were observed feeding directly in the water column on items including juvenile fish, discarded scraps from other fish and faecal matter.

In terms of distances travelled by *T. lunare* during foraging observations, we found significant variation in both the total distance travelled, and the linear distance between its start and finish points, among sites within different proximity to the backreef (Table 5.2b). Pairwise exploration of these revealed significant differences between the distant and

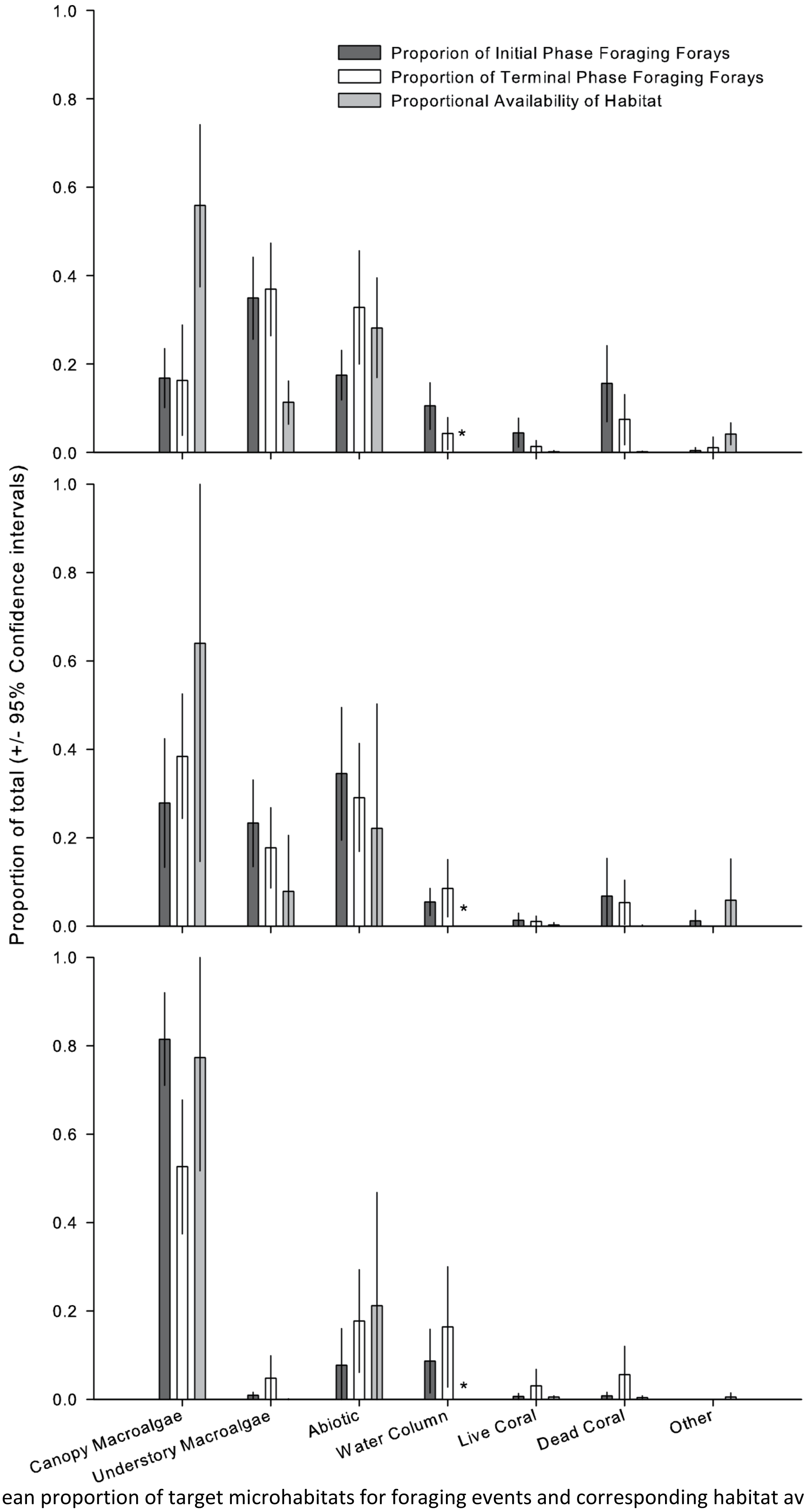

Figure 3. Mean proportion of target microhabitats for foraging events and corresponding habitat availability for (a) lagoonal patches distant from the reef, (b) lagoonal patches proximate to the reef, and (c) macroalgae patches situated on the backreef. * indicates a microhabitat category for which data was not collected.

spatial contexts, with terminal phase fish travelling longer distances and both initial and terminal phases having a larger linear distance between start and end points in sites proximate to the backreef (Fig. 5.4). While fish in sites distant to the reef had a higher median tortuosity ratio compared to the other two spatial contexts, particularly among terminal phase individuals- suggesting a convoluted foraging path. However, due to high levels of variation no significant difference in tortuosity was found at any level (Table 5.2c, Fig. 5.4).

General patterns of movement emerged that typified each of the different spatial contexts and can be seen at the extremes of the range of pathways. In distant patches, individuals more often had shorter travel distances, more convoluted pathways and seldom left their focal patch, even in patches with large areas. (Fig. 5.5 a, b). In contrast, individuals from sites proximate to the reef had larger travel distances and more directed movement, with individuals traversing large distances to access the backreef and moving across open space to access other macroalgal patches (Fig. 5.5c, d). *T. lunare* from sites embedded in the backreef exhibited characteristics from the other two spatial contexts, with wide variation in the distances travelled and pathway convolution, while making use of both available mesohabitats (Fig. 5.5e, f).

