Richardson, Laura Elizabeth (2018) ***Variation in structure and function of reef fish assemblages among distinct coral habitats*****. PhD thesis, James Cook University.**

https://doi.org/10.25903/5b57c26b0beb7

Variation in structure and function of reef fish assemblages among distinct coral habitats

Thesis submitted by

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in March 2018

for the degree of Doctor of Philosophy in Marine Biology

in the Centre of Excellence for Coral Reef Studies,

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ARC CENTRE OF EXCELLENCE
Coral Reef Studies

We must not let a forest full of trees fool us into believing that all is well

Redford, K (1992)

Acknowledgements

During my candidature, I received generous assistance from numerous individuals and organisations. Primarily, I am indebted to my supervisors Andrew Hoey, Nicholas Graham, and Morgan Pratchett. Thank you all for providing me with the opportunity to conduct interesting and rewarding research at the ARC Centre of Excellence for Coral Reef Studies in Townsville. Moreover, thanks for your continuous and patient mentorship, insightful contributions and questions, and unfailingly prompt and timely feedback on written work, field logistics, and data wrangling. I undertook this PhD to learn how to be an independent and rigorous scientist and I have been incredibly fortunate to have been guided by some of the world's leading ecologists. In particular, I thank you Andy for all your contributions, unfailing support, dedication, and thoughtfulness throughout and in particular in my most challenging times. Nick, thanks for all your great advice, clear foresight, guidance and encouragement, especially from the other side of the world. And thanks Morgan, for your all thoughtful advice, insight and recommendations throughout.

Huge thanks go also to the staff of the ARC Centre of Excellence for Coral Reef Studies for the academic, financial and administrative support and assistance provided throughout my candidature, in particular Terry Hughes, Jenny Lappin, Olga Bazaka, Janet Swanson, Vivian Doherty, Rose-Marie Vasiljuk, as well as staff in the Graduate Research School of James Cook University, in particular Jodie Wilson. None of this would have been possible without the never-ending IT support from Andrew Norton and Malcolm Goon Chew, as well as Rick Abom and Glen Ewels – thank you. Invaluable statistics and coding support was provided by Rhondda Jones, Murray Logan, Rie Hagihara, Simon Brandl, Cindy Hutchery, Collin Storlie – this thesis would not have happened without you. I am forever grateful to the following organisations and people who assisted me in my data collection and methods in one form or another: staff at Lizard Island Research Station, Jacob Eurich, Amy Douglas, Brock Bergseth, Bridie Gibbs, Molly Scott, Alexia Graba-Landry, Rob Streit, Eva McClure, Valeriano Parravicini, Emmanuel Mbaru, Kirsty Nash, Mike McWilliam.

Huge thanks to the organisations that funded my project, including: James Cook University Postgraduate Research Scheme and the Australian Research Council (ARC) Centre of Excellence for Coral Reef Studies, in particular the ARC DECRA awards to ASH (DE130100688) and NAJG (DE130101705), and the ARC Centre of Excellence for Coral Reef Studies to LER (Higher Degree Research Enhancement Scheme). Thanks also to the FSBI International Society for Fish Biology and the Australian Coral Reef Society for generous travel grants to international conferences so that I could present my research.

And finally, I am indebted to my friends in Townsville and friends and family overseas for their enduring love, support, laughter, and incredible times.

Statement of contribution of others

This thesis includes some collaborative work with my supervisors Dr Andrew Hoey, Prof Nicholas Graham, and Prof Morgan Pratchett. While undertaking this work, I was responsible for the project concept and design, data collection, analysis and interpretation, and the final synthesis of results into a form suitable for publication. My supervisors provided intellectual guidance, equipment, financial support, and editorial assistance.

Financial support for the project was provided by the Australian Research Council Centre of Excellence for Coral Reef Studies (DECRA grants to ASH: DE130100688, and NAJG: DE130101705), and the James Cook University Graduate Research Scheme. Stipend support was provided by a James Cook University Postgraduate Research Scholarship. Financial support for conference travel was provided by the Australian Research Council Centre of Excellence for Coral Reef Studies, The Australian Coral Reef Society, and the Fisheries Society of the British Isles.

Abstract

Anthropogenic disturbances are altering the abundance and distribution of organisms across biomes, disrupting the function and stability of ecosystems, and the goods and services they provide. On tropical coral reefs, global climate change and a range of local stressors are reducing populations of habitat-building corals, resulting in unprecedented coral loss and marked shifts in coral species dominance due to differential susceptibilities of coral taxa to disturbance. However, the extent to which shifts in coral species composition will alter the organization of associated organisms and undermine the resilience of coral reefs remains unclear. This thesis exploited a natural experiment on reefs surrounding Lizard Island, Australia, where multiple taxonomically distinct coral habitats existed, characterised by dominance of differing coral taxa, to assess the influence of coral species composition on the structure, function and resilience of reef fish assemblages. Specifically, the four data chapters of this thesis (**2–5**) addressed the following questions: (1) How does coral species composition affect the cross-scale structural complexity of coral reef habitats? (2) How does the functional diversity of reef fish assemblages vary among taxonomically distinct coral habitats? (3) To what extent does pre-disturbance coral species composition influence the susceptibility of reef fish assemblages to coral bleaching events? (4) Do critical herbivory functions (browsing and grazing) vary among distinct coral habitats?

Chapter 2 compares the cross-scale structural complexity of four coral habitats (i.e. branching *Porites*, massive *Porites*, *Pocillopora*, soft coral), with degraded habitats (characterized by low coral cover <10%, dead coral, rubble and macroalgae) across five ecologically relevant scales of measurement (4-64 cm). Results show that the structural complexity of habitats was underscored by coral species composition, and was not a simple function of total coral cover. However, among-habitat variation in structural complexity changed with scale. Importantly, the range of scales at which habitat structure was available also varied among habitats. Complexity at the smallest, most vulnerable scale (4 cm) varied the most among habitats, with inferences for as much as half of all reef fishes that remain small-bodied and refuge dependent for much of their lives.

Using an ecological trait-based analysis, **Chapter 3** compares the functional diversity of fish assemblages among six distinct coral habitats (characterised by branching *Porites*, massive *Porites*, staghorn *Acropora*, *Pocillopora*, soft coral, and mixed coral assemblages). Despite comparable species richness and functional evenness of fish assemblages among habitats, functional richness and functional divergence varied significantly. Variation in both metrics of fish functional diversity were best predicted by the relative structural complexity among habitats, and were largely driven by the abundance of small-bodied, schooling planktivores in the *Porites* habitats. The findings suggest that differential structural complexity among coral habitats may act as an environmental filter, altering the distribution and abundance of associated species traits, particularly those of small, habitat-dependent reef fishes.

Chapter 4 compares temporal changes in five complementary trait-based indices of reef fish assemblage structure among six habitats (i.e. branching *Porites*, massive *Porites*, *Pocillopora*, soft coral, mixed coral assemblages, degraded habitats) exposed to a system-wide thermal stress event. The analyses revealed an increased taxonomic and functional similarity of previously distinct reef fish assemblages following mass coral bleaching, with changes characterized by subtle but significant shifts in dominant fish taxa towards small-bodied, algal-farming habitat generalists. The taxonomic and functional richness of fish assemblages did not change across habitats. However, an increase in functional originality indicated an overall loss of functional redundancy, and interestingly, pre-bleaching coral composition better predicted changes in fish assemblage structure, than the magnitude of coral loss.

Finally, **Chapter 5** examines the relationships between coral and fish species composition and critical herbivory processes using *in situ* surveys and experimental assays to compare grazing and browsing functions among three distinct coral habitats (i.e. branching *Porites*, soft coral, and mixed coral assemblages). There was variation in browsing on the red macroalga, *Laurencia* cf. *obtusa*, among habitats, best predicted by differential benthic condition and composition but displaying little relationship with visual estimates of herbivore species biomass. Conversely, there was no variation in the grazing of algal turfs, suggesting that different mechanisms may be driving browsing and grazing processes.

Overall, this research develops a more comprehensive understanding of the role of coral species composition in partitioning available habitat structure, the spatial ecology of reef fishes, and the susceptibility of tropical reef ecosystems to disturbance. The resilience of coral reef ecosystems can hinge upon a range of factors including those considered here: the extent of physical habitat provisioning, the functional diversity and redundancy of associated reef fish assemblages, and the capacity of herbivorous fishes to remove macroalgae following extensive coral loss. However, managers face new governance challenges as species shifts transform reef assemblages with unknown implications for their capacity to maintain key ecosystem functions. This thesis highlights the likely ecological consequences of shifts in species configurations, and provides strong support for assigning greater concern for the composition of habitat-building corals in efforts to promote ecosystem resilience, particularly where they remain present but have undergone taxonomic shifts.

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Chapter 1: General Introduction

1.1 Community ecology and disturbance in the Anthropocene

Human actions are changing the composition of species assemblages across biomes via global climate change and mounting local stressors (Dornelas et al. 2014). Increasing temperatures and changes in biogeochemistry often combine with habitat destruction, overharvesting, pollution and invasive species to modify natural environments and alter the distribution of organisms (Cardinale et al. 2012, Ellis et al. 2013, Nagelkerken and Connell 2015). Critically, disturbances are changing the composition of habitat-building organisms, such as trees (Ellison et al. 2005), canopy-forming seaweeds (Wernberg et al. 2011a), and corals (Pandolfi et al. 2011), altering the availability of microhabitats across scales with direct knock-on effects on the organisation, function, and stability of ecosystems (Levin 1992, Tilman et al. 1997, Peterson et al. 1998, Dossena et al. 2012, Yvon-Durocher and Allen 2012).

Deterministic species turn-over, ordered by the susceptibility of organism traits such as body-size, extent of habitat or diet specialisation, or thermal sensitivity (McKinney 1997), is therefore non-randomly modifying the distribution of species resulting in dominance shifts towards those better adapted to changed environmental conditions (McKinney and Lockwood 1999, Clavel et al. 2011). Rather than a consistent net loss of species, changes in species relative abundance, and local extirpations and introductions are altering the community structure of ecosystems across spatial and temporal scales, causing biotic homogenization of communities as generalist species increasingly replace specialists (Devictor et al. 2007, Abadie et al. 2011, Villéger et al. 2014, Magurran et al. 2015). Such changes are leading to the emergence of novel ecosystem configurations, raising questions regarding their persistence, socio-ecological value, and how they may be best managed (Hobbs et al. 2006, Graham et al. 2014a).

Local species turnover resulting in systemic loss of spatial or temporal β diversity is increasingly considered one of the most pressing, but largely unrecognized, biodiversity crises faced globally (Dornelas et al. 2014, McGill et al. 2015), as changes threaten the functioning and resilience of ecosystems (Purvis and Hector 2000, Hooper et al. 2005b, Cardinale et al. 2012, Nagelkerken and Connell 2015). Resilience theory holds that the maintenance of ecosystems is generated by diverse, but overlapping, functions carried out by multiple species operating within and across scales (Holling 1992, Levin 1992, Peterson et al. 1998). Within this context, two components of species diversity are predicted to ensure ecosystem functioning during community re-organisation: (i) the capacity of one or more species to functionally compensate for the loss of another (functional redundancy); and (ii) the variety of species responses within functional groups to disturbance such that functions may be maintained (response diversity) (Walker 1992, Elmqvist et al. 2003). However, relationships between individual and community level responses to disturbance are confounded by complex ecological interactions between organisms, with their environment, and modified individual behaviours (Nagelkerken and Munday 2016, Goldenberg et al. 2018).

1.2 The coral reef context

On coral reefs, climate change and pervasive local stressors have reduced populations of habitat-building corals at regional scales, resulting in unprecedented coral loss and marked shifts in coral species composition (Gardner et al. 2003, Bruno and Selig 2007, Hughes et al. 2017b). In many instances, coral mortality has led to declines in the structural complexity of reef habitats (Graham et al. 2006, Alvarez-Filip et al. 2009), where colony skeletons gradually erode following coral bleaching or outbreaks of *Acanthaster planci*, or are immediately lost or damaged in severe tropical storms or with particular fishing practices (Hawkins and Roberts 2004, Wilson et al. 2006, Graham et al. 2007). In instances where coral populations are not able to recover, live coral is typically replaced by less structurally robust life forms such as macroalgae, corallimorphs, and sponges (Done 1992, Hughes et al. 2007, Norström et al. 2009). To date, research has primarily sought to understand the impacts of reductions in live coral on the physical structure of reef habitats and the spatial ecology of reef fish assemblages (Wilson et al. 2006, Graham and Nash 2013, Emslie et al. 2014, Pratchett et al. 2014), generally reporting marked declines in reef fish abundance and diversity, and changes in body-size spectra and trophic structure of fish assemblages (Graham et al. 2007, Pratchett et al. 2011b, Chong-Seng et al. 2012, Rogers et al. 2014). However, reductions are confounded by changes in the composition of coral species assemblages that will likely have more subtle consequences that threaten the ecological functional redundancy and response diversity, and with them ecosystem resilience (Alvarez-Filip et al. 2011a, Alvarez-Filip et al. 2013, McWilliam et al. 2018). However, the influence of coral species shifts on ecosystem structure and function is poorly understood (Graham et al. 2014a).

Emerging changes in coral species composition are occurring due to the differential susceptibilities of coral taxa to disturbance and variation in life-history strategies (Marshall and Baird 2000, Pandolfi et al. 2011, Johns et al. 2014). Typically, directional shifts have been characterised by dominance of species that are relatively tolerant to stressors such as climatic thermal anomalies or large storms (i.e. massive *Porites*, *Favia* or *Favites*), or fast growing and quick to colonize (i.e. *Acropora* or

Pocillopora) (Aronson et al. 2004, Pratchett et al. 2011a, Van Woesik et al. 2011, Bento et al. 2015). These altered configurations are predicted to persist into the future due to increased incidence and severity of disturbances, as well as differential recovery potential and adaptation capacity among corals (Pandolfi et al. 2011). However, whilst coral assemblages vary with natural biotic and abiotic factors (Hughes et al. 2012, Williams et al. 2013), the influence of coral species composition on physical habitat provisioning and the structure and function of reef fish assemblages remains uncertain (though see Alvarez-Filip et al. 2011b, Alvarez-Filip et al. 2011c, Messmer et al. 2011, Alvarez-Filip et al. 2013). This represents a critical gap in our understanding of the mechanisms underlying changes in reef ecosystems subject to ongoing climate change and local human stressors (Graham et al. 2014a), exacerbating uncertainty regarding the ecological integrity of these altered, and often simplified, coral configurations.

1.3 Coral species composition and habitat structure

Scleractinian corals are critical ecosystem engineers, creating, modifying and maintaining complex three-dimensional structures on coral reefs (Jones et al. 1996), and disproportionately structuring communities of reef associated organisms and ecological interactions (Hixon and Beets 1993, Friedlander and Parrish 1998, Graham and Nash 2013). Although total coral cover is often related to the structural complexity of reef habitats (Alvarez-Filip et al. 2009, Graham and Nash 2013, Nash et al. 2013), it does not capture variation in reef structure mediated by different coral taxa (Alvarez-Filip et al. 2011a). Corals are morphologically and structurally diverse (Chappell 1980, Edinger and Risk 2000), ranging from species with multiple branches, crevices or holes (i.e. branching, foliose, and tabulate species) to more planar, prostrate structures (i.e. massive, submassive and encrusting species) (Fabricius et al. 2011, Harborne et al. 2012). Indeed, evidence from the Caribbean shows that the community composition of corals in the region can underpin fine-scale habitat structural complexity, driven largely by the relative abundance of corals with different morpho-functional characteristics (Alvarez-Filip et al. 2011b). However, the availability of habitat structure across a range of different spatial scales can be important for determining ecological organization and resilience as animals often use their environment at scales relative to their body-size, for example as spatial refugia from predators (Hixon and Beets 1993, Nash et al. 2014). To date, the influence of coral species composition on cross-scale structural complexity remains largely unexplored. This limits our understanding of: i) how different configurations of corals structure ecosystems via differential habitat provisioning (Jones et al. 1997), and ii) the extent to which habitat structure may be lost, maintained, or enhanced with disturbance-mediated species shifts (Ferrari et al. 2016a). For example, some of the most structurally complex corals (i.e. branching morphologies), are the most susceptible to disturbances such as storms (Harmelin-Vivien 1994), thermal stress (Marshall and Baird 2000), and predation by crown of thorns starfish (Baird et al. 2013). However, whilst reductions in structurally complex taxa typically relate to a physical flattening of reef habitats (Alvarez-Filip et al. 2009), species specific responses to disturbance can also increase habitat structural complexity (Ferrari et al. 2016a).

1.4 Coral species composition and the spatial ecology of reef fishes

Up to sixty-four percent of coral reef associated fishes are dependent on corals, primarily for refuge from predation or environmental stressors, as well as settlement and nutrition (Pratchett et al. 2012, Coker et al. 2014). However, dependency and preferential use of different coral species varies substantially among fishes (Munday et al. 1997, Cole et al. 2008, Kerry and Bellwood 2012, Pratchett et al. 2012). For example, some juvenile and small-bodied species of fishes can be strongly affiliated with complex branching corals such as acroporids, pocilloporids and branching species of *Porites* (Sano et al. 1984, Shulman 1984, Munday et al. 1997), where larger-bodied reef fishes preferentially select shelter under the canopy of tabular corals or undercut edges of massive colonies (Kerry and Bellwood 2012, Kerry and Bellwood 2015a). However, whilst the importance of specific coral microhabitats, and the role of live coral, benthic diversity (Messmer et al. 2011, Komyakova et al. 2013), and habitat structural complexity to the taxonomic structure of fish assemblages has been well established (Pratchett et al. 2008, Graham and Nash 2013), an understanding of how differential coral configurations mediate the composition of fish assemblages is currently lacking (though see Berumen and Pratchett 2006, Alvarez-Filip et al. 2011c, Darling et al. 2017). In particular, by assessing the influence of coral species composition on the distribution, diversity, and susceptibility of fishes to disturbance in terms of their specific functional roles (e.g. using traits such as diet and body-size as proxies for function; Alvarez-Filip et al. 2011c, Graham et al. 2015), research efforts may provide insights into important changes in ecosystem function underlying ecosystem resilience as coral assemblages change under further disturbance (Bellwood et al. 2004, Mouillot et al. 2013b).

1.5 Coral species composition, ocean warming, and ecosystem resilience

As ocean warming continues, understanding how initial habitat configurations prior to disturbance will influence changes in associated communities will be critical for developing forewarnings of resilience loss and the threat of functional collapse, such that management efforts may be appropriately assigned (Graham et al. 2014a, Mumby 2017). Climate-driven thermal anomalies can cause widespread coral loss and the reorganisation of reef-associated fishes (Wilson et al. 2006, Hughes et al. 2017b). However, like corals, reef fishes vary in their susceptibility to disturbances such as thermal-stress or habitat disturbance due to differential vulnerability of species traits such as body-size or diet specialisation (Graham et al. 2011). As a result, reef fish and coral species responses to extreme temperatures can be highly variable (Wilson et al. 2006, Pratchett et al. 2011b). Effective management requires better understanding of how taxonomically distinct coral configurations and the associated functional structure of reef fish assemblages will respond to further disturbances, in particular more frequent coral bleaching events (sensu Hughes et al. 2018), in order to predict the likely impacts on ecological organisation, ecosystem function and stability.

1.6 Coral species composition and herbivory processes

Herbivory promotes coral dominance by controlling algae on tropical reefs, and is considered fundamental to ecosystem resilience by mitigating shifts to macroalgal dominance following extensive coral mortality (Hughes 1994). Through the removal of algal material from the substratum, coral reef herbivores enhance the recruitment, growth and survival of corals, thereby promoting reef recovery (Hughes et al. 2007, Mumby and Steneck 2008). However, both the distribution of herbivores and rates of herbivory can be highly spatially variable (Choat and Bellwood , Cvitanovic and Hoey 2010, Hoey and Bellwood 2010a, Hoey and Bellwood 2010b), and the relationship between coral species composition and herbivory functions is unclear. Studies show that the biomass, abundance, and species composition of herbivores can vary with geographic shelf position (Hoey and Bellwood 2010b, Hoey et al. 2013), depth and reef zonation (Fox and Bellwood 2007), reef condition (Wilson et al. 2006, Rasher et al. 2013, Chong-Seng et al. 2014), and structural complexity (Friedlander and Parrish 1998, Wilson et al. 2006). Similarly, rates of herbivory also vary substantially with reef location (Hoey and Bellwood 2010b), zonation (Fox and Bellwood 2007), and importantly, within habitats (Cvitanovic and Bellwood 2009, Cvitanovic and Hoey 2010). Studies suggest that this variation may be due to differential benthic condition (Cvitanovic and Bellwood 2009, Nash et al. 2016), or the influence of differential benthic composition within habitats (Cvitanovic and Hoey 2010). However, without an understanding of the mechanisms underlying this variation and an elucidation of the role of coral species composition, we are restricted in our capacity to predict the extent to herbivory functions and ecosystem ecological integrity will vary among different configurations of corals.

1.7 Aims and thesis outline

This thesis investigates the potential implications of changes in coral species composition on coral reef structure and the function and resilience of coral reef fish assemblages by quantifying inherent variation in physical habitat partitioning, the spatial ecology of coral reef fishes, and susceptibility of taxonomically distinct coral species configurations to disturbance. Through detailed studies of distinct coral habitats characterised by dominance of differing coral taxa coral at Lizard Island, Australia (14°41′S, 145°27′E), I addressed the following questions:

1. How does coral species composition affect the cross-scale structural complexity of coral reef habitats?
2. How does the functional structure of reef fish assemblages vary among taxonomically distinct coral habitats?
3. To what extent does pre-disturbance coral species composition influence the susceptibility of reef fish assemblages to coral bleaching events?
4. Do critical herbivory functions (browsing and grazing) vary among distinct coral habitats?

The research questions are addressed in the four studies outlined below, which correspond to publications derived from this thesis. **Chapter 2** compares the cross-scale structural complexity of five habitats across five spatial scales of measurement (4–64 cm), and assesses the relative influence of coral species composition versus total coral cover in predicting habitat structure at each scale. **Chapter 3** uses an ecological trait-based analysis to compare the functional diversity of associated reef fish assemblages among six distinct habitats, and quantifies the relative importance of habitat composition, structural complexity, and total coral cover as drivers of variation found. **Chapter 4** investigates the susceptibility of taxonomically distinct coral habitats and their associated reef fish assemblages to thermal disturbance by quantifying temporal changes in the taxonomic and functional structure of reef fish assemblages among six habitats exposed to a system-wide coral bleaching event. Finally, **Chapter 5** examines relationships between coral and fish species composition and critical herbivory functions (grazing and browsing) using *in situ* surveys and experimental assays among three distinct coral habitats.

Chapter 2

Cross-scale habitat structure driven by coral species composition on tropical reefs

2.1 Abstract

The availability of habitat structure across spatial scales can determine ecological organization and resilience. However, anthropogenic disturbances are altering the abundance and composition of habitat-forming organisms. How such shifts in the composition of these organisms alter the physical structure of habitats across ecologically important scales remains unclear. At a time of unprecedented coral loss and homogenization of coral assemblages globally, I investigate the inherent structural complexity of taxonomically distinct reefs, across five ecologically relevant scales of measurement (4-64 cm). I show that structural complexity was influenced by coral species composition, and was not a simple function of coral cover on the studied reefs. However, inter-habitat variation in structural complexity changed with scale. Importantly, the scales at which habitat structure was available also varied among habitats. Complexity at the smallest, most vulnerable scale (4 cm) varied the most among habitats, which could have inferences for as much as half of all reef fishes which are small-bodied and refuge dependent for much of their lives. As disturbances continue and species shifts persist, the future of these ecosystems may rely on a greater concern for the composition of habitat-building species and prioritization of particular configurations for protection of maximal cross-scale habitat structural complexity.

Published:

Richardson, L. E., Graham, N. A. J., & Hoey, A. S. (2017). Cross-scale habitat structure driven by coral species composition on tropical reefs. *Scientific Reports,* **7**, 7557. DOI:10.1038/s41598-017-08109-4

2.2 Introduction

The physical structure of habitats is integral to the organization, function, and resilience of ecosystems (Levin 1992, Peterson et al. 1998, Nash et al. 2014), and therefore the provision of ecosystem goods and services. The diversity and abundance of taxa such as birds, small mammals, lizards, and fish, commonly correlate with the structural complexity of habitats across a range of ecosystems (Huston 1979). Specifically, the availability of microhabitats over a range of spatial scales provides associated organisms of different sizes with refuge from predation, allows for greater niche differentiation and can facilitate other species by mediating competition, and reducing environmental conditions to tolerable levels (Stachowicz 2001). Animals often use their environment at spatial scales relative to their body-size, for example spatial refugia from predators (Nash et al. 2014). However, habitat structural complexity at one scale of measurement is not necessarily synonymous with complexity at other scales (e.g. Bradbury 1984). The availability of fine and coarse scale structural complexity often varies among habitats, with direct implications for the distribution of organisms (Williams et al. 2002, Nash et al. 2013), the maintenance of ecosystem processes (Yvon-Durocher and Allen 2012, Nash et al. 2015), and the resilience of communities (Peterson et al. 1998).

The structural complexity of habitats is typically created by communities of living organisms (i.e. habitat-forming organisms such as trees, canopy-forming seaweeds, oysters, wetland grasses, and corals), as well as abiotic features such as the underlying geomorphology, and/or three-dimensional structures of dead organisms (Bradbury 1984, Jones et al. 1996). Importantly, both the abundance and species composition of habitat-forming organisms can have a strong influence on the structural complexity of habitats. For example, the habitat structural complexity of forests varies with tree species composition (Huston and Huston 1994, Ellison et al. 2005); wetland habitats vary with the composition of forbs, grasses and rushes (Brose 2003); and the structure of subtidal temperate reefs is dependent on the species composition of canopy-forming seaweeds (Wernberg et al. 2011b). Similarly on coral reefs, habitat structural complexity is likely underpinned by the relative abundance of component coral species (Alvarez-Filip et al. 2011b), and can vary independently of total coral cover (Alvarez-Filip et al. 2011a). Corals are structurally diverse taxa, characterized by a range of morphologies (e.g. branching, foliose, massive, or tabulate) that are determined by evolved life history strategies (Darling et al. 2013), genetic variation, and environmental phenotypic plasticity (Todd 2008). Even within these morphological groupings there is considerable variation among species in the size and shape of morphological features (e.g., length and spacing between branches, branching pattern) and hence the interstitial spaces created within, underneath and between colonies (Luckhurst and Luckhurst 1978, Gratwicke and Speight 2005, Harborne et al. 2012).

Globally, pervasive anthropogenic disturbances are reducing species populations, leading to biotic homogenization of communities and changes to the functioning of ecosystems (Ellis et al. 2013, Dornelas et al. 2014). On tropical reefs, climate-change induced warm-water anomalies, severe storms, land-based sources of pollution and sedimentation, overfishing, and predation by crown-of-thorns starfish are leading to marked declines in the abundance, and changes in the composition of habitat-forming corals (De'ath et al. 2012, Hughes et al. 2017b). Differential susceptibilities to disturbance and variation in life-histories among coral species are causing non-random homogenization of coral assemblages, often dominated by species that are relatively more tolerant to stress, or fast growing and quick to colonize (Pratchett et al. 2011a, Guest et al. 2012, Darling et al. 2013, Bento et al. 2015). Some of the most structurally complex corals, such as taxa with branching morphologies, are the most susceptible to a range of disturbances, including storms (Harmelin-Vivien 1994), thermal-bleaching (Marshall and Baird 2000), and crown-of-thorns starfish (Baird et al. 2013). While reductions in the abundance of these structurally complex corals is typically related to reductions in the structural complexity of habitats (Alvarez-Filip et al. 2009), disturbances can also lead to increases in habitat structural complexity, particularly where reefs persist as altered coral-dominated systems (Ferrari et al. 2016a). Consequently, changes in coral composition will likely impact the habitat structural complexity of coral reefs (Ferrari et al. 2016a), with direct implications for the capacity of those reefs to maintain reef functions (Done 1999, Alvarez-Filip et al. 2013), and the provision of coral reef ecosystem goods and services (Moberg and Folke 1999, Hicks and Cinner 2014).

Shifts in the composition of habitat-building coral species are predicted to persist into the future (Pandolfi et al. 2011, Hughes et al. 2017a). Therefore, identifying the structural characteristics of particular coral configurations is critical for the conservation of those systems. However, an understanding of the inherent variation in cross-scale structural complexity of coral reefs is currently lacking. To this end, this study aimed to investigate the influence of coral species composition on cross-scale patterns of habitat structural complexity, at spatial scales of measurement relevant to fish refuge selection (adapted from Nash et al. 2013). Cross-scale structural complexity was quantified at randomly selected sites at Lizard Island in the northern Great Barrier Reef, Australia (14°41′S, 145°27′E), following a step-length geometric series using contour distance measuring wheels of different diameters (4–64 cm) along 10-m transects at each site (Fig. 2.1; see Appendix A Table S1). Specifically, I assessed i) the cross-scale structural complexity of four coral habitats with distinct species configurations and degraded (<10% total coral cover) reef habitat, and ii) cross-scale colony level structural complexity of the dominant coral species at the study location to elucidate the relationship between the complexity of taxa-specific morphologies and colony size.

2.3 Material and methods

Study location

This study was conducted in September 2015 on the reefs surrounding Lizard Island, a granitic island in the northern Great Barrier Reef, Australia (14°41′S, 145°27′E). Benthic composition and cross-scale habitat structural complexity were quantified at twelve randomly selected sites on the leeward side of the island. All sites were shallow (<6-m depth) reef edges (>5-m wide) adjacent to sand. All sites were in areas protected from the prevailing south-east swell, with comparable water clarity and flow, light levels, and geomorphology. Adjacent sites separated by a minimum of 500 m.

Benthic composition was quantified along six replicate 30-m point-intercept transects at each site, recording the substratum directly beneath the transect line at 25-cm intervals (120 points per transect). Transects were positioned parallel to the reef edge at a depth of 2-6-m, with a minimum of 5 m between adjacent transects. Substratum types included hard (scleractinian) corals (identified to genus or species where possible, and growth form noted), soft (alcyonacean) corals, 'other sessile invertebrates' (primarily sponges, giant clams, and ascidians), macroalgae, erect crustose coralline algae, dead coral and pavement, rubble and sand.

Habitat structural complexity

Habitat structural complexity was estimated at five spatial scales of measurement following a step-length geometric series using distance measuring wheels of different diameters (4–64 cm) along four 10-m transects at each site (adapted from Wilding et al. 2007, following Nash et al. 2013). The abundance of fishes has been shown to positively correlate with structural complexity relative to fish body-size (Graham et al. 2007, Wilson et al. 2010), and the aperture diameter of available holes or crevices in the substrate as refuges from predation or environmental stressors (Hixon and Beets 1993). Therefore, the scales of measurement selected correspond to the body-depth distributions of fishes over a gradient of refuge dependency (Nash et al. 2013): ranging from fishes with body-depths <4 cm that would fit into an interstitial space of 4 cm diameter (approximately 50% of reef fishes, highly refuge dependent to avoid predation; Goatley and Bellwood 2016), through to fishes with a body depth up to 64 cm that can be site attached but substantially less likely to be dependent on refuge from predation. The 10-m transects used to quantify structural complexity were positioned within the mid-section (i.e., ~10-20 m) of four of the six 30-m transects used to quantify benthic composition. Adjacent 10-m transects were separated by a minimum of 20m. . The contour distance travelled by each wheel over the reef substratum was estimated by rolling the wheels along the reef surface contour immediately below the length of the taught 10-m transect line, being careful to ensure each wheel followed the detailed surface structure of the benthos (Fig. 2.1). The number of complete rotations and the proportion of each wheel turned for any incomplete rotations were recorded. The contour distance covered by each wheel was calculated by multiplying the number of rotations by the wheel circumference.