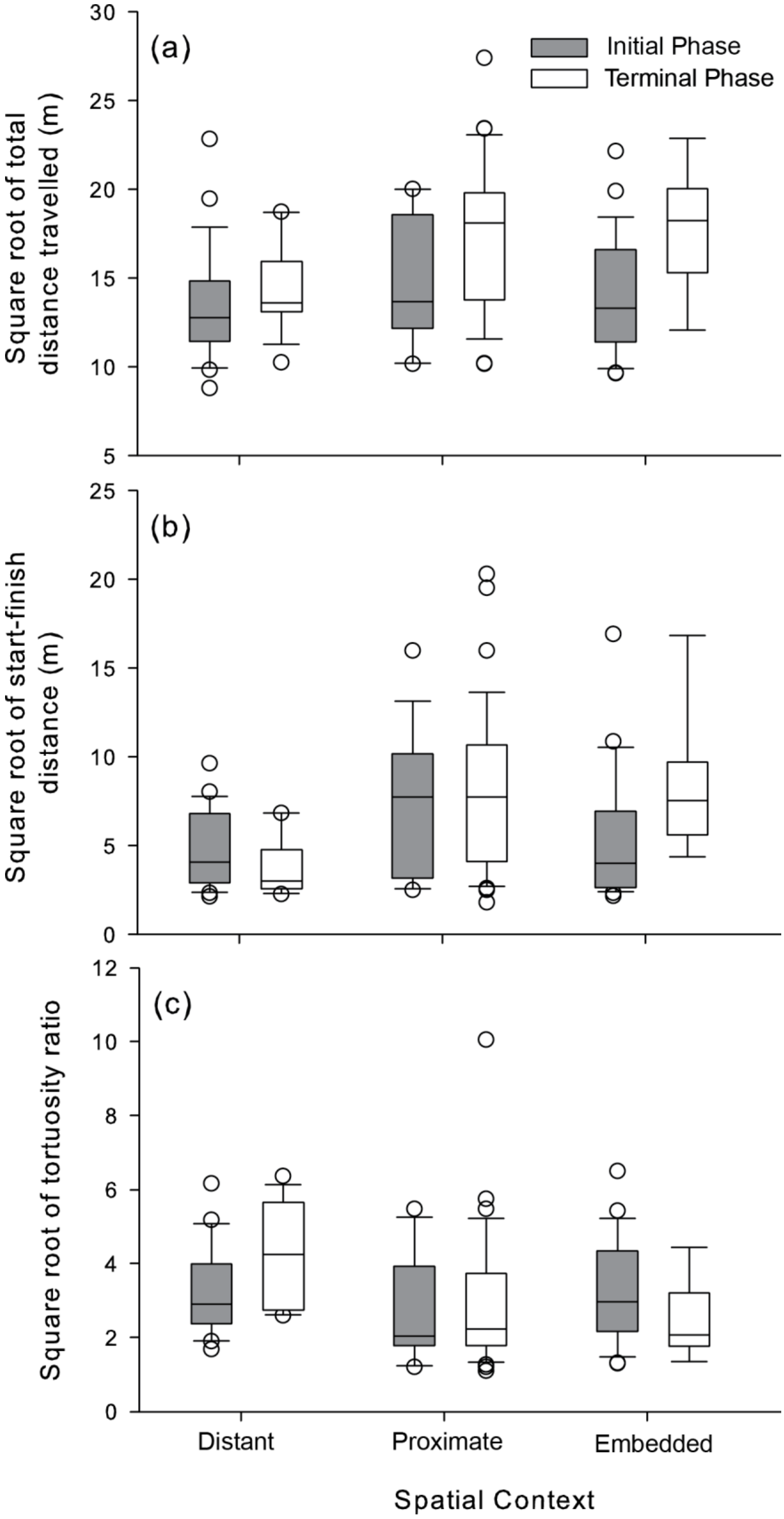

Figure 5.4. The variation in *Thalassoma lunare* movement metrics for (a) total distance travelled, (b) start-finish distance, and (c) tortuosity ratio at different life-history stages and spatial contexts at Ningaloo.

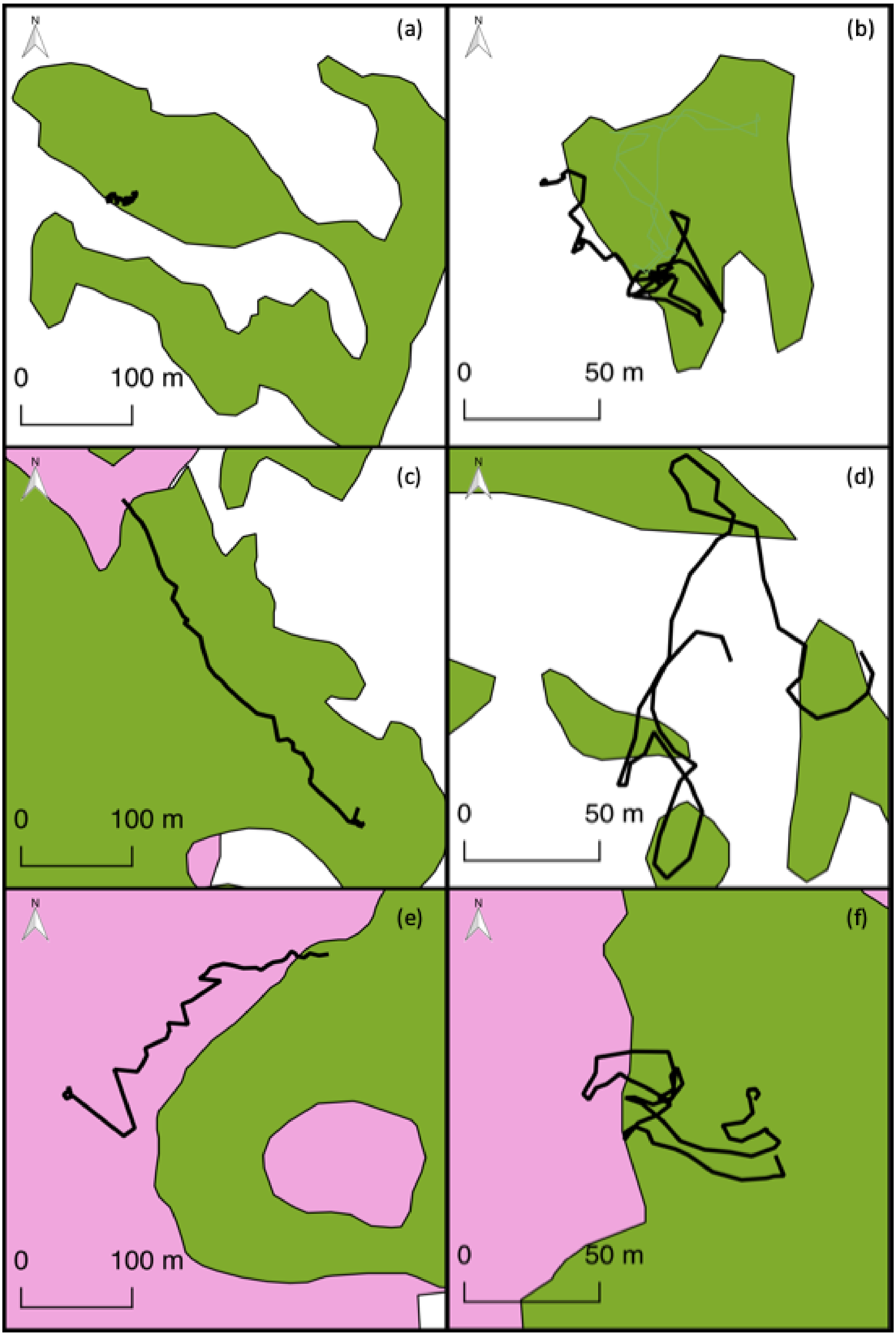

Figure 5.5. Examples of different movement pathways with the top panels showing far patches, the middle panels showing near patches, and the bottom panels showing embedded patches. Pink = coral backreef, green = macroalgae meadows, white = lagoonal soft-sediment.

Discussion

Our results suggest *Thalassoma lunare* is an ecologically versatile fish that is able to exist across the seascape by utilizing a range of habitats for its shelter and foraging activities. In the Ningaloo Reef population, we find that there are ontogenetic-based differences in habitat use across a range of spatial scales, with juveniles showing preference for complex coral structure in coral reef mesohabitats before a general shift in habitat preference as adults to macroalgae meadows. Furthermore, foraging behaviours of adult *T. lunare* appeared to be influenced by broad-scale patterns in the configuration of the seascape, with higher connectedness allowing for the exploitation of proximate mesohabitats, similar to what has been seen in some browsing herbivores (Davis et al. 2014).

T. lunare appears to show habitat specialisation as a recruit, with a high affinity for complex live coral microhabitat structure within coral reef mesohabitats (Berkström et al. 2014), before becoming substantially more general in its habitat use (Green 1996; Wilson et al. 2010) and diet (Kramer et al. 2015). While we found juveniles had a neutral preference towards live coral in coral reef mesohabitats, there is likely some nuance to this result. Firstly, when looking to macroalgae mesohabitats in this study we find a high level of electivity towards live corals. So even though juveniles are a rare occurrence in these habitats, where they are present there is a strong, positive relationship between fish and microhabitat. More broadly, while many fishes associate with live corals as juveniles (Coker et al. 2014), coral morphology can play a significant role in species-specific microhabitat use. For example, Wilson *et al.* (2016) demonstrated that it was specifically the availability of corymbose coral growth forms that were important for the successful recruitment of the damselfish *Pomacentrus moluccensis*. Given that *T. lunare* has previously shown strong associations with structurally complex live coral growth forms like corymbose corals (Berkström et al. 2014), it is likely that our microhabitat category was too broad to pick up on some of these fine-scale differences, but that juveniles are preferentially selecting for live coral microhabitat- particularly as newly settling recruits. Observations that *T. lunare* became more generalist in their niche requirements as they moved through life history stages are consistent with observations in the wider literature relating to both *T. lunare* and other reef fishes. On Lizard Island, in the Great Barrier Reef, adult *T. lunare* were shown to use a much wider array of reef habitat compared to juveniles who were observed almost entirely on the reef slope (Green 1996), while many other fishes have shown ontogenetic changes from habitat specialist to generalist (Coker et al. 2014). However, many of these studies have focused exclusively on coral reefs, so an examination of microhabitat use patterns as they manifest in the fundamentally different environment of macroalgae mesohabitats is also important.