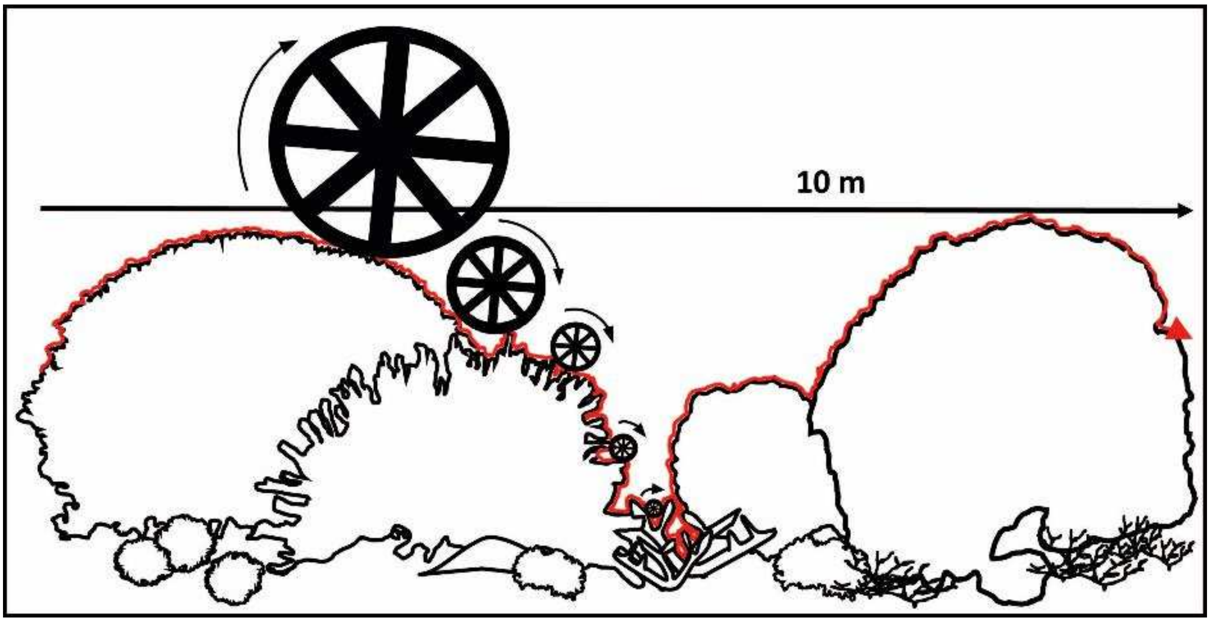

Fig. 2.1 Cross-scale habitat structural complexity estimated by contour distance travelled by five wheels of different diameters (4-64 cm) along a 10 m transect. Wheels closely follow the surface structure of the benthos and number of rotations are counted. Small wheels fit into more holes than larger wheels and thus estimate greater contour distance.

Colony level structural complexity

To assess how the five scales of structural complexity relate to colony size of corals, I quantified the structural complexity of three of the most common hard coral taxa at the study sites. Contour distance travelled by each wheel was estimated across the maximum diameter of individual colonies of *Porites cylindrica*, massive *Porites* (mostly *Porites lutea*), and *Pocillopora damicornis* (measured to the nearest cm with a tape *in situ* over the surface of the colony). Structural complexity estimates were acquired across the range of available colony sizes for each taxa (*P. cylindrica:* 3–350 cm, *n* = 100; massive *Porites:* 3–415 cm, *n* = 100; *P. damicornis:* 3-69 cm, *n* = 72), at other sheltered reef edge sites around Lizard Island.

Data analysis

Variation in benthic composition among sites was investigated with non-metric multi-dimensional scaling (nMDS) based on Bray-Curtis similarities of square root transformed benthic cover data in Primer v6 (Clarke and Warwick 2001). Group-average hierarchical clustering was used to provide an objective assessment of five distinct habitat groups identified with nMDS. Two-way permutational multivariate analysis of variance (PERMANOVA) was used to test the significance of these groupings (9999 permutations), with habitat (fixed; branching *Porites*, massive *Porites*, *Pocillopora*, soft coral, and degraded) and site (random) as factors (PERMANOVA+ add on package). One-way pairwise comparisons between habitat groups were performed with unrestricted permutation of raw data to allow for sufficient permutations to be tested. Similarity Percentage (SIMPER) analysis was used *post hoc* to identify those benthic categories contributing consistently to average similarity within, and dissimilarity between, habitats with a similarity/dissimilarity test ratio of ≥4.0 or 2.0, respectively (Clarke and Warwick 2001).

Differences in (i) contour distances measured at each scale were compared among habitats (fixed effect), and (ii) differences in contour distances measured were compared across scales (fixed effect) within each habitat, using linear mixed effects models, with lme in *nlme* in all instances (R version 3.2.3; R Development Core Team 2015). In each analysis, site was treated as a random effect and Tukey multiple comparison tests were used to identify where differences occurred (with the *multcomp* package). Exploratory graphical analysis of model residuals suggested the data conformed to the assumptions of normality and independence, though there was heterogeneity of variance among habitats at the largest scale. Therefore models were fitted with a constant variance structure to allow for heteroscedasticity at all scales, consequently allowing for cross-scale comparisons. To identify the main sources of variation at each scale, variance components were subsequently extracted using *lme4* and the *MuMIn* package (see Appendix A Table S1).

Multiple linear regression was used to estimate relationships between habitat structural complexity with total coral cover (hard and soft coral) and benthic composition (habitat classification) at each scale. Collinearity between coral cover and habitat type was tested by calculating generalized variance inflation-factors (GVIF^1/2*df*; Fox and Monette 1992). As GVIF values indicated low levels of collinearity (<3; Zuur et al. 2010), information-theoretic model selection was used to determine the relative importance of these covariates in predicting variation in habitat structural complexity (*MuMIn* package). Multi-model inference (including null models) was estimated by ranked changes in AICc <3 (Burnham and Anderson 2002). To determine the scales where changes in structural complexity occurred within habitats, hierarchical modelling was also used to compare contour distances across scales within each habitat, accounting for site effects, followed by Tukey tests. Due to unequal variance across scales within habitats, models were fitted to allow for heterogeneity as previously described. Only one site was identified to be dominated by *Pocillopora*, and subsequently contour distance was compared across scales without site effects for this habitat using the gls function of *nlme*. The relationships between colony size and structural complexity at the same five scales were assessed for massive *Porites*, *P. cylindrica* and *P. damicornis,* using linear regression.

2.4 Results

Habitat classification

Benthic composition varied among the twelve sites, with five distinct habitat groups identified by MDS and hierarchical clustering of benthic composition (Fig. 2.2). PERMANOVA supported these groupings with significant differences in benthic composition among the five groups (Pseudo-F = 11.22, df = 4, P = 0.0001; all pairwise comparisons P = 0.0001; see Appendix A Table S2). SIMPER analysis indicated dominant taxa and substrate types (i.e., *Porites cylindrica*, massive *Porites* – mostly *P. lutea*, *Pocillopora damicornis*, soft coral, dead coral and macroalgae) consistently contributed to average similarity within, or dissimilarity between groups (see Appendix A Table S2). Cover of these dominant coral taxa (including soft coral) ranged from 51.5-90.1% of total live coral in coral-dominated sites (mean total coral cover 51.3% ± 4.6 SE). Conversely, the grouping characterized by dead coral and pavement, rubble, and macroalgae (79.4% ± 1.2 SE benthic cover), had significantly less live coral cover (10.5% ± 1.8 SE; lme, $F_{4,7}$ = 25.83, P = 0.0003; Tukey, all $P \leq 0.03$). Among the coral-dominated groupings, total live coral cover was higher at sites dominated by *Porites cylindrica* than those characterized by *P. lutea*, *Pocillopora damicornis*, or soft coral which had comparable cover (lme, $F_{4,7}$ = 25.83, P = 0.0003). Sites were classified by habitat groupings according to dominant substrata as follows: *Porites cylindrica* (hereafter 'branching *Porites*'; 3 sites), *P. lutea* (hereafter 'massive *Porites*'; 2 sites), *Pocillopora damicornis* (hereafter '*Pocillopora*'; 1 site), soft coral (3 sites), and degraded (3 sites) for all subsequent analyses.

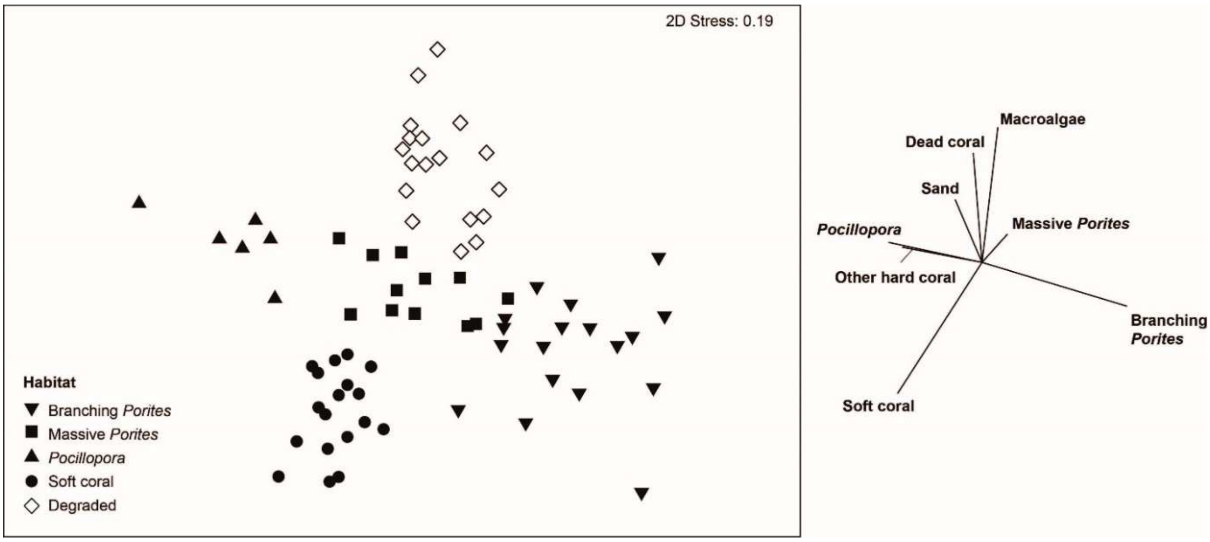

Fig. 2.2 Non-metric multidimensional scaling analysis showing variation in benthic composition among surveyed reef habitats at Lizard Island, using transect level square root transformed data. The relative contribution of benthic categories to the observed variation in benthic composition are illustrated (>0.2 Pearson correlation).

Habitat structural complexity

The structural complexity of habitats quantified using distance measuring wheels of different diameters (4–64 cm) that followed the reef surface contour along four 10-m transects at each site changed with scale of measurement, and varied among habitats with similar levels of coral cover (Fig. 2.3; see Appendix A Table S1 and S3). Modelling multi-scale contour distance with coral cover and benthic composition indicated that at the smallest scales (4-8 cm), total coral cover was a significant predictor of contour distance, but variation in benthic composition (habitat type) was also in the top models with a relative importance of 0.27 (4 cm scale) and 0.17 (8 cm scale). Total coral cover was not present in the top models for structural complexity at larger scales (16-64 cm), indicating that benthic composition better predicted variation in contour distance measured among sites (Table 2.1). Null models featured in the top models for structural complexity at the 8, 16, and 64 cm scales, indicating high variability among transects (scales 8 and 16 cm) and/or sites (64 cm) (see extracted variance components in Appendix A Table S1). Broadly, structural complexity varied significantly among habitats at all scales except 8 cm, though inter-habitat differences were not consistent among scales. Branching *Porites* and massive *Porites* habitats were generally more complex than soft coral, *Pocillopora* and degraded habitats at the small and intermediate scales (4-16 cm). The structural complexity of branching *Porites* habitats reduced to intermediate levels at the 32 cm scale, comparable with degraded habitats; and massive *Porites* and degraded habitats were most complex at the largest scale (64 cm) (Fig. 2.3; see Appendix A Table S3).

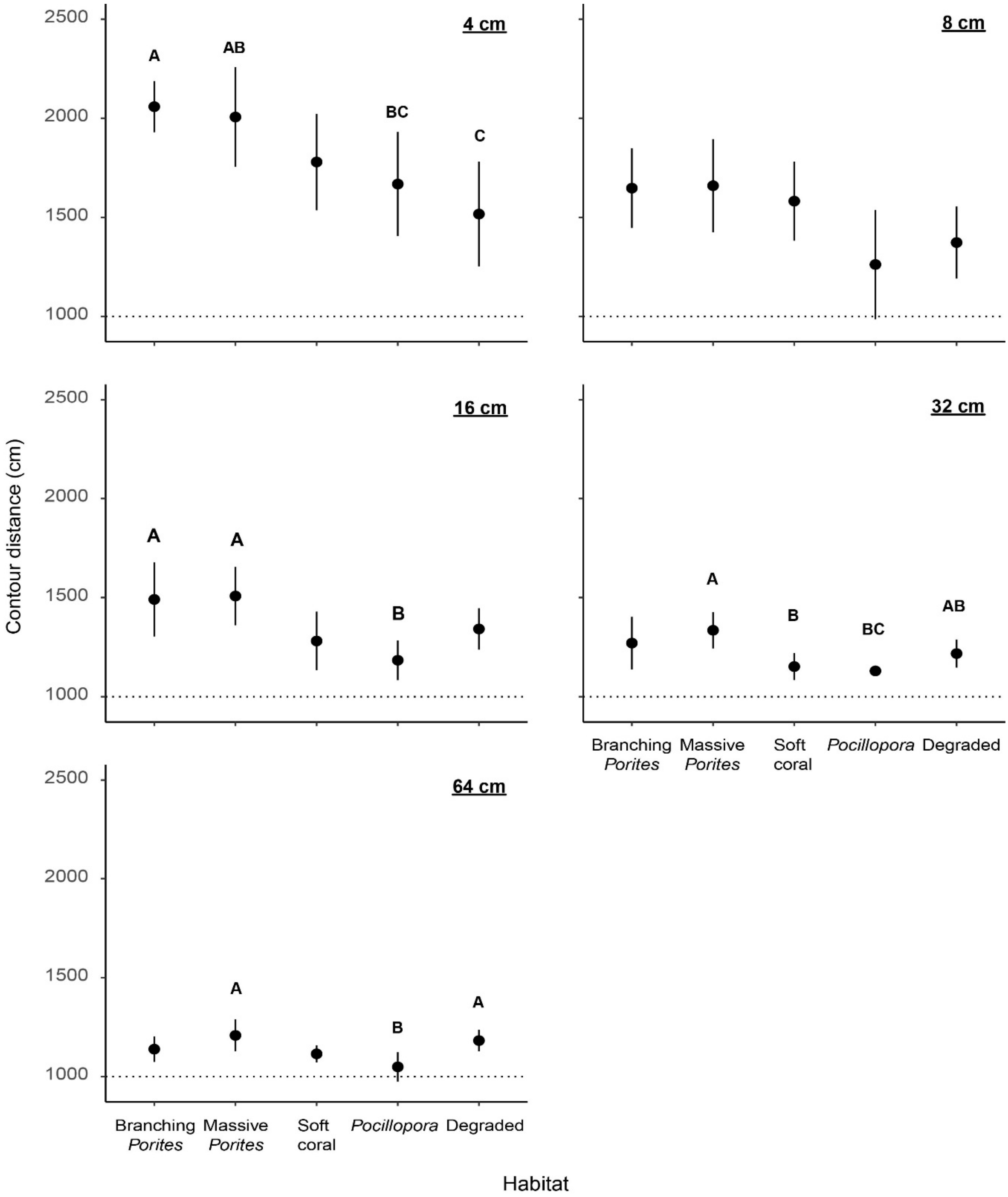

Fig. 2.3 Modelled contour distance (± 95% confidence intervals) measured along 10 m transects at scales 4-64 cm with measuring wheels (wheel diameters, cm: 3.99; 7.97; 15.95; 31.89; 63.79), in different coral reef habitats (n = 4-12 per habitat). Significant differences between habitats revealed by *post hoc* Tukey pairwise comparisons are illustrated by the pairing of letters (P <0.05).

Contour distance travelled along transects declined with increasing wheel size in all habitats, however, the magnitude of change and cross-scale patterns of structural complexity varied among habitats (Fig. 2.4). Branching *Porites* and massive *Porites* had the greatest variation in complexity across scales, while degraded habitat had the least (Fig. 2.4; see Appendix A Table S4). Habitat structural complexity was identified at four distinct scales in the massive *Porites* and branching *Porites* habitats, three in *Pocillopora*, and at two distinct scales in the soft coral and degraded habitats. In soft coral, massive- and branching-*Porites* habitats, structural complexity at the two smallest scales (4 and 8 cm) was significantly greater than structural complexity at the two largest scales (32 and 64 cm). However, in the *Pocillopora* and degraded habitats these distinctions between scales were less apparent. Within the *Pocillopora* habitat, structural complexity at the smallest scale (4cm) was greater than at the remaining scales (8-64cm), while in the degraded habitat structural complexity was similar across all but the largest scale (64cm).

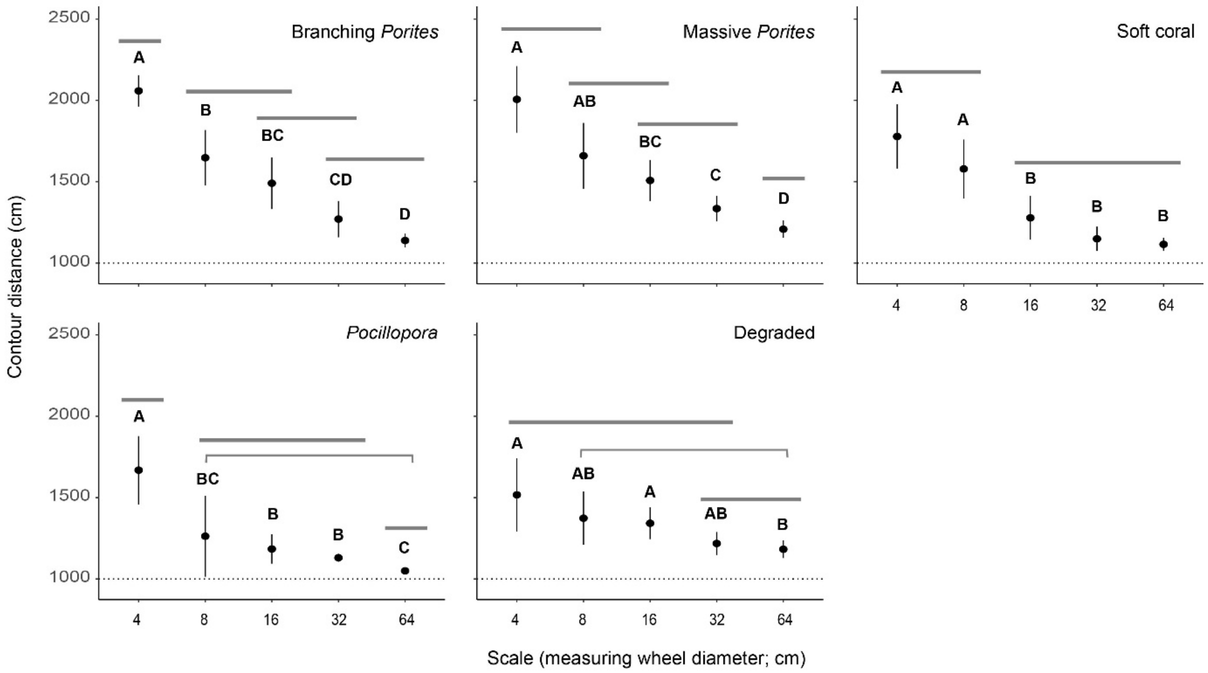

Fig. 2.4 Modelled contour distance (± 95% confidence intervals) measured using wheels representing scales 4-64 cm (wheel diameters, cm: 3.99; 7.97; 15.95; 31.89; 63.79), within each habitat. Significant differences between habitats revealed by linear mixed effects modelling and *post hoc* Tukey pairwise comparisons are illustrated by the pairing of letters (P <0.05). Grey bars across scales further illustrate similarities in structural complexity across scales of measurement in each habitat. Thin grey bars in *Pocillopora* and Degraded habitats denote similarities in contour distance over scales at either end of the bar (i.e. non-consecutive sales).

Colony level structural complexity

Colony level analyses revealed strong linear relationships between the structural complexity of massive *Porites*, *P. cylindrica* and *Pocillopora damicornis* and colony size for each taxa, with constant relationships between contour distance and colony diameter at all five scales (correlation coefficients ranged from 0.96-0.97, 0.93–0.97, and 0.68-0.91, respectively) (Fig. 2.5, see Appendix A Table S5). Visual inspection of regression slopes suggests that both *Porites* taxa were more structurally complex than *Pocillopora damicornis* across their size ranges at all scales. *Porites cylindrica* colonies appear more structurally complex than massive *Porites* colonies of the same size at the 4 cm scale, and to a lesser degree at the 8 cm scale. Conversely, massive *Porites* colonies appear more complex at the 16-64 cm scales (Fig. 2.5, see Appendix A Table S5).

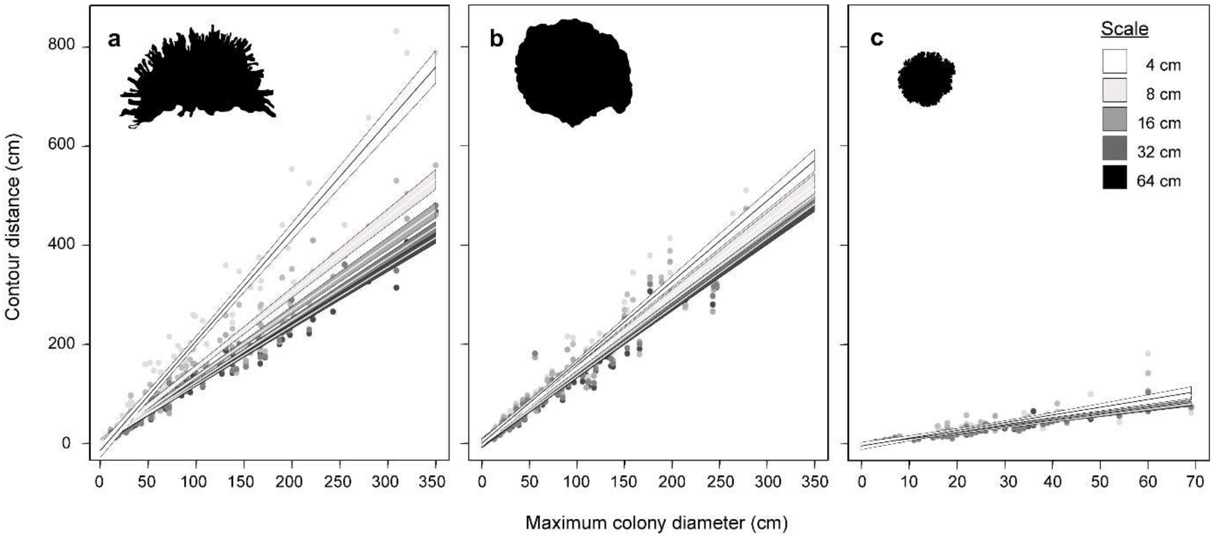

Fig. 2.5 Fitted relationships between maximum colony diameter (cm) and contour distance travelled by measuring wheels of diameters 4-64 cm (± 95% confidence intervals): a) *Porites cylindrica* (R^2 = 0.93 – 0.97); b) massive *Porites* (R^2 = 0.95 – 0.97); and c) *Pocillopora damicornis* (R^2 = 0.68 – 0.91).

Table 2. 1 Top candidate models selected to describe the relationship between habitat structural complexity across scales (4-64 cm), with total coral cover and habitat type (benthic composition). Models are ranked by Akaike's information criteria (AICc), with all models within ΔAICc <3 of the top ranked model. The relative weight of evidence for each model is indicated by Akaike weight (wAICc), and the variables present in each model are indicated with an X. Null models refer to variance explained by site or transect level sampling Outputs are presented for each model, tested using Site as a random effect, and fitted with a constant variance structure to allow for heterogeneity at all scales.

Scale (cm)	Model rank	AICc	*df*	logLik	ΔAICc	wAICc	Total coral cover (%)	Habitat	Model output (lme)
4	1	665.26	8	-322.68	0.00	0.73	**X**		$F_{1,33}$ = 23.06, ***P* <0.0001**
	2	667.29	11	-318.76	2.03	0.27		**X**	$F_{4,7}$ = 6.73, ***P* = 0.02**
8	1	668.63	8	-324.37	0.00	0.57	**X**		$F_{1,33}$ = 5.03, ***P* = 0.03**
	2	670.16	7	-326.60	1.53	0.26	Null model		$F_{1,34}$ = 1112.41, ***P* <0.0001**
	3	671.05	11	-320.64	2.42	0.17		**X**	$F_{4,7}$ = 3.32 , ***P* = 0.08**
16	1	634.33	11	-302.28	0.00	0.80		**X**	$F_{4,7}$ = 6.18, ***P* = 0.02**
	2	637.14	7	-310.09	2.80	0.20	Null model		$F_{1,34}$ = 1187.59, ***P* <0.0001**
32	1	NA	11	-255.26	NA	NA		**X**	$F_{4,7}$ = 8.81, ***P* = 0.01**
64	1	517.18	11	-243.71	0.00	0.69		**X**	$F_{4,7}$ = 4.34, ***P* = 0.04**
	2	518.80	7	-250.93	1.62	0.31	Null model		$F_{1,34}$ = 4792.91, ***P* <0.0001**

2.5 Discussion

Disturbance induced biotic homogenization threatens the architecture of habitats at ecologically relevant scales and the resilience of ecosystems (Ellison et al. 2005, Dornelas et al. 2014). Previous studies have described the physical flattening of habitats associated with the loss of key organisms such as trees, kelp, and corals, and the often profound consequences for biodiversity and related ecosystem services (Steneck et al. 2002, Ellison et al. 2005, Alvarez-Filip et al. 2009). Here, I show that the habitat structural complexity of the studied reefs was inextricably tied to the identity of constituent habitat-building species, and was not shaped solely by the absolute cover of corals. Importantly, the structural complexity of habitats changed with scale of measurement. The greatest differentiation in habitat structural complexity was at the smallest (4 cm) and most vulnerable scale of measurement (Wilson et al. 2010). Furthermore, cross-scale structural complexity varied among all habitats, evident at four distinct scales in both *Porites* habitats, three in *Pocillopora* habitat, and two in soft coral and degraded habitats. It should be noted that the less rigid biota such as soft corals and large macroalgae likely provide elements of structural complexity that may not be effectively captured by the methods used in this study. These findings have substantial implications for the relative suitability of coral reef habitats for associated organisms that are refuge dependent, including other reef invertebrates and small-bodied reef fishes (Wilson et al. 2010, Stella et al. 2011).

Differential habitat structural complexity across scales emphasizes the role of species composition in shaping the physical architecture of reef ecosystems. For example, I show that at small to mid-scales (4 – 16 cm), habitat structural complexity was greatest in massive and branching *Porites* habitats, relative to *Pocillopora*, soft coral and degraded habitats, while at larger scales (32-64 cm), the greatest structural complexity was in massive *Porites* and degraded habitats. Similar differences were evident in colony level complexity for both *Porites* taxa versus *Pocillopora*. Notably, the greatest differentiation in habitat structural complexity was evident at the smallest scales of measurement (4-8 cm). Structural complexity at these scales is largely determined by variation in the surface morphology of individual coral colonies (see Fig. 2.5), and likely provides the most benefit to small bodied and/or juvenile fishes subject to high risk of predation (Wilson et al. 2010). Branching *Porites* colonies were notably more structurally complex at the 4 cm scale, relative to massive *Porites* colonies of the same size, though relatively high contour distances were also observed in the latter (Fig. 2.5; Appendix A Table S5). Branching *Porites* species such as *P. cylindrica* create intricate and discrete interstitial spaces between their branches, whilst large colonies of massive *Porites* species can form fine scale corrugations or crevices in their otherwise relatively planar surfaces thereby providing small-scale microhabitats for small-bodied reef organisms (Wellington and Victor 1985, Gardiner and Jones 2010). Despite greater complexity of branching *Porites* colonies, the differentiation in complexity between *Porites* taxa was lost at the transect level possibly due to variable size distributions of colonies in these habitats. Overall, the high contour distances measured in these *Porites* habitats likely reflect the typically large size of the branching and massive *Porites* colonies, as well as the undercut areas beneath and the vertical relief between colonies.

Whilst *Pocillopora* habitat was the least structurally complex of the four coral-dominated habitats across all scales, at scales finer than those considered in this study (i.e. <4 cm), *P. damicornis* is structurally intricate, and likely provides important refugia for many reef fishes (Coker et al. 2014). However, due to its small size, brooding reproduction and fast growth rates (Darling et al. 2012), *Pocillopora* dominated reefs can be characterised by multiple, tightly-aggregated colonies of similar sizes, offering little relief between them that might otherwise provide greater structural relief across all scales, but particularly at an inter-colony scale of approximately 8-32 cm.

The role of live coral in providing structurally complex tropical reef habitats has received much attention (Alvarez-Filip et al. 2009, Graham and Nash 2013). However, the absolute cover of live corals alone does not capture all of the inherent variation in habitat structural complexity (Alvarez-Filip et al. 2011a, Bozec et al. 2015, Ferrari et al. 2016a, Darling et al. 2017). I found that total coral cover was a good predictor of structural complexity at the two smallest scales (4-8 cm), but the inclusion of habitat composition further increased the predictive capacity of the models. At the larger scales (16 – 64 cm), the relationship between total coral cover and structural complexity of the habitat broke down. These findings are consistent with studies from the Caribbean showing that whilst the fine-scale habitat structural complexity of reefs (0.7 cm scale) increases with coral cover, much of the variance in complexity at high levels of coral cover results from the dominance of particular corals (Alvarez-Filip et al. 2011b). It is important to note that despite differences in structural complexity among habitats at the larger scales (i.e. 8-64 cm), variation in the underlying reef structure, as well as the likely contribution of other benthic organisms, introduced substantial variation in complexity at the transect and site sampling levels. The contribution of the underlying substrata (geomorphological structure and dead reef matrix) to the structural complexity of reef habitats was further highlighted by the greater structural complexity of the degraded habitat found at larger scales (32-64 cm). This supports previous findings comparing multiscale complexity of coral-, and macroalgal-dominated habitats (Nash et al. 2013).

The availability of habitat structural complexity across a range of scales is important for maintaining the organisation of associated organisms, including body-size distributions, food web structure and ecosystem functioning (Holling 1992, Peterson et al. 1998). I found that cross-scale habitat structural complexity varied with coral composition, with multi-scale structure most distinguished in branching and massive *Porites* habitats, relative to *Pocillopora* and soft coral habitats. These coral-dominated habitats all contrasted with the low relief degraded reef habitats across all scales. As reef habitats degrade, they become flatter and more structurally homogenous (Alvarez-Filip et al. 2009), providing fewer potential refuges at different scales (Nash et al. 2013), though large stands of macroalgae also contribute to elements of structural complexity (Hoey and Bellwood 2011). Broadly, the structural complexity of coral reef habitats is evident both within and between colonies, and at larger scales that capture the corrugations of the underlying substratum (Bradbury 1984). More specifically however, these results reveal that cross-scale habitat structural complexity is influenced by the composition of coral species, with habitats providing structure ranging from just two scales measured in this study (e.g. soft coral and degraded habitats), to four scales (e.g. massive-, and branching *Porites* habitats). Interestingly, whilst the *Porites* habitats both displayed structural complexity at four distinct scales of measurement, cross-scale complexity varied between them. For example, structural complexity at the 4 cm scale differed to complexity at the 8 cm scale in branching *Porites* habitats, but not in massive *Porites* habitats. This was supported by colony level analyses indicating greater complexity of branching *Porites* at the 4 cm relative to massive *Porites* resulting from the interstitial spaces created between branches of *P. cylindrica*. Similarly, structural complexity at the 64 cm scale was distinct from complexity at the smaller scales in massive *Porites* habitats, but not branching *Porites* habitats, likely due to the overhangs often created by large colonies of massive *Porites*. The only shared variation in structural complexity occurred between the 8-16 cm and 16-32 cm scales resulting from the similar overall colony surface structures of branching and massive *Porites* at these intermediate scales.

Soft coral habitat structural complexity was unexpectedly high, particularly at the smallest scales (4-8 cm), and surprising given that the study method likely underestimates structural complexity of less rigid biota such as soft coral. While the relative contribution of soft corals to reef structural complexity are apparent due to their physical presence when alive, quantification of their structural complexity is complex due to their only partially calcified structures, and has received little attention (though see Syms and Jones 2001, Ferrari 2017). Despite this, structural complexity of these soft coral habitats was found at two distinct scales of measurement (4-8 cm and 16-64 cm), as the two smallest wheels were able to fit in between adjoining colonies often reaching the substratum below, whereas the larger wheels rolled over the surface of colonies suggesting less relief at larger scales. Similarly, there was little medium- to large-scale structure (16-64 cm) in *Pocillopora* habitat due to the small colony sizes and limited space between them, resulting in the larger wheels remaining on the reef surface. Building upon empirical and modelling studies of Caribbean reefs (Alvarez-Filip et al. 2011a, Alvarez-Filip et al. 2011b, Bozec et al. 2015), these findings show that not only is the identity of constituent corals an important driver of habitat structural complexity, but this occurs across scales. Moreover, the size and number of scales of measurement at which structure is available varies substantially among habitats.