The pattern in which adult *T. lunare* associates with and feeds upon microhabitats in macroalgae-dominated mesohabitats highlights a generalist, but with a preference for structurally complex hard features. Where the three-dimensional soft-structure of macroalgae-dominated mesohabitats has been highlighted as an important predictor of fish distribution and habitat use for a number of species (Wilson *et al.* 2014; Lim *et al.* 2016; Wenger *et al.* 2018; Fulton *et al.* In Press.), *T. lunare* appears to show neutral preference, or avoidance, in the case of juvenile fish, to both canopy and understory macroalgae across its range of activities. In contrast, the macroalgae-associated carnivorous fish *Xenojulis margaritaceus* showed very strong preference for canopy forming macroalgae for all of its activities (Wenger et al. 2018). While some caution must be taken in interpreting our results due to the emphasis placed on use of rare microhabitat categories when calculating electivity indices (Manly et al. 2002), it seems that established predictors of fish distribution and habitat use do not apply to *T. lunare*. Instead, adult fish behaviour in macroalgae mesohabitats appears to respond to aspects of hard structural complexity, and potentially, spatial context (van Lier et al. 2018).

In our study, we found that spatial context influenced the foraging targets of *T. lunare*. In sites distant from the coral backreef, understory macroalgae was targeted disproportionately more than its availability, while canopy macroalgae showed the opposite trend. As site proximity to the coral backreef became closer, foraging forays of both canopy and understory macroalgae became more proportional to their availability. The apparent preference for understory macroalgae on sites furthest from the backreef may relate to targeting of macroalgal taxa that harbour more food resources. An abundant genera of understory macroalgae in the Ningaloo region is *Lobophora* (Lim et al. 2016). This genera possesses a higher density of epifauna than other understory macroalgae (Roff et al. 2013), comparable to epifauna densities observed on canopy forming *Sargassum* (Wenger et al. 2018). Given crustaceans are the main dietary component of *T. lunare* (Berkström et al. 2014; Kramer et al. 2015), and different species of macroalgae can support different epifauna communities (Cacabelos et al. 2010; Gestoso et al. 2010), what we are potentially seeing then is a preference for *Lobophora*-associated epifauna. *Lobophora* is also more common in areas with low wave exposure (Goldberg and Kendrick 2004), most likely found furthest from the backreef. Therefore, potential spatial variation in the distribution of prey species associated with understory macroalgae may be why we found such large variation in electivity indices towards this microhabitat category, as variation at the seascape level was not considered. The potential importance of food availability in helping to determine spatial foraging patterns is highlighted elsewhere in the Ningaloo system with a positive relationship between the abundance of juvenile and predatory fish (of which *T. lunare* is one; Holmes et a. 2012) within different macroalgal patches (Wilson et al. 2014; Wilson et al. 2017).Future studies focusing on specific prey-selection, as well as multi-scale variation in epifauna community structure and the drivers of macroalgae presence and growth, would be helpful in understanding these spatial differences in foraging behaviour.

In addition to variation in foraging targets, we also found movement patterns differed with spatial context. This was largely driven by differences in absolute movement distances, with individuals at sites close to the backreef exhibiting much higher values than those furthest from the backreef. In distant sites, individuals generally moved relatively smaller distances and in convoluted pathways, even in large patches. Based on our *in situ* observations, this was likely related to individuals moving in a way where they would not leave the vicinity of an area of high structural complexity (e.g., live or dead coral structure). When an individual would attempt to leave a patch and cross open sand habitat, it would quickly return to an area of hard structural complexity. As a consequence, there is a high degree of selectivity for live and dead corals within macroalgal mesohabitats that is not apparent on coral reefs where these microhabitats aren't isolated. In contrast to distant sites, sites with higher connectivity (i.e., less time spent over exposed sand habitat) possessed some individuals that demonstrated movement which was relatively directed and over larger distances into different macroalgal patches or the coral backreef.

The different foraging path responses we found between spatial contexts may manifest in fundamentally different predation pressures, processes and resultant prey communities. Here, we find *T. lunare* individuals in distant macroalgae sites tend to cluster around 'islands' of high structural complexity. This could result in localised areas of predation which manifest in a foraging pressure gradient, similar to ecological halos of herbivory observed elsewhere (Madin et al. 2011; Reeds et al. 2018), with very different prey communities at the extremes. In contrast, individuals in sites with contiguous corals and associated complexity forage between sites and over broader areas, potentially reducing local predation pressure and taking advantage of a wider range of prey targets; potentially allowing them to be more resilient to change.

In this study, we add to the growing body of work that explores foraging behaviours in a spatial context (e.g., Davis *et al.* 2014; Sambrook *et al.* 2016). Predation is a key function that is responsible for shaping community structure and maintaining diverse assemblages (Hixon and Beets 1993). Here, we show that a common mesopredator in tropical waters can be found across different mesohabitats, with juveniles being predominantly found on coral reefs before an ontogenetic shift to macroalgae. This shift in habitat use emphasises the need to protect a range of habitat types to successfully conserve species responsible for key ecological processes like predation and energy transfer (Holmes et al. 2012; Thillainath et al. 2016). Furthermore, it is clear that foraging of this generalist mesopredator differs among spatial contexts, possibly due to accessibility of reef structure. To fully realise the implications of different foraging strategies and their effects on the local system, further work is required on the feeding preferences associated with behaviours in different mesohabitats for fishes that are linked to important ecological processes.

Supplementary Material

Table S5.1. Contingency table showing number of observations per life history stage and proportion of available habitat for (a) coral reef and (b) macroalgae mesohabitats.

		Microhabitat category	Frequency of use observed	Proportion of habitat available
a)	Coral Reef			
i.	Juvenile	Abiotic	146	0.49
		Macroalgae	81	0.04
		Dead coral	181	0.22
		Live coral	384	0.24
		Other biotic	3	0.01
		Total	795	1.00
ii.	Initial Phase	Abiotic	324	0.49
		Macroalgae	75	0.04
		Dead coral	150	0.22
		Live coral	165	0.24
		Other biotic	10	0.01
		Total	724	1.00
iii.	Terminal Phase	Abiotic	22	0.49
		Macroalgae	3	0.04
		Dead coral	4	0.22
		Live coral	11	0.24
		Other biotic	0	0.01
		Total	40	1.00
b)	Macroalgae			
i.	Juvenile	Abiotic	11	0.24
		Canopy macroalgae	12	0.66
		Dead coral	3	<0.01
		Live coral	10	<0.01
		Understory macroalgae	3	0.06
		Other biotic	0	0.04
		Total	39	1
ii.	Initial Phase	Abiotic	42	0.24
		Canopy macroalgae	298	0.66
		Dead coral	11	<0.01
		Live coral	4	<0.01
		Understory macroalgae	34	0.06
		Other biotic	5	0.04
		Total	394	1
iii.	Terminal Phase	Abiotic	13	0.24
		Canopy macroalgae	83	0.66
		Dead coral	0	<0.01
		Live coral	2	<0.01
		Understory macroalgae	4	0.06
		Other biotic	0	0.04
		Total	102	1

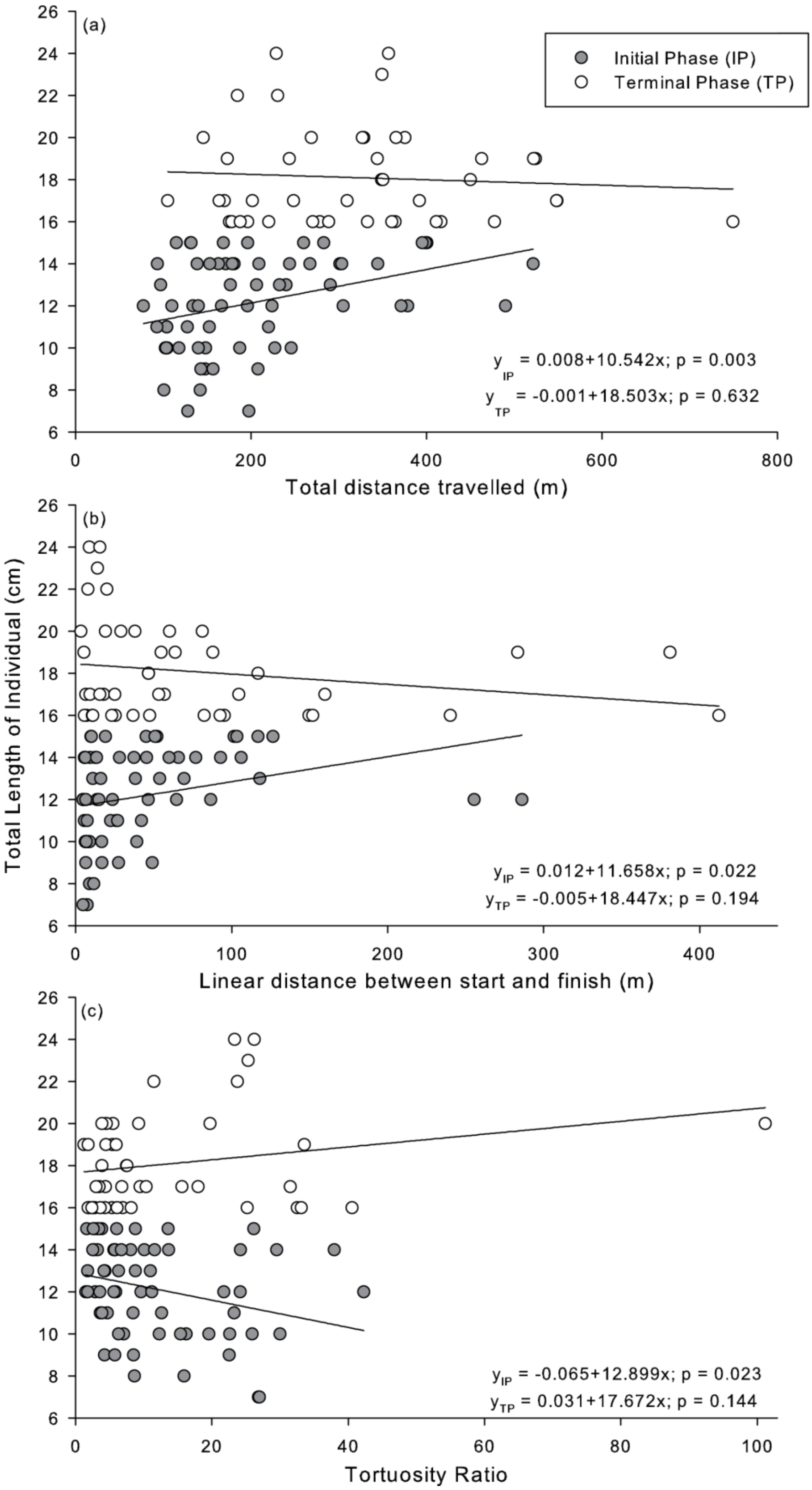

Figure S5.1. Linear relationships between total body length *Thalassoma lunare* individuals and their (a) total distance travelled, (b) start-finish linear distance, and (c) tortuosity ratio for both initial and terminal phase life-history stages. Equations and p-values from linear relevant linear regressions are shown.

Chapter 6

General Discussion

Seascape ecology posits that both complexity and connectivity of habitats are important in structuring and maintaining diverse ecological communities. However, the form of structure (e.g., hard or soft), how it is measured, and its importance at varying spatial and temporal scales varies between systems. Therefore, how reef fishes in classically understudied systems respond to multi-scale variation in the seascape is critical to our understanding of patterns and processes guiding species distribution, abundance and community structure- particularly as we move towards ecosystem-level approaches to conservation and management.