Previous work has shown that broad-scale habitat structural complexity, determined by coral composition and reef condition, can drive the taxonomic and functional diversity of reef fish assemblages (Messmer et al. 2011, Harborne et al. 2012, Graham et al. 2015, **Chapter 3**). More specifically however, the range of scales at which habitat structure is available likely regulates how species organisation is partitioned and ecological processes are maintained (Levin 1992, Nash et al. 2014). Evidence suggests that ecosystems are strongly influenced by processes operating over different scales, and their resilience is determined by diverse, though overlapping, functions at and across those scales (Holling , Peterson et al. 1998). For example, herbivory, a critical process on coral reefs, is mutually reinforced when reef fishes with shared functions can operate across multiple spatial scales, thereby minimising competition between fishes of similar body-sizes (Nash et al. 2015). Therefore, a loss of habitat structural complexity at specific scales may compromise resilience (Nash et al. 2014), even where habitat-building organisms remain present and appear intact, but have undergone species shifts (Redford 1992).

The homogenisation of habitats characterized by increasingly monospecific assemblages of habitat-building species therefore has broader implications than simply the habitat structural complexity of ecosystems. Conservation practitioners responsible for maintaining coral reef ecosystem services are therefore advised to consider changes in the composition of coral assemblages, and not simply total coral cover on reefs (Alvarez-Filip et al. 2011a). Studies suggest that total coral cover alone is a poor surrogate for habitat structural complexity (Alvarez-Filip et al. 2011a), the organization of reef associated species (Alvarez-Filip et al. 2011c), ecological function (Cvitanovic and Hoey 2010), or reef recovery (Johns et al. 2014), as it does not capture sufficient variation in structural complexity driven by benthic composition. Some coral habitats might warrant relatively greater protection as their inherent variation in habitat structural complexity may support enhanced ecosystem resilience (e.g. *Acropora* and *Orbicella* reefs in the Caribbean, Harborne et al. 2008, Mumby et al. 2008, Alvarez-Filip et al. 2013). The strong linear relationships between structural complexity and the dimension of individual colonies of massive *Porites, P. cylindrica*, and *P. damicornis* suggest that data on the composition of habitat-building species may prove to be a useful proxy for cross-scale habitat structural complexity. In this way, a refined surrogate for habitat structural complexity that combines coral cover and composition may offer a more effective resilience indicator, thereby improving the likelihood of success of important and costly conservation initiatives (Mumby et al. 2008, Hermoso et al. 2013). Mechanistic models of structural complexity have been developed to describe the structure of Caribbean reefs at a broad scale in relation to shifts in benthic communities, using simplified colony shapes of explicit volumes (Bozec et al. 2015), or finer scale estimates of coral structural complexity standardised by colony size (Alvarez-Filip et al. 2013). Similar models could be developed for Indo-Pacific reefs using emerging low-cost, effective techniques such as photogrammetry (Figueira et al. 2015, Ferrari et al. 2016b), allowing predictions of cross-scale structural dynamics resulting from shifts in dominance patterns of corals in the region.

The likely outcomes of continued coral loss on the structural complexity of coral reef habitats will be largely dependent on the nature, frequency and severity of future disturbances, and the capacity for different coral taxa to adapt to changing conditions (Pandolfi et al. 2011, Hughes et al. 2017b). Among those habitats considered here, massive *Porites* generally provided the most structurally complex habitat at each scale, arguably due to the sheer size of colonies. Massive *Porites* are relatively slow-growing and tolerant to stressors such as warm-water anomalies (Darling et al. 2013), poor water quality (Fabricius et al. 2011), and large storms (Harmelin-Vivien 1994), and as such is among those taxa predicted to persist into the future (Darling et al. 2013). Similarly, branching *Porites* was structurally complex across scales, but is relatively fast-growing (Darling et al. 2013), and exhibits varied levels of sensitivity to thermal stress (McClanahan 2017). This may afford some optimism for future reefs despite escalating anthropogenic disturbance, as persistent corals that can offer refugia across a range of scales have the potential to mediate predator-prey interactions (Gregor and Anderson 2016), thereby extending fish body-size distributions (Nash et al. 2013), and coral reef food chains (Alvarez-Filip et al. 2011c). Conversely, the cross-scale habitat structural complexity of degraded reefs with little remaining coral cover (<10%) highlight both the vulnerability of fine scale structure to disturbance, and the more robust nature of larger scale reef structure. The loss of fine scale structure has important implications for species and life stages of fishes that rely on it for refugia, and is likely to lead to rapid reductions in small bodied fish species, and lagged declines in larger bodied species that rely on fine scale habitat structural complexity as juveniles (Graham et al. 2007, Wilson et al. 2010).

These results provide new insight into the cross-scale structural dynamics of taxonomically distinct coral reef habitats across spatial scales of measurement relevant to refuge selection by fishes (Hixon and Beets 1993, Nash et al. 2013). However, the outcomes of assemblage shifts can be diverse and spatially variable, such that quantification of the cross-scale habitat structural complexity of additional coral configurations are warranted. For example, tabular and branching *Acropora* is structurally distinctive and typically dominates large areas of undisturbed coral reef habitats in the Indo-Pacific (Johns et al. 2014), but was not locally abundant at Lizard Island during this study. Furthermore, this study focused on shallow, sheltered reefs only, and further investigation into the cross-scale structure of reef habitats on deeper reefs would provide greater generality to these findings. Coral species composition and the morphology of some coral species vary with abiotic conditions (e.g. exposure, depth, water flow, light, Todd 2008), biological processes (e.g. recruitment, competition, predation), and disturbance histories (Pandolfi et al. 2011, Williams et al. 2013), likely causing variation in the structural complexity of habitats. Similarly, the structural complexity of degraded coral reef habitats can be highly variable, influenced by local disturbance histories (e.g. coral bleaching versus large storms, Wilson et al. 2006), the underlying substrate (Nash et al. 2013), and the colonisation of other benthic organisms (e.g. macroalgae, Hoey and Bellwood 2011). Finally, the method employed in this study while useful for capturing some aspects of structural complexity (e.g. spaces under overhangs and in non-vertical recesses) that may be underestimated using approaches such as profile gauges and photographic methods (Wilding et al. 2007), only captures an estimate of the two-dimensional structural complexity of habitats. Coral reef structures are often multidimensional, with different sized holes and passages throughout the matrix itself. Therefore, in seeking to understand how reef structure relates to the distribution of associated organisms, it would be prudent to consider the specific method used for assessing variation in habitat structural complexity (Robson et al. 2005).

These results provide evidence that habitat structural complexity can be multifaceted over ecologically relevant scales, and demonstrates the importance of going beyond a consideration of just the presence of habitat-building organisms, to include taxonomic structure in efforts to maintain ecosystems and the provision of associated goods and services (Moberg and Folke 1999, Alvarez-Filip et al. 2011c). Coral reefs are among the world's most biodiverse but threatened ecosystems (Hughes et al. 2017b). As global conservation increases in response to coral reef degradation (Butchart et al. 2010), assessments of reef condition and the identification of priority areas for protection should consider the composition as well as cover of corals and other habitat forming organisms. Moreover, identifying inherent patterns of cross-scale habitat structural complexity typical of likely future configurations of species may prove critical for understanding the ecology and conservation of those coral reef systems.

Chapter 3

Structural complexity mediates functional structure of reef fish assemblages among coral habitats

3.1 Abstract

Coral community composition varies considerably due to both environmental conditions and disturbance histories. However, the extent to which coral composition influences associated fish assemblages remains largely unknown. Here an ecological trait-based ordination analysis was used to compare functional richness (range of unique trait combinations), functional evenness (weighted distribution of fishes with shared traits), and functional divergence (proportion of total abundance supported by species with traits on the periphery of functional space) of fish assemblages among six distinct coral habitats. Despite no significant variation in species richness among habitats, there were differences in the functional richness and functional divergence, but not functional evenness, of fish assemblages among habitats. Structural complexity of coral assemblages was the best predictor of the differences in functional richness and divergence among habitats. Functional richness of fish assemblages was highest in branching Porites habitats, lowest in Pocillopora and soft coral habitats, and intermediate in massive Porites, staghorn Acropora, and mixed coral habitats. Massive and branching Porites habitats displayed greater functional divergence in fish assemblages than the Pocillopora habitat, whilst the remaining habitats were intermediate. Differences in functional richness and divergence were largely driven by the presence of small schooling planktivores in the massive and branching Porites habitats. These results indicate that differential structural complexity among coral communities may act as an environmental filter, affecting the distribution and abundance of associated species traits, particularly those of small-bodied schooling fishes.

Published:

Richardson, L. E., Graham, N. A. J., Pratchett, M. S., & Hoey, A. S. (2017). Structural complexity mediates functional structure of reef fish assemblages among coral habitats. *Environmental Biology Of Fishes,* **100**, 193-207. DOI 10.1007/s10641-016-0571-0

3.2 Introduction

Scleractinian corals are foundation species on coral reefs, providing important microhabitats and food to a diverse range of reef fishes (reviewed in Coker et al. 2014). Most coral reef fish are associated with the physical structure created by live corals, evidenced by well-established positive correlations between local fish diversity, abundance, and biomass with reef-scale architectural complexity (Graham and Nash 2013). Broad scale loss of coral cover can cause concomitant declines in fish abundance and biomass (Wilson et al. 2006), diversity (Sano et al. 1984), shifts in body-size distributions (Rogers et al. 2014), trophic structure, and loss of specialist species (Bellwood et al. 2006a, Wilson et al. 2008, Pratchett et al. 2011b, Alvarez-Filip et al. 2015). Such marked reductions in coral cover at both local and regional scales have been well documented (Gardner et al. 2003, Bruno and Selig 2007) as a result of anthropogenic stressors such as overfishing, pollution, and sedimentation, compounded by climate change. Despite concerns for comprehensive and widespread mortality of reef-building corals (Hoegh-Guldberg et al. 2007, Veron et al. 2009), it appears likely that many reefs will persist into the future, albeit with an altered composition (Riegl and Purkis 2009, Pandolfi et al. 2011). Increasing evidence suggests that differential vulnerability of coral species to a range of stressors, and variation in recovery potential is leading to shifts in species dominance towards taxa with stress-tolerant and/or weedy life-histories (Aronson et al. 2004, Van Woesik et al. 2011, Darling et al. 2013, Graham et al. 2014b, Bento et al. 2015). Whilst coral communities vary with natural biotic and abiotic factors (Hughes et al. 2012, Williams et al. 2013), predictions of further community shifts associated with anthropogenic disturbance suggest that understanding the role of community composition in structuring reef fish assemblages may be increasingly important in the future. However, evidence for impacts of coral composition on reef fishes is sparse (but see Berumen and Pratchett 2006, Alvarez-Filip et al. 2011c, Messmer et al. 2011).

The level of dependence and preferential use of different coral species varies greatly among fish species (Coker et al. 2014) and ontogenetic stages (Jones et al. 2004). For example, many small-bodied species and juveniles of large-bodied species demonstrate preference for branching corals such as acroporids, pocilloporids, and branching poritids (Shulman 1984, Bonin 2012). Likewise, some larger-bodied fishes such as groupers and snappers have been shown to shelter preferentially under tabular acroporid corals (Kerry and Bellwood 2015a). At a reef scale, structural complexity of Caribbean reefs has been shown to be determined by the identity and cover of corals present (Alvarez-Filip et al. 2011b), which in turn may influence the size-spectra and trophic structure of local fish assemblages (Alvarez-Filip et al. 2011c). On Indo-Pacific reefs, coral diversity has been shown to affect fish assemblage structure (Messmer et al. 2011, Komyakova et al. 2013), but these studies have been limited in their spatial extent (≤ 4 m^2) and not focused on specific configurations of corals *per se*.

A detailed quantitative assessment of how fish assemblages vary among habitats with specific coral configurations is required to understand the likely impact of predicted directional shifts in coral composition.

Traditionally, studies that have investigated fish-habitat associations have focused on changes in the taxonomic composition of fish assemblages (Mouillot et al. 2013b). However, there is an emerging interest in investigating species assemblages in terms of their roles in ecosystem function as opposed to their taxonomic identity (Bellwood et al. 2004). In combination with community surveys, the distribution and abundance of ecological and morphological traits can be assessed, and by doing so provides some insight into the processes driving community assembly (Mouillot et al. 2013b). Ecological theory broadly predicts that two processes may determine community assembly: interactions among species with shared traits (i.e. competition), and interactions between species and their environment (i.e. environmental filtering) (Diamond 1975, Weiher and Keddy 2001). Locally, competition can limit the ecological similarity of species, thereby differentiating co-occurring species (Macarthur and Levins 1967). Environmental filtering reduces the spread of traits within a habitat, reflecting shared ecological tolerances and a reduction in the range of successful ecological strategies among co-occurring species, thereby reducing functional capacity of the community (Keddy 1992, Cornwell et al. 2006). Previous analyses have considered the functional structure of reef fish communities (captured by species traits) in relation to habitat disturbance (Pratchett et al. 2011b), and ecosystem recovery potential (Graham et al. 2015), and have identified predictable outcomes for ecosystem function. These studies focus on the functional implications of catastrophic bleaching and widespread coral mortality, however the extent to which functional diversity varies among reef habitats that remain coral dominated is untested.

The objective of this study is to investigate the variation in functional structure of reef fish assemblages among six distinct coral habitats. Specifically, I use an ecological trait-based ordination analysis to quantify the functional diversity of fish assemblages in relation to benthic composition in order to address the following questions: (1) does the functional richness, functional evenness, and functional divergence of fish assemblages vary with changes in the taxonomic composition of coral habitats?; and (2) do particular benthic characteristics (benthic composition, benthic diversity, structural complexity, and depth) predict these differences?

3.3 Material and methods

Study location

Fish and coral assemblages were surveyed on reefs surrounding Lizard Island, in the northern Great Barrier Reef, Australia (14°41′S, 145°27′E) in October and November 2014. Sampling was conducted on shallow (<6-m) reef slopes on the western (i.e. leeward) side of the island. Sites were selected to represent six distinct coral habitats characterised by: (i) branching *Porites*, (ii) massive *Porites*, (iii) *Pocillopora*, (iv) staghorn *Acropora*, (v) soft coral, and (vi) mixed coral assemblages. Two replicate sites of each habitat were sampled, except staghorn *Acropora* where only one suitable site was located. Sites were >250 m long by >5 m wide reef slopes; with adjacent sites separated by at least 500 m. All sites were in areas protected from fishing and the prevailing SE swells and currents, and had comparable water clarity and geomorphology. At each site, benthic composition, structural complexity, and associated fish assemblages were surveyed along four replicate 50 m transects positioned parallel to the reef edge, with a minimum of 5 m separating adjacent replicates.

Benthic composition and structural complexity

Benthic composition was quantified using the point intercept method, recording substratum types directly beneath 100 points spaced at 50 cm intervals along each transect line. Substratum types were hard (scleractinian) corals (identified to genus and growth form), soft (alcyonacean) corals, macroalgae, ‘other benthos’ (primarily sponges, giant clams, and ascidians), dead coral and pavement, rubble, and sand. Cross-scale structural complexity of the reef was estimated visually at the start, middle and end of each transect using a 6-point scale, with a score of 0 indicating a flat surface, and a score of 5 an exceptionally complex reef with numerous caves and overhangs (following Wilson et al. 2007).

Fish functional structure

The abundance and body-length (total length (TL), to the nearest cm) of all diurnally active non-cryptic fishes were recorded along each transect using underwater visual census. Large, mobile fish (>10 cm TL) were recorded within a 5-m wide belt while simultaneously deploying the transect tape (to minimise disturbance). Smaller, site-attached fish (<10 cm TL) were then recorded within a 1-m wide belt during a return swim along the same transect (following Hoey et al. 2011). Care was taken to minimise the resurveying of individuals that left and subsequently re-entered the transect area. All fish surveys were conducted by a single observer (ASH) and the fish abundances standardised per 250 m^{-2}.

Two hundred and eighteen observed fish species from twenty-six families were assigned traits from six categories relating to their diet, mean observed species body-size, mobility, time of activity, social grouping, and position in the water column (Appendix B Tables S1 and S2; adapted from Mouillot et al. 2013a). These traits were chosen to represent implicit roles performed by reef fishes (following Mouillot et al. 2013a, Mouillot et al. 2013b), as well as having demonstrable relationships with benthic variation (e.g. Pratchett et al. 2011b, Nash et al. 2013). Fish were classified into established trophic categories that cover the main feeding functions performed by fishes on coral reefs, including removal of algae, and trophic mediation via predation. Body-size, that captures variation in both the identity and magnitude of functions relating to feeding, movement, home range size and energetic requirements, was assigned into 10 cm size-class categories based on the mean observed body size of each species. Diet and body-size encompass a large proportion of the implicit functional roles of coral reef fishes (Bellwood et al. 2004, Lokrantz et al. 2008). However, mobility, time of activity, social grouping, and position in the water column provide additional information on the likely spatial and temporal scales at which the various functions are realised/exerted, and are therefore included to capture maximal estimations of functional diversity (Mouillot et al. 2013a).

Data analysis

Variation in benthic composition between coral habitats was visualised using principal component analysis (PCA) based on the covariance matrix of log (x+1) transformed data. The analysis was based on the percent cover of substratum types on transects in each habitat, including: branching *Porites*, massive *Porites*, *Pocillopora*, and staghorn *Acropora*, 'other' hard coral genera, soft coral, macroalgae, 'other benthos' (described above), dead coral and pavement, rubble, and sand. Analysis of benthic composition using a non-metric Multiple Dimension Scaling (nMDS) based on Bray-Curtis similarities showed comparable groupings among habitats and sites (Appendix B Fig. S1). Benthic composition was compared among habitats (fixed) and sites (random) using a two-way permutational multivariate analysis of variance (PERMANOVA) based on Euclidean distances of the log (x+1) transformed data (Primer V6, PERMANOVA + add on package, n = 999 permutations). For consistency with PCA analyses of benthic composition and subsequent extraction of principal components for multiple linear regression analyses, PERMANOVA was based on Euclidean distances rather than Bray-Curtis similarity. Pairwise comparisons were carried out at the transect level based on unrestricted permutation of raw data to allow for a sufficient number of unique permutations (>420) to be tested. Similarity Percentage analysis (SIMPER) was used post-hoc to identify benthic categories consistently contributing to average similarity within, and dissimilarity between habitats with a test ratio value of 1.5 or higher (Clarke and Warwick 2001).

To assess variation in fish assemblage functional structure among surveyed coral habitats, a trait-based ordination analysis was used to generate three complementary indices of functional diversity: functional richness, evenness, and divergence (Fig. 3.1). These independent indices measure all facets of functional diversity (Villéger et al. 2008): (1) functional richness (the number of unique trait value combinations in an assemblage calculated according to the minimum convex hull volume incorporating species present in functional space relative to the total pool of species); (2) functional evenness (the regularity of the distribution of abundance in this volume calculated as the sum of the minimum spanning tree branch length weighted by relative abundance); and (3) functional divergence (species deviance from the mean distance to the centre of the neutral functional space, weighted by relative abundance) (Mason et al. 2005). Based on pairwise Gower's distances between species, principal coordinates analysis (PCoA) was used to construct a synthetic multidimensional ordination from which functional diversity indices were computed by transect. The first four dimensions of the ordination were selected *a posteriori* (following Maire et al. 2015), and single score functional diversity indices were calculated according to species' position in this four-dimensional space. A square root correction for negative eigenvalues was applied for Euclidean representation of distance relationships among species and to avoid biased estimations of functional diversity (Legendre and Legendre 1998).

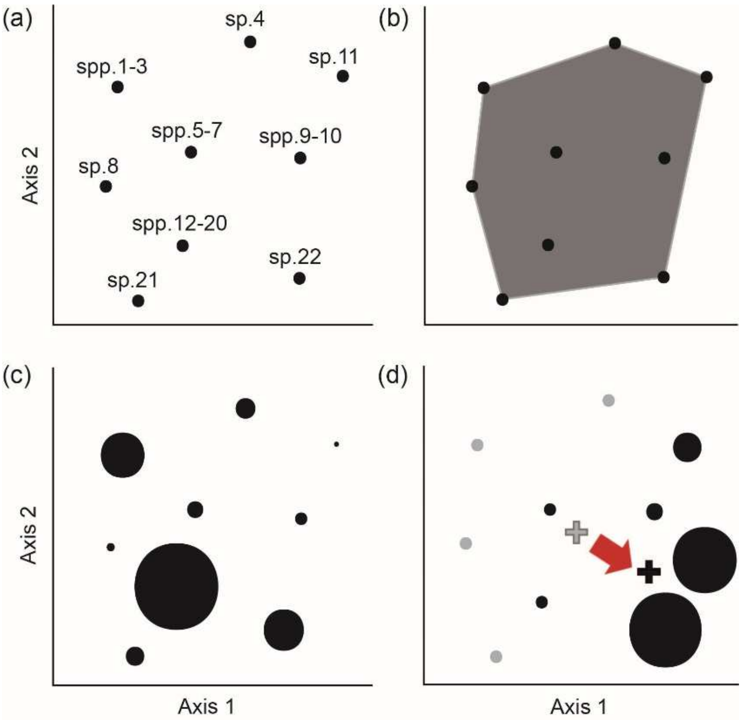

Fig. 3.1 Assessing variation in the functional structure of ecological communities. (a) Species are plotted in multidimensional space according to shared trait values; (b) Functional richness, the proportion of the functional space filled by species, illustrated by the convex surface encompassing species present from the total species pool; (c) Functional evenness, the regularity of abundance distributions in functional space, where circle sizes are proportional to species relative abundances; (d) Functional divergence, the proportion of the total abundance characterised by species with functional traits positioned in towards the periphery of functional space, calculated as the distance from the grey

to black cross (Villéger et al. 2008, Mouillot et al. 2013b). A four-dimensional space was used to assess functional diversity, however two axes are shown here for illustrative purposes.

Variation in functional richness, evenness, and divergence, as well as species richness (total number of species) of fish assemblages among coral habitats was modelled using the lme function from the *nlme* package in R (R Development Core Team 2015), with habitat as a fixed effect, and *post hoc* Tukey multi-comparison tests. Models with and without site as a random effect were compared using the minimisation of corrected Akaike information criterion (AICc; Akaike 1974) to rank alternative models. Since exploratory graphical analysis suggested possible differences in variance among habitats, models which did and did not allow heterogeneity of variance among habitats were also compared. Multiple linear regression was then used to estimate relationships between functional richness, evenness, and divergence with six continuous benthic explanatory variables: benthic diversity (Shannon-Wiener H'), the first two axes of the benthic PCA as proxies of benthic composition (Fig. 3.2), cross-scale structural complexity (hereafter, structural complexity), coral cover, and depth (Fig. 3.3; mean ± SE values detailed in Appendix B Table S3). Collinearity between explanatory variables was assessed using Spearman's correlation coefficients (for numerical values), and variance inflation factors (VIF). All variables had a correlation coefficient of <0.7 and VIF values <3 and so were retained for model selection. Information-theoretic model selection based on the AICc ranking was used to quantify model uncertainty (Burnham and Anderson 2002). The top models, based on ΔAICc values <2 (Burnham and Anderson 2002) are presented and detail the changes in AICc and model weights to illustrate the strength of the optimum model. Parameter estimates and significance values are also presented for the top-ranked models for each functional diversity index. Analyses were performed in R using the packages *ape*, *ade4*, *cluster*, *geometry*, *MuMIn*, *nlme, polycor*, *rcdd*, *vegan*, as well as the function FDchange in the package *FD*, unless otherwise specified.

3.4 Results

Benthic composition and structural complexity

Dominant benthic components in each habitat were those coral taxa identified *a priori* in site selection, covering 22.6-51.6% of total benthos, and 38.5-89.7% of total live coral (Appendix B Table S3). Principal component analysis (PCA) revealed variation in benthic composition among habitats, with transects in each habitat generally grouping together (Fig. 3.2a). Branching *Porites* habitats were clearly separated from soft coral, *Pocillopora*, and staghorn *Acropora* habitats along the first axis (PC1), while soft coral habitats were differentiated from staghorn *Acropora* and *Pocillopora* along PC2. Groupings identified in the PCA were supported by the PERMANOVA with significant differences in benthic composition between habitats (Pseudo-*F* = 3.37, *P* = 0.002, 945 Permutations). Pairwise comparisons and SIMPER analysis indicated that all habitats differed in benthic composition (all *P* ≤0.05, Appendix B Table S4).

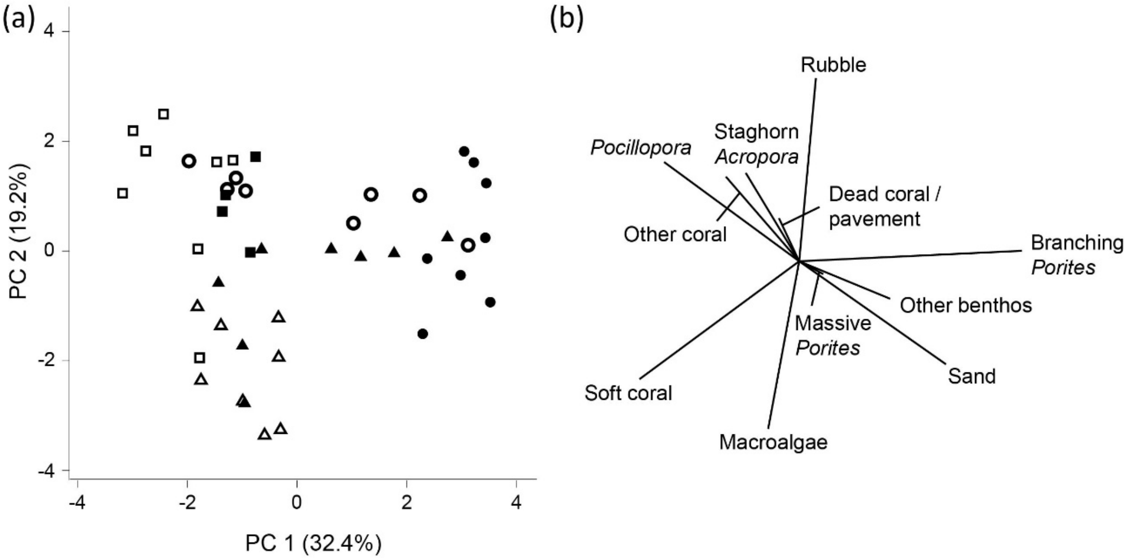

Fig. 3.2 Principal components analysis showing relationships among benthic assemblages across six coral habitats on Lizard Island. (a) Spatial variation in benthic habitat on reefs at the transect level on natural log(x+1) transformed data. Data symbols represent transects within habitats: staghorn *Acropora* (filled square); branching *Porites* (filled circle); massive *Porites* (filled triangle); mixed assemblages (open circle), *Pocillopora* (open square); and soft coral (open triangle). (b) Relative contribution of 10 benthic habitat categories to the observed variation in reef benthic composition.

Fish functional diversity

The first four dimensions of the PCoA cumulatively explained 55.5% of the projected inertia in the distribution of fish species traits (first two independent axes accounted for 38% of the variance and are illustrated in Fig. 3.4 and 3.6). Generally, fish body-size and mobility increased from right to left along the first axis of the PCoA, and social grouping broadly changed along the second axis (

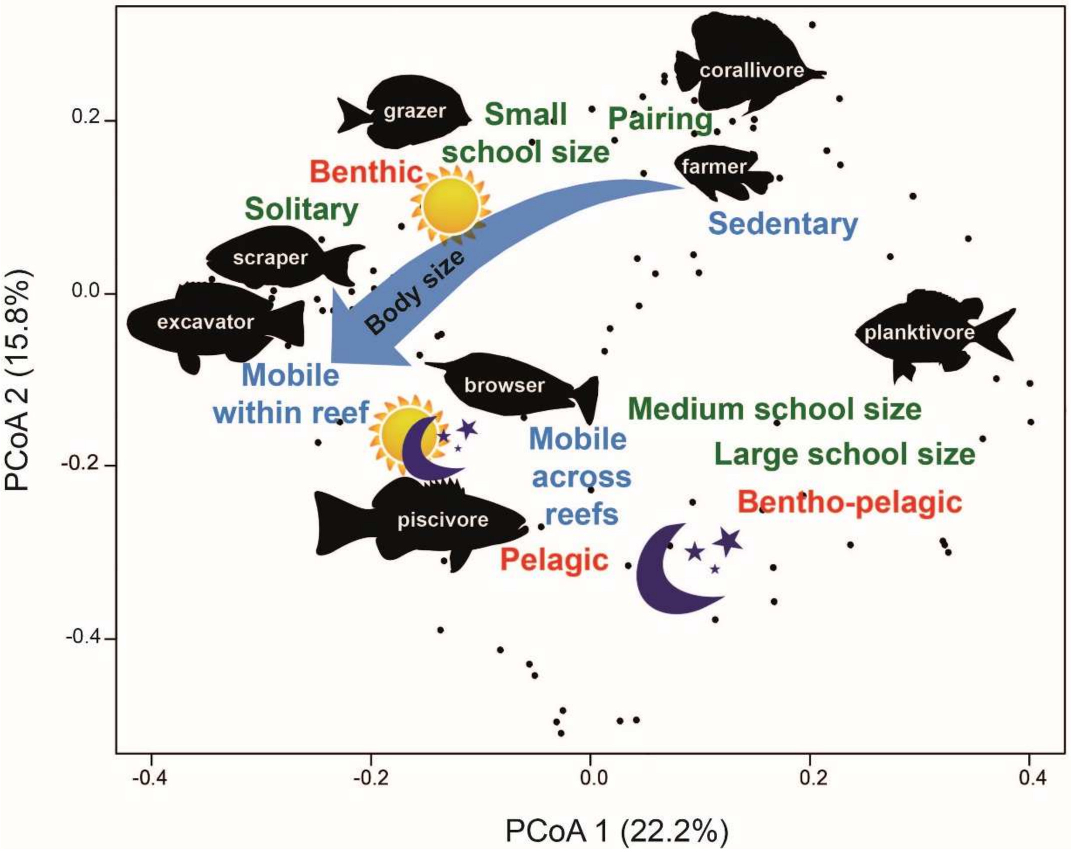

Fig*. 3.4* 3.4). Grazers, scrapers, and excavators were positioned top-left in functional space, and sedentary farmers, and corallivores were in the top-right. Planktivores were positioned in the middle-right, and larger piscivores and mixed-diet feeders typically mobile within reefs were positioned in the bottom-left (Fig. 3.4).

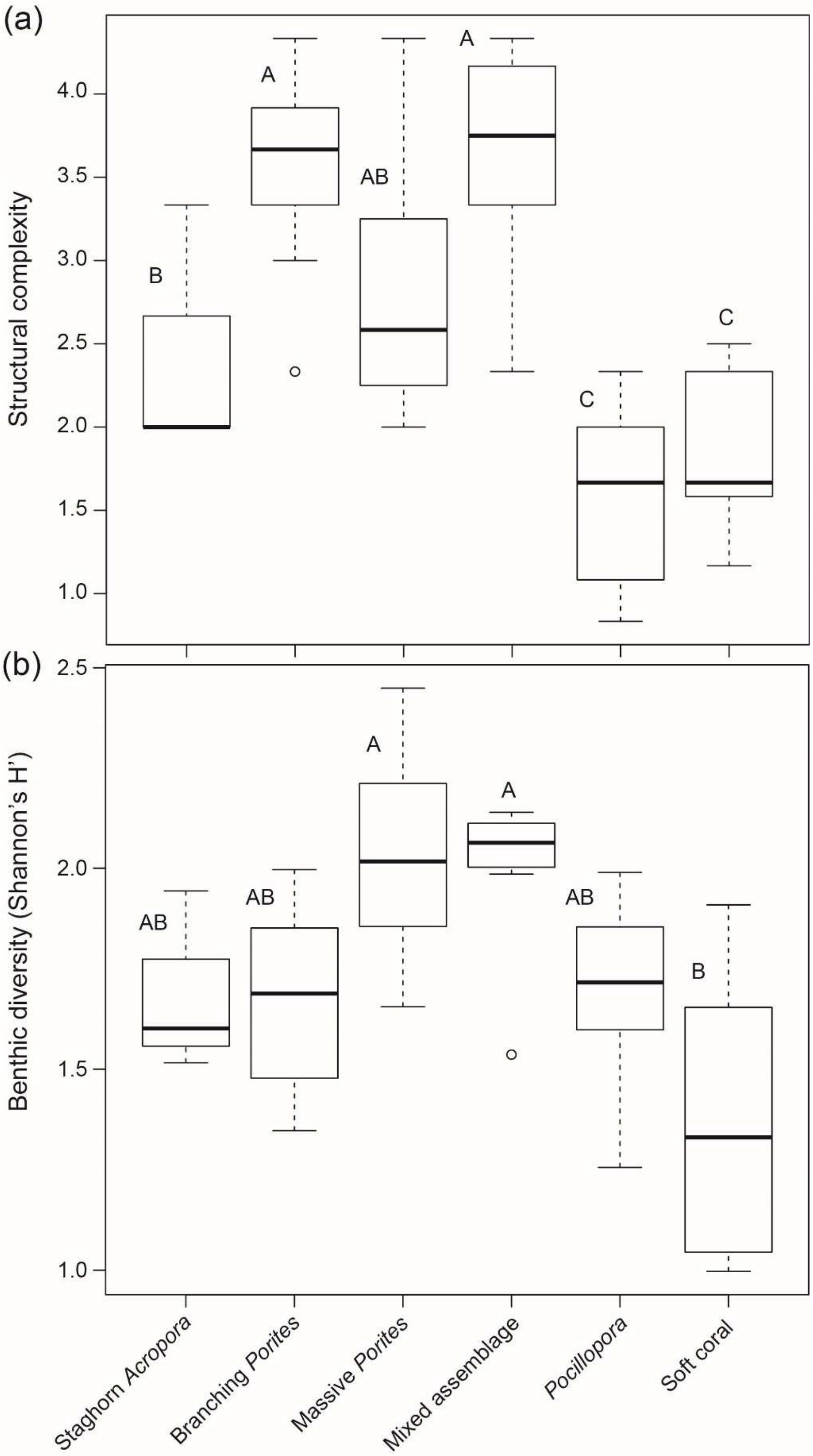

Fig. 3.3 Variation in structural complexity (a), and benthic diversity (b) among surveyed coral habitats (n = 4-8 per habitat). Significant differences between sites revealed by *post hoc* Tukey pairwise comparisons are illustrated by the pairing of letters (A – C; Tukey, all P <0.04).