Looking across a range of temperate mesohabitats, I found that mesohabitat-specific differences in fish community structure all aligned with key aspects of soft three-dimensional structure- namely canopy cover and height (Chapter 2). In the ecologically valuable system of tropical macroalgae meadows, I, for the first time, identified connectivity with a coral reef as important for determining the structure of local fish communities (Chapter 3). However, the importance of connectivity was limited to examinations that explicitly accounted for species identity. When exploring coarser resolutions of diversity (e.g., alpha diversity, functional group structure), local-scale aspects of habitat condition, such as canopy cover, height, and the novel result of hard complexity, were what best predicted observed patterns (Chapter 3). Additionally, in an experimental manipulation, I demonstrated that canopy height of the tropical macroalgae *Sargassum* spp. is a direct driver of fish abundance and diversity (Chapter 4). Furthermore, the unseasonal reduction of canopy height can have long term effects that decreases fish diversity and abundance (Chapter 4). Finally, by highlighting how the mesopredatory fish *Thalassoma lunare* varies its foraging behaviours according to spatial context, I link multi-scale variations in habitat quality to the ecological process of predation (Chapter 5). Overall, my thesis demonstrates the importance of taking a holistic view to understand ecological pattern and process; that, in understanding what comprises a quality habitat for a community, one must account for variation across multiple spatial and temporal scales (Fig. 6.1).

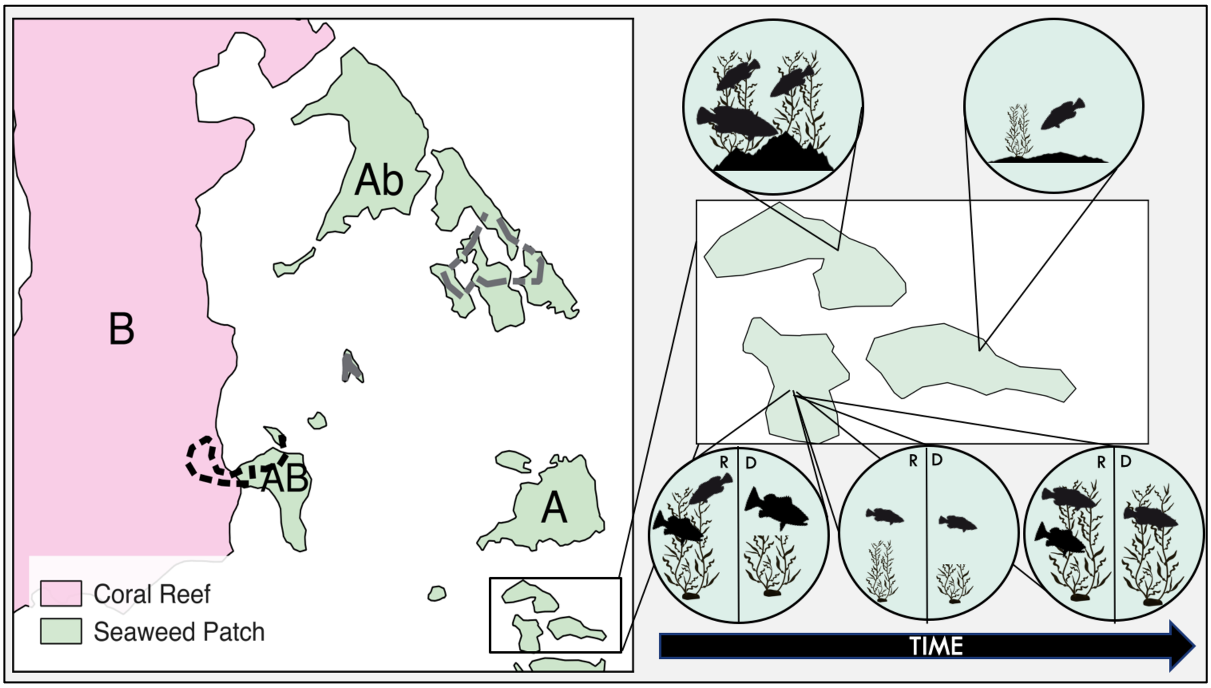

Figure. 6.1. Conceptual diagram showing the philosophy of my thesis. The panel on the left shows a model seascape comprised of coral and macroalgae mesohabitats, where connectivity between different patches and mesohabitats can further augment patterns and processes. Shown here by different community types and foraging pathways. Where A = a typical macroalgae-associated fish community and B = a typical coral-associated fish community. The more connected a patch of macroalgae is to the coral reef the greater the influence the coral reef will have on the macroalgae-associated fish community, represented by the presence/absence and/or capitalisation of the letter 'b'. Foraging pathways shown are represented by a black dashed line = individual foraging through multiple connected mesohabitats; grey-dashed line = individual foraging through connected patches within the same mesohabitat; and solid grey line = individual foraging in an isolated patch. Within the seascape, local-scale processes are also operating that underpin ecological patterns and processes. Circular panels in the top-right show how differences in local habitat condition between two macroalgae patch-habitats manifest in different values of species richness and abundance. While the circular panels on the bottom right highlight the explicit importance of canopy height and the effects unseasonal height reductions can have on fish diversity over the short- (days; left circle), medium- (months; middle circle) and long-term (years; right circle), where R = reference site, and D = disturbed site.

Local soft-structure complexity drives marine fish patterns and processes

Local three-dimensional complexity of rigid benthic components continues to be important for understanding patterns and processes in coastal fish communities (Almany 2004b; Graham and Nash 2013). However, in looking across a variety of soft-structure mesohabitats, I found a strong response of fish to the three-dimensional manifestation of non-rigid habitat-forming organisms. In temperate sponge gardens, areas that had the highest level of microhabitat richness were also the areas with the highest level of fish species richness. These sponge mesohabitats exhibit a high degree of structural complexity through variation in growth form (Boury-Esnault and Rutzler 1997), analogous to those seen by hard corals, which provides a range of available niche space (Bell 2008). This aligns well with niche theory which suggests that a diversity in microhabitats should support the coexistence of an increased number of species in a given area via niche-partitioning (Hardin 1960; Hortal et al. 2009).

Across the range of temperate and tropical mesohabitats examined in my thesis, and in support of recent observational studies (e.g., Harasti et al. 2014; Lim et al. 2016; Wilson et al. 2018), the height of canopy forming organisms was consistently one of the best predictors of fish diversity and community structure. Through my manipulative experiment, I was able to explicitly demonstrate variation in local canopy height as a driver of fish abundance, diversity and community structure. Interestingly, the response to a reduction in canopy height was taxa-specific, with nominal herbivores and lower-order carnivores both showing immediate and sustained decreases in density, while higher-order carnivores exhibited a short-term increase. These different responses are likely due to how fish use space in this third dimension, i.e., height from the substratum. Many nominal herbivores and lower-order carnivores rely on macroalgae for dietary resources by either directly consuming the macroalgae itself, or their resident epifauna (Bellwood et al. 2006b; Lim et al. 2016; Tano et al. 2016; Wenger et al. 2018). So a reduction in canopy height would lead to a direct reduction in the epifauna habitat available, likely decreasing their abundance as an available food resource. This follows similar patterns observed on coral reefs whereby the fish species that show direct trophic links to disturbed basal habitat-forming organisms showed the greatest declines in density (Pratchett et al. 2006; Emslie et al. 2011).

Differences in canopy structure can also affect behaviours related to key processes. Results in coral reefs have demonstrated the role of hard complexity in moderating the effects of predation and piscivory, with decreasing complexity being related to increases in predation success (Beukers and Jones 1997; Almany 2004b). However, here I found that reduction in canopy height precipitated short term, significant increases in higher-order carnivores. The reduction in soft canopy structure has previously been shown to increase foraging efficiencies in some forms of predator (Horinouchi et al. 2009). This suggests that with the canopy height reduction in my study, mobile piscivores were better able to exploit smaller-bodied fishes that had reduced refugia.

I recommend canopy height, among other measures of soft-structure, be included in future studies exploring patterns and processes of fish habitat-interactions. Where benthic cover has previously been a key predictor of fish patterns in soft-structure mesohabitats, particularly tropical macroalgae (reviewed in Fulton et al. In Prep.), this limits examination to a two-dimensional plane and can potentially omit vital information that is accounted for in a three-dimensional exploration, providing a fuller understanding of fish patterns and processes.

The seascape ecology of macroalgae-associated fish patterns and processes

Seascape ecology has highlighted the connectivity and proximity of mesohabitats as an important predictor of the diversity and abundance of terrestrial and marine communities (Berkström et al. 2013; Staveley et al. 2016; Michael et al. 2017). For the first time, I extend the principles of seascape ecology to a patchy network of tropical macroalgae and highlight the importance of connectivity with a coral reef in structuring the suite of fish species observed in macroalgae-dominated patches. Such results provide further support for the prominence of the mass effects paradigm of metacommunity theory in marine seascapes, contrasting other biomes (Leibold et al. 2004; Heino et al. 2015). Mass effects requires that different patches have different local conditions and be sufficiently connected which results in a source-sink dynamic (Leibold et al. 2004). Connectivity between coral reef and macroalgae mesohabitats allows generalist species (e.g., *Thalassoma lunare*) to readily exploit resources in both, expanding their distribution and influence on other components of the system. Connectivity between these mesohabitats also seems to inflate diversity in macroalgal patches, particularly where there are isolated areas of structural complexity (e.g., coral bommies) embedded within the focal patch. Indeed, it is these patches (that possess high complexity and connectivity) that likely allow the coral reef fish to persist in a macroalgal-dominated system. Thus, for these fishes, it is the structural complexity and links between structures that underpin their function, while it is the structure of canopy forming macroalgae that is most important for the more classically recognised macroalgae-associated fish species.

The isolation and area of a patch-habitat arose from studies into Island Biogeography Theory as key predictors of diversity and community structure (MacArthur and Wilson 1963; Simberloff and Wilson 1970). However, in these tropical macroalgae meadows I found both patch area and isolation to be consistently among the poorest predictors of diversity-regardless of the taxonomic resolution investigated. This is in stark contrast to a number of terrestrial studies and other marine mesohabitats, such as coral reefs, where area and isolation have shown to be effective in predicting species richness (Garden et al. 2010; Boström et al. 2011; Shanahan et al. 2011). Instead, my results relating patch size and isolation to fish diversity best align with those from other soft-structure patchy mesohabitats, such as seagrass, that found a limited relationship (Boström et al. 2011).

In addition to explaining ecological patterns, spatial context was also important in predicting ecological processes. I found that the foraging behaviour of a transient mesopredator (*Thalassoma lunare*) was partially explained by the connectivity of the macroalgae-dominated patch it was observed in. Individuals that resided in isolated patches tended to show decreased absolute movement distances and a strong sense of site fidelity. In contrast, individuals from more connected patches showed greater absolute movement distances and would more frequently forage in the neighbouring coral reef mesohabitat. My result here found concordance with other studies that have linked spatial subsidies in foraging to mesohabitat connectivity (e.g., Davis et al. 2014), and begin to fill in the knowledge gap surrounding ecological processes in a spatial context (Pittman and Olds 2015).