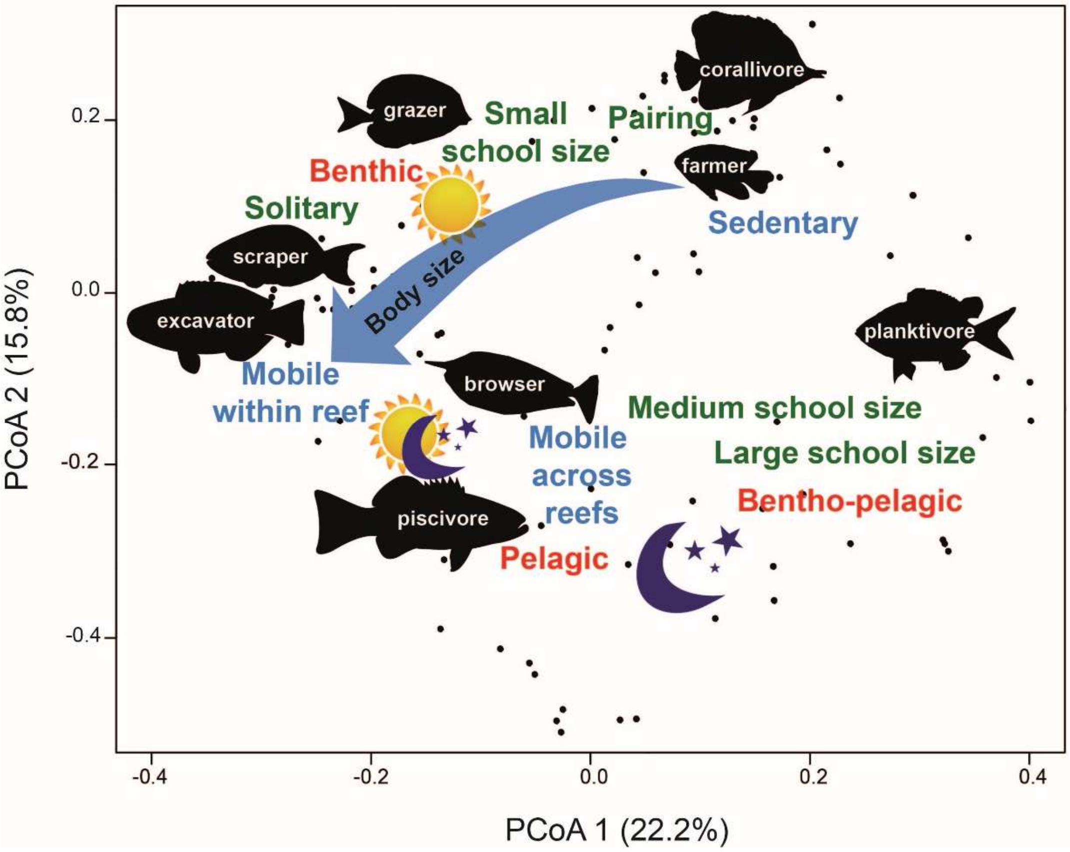

Fig. 3.4 Principal coordinates analysis of fish assemblage functional space. Two hundred and eighteen recorded fish species (black dots) plotted in the first two dimensions (four total) of functional space defined by six traits: mean observed total body length (blue directional arrow indicating increasing size), diet (fish symbols); mobility (blue text); time of activity (sun and/or moon); social grouping (green text); and position in the water column (red text). Illustrations and text show the position of average trait levels in the functional space.

Model comparisons using AICc indicated that neither inclusion of site as a random effect, nor allowing heterogeneity of variance among habitats, improved the model fit for estimations of functional diversity metrics, and were excluded from subsequent analyses. There were significant differences among coral habitats in the average functional richness of fish assemblages (ANOVA, $F_{5, 38} = 3.62$, $P = 0.008$), with branching *Porites* habitats supported functionally richer fish assemblages than both soft coral and *Pocillopora* habitats (Tukey pairwise comparisons, $P = 0.009$ and $P = 0.004$, respectively; Fig. 3.5a and 3.6). Modelling of the individual-scale predictors of functional richness yielded two models within ΔAICc <2 of the top model (Table 3.1). The most parsimonious model (wAICc = 0.7) contained structural complexity alone and was 2.33 times more plausible than the next model (wAICc = 0.3), which included structural complexity and the second axis of the benthic PCA. Structural complexity was the only variable present in both top models, and had a top relative importance of 1 (Table 3.1). The positive parameter estimate for structural complexity (± SE; 0.08 ±

0.02) indicates greater structural complexity to be associated with higher fish functional richness (full model, linear regression, $r^2 = 0.248$, $F_{5,38} = 3.84$, $P = 0.01$; optimal model structural complexity ~ functional richness, $r^2 = 0.296$, $F_{1,42} = 19.08$, $P < 0.001$; Fig. 3.7a). The effect size of PCA axis 2 was less substantial, reflected by its relative importance score (0.30). Total coral cover was a poor predictor of functional richness (and divergence; >2 ΔAICc of the top ranked multiple linear models). Pairwise comparisons revealed that non-overlap of mean convex hull volumes among habitats varied from 20.6 – 40.9% (Appendix B Table S5).

No difference in functional evenness was detected between habitats (ANOVA, $F_{5,38} = 1.01$, $P = 0.43$; Fig. 3.5b). There was also no significant difference in the mean species richness of fish assemblages among coral habitats (best model fit: ANOVA, $F_{5,5} = 1.21$, $P = 0.42$).

Functional divergence varied significantly between habitats (ANOVA, $F_{5,38} = 3.41$, $P = 0.01$) with greater divergence in massive and branching *Porites* habitats than *Pocillopora* habitats (Tukey pairwise comparisons, $P = 0.003$ and $P = 0.03$, respectively; Fig. 3.5c and 3.6). Sensitivity analysis of individual-scale benthic predictors (full model, linear regression, $r2 = 0.077$, $F_{5,38} = 1.72$, $P = 0.15$) yielded 4 models within ΔAICc <2 of the top model (Table 3.2). The top ranked model (wAICc = 0.43; $r2 = 0.123$, $F_{1,4} = 7.03$, $P = 0.01$; Fig. 3.7b) contained structural complexity alone and was 2.05 times more likely than the next model that included structural complexity and the second axis of the benthic PCA (wAICc = 0.21). Structural complexity featured in all four top models, with a high relative importance score of 1.00. The positive parameter estimate for structural complexity (± SE; 0.01 ± 0.004) indicated higher fish functional divergence in coral habitats characterised by greater structural complexity.

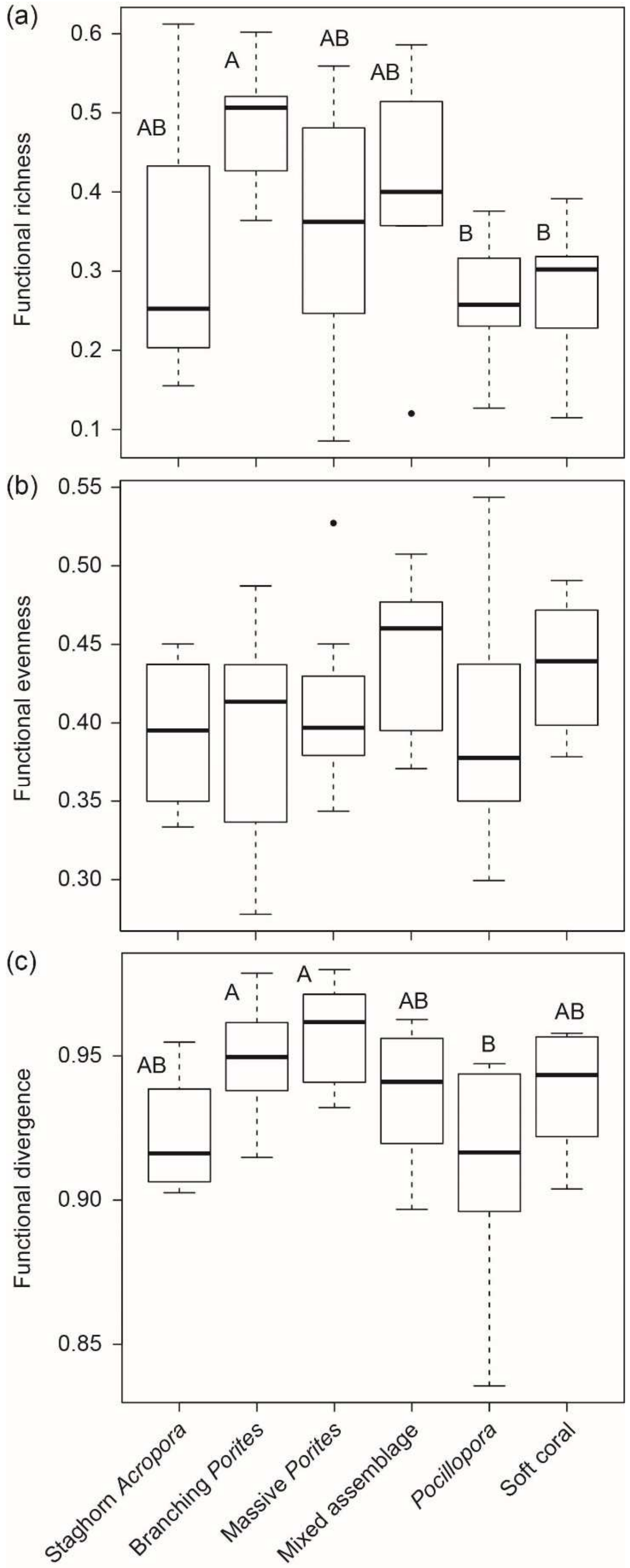

Fig. 3.5 Variation in functional richness (a), evenness (b), and divergence (c) of fish assemblages among the six surveyed coral habitats (n = 4-8 per habitat). Significant differences between sites revealed by *post hoc* Tukey pairwise comparisons are illustrated by the pairing of letters (A – B; Tukey, all P ≤0.05).

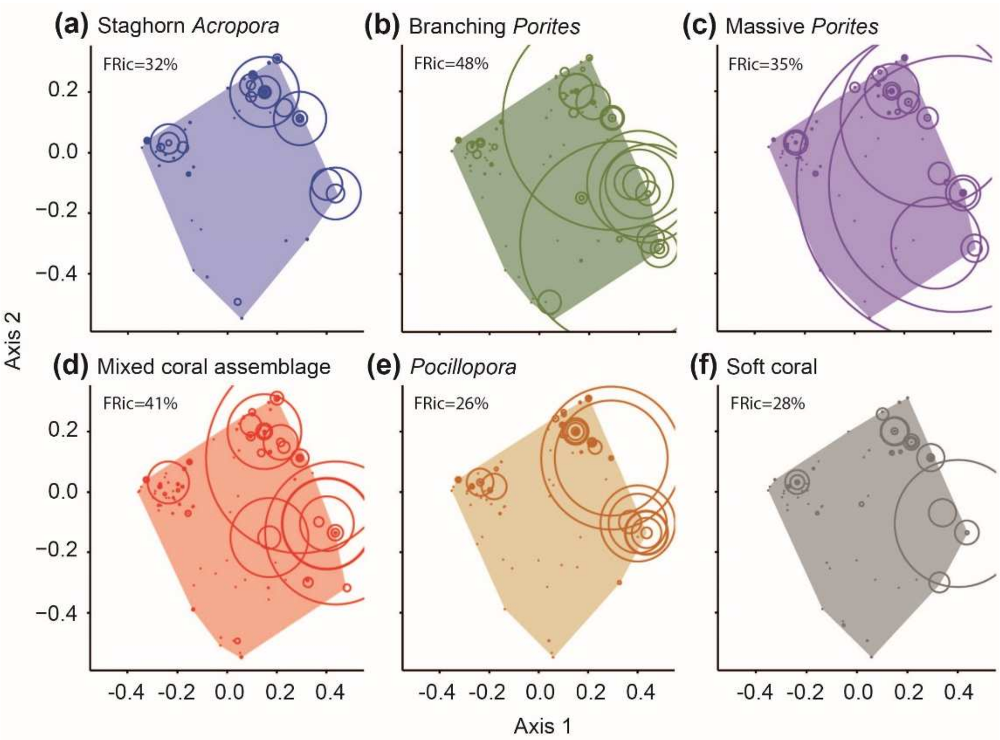

Fig. 3.6 Variation in fish assemblage functional structure among coral habitats (a-f). Shaded convex surfaces illustrate the first two dimensions of functional space filled by species present from the total species pool (functional richness; FRic), and circle sizes are proportional to species mean relative abundances (illustrating patterns in functional divergence).

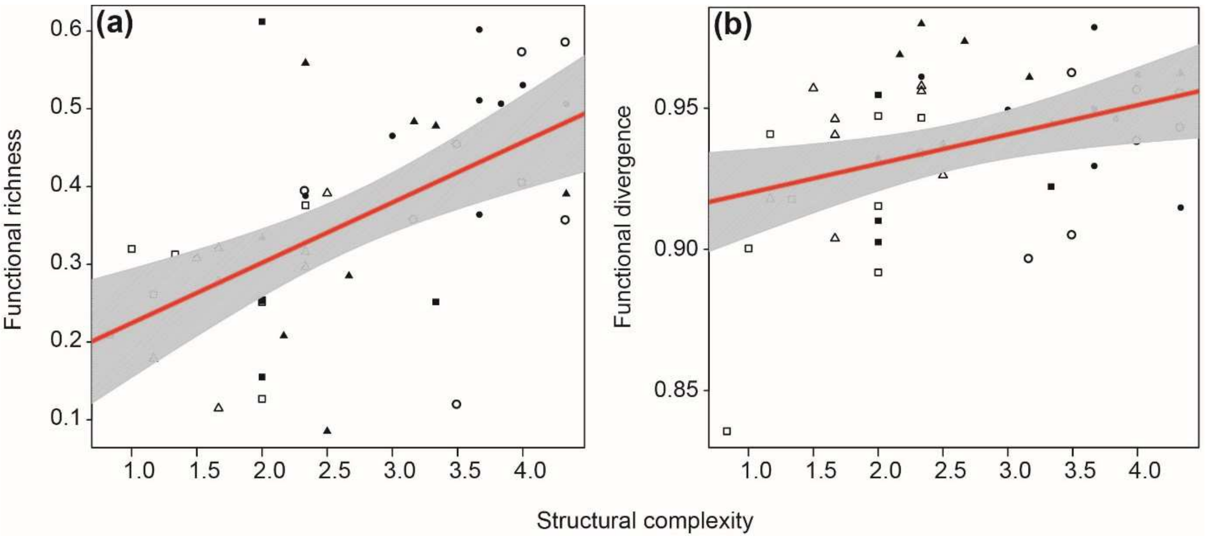

Fig. 3.7 Relationship between structural complexity and (a) fish functional richness, and (b) fish functional divergence (95% CIs). Symbols relate to transects in different coral habitats: Staghorn *Acropora* (filled square); branching *Porites* (filled circle); massive *Porites* (filled triangle); mixed (open circle); *Pocillopora* (open square); and soft coral (open triangle).

Table 3.1 The two candidate models selected to describe the relationship between benthic characteristics and fish assemblage functional richness. Models are ranked by corrected Akaike's information criteria (AICc), with all models within ΔAICc <2 of the top ranked model. The relative weight of evidence for each model is indicated by Akaike weight (wAICc), and the variables present in each model are indicated with an X. The parameter estimates ± unconditional standard errors averaged over the two models are given along with the relative importance of each variable based on the sum of Akaike weights of the models in which the variable is present.

Model rank	AICc	*df*	logLik	ΔAICc	wAICc	Structural complexity	Benthos (PCA axis 2)	Benthos (PCA axis 1)	Benthic diversity (Shannon)	Depth (m)	Model output (lm)
1	-58.27	3	32.44	0.00	0.70	X					$F_{1,42}$ = 19.08, ***P* <0.001**
2	-56.61	4	32.82	1.67	0.30	X	X				$F_{2,41}$ = 9.83, ***P* <0.001**
Relative importance						1.00	0.30	N/A	N/A	N/A	
Model average						0.08 ± 0.02	0.003 ± 0.01	N/A	N/A	N/A	

Table 3.2 The four candidate models selected to describe the relationship between benthic characteristics and fish assemblage functional divergence. Models are ranked by Akaike's information criteria (AICc), with all models within ΔAICc <2 of the top ranked model. The relative weight of evidence for each model is indicated by Akaike weight (wAICc), and the variables present in each model are indicated with an X. The parameter estimates ± unconditional standard errors averaged over the four models are given along with the relative importance of each variable based on the sum of Akaike weights of the models in which the variable is present.

Model rank	AICc	*df*	logLik	ΔAICc	wAICc	Structural complexity	Benthos (PCA axis 2)	Benthos (PCA axis 1)	Benthic diversity (Shannon)	Depth (m)	Model output (lm)
1	-191.27	3	98.94	0.00	0.43	X					*F*1,42 = 7.03, ***P* = 0.01**
2	-189.88	4	99.45	1.39	0.21	X	X				*F*2,41 = 4.00, ***P* = 0.03**
3	-189.79	4	99.41	1.48	0.20	X				X	*F*2,41 = 3.95, ***P* = 0.03**
4	-189.28	4	99.15	1.99	0.16	X			X		*F*2,41 = 3.67, ***P* = 0.03**
Relative importance						1.00	0.21	N/A	0.16	0.20	
Model average						0.01 ± 0.004	-0.001 ± 0.002	N/A	0.001 ± 0.01	0.001 ± 0.002	

3.5 Discussion

The composition and functions of coral reef fish assemblages are mediated by the availability of live coral habitat (reviewed in Pratchett et al. 2008). However, the role of coral community composition, specifically the dominance of different coral taxa, in shaping fish assemblages is not yet well understood. This study revealed variation in the functional diversity of fish assemblages among six surveyed coral habitats. These results suggest that coral composition may act as an environmental filter on the distribution and abundance of associated fish traits. Functional richness and functional divergence, but not functional evenness or taxonomic richness, of fish assemblages varied among coral-dominated habitats, with the structural complexity of the habitats being the best predictor of these measures. Functional richness was highest in branching *Porites* habitats, lowest in *Pocillopora* and soft coral habitats, and intermediate in massive *Porites,* staghorn *Acropora,* and mixed coral habitats. Functional divergence was greatest in branching *Porites* and massive *Porites* habitats, and lowest in *Pocillopora* habitats.

Functional richness reflects the range of unique trait combinations held by coexisting fish species, which for some groups (e.g. herbivores) may indicate the potential resilience of an ecosystem (Rasher et al. 2013, Nash et al. 2015). Results of this study suggest that at a reef-scape scale, coral habitats dominated by complex coral growth forms (such as branching *Porites*) may accommodate a greater range of niches, or functional strategies, than corals that provide less structural complexity (such as *Pocillopora* and soft coral). Fish with particular shared functions were found across all habitats (e.g. solitary grazers, scrapers and excavators, small sedentary farmers, and pairing corallivores). However, others were largely restricted to branching *Porites* habitats, namely nocturnally active, schooling planktivores (i.e. planktivorous species of the Apogonidae and Holocentridae). Branching *Porites* tends to form large dome-shaped colonies that offer potential refugia for other organisms at multiple spatial scales, both between its narrow-spaced branches, between colonies, and under colony ledges. In this way, branching *Porites* contains structural similarities of both branching and massive morphologies, importantly providing structure for fishes across a range of scales (Nash et al. 2013). Nocturnal planktivorous cardinalfishes, in particular, can exhibit high levels of habitat specialisation with branching *Porites*, occupying colonies at diurnal resting sites on the reef (Gardiner and Jones 2005).

Experimental analysis of the effects of coral species richness on fish assemblage diversity shows that habitat specialists are vulnerable to shifting coral composition (Holbrook et al. 2015), in accordance with the specialisation-disturbance hypothesis (Vázquez et al. 2002). Thus, where shifts in coral composition are characterised by the loss of structurally complex corals, reef fish assemblages may become less functionally diverse and dominated by habitat generalists that utilize a range of habitat types at the expense of habitat specialists (Bellwood et al. 2006a, Wilson et al. 2008). Nocturnally active planktivores, such as cardinalfishes, are typically fast growing and short-lived, and have been suggested to play an important role in recycling and concentrating energy on reefs through the provision of a trophic link between emergent (nocturnal) plankton and higher trophic levels (Marnane and Bellwood 2002). Although the functional importance of fish such as cardinalfish is not well understood, a loss of functional richness and ecological complementarity among fish can have important and unexpected consequences for ecosystem function (Bellwood et al. 2003, Bellwood et al. 2006a). For example, certain processes are maintained by just one or a few fish species, making ecosystem function highly vulnerable to the loss of those species (Hoey and Bellwood 2009, Mouillot et al. 2014).

Fish assemblages in massive and branching *Porites* habitats were more functionally divergent than those in *Pocillopora* habitats, driven by the dominance of small, schooling planktivorous fishes in the two *Porites* habitats. Higher functional divergence suggests greater niche specialisation among coral habitats due to higher abundances of species close to the volume borders of the functional space, i.e. specialist species (Mouillot et al. 2013b). Massive *Porites* corals appear to provide little shelter from predation, water movement, or solar radiance for small-bodied fish across the relatively planar colony surface. However, some evidence suggests that small fishes may use massive corals when their primary branching coral microhabitat has been lost (Wellington and Victor 1985, Precht et al. 2010). Branching *Porites* habitats had similarly high functional divergence, and was differentiated from other habitats due to the abundance of schooling, nocturnal planktivores which were absent or in low abundance elsewhere. The branching *Porites* habitat also had the highest abundance of small, sedentary fish (e.g. damselfishes *Pomacentrus moluccensis*, *P. grammorhynchus*, and *Chromis viridis*). Branching *Porites* is somewhat morphologically similar to massive *Porites* in that they both form large mound-shaped colonies providing shelter between colonies or under ledges created by overhangs (Kerry and Bellwood 2015b), with branching *Porites* also providing smaller refuges between its branches.

Differential structural complexity among coral habitats was the best predictor (of the five explanatory variables examined) of fish functional richness and divergence. The relationship between structural complexity and coral composition illustrated in this study is consistent with analyses from the Caribbean emphasising the variable morpho-functional characteristics of individual coral species (Alvarez-Filip et al. 2011b). Studies concerned with impacts of reef degradation demonstrate the importance of habitat structure for reef fish taxonomic diversity and abundance (Graham and Nash 2013), fish body-size distributions (Wilson et al. 2010), trophic structure (Alvarez-Filip et al. 2011c), and habitat selection of recruits and juvenile fishes (Jones et al. 2004). Despite little variation in fish species richness among habitats, the increasing functional richness across a structural complexity gradient in this study is consistent with the concept of environmental filtering, where species with certain ecological or morphological traits were excluded if unsuited to low complexity habitat (Cornwell et al. 2006). The positive correlation between functional divergence and structural complexity also suggests that the performance of particular groups of specialist species may be restricted on low complexity reefs due to limited available refugia from predation or environmental conditions such as water flow or solar radiance (sensu performance filter hypothesis) (Mouillot et al. 2013b). Species can exhibit a range of responses to environmental disturbance, such as increases in herbivores in response to coral loss (Wilson et al. 2006, Pratchett et al. 2011b). Therefore, where functional diversity is greater in more structurally complex coral habitats, a broader range of processes may be supported that underpin ecosystem performance (Rasher et al. 2013).

Coral communities are known to vary with natural physical features (e.g. geomorphology, exposure, reef zonation and depth), biological processes (e.g. recruitment, predation, inter- and intra-specific competition for space), and local disturbance histories (Pandolfi et al. 2011, Hughes et al. 2012, Williams et al. 2013). How these communities will change, and the implications for the functional diversity of reef fish assemblages will be largely dependent on the nature, frequency and severity of future disturbances, and the capacity for different coral taxa to adapt to changing conditions (Hoegh-Guldberg et al. 2007, Pandolfi et al. 2011). Inter- and intra-taxon variation in colony morphology and physiology influence both the susceptibility to various stressors and patterns of larval recruitment and growth, which promote particular corals as more or less competitive, stress-tolerant and/or quick to colonize post-disturbance (reviewed in Darling et al. 2012, Hughes et al. 2012). For example, structurally complex branching corals (e.g. *Acropora* and *Pocillopora*) are often the most susceptible taxa to a range of disturbances such as thermal bleaching (Marshall and Baird 2000), storms (Madin and Connolly 2006), and crown-of-thorns starfish (Baird et al. 2013), yet they are also fast-growing and in areas of sufficient larval supply can quickly dominate areas post-disturbance (e.g. Berumen and Pratchett 2006). Branching *Porites* is similarly fast growing and sensitive to thermal stress, though there is little evidence of long-term recovery potential following disturbance (e.g. Van Woesik et al. 2011, Johns et al. 2014). Conversely, slow-growing coral genera with massive or encrusting life forms, such as massive *Porites*, typically exhibit less sensitivity to thermal stress or colony damage caused by large storms (e.g. Hughes 1994, Van Woesik et al. 2011, but see Guest et al. 2012), and have been predicted to persist in a changing climate characterised by warmer temperatures and high disturbance frequency (Riegl and Purkis 2009, Bento et al. 2015). Soft corals are relatively stress tolerant and opportunistic (Darling et al. 2012), and have been documented to rapidly colonise and dominate benthic assemblages following the widespread mortality of hard corals (reviewed in Norström et al. 2009, Johns et al. 2014). Although the most likely scenarios facing coral reefs will be a shift away from structurally complex branching corals to less complex mound and massive growth forms, or toward benthic communities dominated by other non-coral taxa, the exact nature of these shifts remain uncertain and are likely to vary between locations.

This study provides some initial insights into the role of coral composition in structuring reef fish assemblages via the differential structural complexity provided by coral taxa in shallow, sheltered reef habitats. Despite being conducted at a single location (Lizard Island), with limited availability of habitats with *a priori* defined coral composition, significant differences in the functional diversity of fish assemblages were evident. However, our findings are a snapshot of a complex, dynamic system, influenced by seasonal biological processes (e.g. recruitment), anthropogenic disturbances, and intra- and interspecific interactions between reef fishes and their environment (Jordano 2016). Therefore, further examination of the role of coral species composition in structuring reef fish assemblages over seasons, locations, and environmental gradients (e.g. depth and reef zonation) would better our understanding of these reef fish-coral community associations. Although the assessment of structural complexity captured differences in broad-scale habitat features and was an important predictor of fish functional diversity, more detailed consideration of how multiple scales of complexity correlate with reef fish functional diversity is warranted to improve the understanding of how coral composition may structure ecosystems through differential habitat provision (**Chapter 2**).

Corals do not provide equal resources to reef fishes, so predicted shifts in coral species composition (e.g. Graham et al. 2014a) will likely to have important effects on the functional composition of reef fish assemblages. Recent work has shown substantially altered functional structure of fish assemblages on reefs that have shifted from coral to algal dominance (Hoey and Bellwood 2010b, Wilson et al. 2010, Rasher et al. 2013, Chong-Seng et al. 2014, Graham et al. 2015). This study shows that functional diversity and structure of fish assemblages also varies in coral dominated habitats that differ in composition and structural complexity. These results suggest that despite little variation in taxonomic richness of fish assemblages among coral habitats, coral composition may mediate the distribution and abundance of fish traits, which is likely to influence the maintenance of populations, ecosystem processes to which they contribute, and therefore the resilience of that system (Larsen et al. 2005, Nash et al. 2015). This study highlights the need to delve further into trait-based exploration of the functional implications of altered coral habitats across multiple locations as ecosystem performance may hinge upon it.

Chapter 4

Mass coral bleaching causes biotic homogenization of reef fish assemblages

4.1 Abstract

Global climate change is altering community composition across many ecosystems due to non-random species turnover, typically characterized by the loss of specialist species and increasing similarity of biological communities across spatial scales. As anthropogenic disturbances continue to alter species composition globally, there is a growing need to identify how species responses influence the establishment of distinct assemblages, such that management actions may be appropriately assigned. Here, I use trait-based analyses to compare temporal changes in five complementary indices of reef fish assemblage structure among six taxonomically distinct coral reef habitats exposed to a system-wide thermal stress event. These results revealed increased taxonomic and functional similarity of previously distinct reef fish assemblages following mass coral bleaching, with changes characterized by subtle, but significant, shifts towards predominance of small-bodied, algal-farming habitat generalists. Furthermore, whilst the taxonomic or functional richness of fish assemblages did not change across all habitats, an increase in functional originality indicated an overall loss of functional redundancy. I also found that pre-bleaching coral composition better predicted changes in fish assemblage structure than the magnitude of coral loss. These results emphasise how measures of alpha diversity can mask important changes in the structure and functioning of ecosystems as assemblages reorganize. The findings also highlight the role of coral species composition in structuring communities and influencing the diversity of responses of reef fishes to disturbance. As new coral species configurations emerge, their desirability will hinge upon the composition of associated species and their capacity to maintain key ecological processes in spite of ongoing disturbances.

Published:

Richardson, L. E., Graham, N. A. J., Pratchett, M. S., Eurich, J. & Hoey, A. S. (2018). Mass coral bleaching causes biotic homogenization of reef fish assemblages. *Global Change Biology,* DOI:10.1111/gcb.14119

4.2 Introduction

Pervasive anthropogenic disturbances have altered the structure of ecological communities and the functioning of ecosystems, primarily through habitat change, exploitation, and pollution (Cardinale et al. 2012, Ellis et al. 2013). Species extirpations and introductions modify the composition of local assemblages, often reducing biodiversity within (alpha diversity; α), and among (beta diversity; β) communities (Dornelas et al. 2014, McGill et al. 2015). This resulting species turnover typically occurs non-randomly, often varying with organism characteristics such as body-size, physiology, habitat specialisation and trophic level (McKinney 1997, Graham et al. 2011). Long-term observations of trait-filtering across groups such as plants, mammals, birds, and fishes, indicate declines in specialist species in response to past and current global changes (Clavel et al. 2011). These declines have caused increasing taxonomic and functional similarity (i.e., biotic homogenization) at the community level, threatening ecosystem functioning and resilience (Elmqvist et al. 2003, Olden et al. 2004, Clavel et al. 2011). Two facets of species biodiversity are expected to confer ecosystem resilience to disturbance during ecological reorganization: (i) functional redundancy (the capacity of one or more species to functionally compensate for the loss of another), and (ii) response diversity (the diversity of species responses to environmental change within functional groups such that functions may be maintained) (Walker 1992, Elmqvist et al. 2003, Nyström 2006, Nash et al. 2015).

I focus on coral reefs, one of the world’s most biodiverse but threatened ecosystems (Hughes et al. 2017a), to assess how species response diversity to disturbance among fishes and corals influences ecological organisation across scales (within and across distinct reef habitats). Climate-induced coral bleaching represents the foremost threat to coral reefs, with severe thermal stress events causing widespread coral loss, altering the structure of coral reef habitats and the composition of reef-associated species (Graham et al. 2006, Hoegh-Guldberg et al. 2007, Pratchett et al. 2011b). Mass bleaching has been shown to cause local extirpations of coral reef fishes with corresponding declines in fish species richness and total abundance (Wilson et al. 2006). However, reef fish and coral species responses to extreme thermal stress can be highly variable (Wilson et al. 2006, McClanahan 2017), likely due to inherent differences in the response of corals to ocean warming (Pandolfi et al. 2011), as well as differential trait-vulnerability of fish species associated with distinct coral habitats (Graham et al. 2011, **Chapter 3**). Sustained ocean-warming increases the risk of further mass bleaching events (Hughes et al. 2017b). However, how distinct species assemblages will vary in their susceptibility to change is not well understood.

There is a growing need to understand how different configurations of species on coral reefs respond to disturbance and contribute to ecosystem function (Graham et al. 2014a), such that coral reef management efforts may be allocated appropriately. Previously unseen disturbance-mediated configurations of species are increasingly reported on coral reefs (Pandolfi et al. 2011, Pratchett et al. 2011a, Bento et al. 2015). Given inherent differences in the responses and vulnerability of species, disturbances cause shifts in coral species dominance, as well as overall declines in species diversity (Aronson et al. 2004, Pratchett et al. 2011a, Alvarez-Filip et al. 2013). These altered configurations are predicted to persist into the future due to increased incidence and severity of disturbances, as well as differential recovery potential and adaptation capacity among corals (Pandolfi et al. 2011). The composition of coral assemblages and associated structure of reef habitats exerts considerable influence over the structure of reef fish assemblages (Luckhurst and Luckhurst 1978, Roberts and Ormond 1987, Friedlander and Parrish 1998, Darling et al. 2017), important ecosystem processes such as herbivory (Cvitanovic and Hoey 2010), predator-prey dynamics (Hempson et al. 2017), and other intraspecific and interspecific fish species interactions (Kok et al. 2016). Indeed, shifts in coral assemblage composition have also shaped novel reef fish assemblages, where despite regaining pre-disturbance coral cover in some instances, populations of some fish species show little evidence of recovery generations later (Berumen and Pratchett 2006, Bellwood et al. 2012).

Here I assess the susceptibility of distinct species configurations to the impacts of mass coral bleaching to elucidate the influence of pre-disturbance coral species composition on the resilience of tropical reefs, and consider the effects of response diversity on ecological organisation. Specifically, I use trait-based approaches to compare the taxonomic and functional structure of reef fish assemblages among six taxonomically distinct coral reef habitats seven months before, during, and six months after severe coral bleaching at Lizard Island, in the northern Great Barrier Reef, Australia.

4.3 Materials and methods

Study location

Lizard Island (14°41′S, 145°27′E) is a granitic mid-shelf island located 30 km offshore from mainland Australia, in the northern section of the Great Barrier Reef. The island is largely encircled by well-developed fringing reefs and an extensive lagoonal system of patch reefs. In 2016, the northern Great Barrier Reef (including Lizard Island) was subject to extreme temperature stress, with peak daily sea surface temperatures reaching 32.8 °C in February 2016, and a high thermal load of >8 degree heating weeks (°C-weeks) by April 2016, triggering mass coral bleaching (Hughes et al. 2017b).

Benthic and fish assemblages were surveyed at 16 sites on the leeward side of Lizard Island seven months before, during and approximately six months after the bleaching event, in September 2015, April 2016, and October 2016 respectively. Sites were randomly selected in September 2015 within the following constraints: there was >250 m x 5 m of contiguous reef, adjacent sites were separated by >500 m, and were protected from prevailing south-east swell with comparable water clarity and geomorphology.

Assessment of benthic and fish assemblages

Benthic and fish assemblages were surveyed along six replicate 30 m transects at each site, positioned on shallow (<6 m) reef edges and parallel to the reef–sand interface in each time-period. Transect position was initially random in September 2015, and the starting position of individual transects were subsequently identified visually within the same approximate area (within 1–2 m) by the same surveyors (LR and JE) for the following survey periods.

The point-intercept method was used to quantify benthic composition and coral bleaching extent, recording the substrate immediately below the transect tape at 25 cm intervals (120 points per transect). Substratum categories were hard (scleractinian) and soft (alcyonacean) corals recorded to genus (or species where possible) and growth form, 'other sessile invertebrates' (primarily sponges, giant clams, and ascidians), macroalgae, erect crustose coralline algae, 'dead substrate' (dead coral and pavement), rubble, and sand. The extent of coral bleaching (recorded in April and October 2016) was estimated on live coral tissue that lay beneath the survey points. A 6-point colour saturation scale based on the CoralWatch colour reference card was used *in situ* to minimise subjective assessment of bleaching state (Siebeck et al. 2006). Coral tissue with saturation score of 1–2 was considered bleached and 3—6 unbleached to provide an estimate of the percent cover of bleached coral along each transect. No explicit account was made of bleaching variation within coral colonies.

The species identity, abundance, and body-size (total length; TL, to the nearest cm) of all non-cryptic fishes were recorded on transects. Larger, more mobile species (>10 cm TL) were counted as transects were laid in a 5 m wide belt, and smaller fishes (≤10 cm) were surveyed in a 1 m belt on the return pass. All fish surveys were conducted by a single observer (JE) and the fish abundances standardised per 150 m^2. Fish species were classified into functional entities according to six ecological and morphological species traits: diet, mean observed body-size (TL; 10 cm size categories), social grouping, mobility within/between reefs, time when active, and position in the water column (following Mouillot et al. 2013a) (Appendix C Table S1). Body-size was estimated with the mean observed sizes of each species in the September 2015 and October 2016 surveys, unless species were observed only in April 2016 whereby mean size was estimated for that period only.

Data analysis

Benthic composition

Pre-bleaching variation in benthic composition among sites was visualized with non-metric Multidimensional Scaling (nMDS) based on a Bray-Curtis similarity matrix of square root transformed transect level data. Groupings identified with nMDS were tested using a two-way nested PERMANOVA (maximum permutations = 9999), using habitat grouping (fixed) and site (random) as factors. One-way unrestricted permutations of raw data was used for pairwise comparisons between habitats to allow testing of sufficient permutations, followed by percentage similarity analysis (SIMPER) to identify substratum categories consistently contributing to mean similarity within or dissimilarity between habitats (with similarity/dissimilarity test ratio of >4.0 or 2.0 respectively, Clarke and Warwick 2001; Appendix C Table S2). The percentage of total coral cover (hard and soft coral) that bleached was compared among habitats using linear mixed-effects analyses (with lme in *nlme*; R Development Core Team 2016), using habitat as a fixed effect and site as a random effect. Changes in total percentage coral cover (hard and soft coral) among habitats following the bleaching event were assessed with habitat and period (and their interaction) as fixed effects and site (random effect). *Post hoc* multiple comparison Tukey tests were used to identify where differences occurred.

Fish assemblage structure

Trait-based functional diversity was calculated by constructing a principal coordinates analysis (PCoA) of species pairs based on trait combinations and a Gower distance matrix, with a square root correction for negative eigenvectors (Legendre and Legendre 1998). Four synthetic PCoA axes summarizing species distribution within functional trait space were then combined with species abundances to calculate three complementary indices of functional diversity for each transect in all periods: functional richness, functional dispersion, and functional originality (Mouillot et al. 2013b, Maire et al. 2015). Functional richness is calculated as the proportional convex hull volume occupied by a species assemblage in multidimensional functional space (PCoA), and represents the range of unique trait combinations. Functional dispersion measures the abundance-weighted deviation of species traits in an assemblage from the centroid of all species in functional space, and reflects the assemblage spread, or variability, of species traits (Laliberté and Legendre 2010). Functional originality is calculated as the mean pairwise distance between species in an assemblage where greater mean distance infers greater functional originality and isolation of species in functional space. Functional richness and functional dispersion provide presence-absence and abundance-weighted facets of functional diversity respectively, whilst functional originality indicates how changes in species abundances modify the functional redundancy among species (Mouillot et al. 2013b). Variation in the functional structure of fish assemblages through time was assessed using community-weighted transect means (CWM) of assemblages in each habitat before, during and after bleaching, measured using the four PCoA axes combined with species abundance values.

Linear mixed-effects models were used to assess variation in the structure of fish assemblages in two distinct analyses, both (i) within each habitat across time-periods, and (ii) among habitats within each time-period. First, within-habitat variation in fish assemblage structure over time was assessed using habitat type, time-period, and their interaction fitted as fixed effects, site as a random effect, and planned comparisons used *post hoc* to identify where changes occurred. Second, among-habitat variation in assemblage structure was assessed in each time-period using habitat (fixed effect), site (random effect), and Tukey multiple comparisons *post hoc* to identify where differences occurred (with *multcomp*). Count data models of fish species richness and total fish abundance were fit with Poisson, and negative binomial distributions respectively, to accommodate non-stable variances and alternative exponential residual distributions (with glmer in *lme4*). Continuous measures of fish functional richness, functional dispersion, functional originality, and the CWM values for all four PCoA axes were normally distributed and were fitted with a Gaussian residual structure (with lme in *nlme*). Functional originality was fitted with a constant variance structure to allow for existing heterogeneity of variance. Inter-habitat variation in the taxonomic composition of fish assemblages was tested using two-way nested PERMANOVAs for each period (maximum permutations = 9999) on square root transformed data, with habitat (fixed factor) and site (random factor). Due to limited available permutations, Monte Carlo sampling was used to estimate *post hoc* pairwise comparisons (Anderson and Robinson 2003).

The relative influence of coral loss on variation in fish species richness, total abundance, functional richness, functional dispersion and functional originality was estimated using mixed effects multiple linear regression (total coral cover %, time-period, habitat, and period-habitat interaction as fixed effects, and site as a random effect). Information-theoretic model selection based on AICc ranking (ΔAICc values <2) was used to quantify model uncertainty and the relative importance of each explanatory variable (all predictors had Spearman's correlation coefficients <0.4 and variance inflation factors, GVIF^(1/(2**df*)) <3) (Burnham and Anderson 2002). Models within ΔAICc <2 with the fewest degrees of freedom were considered the most parsimonious.

Exploratory graphical analyses of residuals were used to confirm that assumptions of homogeneity of variance, normality, and independence were met for all linear regression modelling, and generalised mixed effects models fit with Poisson or negative binomial distributions were tested for overdispersion. Multivariate analyses of benthic composition were performed in Primer v6 with +PERMANOVA add on package (Clarke and Warwick 2001). All other analyses were performed in

R (R Development Core Team 2016), and the packages *ape*, *cluster*, *geometry*, *polycor*, *rcdd*, *vegan*, and the function *FDchange* in *FD*.

4.4 Results

Benthic composition

Analyses of benthic composition across the 16 study sites revealed six major habitat groupings characterised by a disproportionate cover (25–58% of the total benthos) of (i) *Porites cylindrica* (hereafter branching *Porites*), (ii) massive *Porites* (mostly *Porites lutea*), (iii) *Pocillopora damicornis* (hereafter *Pocillopora*), (iv) soft coral, (v) mixed coral assemblages, and (vi) dead coral and macroalgae (<10% live coral cover, hereafter referred to as low coral cover) (Appendix C Fig. S1; PERMANOVA: Pseudo-F = 8.09, P = 0.0001, all pairwise comparisons $P \leq 0.0002$; Appendix C Table S2 and S3). Four of the six broad habitat groupings were represented by three sites, while massive *Porites* and *Pocillopora* habitats were represented by two and one site(s), respectively. Prior to the bleaching event, total coral cover (hard and soft coral) was similar among surveyed coral habitats (mean ± SE: 50.4 ± 3.6), which all had significantly greater cover of live coral than low coral cover habitats (Tukey, all $P < 0.002$). Coral bleaching was widespread across surveyed sites in April 2016 affecting 51% of total coral cover (31 out of 36 coral taxa; Appendix C Table S4), and did not vary significantly among habitats (percentage bleached of total coral cover; all pairwise comparisons, $P > 0.05$) (Table 4.1). However, coral mortality following the bleaching event varied among taxa (primarily affecting soft coral, branching *Porites* and *Acropora*; Appendix C Fig. S2), causing significant declines in coral cover by October 2016 in just three habitats: soft coral (31%), mixed coral (18%), and branching *Porites* (15%) habitats (Table 4.2; Fig. 4.1; Appendix C Table S5). Coral cover remained higher in all coral habitats relative to the low coral cover habitat in October 2016 (Tukey, all $P < 0.01$).

Table 4.1 Mean ± SE percent cover of benthic composition and coral bleaching extent within habitats from September 2015 to October 2016.

Habitat	September 2015	April 2016			October 2016	Change in coral cover (Sept. 2015–Oct. 2016)
	Total coral cover	Total bleached coral cover	Percent bleached of total coral cover	Percent bleached of dominant coral taxa	Total coral cover	
Branching *Porites*	57.13 ± 2.79	21.81 ± 1.80	43.73 ± 2.92	45.86 ± 4.39	42.08 ± 2.30	-15.01 ± 3.39
Low coral cover	10.46 ± 1.80	7.04 ± 0.96	59.80 ± 4.74	-	14.63 ± 1.87	4.12 ± 3.39
Massive *Porites*	49.37 ± 2.81	23.82 ± 1.55	47.61 ± 4.06	46.96 ± 4.58	46.60 ± 3.19	-2.78 ± 4.15
Mixed coral	46.63 ± 3.07	15.03 ± 1.65	45.72 ± 4.18	-	29.03 ± 2.43	-17.88 ± 3.05
Pocillopora	39.31 ± 6.01	25.69 ± 1.73	56.68 ± 4.64	57.86 ± 4.58	35.83 ± 3.41	-3.47 ± 5.87
Soft coral	59.49 ± 1.93	27.27 ± 2.32	67.15 ± 3.23	67.95 ± 3.58	28.56 ± 2.65	-30.93 ± 3.39

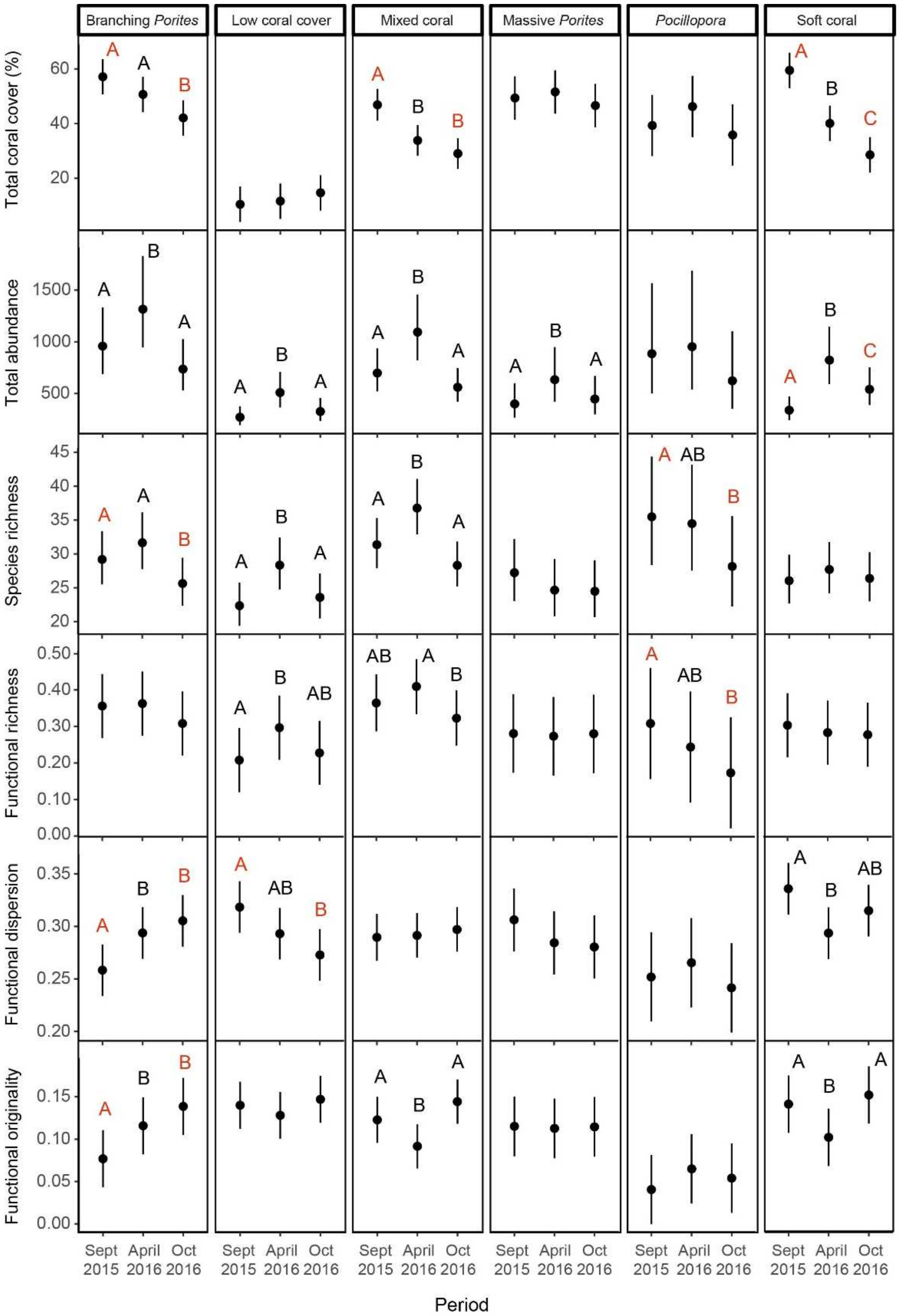

Fig. 4.1 Within-habitat variation (fitted values ± 95% confidence intervals) in total coral cover (%), fish species richness, total fish abundance, fish functional richness, functional dispersion, and functional originality over survey periods. Contrasting letters indicate significant planned comparisons within habitats over time (red letters highlight differences between September 2015 and October 2016).

Due to differential coral loss, coral cover varied among coral habitats following the bleaching, with cover in mixed coral, and soft coral habitats significantly lower than branching- and massive- *Porites* habitats, and *Pocillopora* habitat remaining intermediate (Tukey, all $P < 0.02$).

Fish assemblage structure

The four PCoA axes cumulatively explained 56.8% of the projected inertia in the distribution of fish species traits (Fig. 4.2 and 4.3). Generally, fish body-size and mobility increased along PCoA 1 and 2, with diet groupings positioned along those gradients, ranging from small-bodied site attached farming species through to larger, more mobile, piscivorous fish species (Fig. 4.2). Nocturnally active, schooling planktivores occupied the left of PCoA1, and browsers were positioned in the centre of PCoA 1 and 2. Generally, species clustered more closely on PCoA 3 and 4. However, PCoA 4 separated excavating (PCoA3 left), farming (PCoA3 centre), and mixed diet feeding species (PCoA3 right), from all other species (Fig. 4.2).

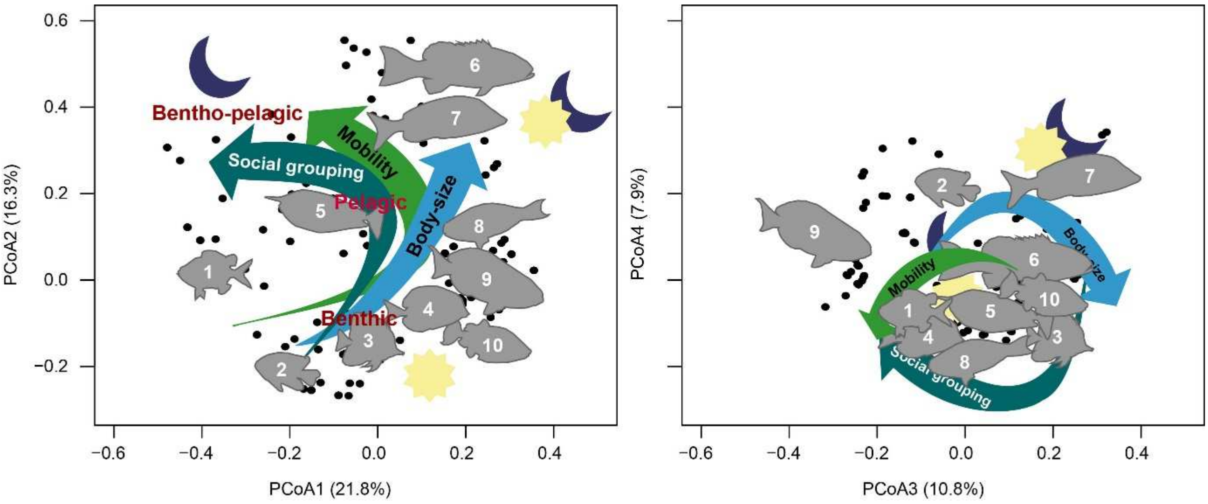

Fig. 4.2 Trait-based principal coordinates analysis of surveyed fish in functional space. Two hundred and seventeen surveyed fish species (black dots) plotted four dimensions of functional space defined by six traits: mean observed body-size (blue arrow indicating increasing size); diet (fish symbols: 1, planktivore; 2, farmer; 3, corallivore; 4, grazer/detritivore; 5, browser; 6, piscivore; 7, mixed diet; 8, scraper; 9, excavator; 10, invertivore); mobility (green arrow indicating increasing mobility); social grouping (dark blue arrow indicating gradient from solitary fishes to large schools); time of activity (sun and/or moon); and position in the water column (red text). Illustrations show the average position of traits in the functional space.

Analysis of within-habitat variation in fish assemblage structure revealed changes in taxonomic (species richness and total abundance) and functional (functional richness, dispersion, and originality) characteristics in response to the bleaching event (Fig. 4.1 and 4.3). However, the nature of these changes varied among habitats (Table 4.2; Fig. 4.1; Appendix C Table S5 and S6). Between September 2015 and October 2016, fish species richness declined in branching *Porites* and *Pocillopora* habitats; total fish abundance increased in soft coral habitats; functional richness declined in *Pocillopora* habitat; functional dispersion increased in branching *Porites* habitats, and decreased in low coral cover habitats; and functional originality increased in branching *Porites* habitats (Fig. 4.1 and 4.3).

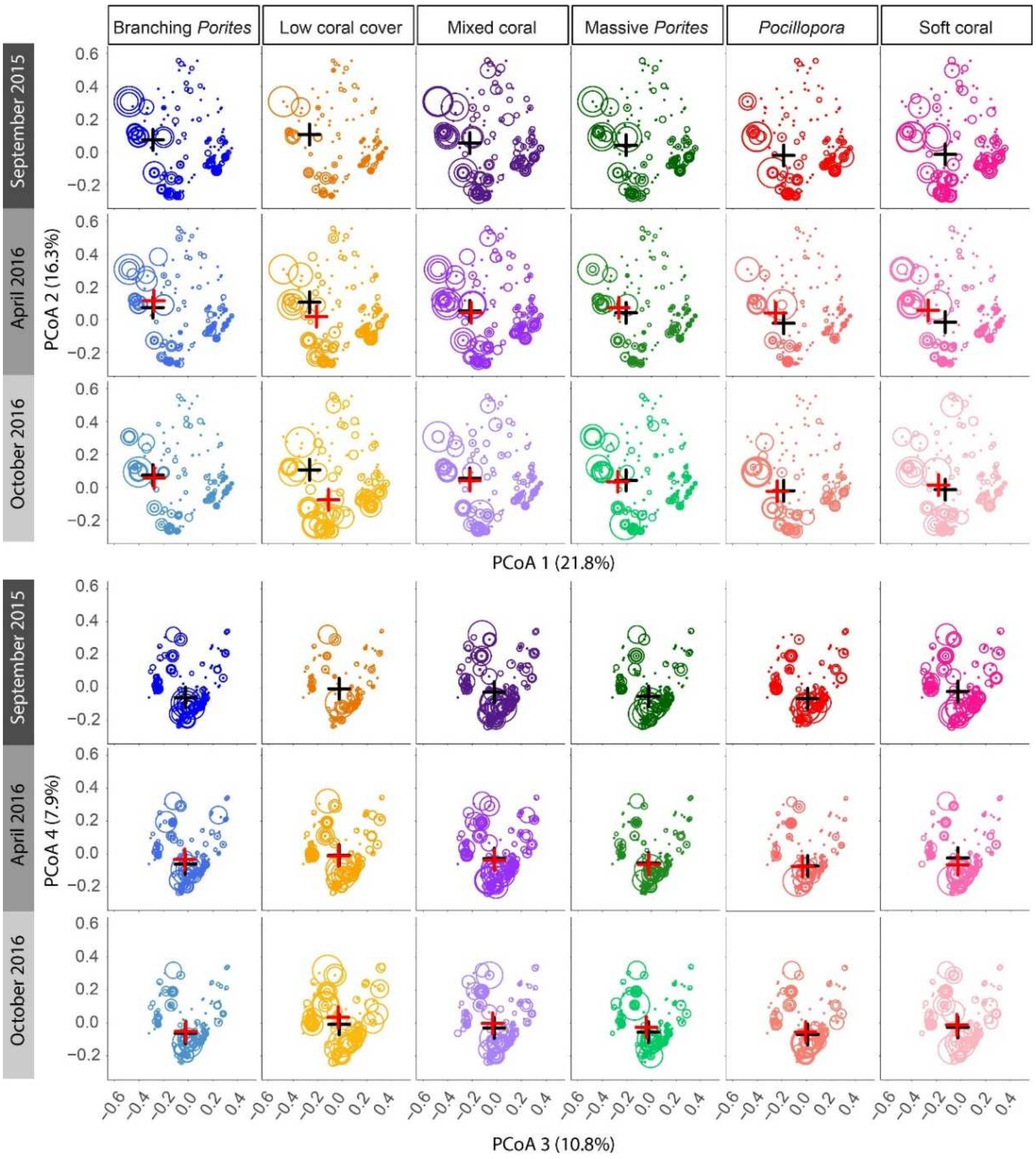

Fig. 4.3 Principal coordinates analyses (PCoA) of fish assemblage functional structure in habitats in each period, showing the first two (top: PCoA 1 and 2), and second two (bottom: PCoA 3 and 4), dimensions of functional trait space. Circle sizes are proportional to species mean relative abundances. Crosses mark community weighted mean centroids in each period (black: September 2015; red: April 2016, or October 2016).

Table 4.2 Significant planned comparisons (contrast effect size and 95% confidence intervals; CI) of within-habitat variation in total coral cover and fish assemblage responses between September 2015 and October 2016 among habitats.

Response	Habitat	Period contrast	Lower CI	Upper CI	Test stat	*df*	*P*
Total coral cover	Branching *Porites*	-15.049	-21.725	-8.373	-4.44	265	<0.001
	Mixed coral	-17.875	-23.882	-11.867	-5.86	265	<0.001
	Soft coral	-30.927	-37.603	-24.251	-9.12	265	<0.001
Fish species richness	Branching *Porites*	0.879	0.775	0.996	-2.03	266	0.04
	Pocillopora	0.793	0.648	0.972	-2.25	266	0.02
Total fish abundance	Soft coral	1.597	1.210	2.108	3.32	265	<0.001
Functional richness	*Pocillopora*	-0.135	-0.255	-0.015	-2.22	265	0.03
Functional dispersion	Branching *Porites*	0.047	0.018	0.077	3.14	265	0.002
	Low coral cover	-0.046	-0.075	-0.016	-3.04	265	0.003
Functional originality	Branching *Porites*	0.062	0.024	0.099	3.24	260	0.001

These changes caused an increased overall similarity in the taxonomic and functional diversity of fish assemblages across distinct habitat types. Analysis of among habitat variation in fish assemblage structure over time revealed that prior to the bleaching event there was significant variation in species richness, total fish abundance, fish functional dispersion, and functional originality, with habitat type accounting for 14–39% of the variation in these indices (not including fish abundance). Eight months after the bleaching event, however, this variation was almost entirely lost, with habitat type accounting for just 8–17%) of the variation in those measures (Table 4.3; Fig. 4.4). There was also an increased similarity in the taxonomic and functional composition of fish assemblages after the bleaching event. The number of pairwise differences in taxonomic composition among habitats declined from 7 in September 2015, to 5 in April 2016, and just 4 by October 2016 (PERMANOVAs: September 2015: Pseudo-$F = 2.42$, $df = 5$, $P = 0.0001$, all pairwise comparisons $P < 0.05$; April 2016: Pseudo-$F = 2.02$, $df = 5$, $P = 0.001$, all pairwise comparisons $P < 0.05$; October 2016: Pseudo-$F = 1.94$, $df = 5$, $P = 0.001$, all pairwise comparisons $P < 0.03$). Similarly, the number of pairwise differences in functional composition indicated by CWMs across the four PCoA axes declined from 11 in September 2015, to two in April 2016, and 4 by October 2016 (Table 4.4). Changes in CWM for PCoA axes 1 and 2 indicated no changes in dominant traits across habitats though time. However, CWM values on PCoA 3 and 4 exhibited significant directional shifts overall between September 2015 and October 2016, indicated by black (September 2015) and red (October 2016) centroid cross markers, towards small-bodied habitat generalist algae-farming species (Table 4.4; Fig. 4.2 and 4.3).

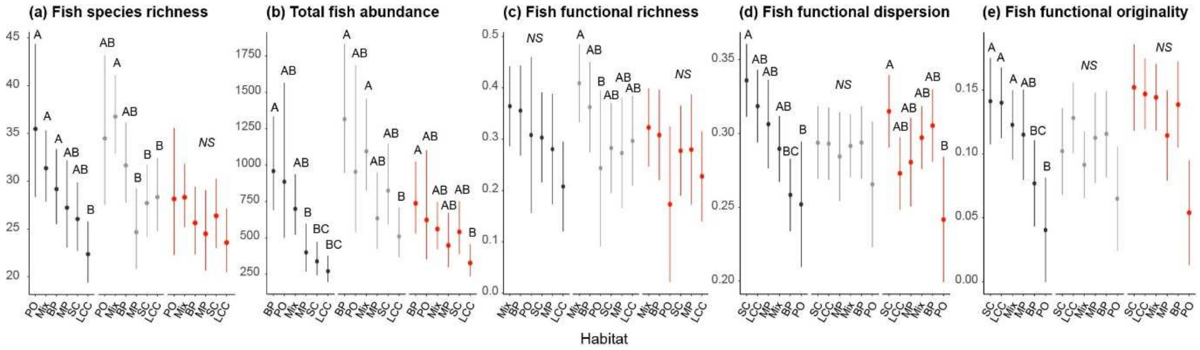
(a) Fish species richness (b) Total fish abundance (c) Fish functional richness (d) Fish functional dispersion (e) Fish functional originality

Fig. 4.4 Among-habitat variation in fish assemblage structure within each time-period (fitted values ± 95% confidence intervals): September 2015 (black); April 2016 (grey), and; October 2016 (red). Different letters illustrate significant differences among habitats within each period revealed by linear mixed effects models (habitat as fixed effect) and Tukey pairwise comparisons *post hoc* (P <0.05). Habitats: BP, branching *Porites;* LCC, low coral cover; Mix, mixed coral; MP, massive *Porites*; PO, *Pocillopora*; and SC, soft coral.

Table 4.3 Components of variation for mixed effects models of fish assemblage structure among habitats in each survey period and Tukey multiple comparisons (number of among-habitat differences in brackets shown in bold). Habitats: BP, branching *Porites*; LCC, low coral cover; Mix, mixed coral; MP, massive *Porites*; PO, *Pocillopora*; SC, soft coral.

Fish response metric	Period	R^2 fixed (habitat)	R^2 random (site)	R^2 residuals (transects)	Habitat differences (P <0.05)
Species richness	Sept-15	0.28	0.11	0.61	**(3)** LCC ≠ BP, Mix, PO
	April-16	0.32	0.13	0.55	**(3)** Mix ≠ LCC, MP, SC
	Oct-16	0.08	0.22	0.69	**(0)**
Total fish abundance †	Sept-15				**(7)** BP ≠ LCC, MP, SC; Mix, PO ≠ LCC, SC
	April-16				**(2)** BP, Mix ≠ LCC
	Oct-16				**(1)** BP ≠ LCC
Functional richness	Sept-15	0.14	0.31	0.55	**(0)**
	April-16	0.23	0.13	0.64	**(1)** SC ≠ Mix
	Oct-16	0.10	0.26	0.64	**(0)**
Functional dispersion	Sept-15	0.33	0.10	0.57	**(3)** BP ≠ LCC, SC; SC ≠ PO
	April-16	0.02	0.09	0.89	**(0)**
	Oct-16	0.14	0.02	0.84	**(1)** SC ≠ PO
Functional originality	Sept-15	0.39	0.03	0.59	**(7)** BP, PO ≠ LCC, Mix, SC; PO ≠ MP
	April-16	0.04	0.05	0.91	**(0)**
	Oct-16	0.15	0.24	0.60	**(0)**

† R^2 estimations not available for generalized linear mixed models with negative binomial distribution.