Applications to conservation and management of coastal marine fishes

While contributing to broader ecological theory, the results from my thesis also have tangible benefits to the conservation and management of coastal marine fishes in several areas. I provide broad support for macroalgae meadows as having high ecological value (i.e., unique macroalgae-associated fish community), and given their global prevalence in tropical seas (Fulton et al. *In Review*), these should be integral parts of any marine protected area. In that regard, I recommend the inclusion of macroalgae meadows and their associated fauna in any monitoring program for the Ningaloo Marine Park.

Placing marine reserves or protected areas in parts of the seascape that facilitate connectivity between different mesohabitats is also critical. Many fish move throughout the seascape mosaic in the course of their diel movements and my research contributes to a building body of work that show greater seascape connectivity enhances both the diversity and productivity of marine protected areas (Olds et al. 2016). Furthermore, tropical macroalgae meadows are increasingly being seen as important nursery habitats for a number of reef fishes, particularly in regions that lack traditionally recognised nursery habitats like seagrass (Evans et al. 2014; Tano et al. 2017). Typically, recruitment occurs in macroalgal mesohabitats before ontogenetic migrations to the reef when fishes become larger (e.g., Wilson et al. 2017). However, here I demonstrate that the pattern can be reversed with fish recruiting to reefs and moving to macroalgal meadows as they get older. This highlights that ontogenetic movements can go both directions and emphasises the importance of protecting both systems, and the corridors that connect them, to maintain healthy fish populations, which is particularly pertinent for exploited fisheries.

I have demonstrated that local habitat quality can vary spatially. Therefore, in assessing areas of high connectivity for improved protection, care should also be taken to examine the condition of the local macroalgal patch. Specifically, priority should be given to areas that possess a combination of high hard complexity, canopy cover and height to increase niche space and support the largest suite of fishes. Furthermore, given the ubiquity of canopy height as a predictor of fish diversity, I propose its use as an efficient and cost-effective bio-indicator tool. Key to the wide-scale success of such an approach would be further exploration and refinement of new technologies (e.g., hyperspectral sensing and satellite imagery - dark colouration and sea surface breaching of tall *Sargassum*) that can identify these aspects of habitat quality over broad scales.

Future directions

I have demonstrated how different attributes of soft complexity can influence the diversity of macroalgae-associated fishes (e.g., canopy cover or height). However, hard structural complexity was another aspect of local habitat condition I identified as important for predicting fish diversity and abundance in tropical macroalgae meadows. This has been well documented in coral-dominated systems (Graham and Nash 2013; Darling et al. 2017), but has had limited attention in the general marine macrophyte literature (e.g., Cheminée et al. 2016; Cuadros et al. 2017), and is a novel result in macroalgae. I recommend that some measure of hard complexity be included in future fish-macroalgae studies aiming to understand patterns of diversity and ecological processes. Furthermore, I view *in situ* manipulative studies that alter available hard complexity in macroalgal mesohabitats, and identify the species most strongly associating with it, as being productive in gaining a greater understanding of their role in structuring fish communities and underpinning processes such as predation.

While several studies are beginning to link patterns in fish diversity with the spatial context they are found in (e.g., Grober-Dunsmore et al. 2007; Olds et al. 2012; Berkström et al. 2013), these studies largely examine this relationship at a single time-step. How the relative importance of seascape variables contribute to community structure changes through time is an exciting avenue of future research. For example, Staveley et al. (2016) found that seascape configuration influenced temperate seagrass-associated fish communities significantly more in the boreal summer compared to autumn due to differences in fish life-history processes. In the Sargassum meadows of Ningaloo, which show temperature-related seasonal cycling in canopy structure (Fulton et al. 2014), understanding how a changing and fragmented seascape can affect the movement and diversity of local fishes through time is critical for understanding patterns of diversity and function. Therefore, I believe that a multi-season investigation of the relative importance of local- and broad-scale variables for fish diversity in the seasonally dynamic macroalgae meadows is an essential and logical next step.

Ecological halos, areas of high herbivory in close proximity to a central structure, are typically thought of as driven by predator relief (Madin et al. 2011; Reeds et al. 2018). However, results in my thesis highlight the potential for a form of ecological halo to occur whereby predation is concentrated around a central structure. The mesopredator *Thalassoma lunare*, was found to exhibit decreased foraging distance in isolated macroalgae patches. This, combined with a preference for hard structural complexity, mean it is potentially foraging in a tightly concentrated area, and causing high predation stress for prey species. By investigating the prey selection of this fish (or others that exhibit similar behaviours), alongside a comparison of the prey community between different buffer distances around a central high complexity structure (and control area with no central structure), greater insights could be had into predator-prey dynamics and community assemblage at different spatial scales.

Concluding Remarks

My thesis highlights the need for taking a holistic view in understanding ecological patterns and processes. I provide the first study to look at the relative importance of seascape metrics for fishes in tropical macroalgae- an ecologically important and ubiquitous mesohabitat type.

Furthermore, I stress the importance of accounting for three-dimensional complexity at the local scale in soft-structure environments when examining the abundance, distribution and diversity of reef fishes. My results provide substantive contributions to the theories underpinning community assembly, particularly as a test of the application of theories developed in terrestrial settings to marine biomes. My findings also provide tangible applications to the design and monitoring of marine reserves by considering predictors and drivers of fish diversity at multiple scales. Finally, in seeking to answer questions of ecological significance, I have raised further ones and identified and outlined several I view as critical to further developing the field of seascape ecology.

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