Table 4.4 Variation in community abundance-weighted means on each PCoA axes indicating change in the functional structure of fish assemblages through time, and differences among habitats (Tukey, P <0.05). The number of inter-habitat differences within each period are shown for each axis. Habitats: BP, branching *Porites*; LCC, low coral cover; Mix, mixed coral; MP, massive *Porites*; PO, *Pocillopora*; SC, soft coral.

PCoA axis	PCoA axis inertia explained (%)	Change (Sept 2015 – Oct 2016)	Overall habitat differences	Habitat differences (P <0.05)		
				Sept 2015	April 2016	Oct 2016
PCoA 1	21.8	No	BP ≠ LCC, Mix, SC	2	0	2
PCoA 2	16.3	No	BP ≠ LCC, Mix	0	2	1
PCoA 3	10.8	Yes	PO ≠ LCC	5	0	1
PCoA 4	7.9	Yes	n/a	4	0	0

Changes in fish assemblage structure across habitats between September 2015 and October 2016 were largely unrelated to levels of coral loss (Table 4.2; Fig. 4.1; Appendix C Table S5). For example, in the three habitats that experienced significant coral loss, there were either no detected changes in fish assemblages (mixed coral); total abundance increased (soft coral); or species richness declined, and functional dispersion and functional originality increased (branching *Porites*) (Fig. 4.1; Appendix C Table S6). Additionally, species- and functional richness declined in *Pocillopora* habitat, and fish functional dispersion increased in low coral cover habitats despite no change in coral cover (Table 4.2; Fig. 4.1). Analyses of the relative influence of coral loss on variation in all five measures of fish assemblage structure revealed total coral cover in all top candidate multiple linear regression models. However it was not the best predictor of variation in any metric (species richness, total abundance, functional richness, functional dispersion and functional originality) relative to the influence of time-period or habitat type (or their interaction; Appendix C Table S7).

4.5 Discussion

This study of the impacts of mass coral bleaching on coral reef fish assemblage structure across six taxonomically distinct reef habitats revealed three key findings. First, I show that bleaching disturbance increased the taxonomic and functional similarity of fish assemblage structure due to species turnover among previously differentiated fish assemblages (i.e., biotic homogenization). Second, I found that despite limited change in taxonomic or functional richness across all habitats, the functional originality of fish assemblages increased. This is potentially important because it suggests that there was a net loss of functional redundancy at the system level. Third, I found that pre-bleaching coral species composition was a better predictor of changes in fish assemblage structure, than absolute coral loss. These results emphasize how measures of alpha diversity (taxonomic or functional richness) can mask important changes in ecosystems as assemblages reorganize with implications for ecosystem function. The findings also highlight the important but poorly understood role of coral species composition in structuring communities and influencing cross-scale resilience to system-wide disturbance due to the response diversity of corals and reef fishes.

The system-wide biotic homogenization among previously differentiated reef fish assemblages was evident by the increased similarity in the taxonomic and functional composition of fish assemblages following the bleaching event. Prior habitat-related differences in fish species richness, total abundance, functional dispersion, functional originality, and the taxonomic and functional composition of fish assemblages was largely lost after the bleaching event, despite no change in the taxonomic or functional richness across all surveyed reefs (local alpha diversity). Biotic homogenization is increasingly considered a central component of the broader biodiversity crisis (McKinney and Lockwood 1999, Olden et al. 2004, McGill et al. 2015). Whilst disturbance-mediated loss of species has occurred across ecosystems (Olden et al. 2004, Butchart et al. 2010), meta-analyses show no systematic loss of species richness, rather a loss of beta diversity, suggestive of increasing biotic homogenization at a global scale (Dornelas et al. 2014). Biotic homogenization has been documented across several groups including temperate marine fishes (Magurran et al. 2015), freshwater fishes (Villéger et al. 2014), birds (Cassey et al. 2007), and plants (Schwartz et al. 2006, Rooney 2009). I add to these studies with evidence of a high diversity coral reef ecosystem response to climatic disturbance, showing that isolated measures of α diversity (i.e. richness) can conceal important spatial beta diversity trends, such that the presence of species does not capture the rapid reorganisation of assemblages (Magurran et al. 2015, McGill et al. 2015).

The consequences of biotic homogenization are not yet well understood (Olden et al. 2004). However, trait-based functional approaches are increasingly used to provide insight into ecological changes that may influence the functional stability of ecosystems (Mouillot et al. 2013b, Graham et al. 2015). I observed an increased similarity of functional dispersion (trait variability), functional originality (trait uniqueness), and functional composition of reef fish assemblages following the bleaching event. Furthermore, I found subtle but significant directional shifts in dominant fish traits across habitats towards algae-farming, small-bodied habitat generalists, causing an increased homogenization of trait space. These findings are consistent with reports of functional homogenization occurring across scales and ecosystems (Devictor et al. 2007, Abadie et al. 2011, Pool and Olden 2012, Villéger et al. 2014). The susceptibility of a species to extirpation is typically non-random, and related to organism traits such as body-size, diet, fecundity, growth-rate, habitat specialisation, social grouping and abundance (McKinney 1997, Graham et al. 2011). As predicted by niche theory (Hutchinson 1957), building evidence suggests that global changes are causing worldwide declines of specialist species which have effectively been replaced by generalists thereby increasing functional similarity at the community level (Clavel et al. 2011). Indeed, severe coral bleaching events tend to favour larger-bodied, habitat generalists at the expense of obligate coral feeders and small-bodied fishes reliant on live coral habitat structure (Wilson et al. 2006, Pratchett et al. 2011b). However, trait vulnerability to bleaching events can vary with the rate and extent that coral tissue mortality also leads to the loss of the physical coral structures (Wilson et al. 2006). Within the current study, coral tissue mortality caused a loss of soft coral colony structures (as previously reported by Ferrari 2017), but not of hard corals whose carbonate colony structures remained largely intact by October 2016. Experimental evidence suggests that soft coral exerts little direct influence on reef fish assemblages (Syms and Jones 2001). Therefore, shifts in dominant traits from habitat specialists to generalists appear likely to result from the loss of coral tissue rather than habitat structural complexity.

Together with taxonomic and functional homogenization, I detected an increase in functional originality at the system level, inferring overall loss of functional redundancy of fish assemblages following coral bleaching, and providing further evidence of non-random trait filtering. The increase in functional originality was largely driven by changes in species composition in branching *Porites* habitats, where live coral tissue was lost though colony structures remained intact. Within this habitat fishes with a strong preference for live branching coral (e.g. small-bodied, site-attached, schooling planktivores), were replaced by a range of other functional entities including algae-farming, habitat generalists. As habitat disturbance reduces the abundance of functionally similar species, the number of species contributing to any one function (i.e., functional redundancy) may decline as remaining species become relatively more functionally unique (Walker 1992, Reich et al. 2012). I found that trait-filtering of habitat specialists likely reduced the competitive exclusion of other functional entities, facilitating habitat use by a range of other groups and reducing functional redundancy at the community level (Macarthur and Levins 1967). I provide clear data showing that whilst functional richness remained consistent across the bleaching event, the turnover of fish species altered the distribution of traits in specific habitats. However, changes were poorly predicted by the loss of coral at the system level.

Interestingly, pre-bleaching coral species composition was a better predictor of changes in fish assemblage structure following the bleaching event than the specific level of coral loss within each habitat type. Whilst substantial coral loss typically incurs concurrent declines in the species richness and total abundance of reef fishes after bleaching (>20% total cover and reduction in absolute cover below 10%; Wilson et al. 2006), I show that observed changes in fish assemblage structure (including species richness and total abundance) were variable among habitats and inconsistent with changes in coral cover. For example, the greatest changes in fish assemblage structure occurred in branching *Porites* habitats that lost 15% coral cover. However, in mixed and soft coral habitats that experienced greater coral loss (18% and 31%, respectively), fish assemblage structure only changed in soft coral habitats (the only habitat where the physical coral structures were also lost) where total fish abundance increased. Further, changes in fish assemblage structure were evident in habitats where significant coral loss was not detected (e.g. reduced taxonomic and functional richness in *Pocillopora* habitat). With widespread coral bleaching across habitats, these results illustrate the differential susceptibility of distinct reef fish assemblages, governed primarily by the vulnerability of particular fish traits associated with specific coral configurations. Coral habitats provide a range of niche spaces for the coexistence of diverse but functionally unbalanced fish assemblages (Mouillot et al. 2014, Brandl et al. 2016, **Chapter 2**). Some provide particular niche habitat to specialist guilds of fishes (**Chapter 3**), such that relatively small habitat disturbance may incur disproportionate change in fish assemblage structure. Indeed, I found that fish assemblages in branching coral habitats (branching *Porites* and *Pocillopora*) were most negatively impacted by the bleaching event, despite differential coral loss. Conversely, coral reefs with high or diverse initial coral cover that incur coral loss may have limited effects on fish populations if the availability of required habitat remains sufficient (e.g. corallivores, Pratchett et al. 2006), such as in mixed coral habitats in the study.

These results provide some insight into the underlying dynamics of coral bleaching on reef fish assemblages, and highlight the role of coral species composition in determining the susceptibility of assemblage structure to disturbance. However, further examination of coral habitats across locations, particularly reefs characterised by dominant though thermally sensitive *Acropora*, and environmental gradients such as depth would enable better understanding of how shifts in coral species composition may affect changes in fish assemblage structure at a broader scale. Furthermore, these results only provide a snapshot of a highly dynamic system, influenced by seasonal biological processes such as recruitment, and complex ecological interactions between species and their environment, and therefore caution is recommended for applying these findings to longer-term predictions. It is unknown if the observed functional trait shifts constitute a temporary phase in the reassembly of coral reefs directly following acute bleaching disturbance, or if shifts will be sustained (Bellwood et al. 2012). Similarly, lag-responses to bleaching events have been observed in corals (e.g. disease, Bruno et al. 2007, Miller et al. 2009), and populations of coral reef fishes where the delayed erosion of dead coral structures has caused substantial declines in smaller size-classes of reef fish (Wilson et al. 2006, Graham et al. 2007). There is much uncertainty about how distinct and emerging configurations of species will respond to ongoing disturbances and how important ecosystem processes will be maintained (Graham et al. 2014a). A great deal more research is needed in this area to understand reef dynamics in the Anthropocene, so to guide viable and pragmatic management approaches (Norström et al. 2016). Finally, whilst trait-based estimations of ecological diversity provide a useful tool for assessing the functional trajectory of disturbed ecosystems, I acknowledge that they remain coarse approximations based on our current understanding of species' roles that do not likely capture finer-scale, nuanced niche partitioning (McGill et al. 2006).

Climate induced mass coral bleaching often devastates coral reef ecosystems, threatening the livelihoods of people that rely upon the ecosystem services that reefs provide (Moberg and Folke 1999, Norström et al. 2016). As global temperatures rise, new governance challenges are faced by managers as non-random species shifts transform reef assemblages into novel configurations of species (Graham et al. 2014a), with unknown implications for their capacity to maintain key ecosystem functions (Norström et al. 2016, Hughes et al. 2017a). Comparing the impacts of bleaching on reef fish assemblage structure across distinct reef habitats provided some insight into the variable responses of both corals and fishes to thermal stress, and highlighted the potential homogenization of fish assemblages across scales. Biotic homogenization is increasingly considered one of the most pressing, but largely unrecognized, biodiversity crises faced globally (Dornelas et al. 2014, Magurran et al. 2015, McGill et al. 2015). The results underscore the importance of coral species composition in determining ecological organisation and the susceptibility of reef ecosystems to disturbance. As species shifts persist, the suitability of coral reef management and the value of different coral dominated states will likely hinge upon the capacity of those ecosystems to maintain key ecological processes with ongoing disturbance.

Chapter 5

Differential response of key ecosystem processes to coral composition

5.1 Abstract

Herbivory is a critical process, mediating plant-coral interactions on coral reefs and facilitating ecosystem recovery following disturbance. As ongoing climate change and local stressors change coral species composition and threaten further coral loss, the capacity of these altered coral configurations to support viable herbivore populations and maintain herbivory functions will be central to ecosystem stability. However, relationships between coral species composition and herbivory is not well understood. This study examines the relationships between coral and fish species composition and key herbivory processes using in situ surveys and algal assays to compare grazing and browsing among three taxonomically distinct coral habitats: branching *Porites*, soft coral, and mixed coral assemblages. Results show browsing on the red macroalga *Laurencia* cf. *obtusa* varied among habitats, and was best predicted by differential benthic composition and condition, and poorly reflected by visual estimates of herbivore biomass. However, contrary to expectations, the lowest removal of *L*. cf. *obtusa* occurred in the branching *Porites* habitat. This habitat had the greatest cover of coral and was the most structurally complex of the three habitats examined. The low browsing in this habitat may be related to scale-dependent effects of habitat structure inhibiting foraging activity. Conversely, grazing on turf assays was evident across habitats, but there was no detectable differences among habitats. These differential responses of grazing and browsing among habitats suggest that different mechanisms are shaping these two key processes. The results carry sobering implications for the stability of distinct reef species assemblages where inherent habitat characteristics may restrict the control of algal succession and growth following coral loss, thereby threatening functional collapse.

5.2 Introduction

Climate change is rapidly deteriorating ecosystems via species extirpations and introductions, modifying the composition of assemblages and threatening ecological function and resilience (Olden et al. 2004, Gross and Cardinale 2005, Dornelas et al. 2014). Non-random species turnover, ordered by the susceptibility of organism traits such as body-size, extent of diet or habitat specialisation, and physiology (McKinney 1997), are increasing the taxonomic and functional similarity of communities (Clavel et al. 2011, McGill et al. 2015), altering habitats (Ellison et al. 2005, Alvarez-Filip et al. 2013) and the distribution, and size structure of associated organisms (Thrush et al. 2006, Nash et al. 2013). Across a range of ecosystems, such changes disrupt ecological functions such as habitat provisioning (Ellison et al. 2005, Alvarez-Filip et al. 2013), primary productivity (Tilman et al. 1997, Yvon-Durocher and Allen 2012), nitrogen cycling (Hooper and Vitousek 1997), detrital decomposition (Dossena et al. 2012), pollination (Larsen et al. 2005), and trophic energy flow (Hempson et al. 2018). However, relationships between community structure, ecosystem function, and disturbance dynamics can be complex, and confounded by environmental change (Loreau et al. 2001, Nagelkerken and Munday 2016, Goldenberg et al. 2018). Whilst ample evidence exposes a coherent pattern of ecological change across biomes, ecosystem changes are occurring across substantial environmental and biological gradients, and communities at opposite ends of these gradients can generate different biological responses (Walther et al. 2002). Our current understanding of the relationships between species composition and ecosystem function is largely based on evidence from terrestrial or freshwater systems, such as grasslands, desserts, temperate forests, and river systems that are typically characterised by relatively low biodiversity (though see Alvarez-Filip et al. 2013, Hempson et al. 2017, Goldenberg et al. 2018). However, some of the most biodiverse systems, such as coral reefs, are also the most threatened (Hughes et al. 2018). With community shifts in on coral reefs increasingly reported and predicted to persist (Pandolfi et al. 2011, Hughes et al. 2017b), there is growing concern for how they will function (Purvis and Hector 2000, Mumby 2017, Hughes et al. 2018).

On coral reefs, climate change has reduced populations of habitat-building corals, resulting in unprecedented coral loss and marked shifts in coral species composition due to differential susceptibilities of coral taxa to thermal stress, large tropical storms, altered ocean chemistry, and local water quality (Fabricius 2005, Fabricius et al. 2011, Hughes et al. 2017b). As a result, non-random shifts towards more stress-tolerant and/or weedy coral taxa are reported, with erect branching corals (e.g. *Acropora*) often being replaced by more robust and prostrate corals (e.g. *Porites*) (Marshall and Baird 2000, Loya et al. 2001, Aronson et al. 2004, Alvarez-Filip et al. 2011b, Johns et al. 2014). These altered configurations are likely to become more dominant into the future (Riegl and Purkis 2009, Pandolfi et al. 2011, Darling et al. 2013), however, there is substantial uncertainty regarding the ecological integrity of these often simplified coral configurations (Graham et al. 2014a, Hughes et al.

2017a). Coral species composition has been shown to underscore the structural complexity of reef habitats (Alvarez-Filip et al. 2011b, Chapter 2), exert considerable influence over the taxonomic and functional structure of associated reef fish communities (Alvarez-Filip et al. 2011c, Messmer et al. 2011, Chapter 3), and mediate the susceptibility of reef species assemblages to disturbance (Richardson et al. 2018: **Chapter 4**). Critically, the resilience of altered reef species configurations will hinge upon their capacity to support critical ecosystem functions such as herbivory in the wake of further disturbance (Bellwood et al. 2004, Hughes et al. 2007, Cheal et al. 2010, Graham et al. 2015).

Herbivory promotes coral dominance by removing algae from the benthos thereby mediating competitive interactions with corals (Burkepile and Hay 2008), and facilitating the recovery of disturbed coral reefs by mitigating shifts to macroalgal dominance following coral loss (Hughes et al. 2007). However, herbivory processes are diverse (Bellwood et al. 2004), and can be highly variable across spatial scales (e.g. Cvitanovic and Bellwood 2009, Hoey and Bellwood 2010a). Rates of herbivory vary among regions (e.g. Hay et al. 1983, Hixon and Brostoff 1996, Hughes et al. 2007, Chong-Seng et al. 2014), latitudes (Bennett and Bellwood 2011), distance across the continental shelf (Hoey and Bellwood 2010b), and among distinct reef zones (Fox and Bellwood 2007, Hoey and Bellwood 2010a). Importantly, herbivory rates also vary within reef zones (Cvitanovic and Bellwood 2009, Cvitanovic and Hoey 2010), with studies relating this variation to differences in structural complexity (Hay et al. 1983, McClanahan 1999), the cover of live coral (i.e. reef condition) (Nash et al. 2012, Chong-Seng et al. 2014), the relative palatability of resident algal communities (Hoey and Bellwood 2010b, Rasher et al. 2013), predation pressure or competition for resources (Francini-Filho et al. 2009, Vergés et al. 2011), and management status (Rasher et al. 2013, Nash et al. 2016). However, the extent to which the composition of coral species assemblages explicitly influences herbivory processes is unknown, restricting our understanding of how shifts in coral species dominance may compromise reef functionality and ecosystem stability.

As ocean warming continues and threatens further coral loss, the need to understand the extent to which different configurations of corals maintain populations of herbivorous fishes and support fundamental processes of herbivory for avoiding phase-shifts from coral to macroalgal dominance is paramount for the management and optimisation of coral reef integrity. To this end, this chapter compares two critical and functionally distinct herbivory processes (grazing and browsing) among taxonomically distinct coral habitats. Grazing herbivores closely crop algal turfs, sediment, detritus and invertebrates on coral reefs, facilitating settlement, growth and survival of corals and coralline algae, and preventing algal growth, community succession, and phase shifts (Bellwood et al. 2004). Browsing herbivores remove mature macroalgae, reducing coral overgrowth and shading by macroalgae, and have the potential to reverse a phase shift (Bellwood 2004, Hughes et al. 2007) . Specifically, using *in situ* surveys and algal assays I compare: i) the structure of nominally herbivorous fish assemblages across six functional groups due to potential dietary flexibility or behavioural plasticity (*sensu* Bellwood et al. 2006b), and the limitation of precise, context-specific functional designations for all species (Edwards et al. 2014); and ii) directly quantify grazing of algal turfs and macroalgal browsing across three replicated habitats characterised by the predominance of distinct coral taxa, and assess the relative influence of coral species composition, coral cover, and the biomass of nominal herbivore groups on these two herbivory functions.

5.3 Materials and methods

Study sites

This study was conducted in April and May 2016 on leeward reefs surrounding Lizard Island, in the northern Great Barrier Reef (14°41′S, 145°27′E). Three replicate sites of three distinct coral communities were selected on shallow (<6 m) reefs, based on surveys completed in September 2015 (**Chapter 2**). The three coral communities were characterised by predominant cover of: i) branching *Porites* (mostly *P. cylindrica*); ii) soft coral (mostly *Lobophyton*, *Sarcophyton*, and *Sinularia*); and iii) mixed coral assemblages. The study coincided with a large-scale pantropical coral-bleaching event that impacted reefs at Lizard Island (Hughes et al. 2017b). Six months prior to the bleaching, there was no significant variation in total coral cover (hard and soft corals) among the three habitats (Fig. 4.1A; **Chapter 4**). At each site, I quantified benthic and fish assemblages, the consumption of algal turfs, and a common macroalga. All sites (each >250 m x 5 m) were protected from the prevailing south-east swell, had comparable geomorphology and water clarity, and were separated by >500 m.

Benthic composition and herbivore assemblage structure

Benthic composition was quantified along six 30 m point-intercept transects at each site, recording the substratum immediately under the transect tape every 25 cm (120 points per transect). Transects were positioned approximately 2.5 m from, and parallel to, the reef-sand interface. Substratum categories were hard (scleractinian) corals identified to genus (or species where possible) and morphology, soft (alcyonacean) corals identified to genus, ‘other sessile invertebrates’ (mainly clams, sponges, and ascidians), macroalgae, ‘dead substrata’ (dead coral and pavement), rubble, and sand. For corals that were directly under surveyed points, the extent of bleaching was assessed *in situ* using the CoralWatch colour reference card. The colour saturation of coral tissue was estimated on a 6-point scale, where 1-2 was considered ‘bleached’ (Siebeck et al. 2006).

The abundance and total length (TL; nearest cm) of all non-cryptic nominally herbivorous fishes (i.e. Acanthuridae, Kyphosidae, Pomacanthidae, Scarinae, Siganidae, Pomacentridae) were visually censored along the same six 30-m transects used to quantify benthic assemblages. Fishes >10 cm TL were recorded within a 5 m wide belt while initially deploying the transect tape to minimise disturbance to fish assemblages, and those ≥10 cm TL were recorded within a 1 m wide belt on the return swim. Fish abundance estimates were standardised per 150 m^2 and converted to biomass (kg ha^{-1}) using published species' length-weight relationships (Appendix D Table S1). To allow comparisons of the functional composition of herbivore assemblages among habitats, all surveyed species were categorised into six groups (i.e., macroalgal browsers, grazers/detritivores, scrapers, excavators, farmers, and omnivorous herbivores) based on their diet and feeding behaviour (Appendix D Table S1).

Algal consumption

To quantify rates of grazing on algal turfs among habitats, I exposed six terracotta tiles (10 x 10 x 1 cm) with established turf algal communities to resident herbivore assemblages at each site for seven days. To establish turf algal communities the tiles they were deployed at a single shallow reef site (~2 m depth) at Lizard Island, covered in a large plastic mesh (5 cm square mesh) to exclude feeding by large herbivorous fishes, but allow for continuous cropping by small grazing herbivores, and left *in situ* for six months. After this period, all tiles were collected, and eight or nine haphazardly selected tiles were deployed at each site by securing to individual cement pavers with a galvanized steel nut and bolt through the centre of the tile. The pavers were placed on horizontal surfaces that were free of live coral. Six tiles were exposed to herbivores at each site with >10 m between adjacent tiles. To determine if observed changes in turf height were due to herbivory, the remaining two (or three) tiles were placed inside freestanding herbivore exclusion cages (approximately 300 x 300 x 300 mm; 12 mm^2 steel mesh) at each site. Exclusion cages were cleaned of fouling organisms (mostly algae) every 2-3 days. The initial height of the turf algal community was quantified at nine uniformly spaced points *in situ* using callipers (to the nearest mm) across the upper surface of the tile immediately after deployment (mean ± SE = 4.89 mm ± 0.13; no significant variation among habitats, lme, $F_{2,6} = 1.14$, $P = 0.38$), and again after seven days.

To quantify macroalgal browsing among habitats, assays of the red macroalga *Laurencia* cf. *obtusa* were used. *L.* cf. *obtusa* was selected as it was the most common macroalga on reefs surrounding Lizard Island at the time of the study, and is known to be consumed by herbivorous reef fishes on the Great Barrier Reef (Mantyka and Bellwood 2007, Fox et al 2009, Loffler et al. 2015). Thalli of *L.* cf. *obtusa* were collected by hand from a shallow reef flat on the southern aspect of the island and placed in a large (6000 l) aquarium with flow-through seawater within 30 min of collection. Whole thalli of similar size were selected, spun in a salad spinner for 30 s to remove excess water, and the wet weight recorded (to the nearest 0.1 g). The initial mass (mean ± SE) of each assay was 45.4 ± 1.0 g. Six haphazardly selected assays were transplanted to each site between 0930 and 1030 hrs, with three assays exposed to resident herbivores and three assays placed within adjacent herbivore exclusion cages (300 x 300 x 300 mm) for 24 hr. Each caged assay was positioned approximately 2m from its paired exposed assay, and adjacent assay pairs were separated by a minimum of 10 m. Assays were deployed by wrapping a short (<10 cm) length of PVC coated wire (2 mm diameter) around the base of the thallus and attaching to a small lead weight. A numbered, small plastic tag placed adjacent to the assay was used to identify individual replicates. After 24 hr, assays were collected, spun and weighed as described previously. This procedure was replicated on three non-consecutive days at each site (total $n = 9$ exposed per site).

To identify herbivorous fish species responsible for removing *L.* cf. *obtusa* biomass, small stationary underwater video cameras (GoPro) were used to record feeding activity on up to three (mean = 2.2 assays) haphazardly selected assays at each site on each day. Each camera was attached to a dive weight (2 kg) and positioned approximately 1 m away from each assay, with a scale bar temporarily placed adjacent to each filmed assay at the start of filming to allow calibration of fish sizes on the video footage. Filming commenced immediately after assays were deployed and was continuous for 2.2-4.4 hr (the variable duration was due to differences in battery life among cameras). This procedure was replicated on each day of the experiment (3 days per site), resulting in 20.5 ± 1.7 hr (mean ± SE) of video observations for each site (189 h in total). The body-size (TL) and number of bites taken from the *L.* cf. *obtusa* by each species on the video footage was recorded. To account for variation in fish body-size on the amount of algal mass removed per bite a mass-standardised bite impact was calculated as the product of the number of bites and the estimated body mass for each individual (following Hoey and Bellwood 2009). Bite impact was then standardised per hour to account for varying video recording lengths (mass-standardised bites.hr^{-1}).

Data analysis

Benthic composition and herbivore assemblage structure

Variation in the total cover of hard and soft coral, bleached coral (hard and soft), macroalgae, and dead coral and algae among habitats was analysed with linear mixed effects models in *nlme* (fixed factor: habitat, random factor: site), with Tukey's pairwise multiple comparisons *post hoc* to identify significant differences (in *multcomp*).

Variation in the taxonomic and functional composition of herbivorous fish assemblages among habitats was assessed with two-factor nested PERMANOVAs (9999 permutations) on biomass (kg ha^{-1}; log transformed) data. Each analysis used factors habitat (fixed) and site (random nested in habitat), and Monte Carlo estimated pairwise comparisons. Variation in total biomass (kg ha^{-1}; log transformed) of all herbivores and each herbivore functional group among habitats was assessed using linear mixed effects models fitted with Gaussian residual structures (with lme in *nlme*; fixed factor: habitat, random factor: site). Variation in herbivore species richness and total abundance was assessed with generalised mixed models, with Poisson and negative binomial distributions respectively, to accommodate non-stable variances and alternative exponential residual distributions (with glmer in *lme4*). Tukey's pairwise multiple comparisons were used to identify significant differences among habitats (in *multcomp*).

Algal consumption

Linear mixed effects models were used to analyse variation in the reduction in height of algal turfs, and reduction in biomass of *L.* cf. *obtusa* assays among habitats with a Gaussian residual structure (with lme in *nlme*). Models included habitat, treatment (two levels: exposed and caged-control), and their interaction as fixed effects, and site, and day of deployment (*L.* cf. *obtusa* weight change only) as random effects. A generalised mixed effects model with a gamma distribution and log-link function was used to assess variation in rates of removal of *L.* cf. *obtusa* (total mass-standardised bites.h^{-1}) due to exponential residual distribution, fitted with habitat (fixed), site, and day of deployment (both random). Multiple linear regression and information-theoretic model selection was used to assess the relative influence of centred site-mean environmental variables on the change in exposed assays (assay loss) where significant differences were found among habitats (Legendre and Legendre 1998): the first axis of a principal components analysis of benthic composition (accounting for 61.7% variation in benthic composition, distinguishing transects according to habitat type benthic composition), the percent cover of dead coral and algae, and the biomass of nominal herbivore functional groups considered responsible for removal, i.e. grazers or browsers. Total coral cover was not included as it was collinear with the cover of dead coral and algae. All variables had variance inflation factors <2, and multi-model inference (including null models) was estimated by ranked changes in AICc <2.

For those fish species that were observed to account for >5% of total bites, variation in feeding rates (from video observations; log transformed mass-standardised bites.hr^{-1}) and biomass (from visual surveys) were compared among habitats using linear mixed effects models with lme in *nlme* (fixed effect: habitat; random effects: site and day).

All model assumptions were validated with visual assessment of diagnostic plots of Pearson residuals. Where variance was heterogeneous among habitats, models were fitted with a constant covariance structure in *nlme* (i.e. logged biomass of grazers/detritivores, farmers and omnivorous herbivores, logged biomass of *Naso brevirostris*; and mass-standardised bites by *Naso vlamingii* and *Siganus doliatus*; change in macroalgal weight; total macroalgae cover; total cover of bleached coral; total hard and soft coral cover). All analyses were performed in R (R Core Team 2016), and Primer v6 with PERMANOVA+ package (Clarke and Warwick 2001).

5.4 Results

Benthic composition and herbivore assemblage structure

Total coral cover was significantly higher (and the cover of dead coral and algae was lower) in branching *Porites* habitats than mixed coral habitats (confidence intervals, CI: -27.48 | -5.67, and 3.09 | 31.36 respectively) and intermediate in soft coral habitats (Fig.1A; Appendix D Table S2). There was no significant variation in the total cover of bleached coral or the cover of macroalgae among habitats (Fig. 5.1A; Appendix D Table S2).

The taxonomic composition of herbivore fish assemblages differed among habitats, with herbivore assemblages within branching *Porites* habitats being characterised by a diversity of species including *Acanthurus blochii*, *Chlorurus microrhinos*, *Neoglyphidodon nigroris*, *Pomacentrus grammorhynchus, Stegastes nigricans*, *Scarus niger*, and *Scarus rivulatus*, while those in soft coral habitats were characterised by *Ctenochaetus striatus* and *P. chrysurus* (PERMANOVA, Pseudo-F = 2.47, df = 2, 53, P = 0.004, unique permutations = 280; pairwise test, P (MC) = 0.004). Herbivore species richness and total herbivore biomass (kg ha^{-1}) were significantly greater in mixed coral habitats than soft coral habitats (Fig. 5.1B and C; Appendix D Table S2). The total abundance of herbivores was greater in mixed coral habitats than in branching *Porites*, and soft coral habitats (Appendix D Table S2). There were no significant differences among habitats in the biomass of individual functional groups, except for omnivorous herbivores which was significantly higher in mixed coral, and branching *Porites* habitats than soft coral habitats (Appendix D Table S3).

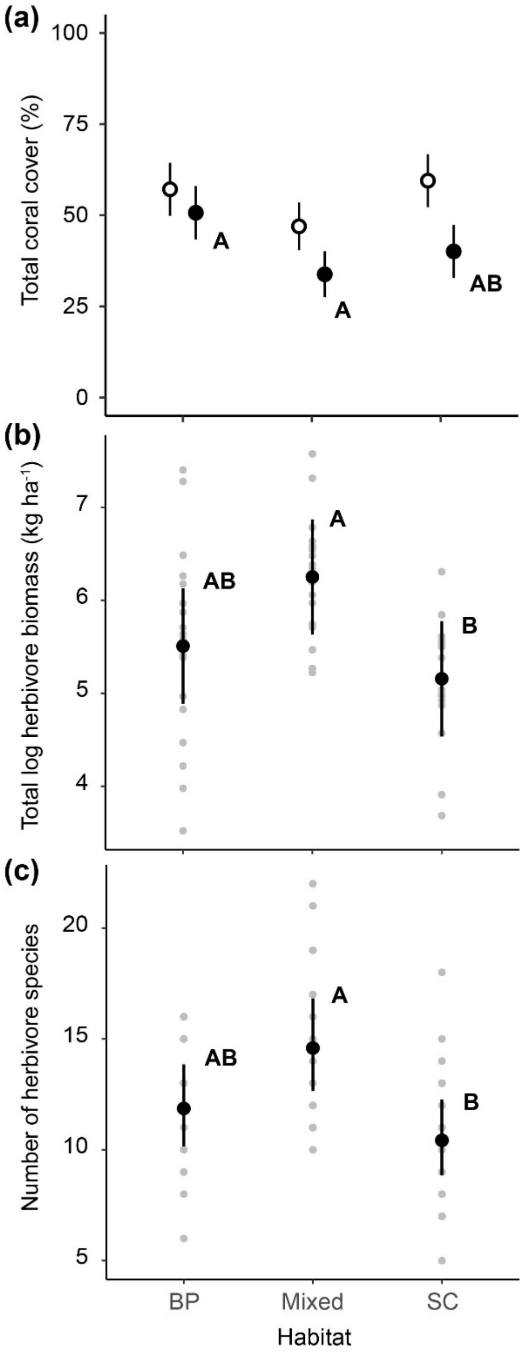

Fig. 5.1 Among habitat variation (fitted values ± 95% confidence intervals) in, (a) total coral cover (%, hard and soft coral) in September 2015 (white; **Chapter 4**), and April 2016 (black); (b) total herbivore biomass (log transformed, kg ha^{-1}); and (c) number of herbivore species. Partial residuals of linear mixed effects models shown in grey. Contrasting letters indicate significant differences among habitats (Tukey, $P < 0.05$). Habitats: BP, branching *Porites*; Mixed, mixed coral; SC, soft coral.

Algal consumption

The reduction in turf height on both exposed and caged tiles differed among habitats, however the difference between caged and exposed tiles was consistent among habitats (CI: 0.21 | 1.38; Fig. 5.2A; Appendix D Table S4). The change in turf height of both caged- and exposed turf assays combined in branching *Porites* habitats was significantly greater than those combined in soft coral habitats (CI: 0.73 | 3.50; Fig. 5.2A).

The reduction in *L.* cf. *obtusa* biomass was greater for exposed than caged assays in mixed coral and soft coral habitats, but not in branching *Porites* habitats where the change in weight of assays expose to local herbivore assemblages did not differ significantly to caged assays (Fig. 5.2B; Appendix D Table S4). Model selection of variables that explained the reduction in mass of *L.* cf. *obtusa* assays yielded three models within ΔAICc <2 of the top model (Table 5.1). The most parsimonious included the cover of dead coral and algae (relative importance: 1.00) and first axis of the principal component of benthic composition among habitats (PC1; relative importance: 0.43), and was 1.1 times more plausible than the second ranked model (Table 5.1). Across all three top models, dead coral and algae had a significant (CI: 0.07 | 0.99) and positive effect on assay weight change, whilst neither PC1 (CI: -1.76 | 0.29), nor browser biomass (CI: -0.16 | 0.05) had a significant effect (Table 5.1).

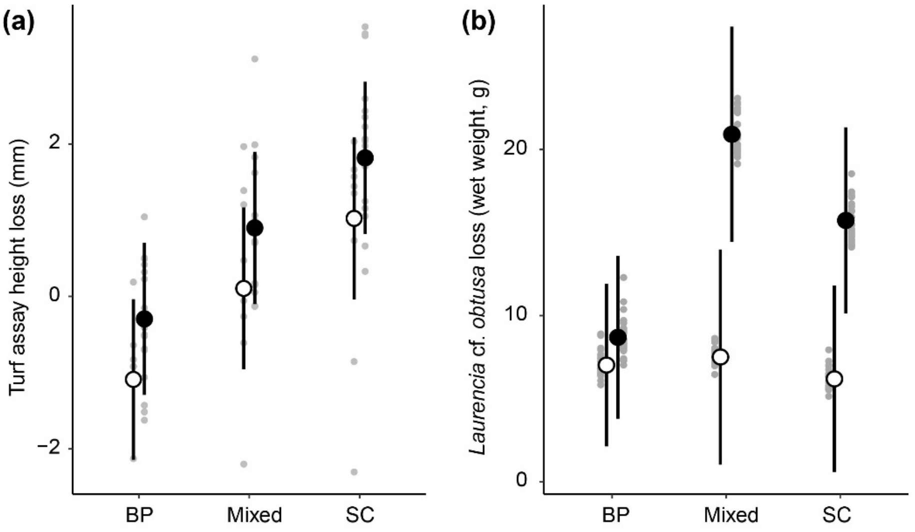

Fig. 5.2 Among-habitat variation (fitted values ± 95% confidence intervals) in assay loss of: (A) turf algae (mean turf height (mm); and B) *L.* cf. *obtusa* (wet weight, g). Caged assays (white), exposed assays (black). Partial residuals of linear mixed effects models shown in grey. Habitats: BP, branching *Porites*; Mixed, mixed coral; SC, soft coral.

Feeding on *L.* cf. *obtusa* assays was significantly lower in the branching *Porites* habitat than soft coral habitat, and intermediate in the mixed coral habitat (CI: 2.34 | 1242.43; Fig. 5.3; Appendix D Table S4). Analysis of video footage revealed 35 species of reef fishes were recorded taking bites from exposed assays across all habitats, with four species accounting for 96% of total mass-standardised: *Naso brevirostris* (69%), *Siganus doliatus* (13%), *N. vlamingii* (9%), and *Pomacanthus sexstriatus* (6%). Feeding by these species was similar in mixed coral, and soft coral habitats, but only *P. sexstriatus* was recorded feeding in branching *Porites* habitats. Estimated biomass of these four species from UVC transects poorly reflected observed feeding activity (Fig. 5.3; Appendix D Table S4).

Table 5.1 Top candidate multiple linear regression models for predicting loss of *Laurencia* cf. *obtusa* wet weight (g) with centred, site-mean environmental variables. Models are ranked by Akaike's information criteria (AICc), with all models within ΔAICc <2 of the top ranked model. The relative weight of evidence for each model is indicated by Akaike weight (wAICc), and the variables present in each model are indicated with an X. The relative importance of each variable based on the sum of Akaike weights of the models in which the variable is present, and parameter estimates ± standard errors and confidence intervals are provided.

Model rank	AICc	*df*	logLik	ΔAICc	wAICc	Dead coral and algae (%)	Benthic composition (PC1)	Browsers (kg ha^{-1})
1	651.56	8	-316.78	0.00	0.43	X	X	
2	651.83	7	-318.15	0.28	0.38	X		
3	653.22	8	-317.61	1.67	0.19	X		X
Model average estimate						0.53 ± 0.20	-0.32 ± 0.46	-0.01 ± 0.04
Confidence intervals (2.5% | 97.5%)						0.07 | 0.99	-1.75 | 0.29	-0.16 | 0.05
Relative importance						1.00	0.43	0.19

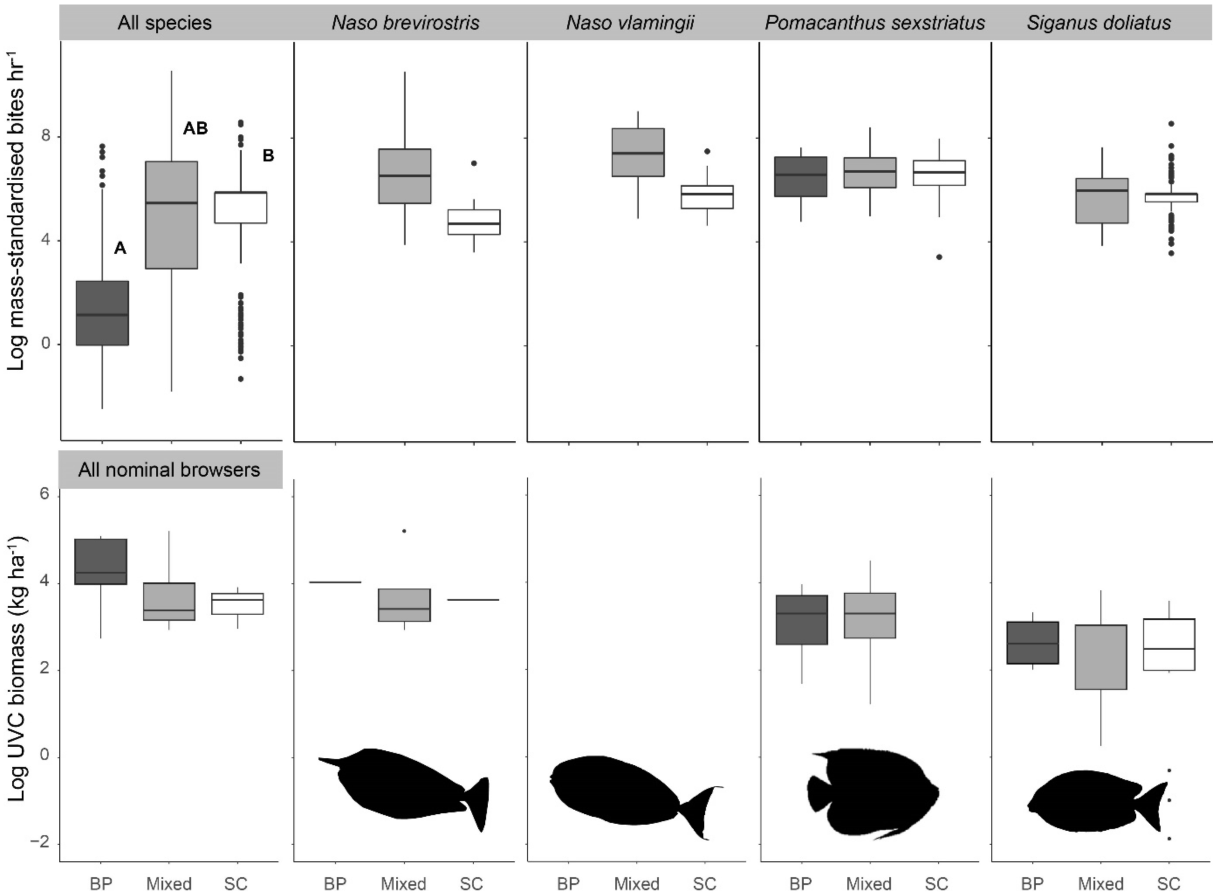

Fig. 5.3 Among-habitat variation in: videoed feeding rates on *Laurencia* cf. *obtusa* assays (top row) by all species and those species responsible for >95%; and visual biomass estimates (bottom row) of all nominal browsing herbivores, and those species accounting for >95% assay removal. Contrasting letters indicate significant differences among habitats (Tukey, *P* <0.05). Habitats: BP, branching *Porites*; Mixed, mixed coral; SC, soft coral.

5.5 Discussion

Climate change is transforming the composition of corals on tropical reefs globally (Pandolfi et al. 2011, Hughes et al. *in press*), with consequent shifts in the composition of organisms that rely on corals for food and/or shelter (Berumen and Pratchett 2006, Wilson et al. 2006, Bellwood et al. 2012). However, the extent to which changes in habitat-building coral communities impact associated organisms and the functions they provide is largely unknown. Comparing the composition of herbivorous assemblages and two critical herbivory functions among taxonomically distinct coral habitats, we show that the taxonomic, but not functional, composition of herbivorous fish assemblages and rates of browsing, but not grazing, differed among coral habitats. The rate of browsing on the red macroalga *Laurencia* cf. *obtusa* was greatest in soft coral and mixed coral habitats, and lowest in branching *Porites* habitats. These differences in the consumption of *Laurencia* were best predicted by variation in benthic composition and condition, with the highest rates of removal in habitats with the lowest coral cover. Interestingly, rates of browsing on *Laurencia* were poorly predicted by visual estimates of the biomass of browsing fishes or all herbivorous fishes collectively. Analysis of video footage revealed that four species (*Naso brevirostris*, *Siganus doliatus*, *N. vlamingii*, and *Pomacanthus sexstriatus*) accounted for >95% of browsing on *Laurencia*, with among habitat differences in bite rates due to an absence of feeding by three of the four species (all except *P. sexstriatus*) in the branching *Porites* habitat. In contrast to rates of browsing, grazing on algal turfs did not differ among habitats, suggesting that different mechanisms may be driving browsing and grazing processes on coral reefs.

Observed differences in rates of browsing among habitats were best predicted by the cover and composition of benthic communities, indicating that particular habitat characteristics may influence foraging behaviour and/or habitat selection by herbivorous reef fishes. Although rarely tested explicitly, differences in the composition and cover of coral communities may have contributed to reported variation in the abundance, biomass or composition of herbivorous coral reef fishes (e.g. latitude: Floeter et al. 2005, continental shelf: Hoey and Bellwood 2008, reef zones: Fox and Bellwood 2007), and rates of herbivory across a range of spatial scales (latitude: Bennett and Bellwood 2011, continental shelf: Hoey and Bellwood 2010b, sites: Cvitanovic and Bellwood 2009, reef zones: Vergés et al. 2011). Of the few studies that have related benthic composition to rates of herbivory, most have used broad taxonomic categories, comparing total coral and/or macroalgal cover to rates of herbivory, and have shown that rates of removal of brown macroalga *Sargassum* spp. are positively related to coral cover (Hoey and Bellwood 2010a, Chong-Seng et al. 2014). Further, Cvitanovic and Hoey (2010) reported that browsing on two species of *Sargassum* on inshore reefs of the Great Barrier Reef were related to benthic composition, with browsing rates being positively correlated to the cover of plating corals and hypothesised this may be related to the structural complexity of the habitat. In contrast, we found that browsing on *Laurencia* was greatest in habitats with lower coral cover and lower structural complexity. Despite the branching *Porites* habitat being the most structurally complex across a range of scales (**Chapter 2**), having the highest coral cover, and comparable biomass of herbivorous fishes of the three habitats examined, no significant reduction in *Laurencia* biomass was detected over a 24 hr period. The negative relationship between reef condition and browsing rates may be related to reduced levels of visual occlusion and hence greater risks in structurally complex habitats (Rilov et al. 2007, Nash et al. 2016), the relative availability of alternate algal resources (Francini-Filho et al. 2009, Cvitanovic and Hoey 2010), or differences in foraging behaviours among habitats (Nash et al. 2012).

The cover of live coral and structural complexity of reef habitats are generally viewed as having positive effects on the abundance, biomass, and diversity of herbivorous fish communities (Friedlander and Parrish 1998, Graham and Nash 2013). Indeed, it has long been recognised that the intensity of herbivory is positively related to the proximity to structurally complex habitat patches (Randall 1961, Ogden et al. 1973). However, recent studies have shown that at particular scales, the physical topography of structurally complex habitats can inhibit access to, and hence consumption of algal resources at fine scales (i.e. between coral branches, Bennett et al. 2010), and can alter the foraging behaviour of fishes by reducing their visual fields and thereby enhancing perceived predation risk (Rilov et al. 2007, Nash et al. 2016). Indeed, several studies have reported higher feeding rates by coral reef fishes in areas of lower structural and topographic complexity (Beukers and Jones 1998, Hoey and Bellwood 2011, Fox 2018). Such findings reflect patterns of habitat use in some terrestrial systems where grazing herbivores favour open grasslands over woodlands due to the enhanced ability to detect approaching predators and initiate an escape response (Riginos and Grace 2008). Interestingly, of the four main species recorded feeding on the *Laurencia* assays, only *Pomacanthus sexstriatus* was recorded feeding within the structurally complex branching *Porites* habitat, despite two of the other species (*N. brevirostris* and *S. doliatus*) being recorded in visual surveys of that habitat. *P. sexstriatus* was the largest-bodied species observed (mean biomass ± SE: 670 g ± 77; other species mean biomass 195-539 g), potentially reducing predation risk and enabling less discriminant foraging activity (Wainwright and Richard 1995, Goatley and Bellwood 2016).

The availability of dietary (i.e. algal) resources may also influence foraging patterns and rates of herbivory among habitats (Francini-Filho et al. 2009, Cvitanovic and Hoey 2010). By foraging in areas where resources are more available, fishes likely benefit from lower energetic costs of movement between outcrops or patches of algae (MacArthur and Pianka 1966, Wilson et al. 2012), and reduced risk of predation associated with longer travel distances between forays (Holbrook and Schmitt 1988). However, negative relationships between local macroalgal cover and rates of macroalgal browsing using assays have been reported in studies encompassing broad ranges (ca. 0–50%) of macroalgal cover (Fox and Bellwood 2008, Hoey and Bellwood 2010b, Chong-Seng et al. 2014, Bauman et al. 2017, Bonaldo et al. 2017), that has been suggested to be related to the dilution of herbivore feeding across abundant resources (Hoey and Bellwood 2010b, Vergés et al. 2011), or the avoidance of areas of dense macroalgae (Hoey and Bellwood 2011). However, relationships between macroalgal cover and rates of browsing are not evident over smaller ranges in macroalgal cover (e.g. Hoey and Bellwood 2010a), such as those in the present study (mean cover: 0.3–1.4%). Further, increases in the cover of algae (predominately turf algal communities) following large-scale coral mortality and the subsequent increases in the abundance and/or biomass of herbivorous fishes (e.g. Adam et al. 2011, Gilmour et al. 2013), has led to suggestions that herbivorous fish populations may be food limited, especially in areas of high coral cover (Mumby and Steneck 2008). A severe bleaching event approximately one month prior to this study caused considerable coral mortality and increased availability in the cover of algal turfs (Fig. 5.1A; **Chapter 4**) at our study sites (between 52.4–71.4% cover of dead coral and algae), however there was no significant variation in the biomass of any herbivore feeding guilds among habitats (the only exception being a greater biomass of omnivores in branching *Porites* and mixed coral habitats than soft coral habitat).

Visual estimates of browser biomass featured in the top three models of reductions in *Laurencia* biomass, however it was a poor predictor of browsing rates. Further, visual census estimates of the biomass of the four species observed to be primarily responsible for consuming the *Laurencia* assays (*N. brevirostris*, *N. vlamingii*, *P. sexstriatus*, and *S. doliatus*), were poor predictors of browsing rates. For example, *N. vlamingii* was not recorded in the visual surveys across all habitats, but accounted for 9% and 8% of bites in the mixed coral and soft coral habitats. This is consistent with previous studies using assays of the brown macroalgae *Sargassum* spp. where visual estimates of herbivorous fishes show little relation to their functional impact, with the density of species either underestimated or not recorded during visual surveys (Fox and Bellwood 2008, Cvitanovic and Bellwood 2009, Hoey and Bellwood 2009, Chong-Seng et al. 2014). These discrepancies may reflect high mobility and opportunistic foraging behaviour of roving herbivores (Fox and Bellwood 2014, Welsh and Bellwood 2014), particularly across habitats with relatively high coral cover (34-51%) and low cover of naturally occurring macroalgal resources (<2%) (Chong-Seng et al. 2014), or the diver-negative behaviours of some fishes (Gotanda et al. 2009). The accuracy of visual estimates of browsing herbivores as a proxy for macroalgal removal may be further hindered by the plasticity and opportunistic nature of diets among herbivorous fishes (Choat et al. 2002, Chong-Seng et al. 2014), and a potential bias in the classification of browsers towards those known to feed on large brown macroalgae versus those that consume other fleshy macroalgae (Mantyka and Bellwood 2007, Puk et al. 2016).

In contrast to browsing, there were no detectable differences in grazing on the algal turf assays among distinct coral habitats. Although there were among habitat differences in the height of the algal turfs on both tiles exposed to, and excluded from (i.e. caged) local herbivorous fish assemblages, the differences between caged and exposed tiles was consistent among habitats. This lack of among habitat variation in grazing rates may be related to the high diversity of fishes that feed on algal-turf covered substrata (Bellwood et al. 2004), and the diversity of their responses to changes in benthic composition (Pratchett et al. 2011b). For example, feeding rates and foraging behaviours (inter-foray distances, foraging ranges) of individual grazing coral reef fish species have been shown to vary with the condition and structure of reef habitats, however the responses tend to be species specific (Nash et al. 2012). Similarly, changes in the abundance of grazing fishes following large reductions in coral cover and concomitant increases in algal cover are highly variable, with some species increasing and others decreasing in abundance (Wilson et al. 2006, Pratchett et al. 2011b). The among-habitat variation in the changes in the turf height on caged tiles was interesting and may be related to differences in algal productivity and/or grazing by small invertebrates (Lobel 1980, Russ 1987).

Similarly, the negative values of turf height loss for both caged and exposed assays in branching *Porites* habitats may be due to high algal productivity in that habitat, and warrants further investigation. Interestingly, while grazing activity was not reflected by variation in total herbivore biomass, or herbivore species richness among habitats, it was reflected by the estimated biomass of nominal grazing herbivores which was also comparable among habitats, suggesting that there may be different mechanisms may be driving browsing and grazing processes on the studied reefs.
Our results provide new empirical evidence of the variable influence of benthic composition on two key functions on coral reefs: grazing and browsing. While the use of a single macroalga, *L.* cf. *obtusa*, has provided valuable information on the variable browsing behaviour among habitats, macroalgal browsing selectivity can vary among fish species (Mantyka and Bellwood 2007, Loffler et al. 2015). Therefore, further investigation with other commonly occurring macroalgal species may offer insight into behavioural variation among habitats of a broader suite of herbivore species. Similarly, we focus on shallow, sheltered reefs to investigate the influence of coral species composition on herbivory processes. However, coral morphology and community composition, the distribution of herbivores, and herbivory processes can vary with depth, exposure, and reef zonation (Russ 1984, Fox and Bellwood 2007, Todd 2008, Bejarano et al. 2017). Therefore, further study across environmental gradients and reef zones is now needed. Our study coincided with a large-scale thermal bleaching event (Hughes et al. 2017b) that resulted in rapid coral loss and changes in reef fish assemblage structure among our study sites (**Chapter 4**), and likely affected the foraging behaviour of a range of reef fish species including herbivores (Lewis 1998, Adam et al. 2011, Nagelkerken and Munday 2016). Although the present study provides insights into how herbivory processes can vary with coral species composition, disturbance dynamics are complex (Nyström et al. 2000, Wilson et al. 2006) and it is likely that fish assemblages are in transition, and in the process of reassembling following large declines in coral cover. Further research into the spatial variation in foraging behaviour and impact of individual herbivores, and temporal variation following disturbance is needed to better understand how changing reef configurations influence critical ecological functions (Nagelkerken and Munday 2016, Goldenberg et al. 2018).

Increasingly, large-scale disturbances are resulting in unprecedented net loss of corals, increases in algae and shifts in the community composition and function of coral reef ecosystems (Alvarez-Filip et al. 2013, Hughes et al. 2017b). Whether herbivores can compensate for this increased algal production in the wake of ongoing disturbances, and maintain critical rates of algal consumption will be fundamental to the persistence of altered coral-dominated systems (Mumby and Steneck 2008, Graham et al. 2014a). Our results show browsing, but not grazing, differed among taxonomically distinct coral habitats, suggesting that different mechanisms may be responsible for shaping these key processes on coral reefs. Benthic composition and reef condition were the best predictors of variation in browsing, with highest rates recorded in mixed and soft coral habitats. With ongoing degradation of coral reefs and the homogenization of both coral and fish assemblages (Hughes et al. *in press*, **Chapter 4**), these results suggest that maintained reef functionality will likely vary among reefs, according to both the differential vulnerability of corals to disturbances as well as the ecological interactions between reef fishes and their environment (Nagelkerken and Munday 2016). Where high susceptibility of particular corals, such the higher thermal sensitivity of mixed coral and soft coral habitats relative to branching *Porites* habitats (**Chapter 4**), combines with a reduced abundance or functional impact of associated key species or functional groups, functional collapse may follow where algal growth is not sufficiently supressed (Hughes 1994).

Chapter 6: General Discussion

Elucidating the role of coral species composition in ecosystem structure and function is central to understanding and predicting the likely future trajectories of coral reefs. Previous studies have established the importance of live coral and habitat structural complexity to reef fish assemblage structure (Pratchett et al. 2009, Graham and Nash 2013), the influence of coral diversity on fish abundance and diversity (Messmer et al. 2011, Holbrook et al. 2015), and the species level dependence of reef fishes on different coral taxa (Coker et al. 2014). Building on growing evidence from the Caribbean (e.g. Alvarez-Filip et al. 2011b, Alvarez-Filip et al. 2011c, Alvarez-Filip et al. 2013, Bozec et al. 2015), this thesis has shown that the composition of distinct coral configurations underscores the structural complexity of tropical reef habitats across ecologically relevant scales, with some habitats providing structure across a greater range of scales (i.e. branching *Porites*, and massive *Porites* habitats) than others (i.e. *Pocillopora*, and soft coral habitats) (**Chapter 2**). This variation in structural complexity can act as an environmental filter, influencing the distribution of associated species traits, specifically those of small-bodied schooling fishes, thereby mediating the functional structure of reef fish assemblages (**Chapter 3**). However, the susceptibility of these distinct coral and fish species assemblages to reorganisation with a system-wide thermal stress event can be highly variable due to the differential susceptibility of both corals and fishes, leading to non-random and habitat-specific community turnover that caused overall biotic homogenization at the system level (**Chapter 4**). Critically, two key ecosystem functions, grazing on algal turfs and browsing on macroalgae, showed varying responses across taxonomically distinct coral habitats; browsing varied significantly with both the composition and condition of coral habitats, whilst grazing was relatively constant. Such contrasts highlight how different environmental mechanisms may shape the shape the abundance and delivery of functional impact of key species and functional groups as species configurations change under mounting stressors (**Chapter 5**).

The abundance and overall cover of live corals are important facets of reef fish distribution and abundance, often used as a proxy for the health and resilience of tropical reef ecosystems (Mumby et al. 2007, Mumby and Steneck 2008). However, consistent with evidence from the Caribbean (e.g. Alvarez-Filip et al. 2011a, Alvarez-Filip et al. 2015), the findings in this thesis demonstrate that the absolute cover of live coral *per se* does not capture important variation in the cross-scale structural complexity of reef habitats (**Chapter 2**), or variation in the functional structure of associated reef fish assemblages (**Chapter 3**). Further, comparisons of fish and coral assemblages over a major thermal stress event in the northern Great Barrier Reef (Hughes et al. 2017b) demonstrated that pre-disturbance cover of live coral does not ensure resilience to community turnover, and the magnitude of coral loss poorly predicted changes in fish assemblage structure (**Chapter 4**). This body of work, together with evidence of cryptobenthic fish assemblages failing to reassemble following the recovery of live coral cover, but not coral assemblage structure (Bellwood et al. 2012) highlights the importance of coral composition, rather than coral cover, in shaping the structure and function of reef fish assemblages.

The biological and/or physical attributes of dominant corals appear to underscore critical variation in reef habitat structures and the distribution of reef fishes, and mediate the ecological responses of reef systems to disturbance. Extensive coral loss and the erosion of carbonate reef structures undoubtedly have significant and widespread impacts on the structure and functioning of reef ecosystems (Sano et al. 1984, Wilson et al. 2006, Pratchett et al. 2009, Graham et al. 2015). However, shifts in coral species dominance will likely have subtle but ecologically important consequences such that accounting for variation in coral species composition as well as overall coral cover is likely to provide a better understanding of the capacity of altered reef systems to maintain critical ecological functions.

6.1 Future trajectories for coral reefs

Ongoing loss of corals and altered coral species configurations are predicted to characterise tropical reefs in the Anthropocene (Pandolfi et al. 2011, Graham et al. 2014a, Hughes et al. 2017a). Although the outcomes of such changes will likely vary by location (e.g. Aronson et al. 2004, Pratchett et al. 2011a, Bento et al. 2015), shifts towards novel coral configurations dominated by one or two species will likely incur predictable ecological changes characterised by greater structural homogenization within habitats (Alvarez-Filip et al. 2011b, **Chapter 2**), leading to the filtering of associated species with particular traits (e.g. particular body-sizes, Alvarez-Filip et al. 2011c, Bellwood et al. 2012, Nash et al. 2013, **Chapter 3**). By influencing the trait structure of communities, coral species shifts will likely disrupt community assembly (Macarthur and Levins 1967, Diamond 1975), with cascading effects on ecosystem functioning (Tilman et al. 1997, Hooper et al. 2005a, Larsen et al. 2005). Additionally, due to the differential and deterministic extinction risk of both corals (Darling et al. 2013) and reef fishes (Graham et al. 2011), distinct reef species assemblages will vary in their susceptibility to sudden reorganisation and functional collapse (McWilliam et al. 2018, **Chapter 2-4**). In particular, where disturbance results in a loss of functional redundancy among species, the overall stability and resilience of these altered coral reef ecosystems may be compromised (Nyström 2006, Brandl et al. 2016, **Chapter 4**). However, ecological interactions and disturbance dynamics are complex (Redford 1992, Nagelkerken et al. 2015, Jordano 2016), and our capacity for precise predictions of coral reef futures is limited by uncertainty regarding the adaptive capacity of organisms under ongoing environmental change (Pandolfi et al. 2011, Nagelkerken and Munday 2016).

6.2 Implications for management

Understanding relationships between community composition and ecosystem function is of increasing concern in conservation ecology (Peterson et al. 1998, Tilman 1999, Purvis and Hector 2000, Walther 2010, McGill et al. 2015). In particular, quantifying how disturbance-mediated community shifts will affect ecosystem functioning is central to our capacity to anticipate whether different coral reef configurations will deliver essential ecosystem goods and services to human societies (Moberg and Folke 1999, Hicks and Cinner 2014, Hughes et al. 2017a). The findings in this thesis provide explicit support for assigning greater concern to the composition of habitat-building corals in assessments of coral reef function (**Chapter 2, 3, 5**) and stability (**Chapter 4**) geared towards understanding the consequences of species shifts on coral reef dynamics. Some coral configurations might warrant greater protection than other as inherent variation in habitat structural complexity may support enhanced ecosystem resilience (e.g. massive *Porites*, mixed coral assemblages; **Chapter 2-5**), and likelihood of recovery from climate-driven disturbances (Graham et al. 2015). Similarly, the structural complexity created by particular coral communities will likely provide important coastal protection from waves under rising sea levels (Harris et al. 2018), and support increased fisheries productivity (Rogers et al. 2014). Accordingly, new governance challenges are characterised by the need for adaptive science and more nuanced approaches to management of these altered coral-dominated systems (Norström et al. 2016, Hughes et al. 2017a, Mumby 2017).

6.3 Future research

Adding to a growing body of literature that is looking beyond coral cover to consider the importance of component species, this thesis develops an understanding of the consequences of species shifts on coral reefs by linking important components of the role of coral species composition in reef ecosystems. Comparisons among different coral species configurations and across geographical and environmental gradients will provide greater insight into the dynamics and future trajectories of these systems. For example, coral species composition, habitat structural complexity, and the structure of reef fish assemblages can vary across depth, latitude, and exposure gradients (Hughes et al. 2012, Graham et al. 2014b, Jankowski et al. 2015, Bridge et al. 2016). However, this thesis focusses on shallow reefs (< 6m) in a single location. Similarly, tabular and branching *Acropora* can be vulnerable to disturbance but relatively fast growing. However, whilst they typically dominate large areas of undisturbed coral reef habitats in the Indo-Pacific (Johns et al. 2014), they were not locally abundant at Lizard Island during this study. Similarly, there is much uncertainty about how distinct and emerging configurations of species will respond to ongoing disturbance from multiple anthropogenic stressors, and how important ecosystem processes will be maintained (Mumby and Steneck 2008, Graham et al. 2014a). To this end, a great deal more research is needed to develop early warnings of critical resilience loss in order to guide viable and pragmatic management approaches (Norström et al.

2016, Mumby 2017). Such research should include assessment of the longer-term outcomes of disturbance on the reorganisation of coral reefs in order to incorporate lag responses of assemblages to environmental change (Graham et al. 2007). A better understanding is also needed of how different stressors such as fishing, large storms or reduced water quality influence ecological interactions and compound community-level responses to species shifts (Hughes et al. 2017a). Further research into the spatial and temporal variation in the behaviour of key species and functional groups would provide a more integrated understanding of the mechanisms and processes connecting individuals to community assembly and ecosystem functions under ongoing disturbance.

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Appendix A. Supplemental information for Chapter 2: Cross-scale habitat structure driven by coral species composition on tropical reefs

Table S1 Linear distance across scales at each habitat and components of variation in linear distance at each level: Habitat, Site, and Transect. Variance components are shown as percentages of total variance explained (extracted with *lme4* and *MuMIn* in *R*).

Scale (cm)	Wheel (cm)		Mean ± SE linear distance (m)					Variance components (%)		
	Diameter	Circumference	Branching *Porites*	Degraded	Massive *Porites*	*Pocillopora*	Soft coral	Habitat	Site	Transect
4	3.99	12.53	20.59 ± 0.48	15.17 ± 1.07	20.06 ± 1.01	16.68 ± 0.98	17.81 ± 0.99	36.82	0.00	63.18
8	7.97	25.05	16.48 ± 0.85	13.73 ± 0.77	16.60 ± 0.99	12.62 ± 1.17	15.82 ± 0.85	21.13	0.00	78.87
16	15.95	50.10	14.91 ± 0.79	13.42 ± 0.44	15.08 ± 0.62	11.84 ± 0.42	12.81 ± 0.62	22.96	0.00	77.04
32	31.89	100.20	12.71 ± 0.56	12.18 ± 0.30	13.35 ± 0.39	11.30 ± 0.11	11.52 ± 0.29	21.83	0.00	78.17
64	63.79	200.40	11.39 ± 0.21	11.82 ± 0.18	12.08 ± 0.26	10.49 ± 0.09	11.18 ± 0.11	35.05	5.46	59.49

Table S2 One-way PERMANOVA pairwise comparisons of benthic composition among coral habitats. Comparisons based on Bray-Curtis similarities of unrestricted permutation of raw data (>6835 permutations). Benthic variables consistently contributing to average similarity within (sim/SD >4; grey shaded boxes), and dissimilarity between habitats, (unshaded boxes; diss/SD >2) identified in one-way SIMPER are listed.

	Branching *Porites*	Massive *Porites*	*Pocillopora*	Soft coral	Degraded
Branching *Porites*	Branching *Porites* Dead coral **Av. sim. 74.7%**	Branching *Porites* Massive *Porites* **Av. dissim. 38.2%**	Branching *Porites* *Pocillopora* **Av. dissim. 50.5%**	Branching *Porites* Soft coral **Av. dissim. 46.2%**	Branching *Porites* Macroalgae **Av. dissim. 44.1%**
Massive *Porites*	**P=0.0001**	Massive *Porites* Dead coral Soft coral **Av. sim. 79.7%**	Massive *Porites* *Pocillopora* **Av. dissim. 42.9%**	Massive *Porites* Soft coral **Av. dissim. 36.3%**	Massive *Porites* Macroalgae **Av. dissim. 35.3%**
Pocillopora	**P=0.0001**	**P=0.0001**	*Pocillopora* Dead coral Soft coral **Av. sim. 80.1%**	Soft coral *Pocillopora* **Av. dissim. 43.4%**	*Pocillopora* Macroalgae **Av. dissim. 45.7%**
Soft coral	**P=0.0001**	**P=0.0001**	**P=0.0001**	Soft coral Dead coral Rubble **Av. sim. 80.9%**	Soft coral Macroalgae **Av. dissim. 44.3%**
Degraded	**P=0.0001**	**P=0.0001**	**P=0.0001**	**P=0.0001**	Dead coral **Av. sim. 76.8%**

Table S3 Summary of mixed effects linear regression analyses of habitat (fixed), and site (random) predicting linear distance measured at multiple scales (4-64 cm), and Tukey multiple comparison tests.

Scale (cm)	$F_{4,7}$	*P*	R^2 (habitat)	Tukey *P* (all)	Inter-habitat variation
4	6.73	**0.02**	0.64	**≤0.01**	Branching *Porites*, Massive *Porites* > Degraded; Branching *Porites* > *Pocillopora*
8	3.32	0.08	0.19	NA	NA
16	6.18	**0.02**	0.14	**≤0.01**	Branching *Porites*, Massive *Porites* > *Pocillopora*
32	8.81	**0.01**	0.11	**≤0.04**	Degraded, Massive *Porites* > *Pocillopora*; Massive *Porites* > Soft coral
64	4.34	**0.04**	0.25	**<0.01**	Degraded, Massive *Porites* > *Pocillopora*

Table S4 Summary of mixed effects linear regression analyses of linear distance measured at multiple scales (4-64 cm; fixed) within habitats, using site as a random factor, and Tukey multiple comparison tests.

Habitat	*F*	*df*	*P*	R^2 (scale)	Tukey *P* (all)	Inter-scale (cm) variation
Branching *Porites*	82.92	4,53	**<0.001**	0.79	**<0.001**	4 > 8, 16, 32, 64; 16 > 32, 64; 16 > 64
Degraded	6.27	4,53	**<0.001**	0.09	**<0.02**	4, 16 > 64
Massive *Porites*	21.37	4,34	**<0.001**	0.49	**<0.05**	4 > 16, 32, 64; 16 > 32, 64; 16 > 64; 32 > 64
Pocillopora	18.30	4,15	**<0.001**	0.48	**<0.02**	4 > 8, 16, 32, 64; 16, 32 > 64
Soft coral	20.55	4,43	**<0.001**	0.42	**<0.04**	4 > 16, 32, 64; 8 > 16, 32, 64

Table S5 Regression coefficients and R^2 of linear distance and colony size for *Porites cylindrica*, massive *Porites* (mostly *P. lutea*) and *Pocillopora damicornis*.

Scale (cm)	*P. cylindrica*			Massive *Porites*			*P. damicornis*		
	Intercept	Slope	R^2	Intercept	Slope	R^2	Intercept	Slope	R^2
4	-14.6890	2.2142	0.93	1.52052	1.61221	0.96	-4.037	1.559	0.68
8	-0.27129	1.52378	0.95	3.96408	1.47673	0.95	-2.03474	1.43967	0.78
16	-0.06219	1.34541	0.96	3.09503	1.45661	0.95	-1.91172	1.27025	0.87
32	-0.92919	1.25057	0.97	-0.92543	1.44113	0.97	-2.34713	1.23802	0.90
64	-0.32606	1.18825	0.97	-4.43976	1.40474	0.97	-2.67417	1.19909	0.91

Appendix B. Supplemental information for Chapter 3: Structural complexity mediates functional structure of reef fish assemblages among coral habitats

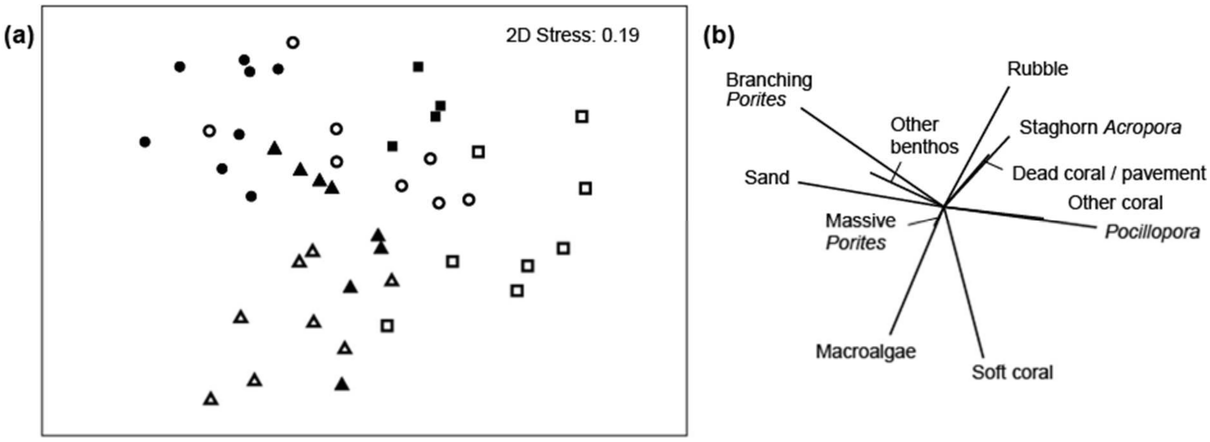

Fig. S1 Non-metric multidimensional scaling analysis showing relationships among benthic assemblages across six coral habitats on Lizard Island (a) Spatial variation in benthic composition on reefs at the transect level on log(x+1) transformed data. Data symbols represent transects within habitats: staghorn *Acropora* (filled square); branching *Porites* (filled circle), massive *Porites* (filled triangle); mixed assemblages (open circle), *Pocillopora* (open square); and soft coral (open triangle); (b) Relative contribution of benthic habitat categories to the observed variation in reef benthic composition.

Table S1 Assigned fish trait categories and descriptions. Categories adapted from Mouillot et al. (2013).

Trait	**Categories**	**Description**
Diet	Herbivores:	Algae feeders:
	Scraper	Feeds on epilithic algal turf by closely cropping or scraping the reef surface leaving shallow scrape marks on the substratum
	Excavator	Feeds on epilithic algal turf by taking deep excavating bites of the reef surface, removing greater quantities of the substratum as it feeds than scrapers
	Grazer/detritivore	Feeds on algal turf and detritus found in the epilithic algal matrix, but does not scrape or excavate the reef substratum as it feeds
	Browser	Feeds on macro-algae
	Farmer	Territorial algal farming species
	Mixed diet feeder	Feeds on multiple food items (e.g. animal and plant, or fish and invertebrates)
	Piscivore	Feeds on fish
	Invertivore	Feeds on invertebrates (excluding corals)
	Corallivore	Feeds on corals
	Planktivore	Feeds on plankton
Body-size	≤10, 11-20, 21-30, 31-40, 41-50, 51-60, >60 cm	Mean observed total body length in the survey: 10 cm size-class categories
Mobility	Sedentary	Generally site attached species which stay within a restricted area (1 – few 100 m^2)
	Mobile within reefs	Species which stay within a restricted area (100 m^2 – several hectares) for periods of several days to months
	Mobile across reefs	Wide ranging species which may change from one reef to another within a short period of time (1 – several days)
Time of activity	Diurnal	Active during the day
	Nocturnal	Active during the night
	Both diurnal and nocturnal	Active during both day and night
Social grouping	Solitary	Species which tend to be found single
	Pairing	Species generally found in pairs
	Schooling:	Species generally found in schools:
	Small groups	Approximately 3-20 individuals
	Medium groups	Approximately 20-50 individuals
	Large groups	Approximately >50 individuals
Position in the water column	Benthic	Species which spend most of the time closely by the benthos
	Bentho-pelagic	Species generally found just above the benthos
	Pelagic	Species generally swimming high above the benthos

Table S2 Assigned fish trait by species observed. Traits assigned based on published literature (Wilson et al. 2008; Green et al. 2009; Pratchett et al. 2011; Mouillot et al. 2013), and FishBase (Froese and Pauly 2014). Schooling trait categories abbreviated as follows: Small groups (SmallG); medium groups (MedG); large groups (LargeG).

Species	Observed mean size (cm)	Diet	Mobility	Time of activity	Social grouping	Position in water
Acanthurus blochii	21-30	Grazer/detritivore	Mobile within reef	Diurnal	SmallG	Benthic
Acanthurus nigricauda	11-20	Grazer/detritivore	Mobile within reef	Diurnal	SmallG	Benthic
Acanthurus nigrofuscus	11-20	Grazer/detritivore	Sedentary	Diurnal	SmallG	Benthic
Acanthurus xanthopterus	21-30	Grazer/detritivore	Mobile within reef	Diurnal	MedG	Benthic
Ctenochaetus binotatus	11-20	Grazer/detritivore	Sedentary	Diurnal	Solitary	Benthic
Ctenochaetus striatus	11-20	Grazer/detritivore	Sedentary	Diurnal	MedG	Benthic
Naso brevirostris	11-20	Browser	Mobile across reefs	Diurnal	LargeG	Bentho-pelagic
Naso lituratus	21-30	Browser	Mobile within reef	Diurnal	SmallG	Benthic
Naso unicornis	21-30	Browser	Mobile within reef	Diurnal	SmallG	Benthic
Naso vlamingii	11-20	Planktivore	Mobile across reefs	Diurnal	SmallG	Bentho-pelagic
Zebrasoma scopas	11-20	Grazer/detritivore	Mobile within reef	Diurnal	SmallG	Benthic
Zebrasoma velifer	11-20	Grazer/detritivore	Mobile within reef	Diurnal	Pairing	Benthic
Apogon compressus	<11	Planktivore	Sedentary	Nocturnal	MedG	Bentho-pelagic
Apogon cyanosoma	<11	Planktivore	Sedentary	Nocturnal	MedG	Bentho-pelagic
Apogon sp	<11	Planktivore	Sedentary	Nocturnal	MedG	Benthic
Archamia zosterophora	<11	Planktivore	Sedentary	Nocturnal	MedG	Bentho-pelagic
Cheilodipterus artus	<11	Piscivore	Sedentary	Nocturnal	SmallG	Bentho-pelagic
Cheilodipterus macrodon	11-20	Mixed diet	Sedentary	Nocturnal	Solitary	Bentho-pelagic
Cheilodipterus quinquelineatus	<11	Mixed diet	Sedentary	Nocturnal	SmallG	Bentho-pelagic
Sphaeramia nematoptera	<11	Invertivore	Sedentary	Nocturnal	MedG	Bentho-pelagic
Zoramia fragilis	<11	Planktivore	Sedentary	Nocturnal	LargeG	Bentho-pelagic
Balistapus undulatus	21-30	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Balistoides viridescens	31-40	Corallivore	Mobile within reef	Diurnal	Solitary	Benthic
Sufflamen chrysopterum	11-20	Invertivore	Sedentary	Diurnal	Solitary	Benthic
Caesio cuning	11-20	Planktivore	Mobile across reefs	Diurnal	LargeG	Pelagic
Pterocaesio marri	11-20	Planktivore	Mobile across reefs	Diurnal	LargeG	Pelagic
Caranx melampygus	31-40	Piscivore	Mobile across reefs	Both	SmallG	Pelagic

Trachinotus blochii	41-50	Invertivore	Mobile across reefs	Both	SmallG	Pelagic
Chaetodon aureofasciatus	<11	Corallivore	Sedentary	Diurnal	Pairing	Benthic
Chaetodon auriga	11-20	Corallivore	Sedentary	Diurnal	Pairing	Benthic
Chaetodon baronessa	11-20	Corallivore	Sedentary	Diurnal	Pairing	Benthic
Chaetodon citrinellus	<11	Corallivore	Sedentary	Diurnal	Pairing	Benthic
Chaetodon ephippium	11-20	Corallivore	Sedentary	Diurnal	Pairing	Benthic
Chaetodon kleinii	<11	Corallivore	Sedentary	Diurnal	Pairing	Bentho-pelagic
Chaetodon lineolatus	11-20	Corallivore	Sedentary	Diurnal	Pairing	Benthic
Chaetodon lunulatus	<11	Corallivore	Sedentary	Diurnal	Pairing	Benthic
Chaetodon melannotus	11-20	Corallivore	Sedentary	Diurnal	Pairing	Benthic
Chaetodon plebeius	<11	Corallivore	Sedentary	Diurnal	Pairing	Benthic
Chaetodon rainfordi	11-20	Corallivore	Sedentary	Diurnal	Pairing	Benthic
Chaetodon semeion	11-20	Mixed diet	Sedentary	Diurnal	Pairing	Benthic
Chaetodon speculum	11-20	Corallivore	Sedentary	Diurnal	Solitary	Benthic
Chaetodon trifascialis	<11	Corallivore	Sedentary	Diurnal	Pairing	Benthic
Chaetodon ulietensis	11-20	Corallivore	Sedentary	Diurnal	Pairing	Benthic
Chaetodon unimaculatus	11-20	Corallivore	Sedentary	Diurnal	Pairing	Benthic
Chaetodon vagabundus	11-20	Corallivore	Sedentary	Diurnal	Pairing	Benthic
Chelmon rostratus	11-20	Invertivore	Sedentary	Diurnal	Pairing	Benthic
Heniochus acuminatus	11-20	Planktivore	Sedentary	Diurnal	Pairing	Benthic
Heniochus chrysostomus	11-20	Corallivore	Sedentary	Diurnal	Pairing	Benthic
Heniochus varius	21-30	Invertivore	Sedentary	Diurnal	Pairing	Benthic
Platax orbicularis	31-40	Mixed diet	Mobile across reefs	Diurnal	MedG	Bentho-pelagic
Platax pinnatus	31-40	Mixed diet	Mobile across reefs	Diurnal	MedG	Bentho-pelagic
Diagramma pictum	31-40	Invertivore	Mobile within reef	Diurnal	MedG	Benthic
Plectorhinchus albovittatus	>60	Mixed diet	Mobile within reef	Diurnal	Solitary	Bentho-pelagic
Plectorhinchus chaetodonoides	31-40	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Plectorhinchus chrysotaenia	31-40	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Plectorhinchus gibbosus	31-40	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Plectorhinchus lineatus	31-40	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Myripristis sp	11-20	Planktivore	Sedentary	Nocturnal	Pairing	Benthic
Neoniphon sammara	11-20	Invertivore	Mobile within reef	Nocturnal	SmallG	Bentho-pelagic
Sargocentron sp	21-30	Invertivore	Sedentary	Nocturnal	Pairing	Benthic

Kyphosus cinerascens	31-40	Browser	Mobile across reefs	Diurnal	MedG	Bentho-pelagic
Kyphosus vaigiensis	31-40	Browser	Mobile across reefs	Diurnal	MedG	Bentho-pelagic
Anampses caeruleopunctatus	11-20	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Anampses geographicus	11-20	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Anampses neoguinaicus	11-20	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Bodianus axillaris	11-20	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Bodianus mesothorax	11-20	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Cheilinus chlorourus	11-20	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Cheilinus fasciatus	11-20	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Cheilinus trilobatus	11-20	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Cheilinus undulatus	51-60	Mixed diet	Mobile within reef	Diurnal	Solitary	Benthic
Choerodon anchorago	11-20	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Choerodon fasciatus	11-20	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Choerodon schoenleinii	21-30	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Cirrhilabrus exquisitus	<11	Planktivore	Sedentary	Diurnal	MedG	Bentho-pelagic
Coris aygula	51-60	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Coris batuensis	<11	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Epibulus insidiator	11-20	Piscivore	Mobile within reef	Diurnal	Solitary	Benthic
Gomphosus varius	11-20	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Halichoeres chloropterus	11-20	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Halichoeres hortulanus	21-30	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Halichoeres marginatus	11-20	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Halichoeres melanurus	<11	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Halichoeres nebulosus	<11	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Halichoeres scapularis	11-20	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Hemigymnus fasciatus	11-20	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Hemigymnus melapterus	11-20	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Labrichthys unilineatus	11-20	Corallivore	Sedentary	Diurnal	Solitary	Benthic
Labroides dimidiatus	<11	Invertivore	Sedentary	Diurnal	Pairing	Benthic
Macropharyngodon choati	<11	Invertivore	Sedentary	Diurnal	Solitary	Benthic
Macropharyngodon meleagris	11-20	Invertivore	Sedentary	Diurnal	SmallG	Benthic
Oxycheilinus digramma	11-20	Piscivore	Mobile within reef	Diurnal	Solitary	Bentho-pelagic
Oxycheilinus sp	11-20	Mixed diet	Mobile within reef	Diurnal	Solitary	Benthic

Pseudocheilinus evanidus	<11	Invertivore	Sedentary	Diurnal	Solitary	Benthic
Stethojulis bandanensis	<11	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Stethojulis interrupta	<11	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Stethojulis strigiventer	11-20	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Thalassoma hardwicke	11-20	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Thalassoma lunare	11-20	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Lethrinus atkinsoni	11-20	Piscivore	Mobile across reefs	Nocturnal	MedG	Benthic
Lethrinus nebulosus	31-40	Mixed diet	Mobile across reefs	Nocturnal	MedG	Benthic
Lethrinus obsoletus	11-20	Mixed diet	Mobile within reef	Nocturnal	SmallG	Benthic
Lethrinus ornatus	11-20	Invertivore	Mobile across reefs	Nocturnal	SmallG	Benthic
Lethrinus reticulatus	21-30	Mixed diet	Mobile across reefs	Nocturnal	SmallG	Benthic
Monotaxis grandoculis	11-20	Invertivore	Mobile within reef	Nocturnal	Solitary	Bentho-pelagic
Lutjanus bohar	21-30	Piscivore	Mobile within reef	Nocturnal	MedG	Bentho-pelagic
Lutjanus carponotatus	21-30	Mixed diet	Mobile within reef	Nocturnal	MedG	Bentho-pelagic
Lutjanus ehrenbergii	21-30	Mixed diet	Mobile within reef	Both	SmallG	Bentho-pelagic
Lutjanus fulviflamma	21-30	Mixed diet	Mobile within reef	Both	MedG	Bentho-pelagic
Lutjanus fulvus	21-30	Piscivore	Mobile within reef	Both	SmallG	Bentho-pelagic
Lutjanus gibbus	21-30	Piscivore	Mobile within reef	Both	MedG	Benthic
Lutjanus kasmira	11-20	Mixed diet	Mobile within reef	Nocturnal	LargeG	Bentho-pelagic
Lutjanus quinquelineatus	11-20	Mixed diet	Mobile within reef	Nocturnal	LargeG	Bentho-pelagic
Lutjanus russelli	21-30	Piscivore	Mobile within reef	Nocturnal	SmallG	Bentho-pelagic
Lutjanus sebae	31-40	Piscivore	Mobile within reef	Nocturnal	SmallG	Bentho-pelagic
Oxymonacanthus longirostris	<11	Corallivore	Sedentary	Diurnal	Pairing	Benthic
Mulloidichthys flavolineatus	21-30	Invertivore	Mobile within reef	Diurnal	MedG	Benthic
Parupeneus barberinus	21-30	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Parupeneus multifasciatus	21-30	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Scolopsis bilineata	11-20	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Scolopsis lineata	11-20	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Scolopsis margaritifer	11-20	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Scolopsis monogramma	21-30	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Centropyge bicolor	11-20	Grazer/detritivore	Sedentary	Diurnal	Pairing	Benthic
Centropyge vrolikii	<11	Grazer/detritivore	Sedentary	Diurnal	Pairing	Benthic
Pomacanthus sexstriatus	21-30	Mixed diet	Sedentary	Diurnal	Solitary	Benthic

Pomacanthus xanthometopon	21-30	Invertivore	Sedentary	Diurnal	Solitary	Benthic
Abudefduf bengalensis	11-20	Planktivore	Sedentary	Diurnal	MedG	Bentho-pelagic
Abudefduf sexfasciatus	<11	Planktivore	Sedentary	Diurnal	MedG	Bentho-pelagic
Abudefduf vaigiensis	<11	Mixed diet	Sedentary	Diurnal	MedG	Bentho-pelagic
Abudefduf whitleyi	<11	Planktivore	Sedentary	Diurnal	MedG	Bentho-pelagic
Acanthochromis polyacanthus	<11	Planktivore	Sedentary	Diurnal	MedG	Benthic
Amblyglyphidodon curacao	<11	Planktivore	Sedentary	Diurnal	MedG	Bentho-pelagic
Amblyglyphidodon leucogaster	<11	Planktivore	Sedentary	Diurnal	MedG	Bentho-pelagic
Amphiprion clarkii	<11	Planktivore	Sedentary	Diurnal	SmallG	Benthic
Amphiprion melanopus	<11	Planktivore	Sedentary	Diurnal	SmallG	Benthic
Cheiloprion labiatus	<11	Corallivore	Sedentary	Diurnal	Solitary	Benthic
Chromis atripectoralis	<11	Planktivore	Sedentary	Diurnal	LargeG	Bentho-pelagic
Chromis ternatensis	<11	Planktivore	Sedentary	Diurnal	MedG	Bentho-pelagic
Chromis viridis	<11	Planktivore	Sedentary	Diurnal	LargeG	Bentho-pelagic
Chromis weberi	<11	Planktivore	Sedentary	Diurnal	MedG	Bentho-pelagic
Chrysiptera rollandi	<11	Planktivore	Sedentary	Diurnal	SmallG	Benthic
Chrysiptera unimaculata	<11	Mixed diet	Sedentary	Diurnal	SmallG	Benthic
Dascyllus aruanus	<11	Planktivore	Sedentary	Diurnal	MedG	Benthic
Dascyllus reticulatus	<11	Planktivore	Sedentary	Diurnal	MedG	Benthic
Dascyllus trimaculatus	<11	Planktivore	Sedentary	Diurnal	SmallG	Benthic
Dischistodus melanotus	<11	Farmer	Sedentary	Diurnal	Solitary	Benthic
Dischistodus perspicillatus	11-20	Farmer	Sedentary	Diurnal	SmallG	Benthic
Dischistodus prosopotaenia	<11	Farmer	Sedentary	Diurnal	SmallG	Benthic
Dischistodus pseudochrysopoecilus	<11	Farmer	Sedentary	Diurnal	SmallG	Benthic
Hemiglyphidodon plagiometopon	11-20	Grazer/detritivore	Sedentary	Diurnal	SmallG	Benthic
Neoglyphidodon melas	<11	Corallivore	Sedentary	Diurnal	Solitary	Benthic
Neoglyphidodon nigroris	<11	Mixed diet	Sedentary	Diurnal	SmallG	Benthic
Neopomacentrus azysron	<11	Planktivore	Sedentary	Diurnal	LargeG	Bentho-pelagic
Neopomacentrus bankieri	<11	Planktivore	Sedentary	Diurnal	LargeG	Bentho-pelagic
Neopomacentrus cyanomos	<11	Planktivore	Sedentary	Diurnal	LargeG	Bentho-pelagic
Plectroglyphidodon lacrymatus	<11	Farmer	Sedentary	Diurnal	Solitary	Benthic
Pomacentrus adelus	<11	Farmer	Sedentary	Diurnal	SmallG	Benthic
Pomacentrus amboinensis	<11	Planktivore	Sedentary	Diurnal	MedG	Benthic

Pomacentrus brachialis	<11	Farmer	Sedentary	Diurnal	MedG	Bentho-pelagic
Pomacentrus chrysurus	<11	Farmer	Sedentary	Diurnal	SmallG	Benthic
Pomacentrus coelestis	<11	Planktivore	Sedentary	Diurnal	MedG	Benthic
Pomacentrus grammorhynchus	<11	Farmer	Sedentary	Diurnal	SmallG	Benthic
Pomacentrus lepidogenys	<11	Planktivore	Sedentary	Diurnal	SmallG	Benthic
Pomacentrus moluccensis	<11	Planktivore	Sedentary	Diurnal	MedG	Benthic
Pomacentrus nagasakiensis	<11	Planktivore	Sedentary	Diurnal	SmallG	Benthic
Pomacentrus reidi	<11	Mixed diet	Sedentary	Diurnal	SmallG	Benthic
Pomacentrus simsiang	<11	Mixed diet	Sedentary	Diurnal	SmallG	Benthic
Pomacentrus tripunctatus	<11	Mixed diet	Sedentary	Diurnal	SmallG	Benthic
Pomacentrus wardi	<11	Farmer	Sedentary	Diurnal	SmallG	Benthic
Premnas biaculeatus	<11	Grazer/detritivore	Sedentary	Diurnal	SmallG	Benthic
Stegastes apicalis	<11	Farmer	Sedentary	Diurnal	SmallG	Benthic
Stegastes fasciolatus	11-20	Farmer	Sedentary	Diurnal	SmallG	Benthic
Stegastes nigricans	<11	Farmer	Sedentary	Diurnal	MedG	Benthic
Priacanthus hamrur	31-40	Mixed diet	Mobile within reef	Nocturnal	SmallG	Bentho-pelagic
Pseudochromis fuscus	<11	Invertivore	Sedentary	Diurnal	Solitary	Benthic
Bolbometopon muricatum	>60	Excavator	Mobile across reefs	Diurnal	MedG	Benthic
Cetoscarus ocellatus	11-20	Excavator	Mobile within reef	Diurnal	SmallG	Benthic
Chlorurus bleekeri	21-30	Excavator	Mobile within reef	Diurnal	SmallG	Benthic
Chlorurus microrhinos	21-30	Excavator	Mobile within reef	Diurnal	SmallG	Benthic
Chlorurus sordidus	11-20	Excavator	Mobile within reef	Diurnal	SmallG	Benthic
Hipposcarus longiceps	21-30	Scraper	Mobile within reef	Diurnal	MedG	Benthic
Scarus altipinnis	21-30	Scraper	Mobile within reef	Diurnal	LargeG	Benthic
Scarus chameleon	21-30	Scraper	Mobile within reef	Diurnal	Solitary	Benthic
Scarus dimidiatus	21-30	Scraper	Mobile within reef	Diurnal	SmallG	Benthic
Scarus flavipectoralis	11-20	Scraper	Mobile within reef	Diurnal	Solitary	Benthic
Scarus frenatus	21-30	Scraper	Mobile within reef	Diurnal	Solitary	Benthic
Scarus ghobban	21-30	Scraper	Mobile within reef	Diurnal	SmallG	Benthic
Scarus globiceps	11-20	Scraper	Mobile within reef	Diurnal	Solitary	Benthic
Scarus niger	11-20	Scraper	Mobile within reef	Diurnal	Solitary	Benthic
Scarus oviceps	21-30	Scraper	Mobile within reef	Diurnal	Solitary	Benthic
Scarus psittacus	11-20	Scraper	Mobile within reef	Diurnal	MedG	Benthic

Scarus rivulatus	21-30	Scraper	Mobile within reef	Diurnal	MedG	Benthic
Scarus schlegeli	11-20	Scraper	Mobile within reef	Diurnal	MedG	Benthic
Scarus sp	<11	Scraper	Mobile within reef	Diurnal	SmallG	Benthic
Scarus spinus	11-20	Scraper	Mobile within reef	Diurnal	Solitary	Benthic
Cephalopholis argus	11-20	Piscivore	Sedentary	Both	Solitary	Benthic
Cephalopholis boenak	<11	Mixed diet	Sedentary	Both	Solitary	Benthic
Cephalopholis cyanostigma	21-30	Mixed diet	Sedentary	Both	Solitary	Benthic
Epinephelus hexagonatus	21-30	Mixed diet	Mobile within reef	Both	Solitary	Benthic
Epinephelus merra	11-20	Mixed diet	Mobile within reef	Both	Solitary	Benthic
Epinephelus ongus	11-20	Mixed diet	Mobile within reef	Both	Solitary	Benthic
Plectropomus laevis	41-50	Piscivore	Mobile within reef	Diurnal	Solitary	Benthic
Plectropomus leopardus	31-40	Piscivore	Mobile within reef	Diurnal	Solitary	Benthic
Siganus corallinus	11-20	Grazer/detritivore	Mobile within reef	Diurnal	Pairing	Benthic
Siganus doliatus	21-30	Grazer/detritivore	Mobile within reef	Diurnal	Pairing	Benthic
Siganus lineatus	31-40	Grazer/detritivore	Mobile across reefs	Diurnal	MedG	Benthic
Siganus puellus	11-20	Grazer/detritivore	Mobile within reef	Diurnal	Pairing	Benthic
Siganus punctatissimus	11-20	Grazer/detritivore	Mobile within reef	Diurnal	Pairing	Benthic
Siganus punctatus	11-20	Grazer/detritivore	Mobile within reef	Diurnal	Pairing	Benthic
Siganus spinus	<11	Grazer/detritivore	Mobile across reefs	Diurnal	LargeG	Benthic
Siganus vulpinus	21-30	Grazer/detritivore	Mobile within reef	Diurnal	Pairing	Benthic
Sphyraena flavicauda	21-30	Piscivore	Mobile across reefs	Nocturnal	LargeG	Pelagic
Arothron hispidus	21-30	Mixed diet	Mobile within reef	Diurnal	Solitary	Benthic
Arothron nigropunctatus	21-30	Corallivore	Mobile within reef	Diurnal	Solitary	Benthic
Arothron stellatus	51-60	Mixed diet	Mobile within reef	Diurnal	Solitary	Benthic
Canthigaster amboinensis	11-20	Mixed diet	Sedentary	Diurnal	Solitary	Benthic
Zanclus cornutus	11-20	Mixed diet	Mobile within reef	Diurnal	SmallG	Benthic

Table S3 Mean ± SE values for variables and fish assemblage functional diversity indices for each coral habitat.

Coral habitat	Dominant taxa as percentage of total live coral	Structural complexity (0-5)	Depth (m)	Benthic diversity (Shannon)	Functional richness	Functional evenness	Functional divergence
Staghorn *Acropora*	67.42 ± 8.39	2.33 ± 0.33	2.75 ± 0.26	1.67 ± 0.09	0.32 ± 0.10	0.39 ± 0.03	0.92 ± 0.01
Branching *Porites*	80.41 ± 3.80	3.56 ± 0.22	4.85 ± 0.21	1.67 ± 0.08	0.48 ± 0.03	0.39 ± 0.03	0.95 ± 0.01
Massive *Porites*	38.49 ± 5.86	2.81 ± 0.27	4.25 ± 0.29	2.03 ± 0.09	0.35 ± 0.06	0.41 ± 0.02	0.96 ± 0.01
Mixed	-	3.65 ± 0.24	4.56 ± 0.17	2.00 ± 0.07	0.41 ± 0.05	0.44 ± 0.02	0.94 ± 0.01
Pocillopora	45.42 ± 9.86	1.58 ± 0.20	2.13 ± 0.33	1.70 ± 0.08	0.26 ± 0.03	0.40 ± 0.03	0.91 ± 0.01
Soft coral	89.66 ± 2.90	1.85 ± 0.17	3.50 ± 0.57	1.37 ± 0.13	0.28 ± 0.03	0.44 ± 0.02	0.94 ± 0.01

Table S4 PERMANOVA pairwise comparisons for the significant variation in benthic composition among coral habitats at the transect level (grouped benthic categories). Comparisons based on Euclidean distances of log (x+1) transformed data, *P* values obtained by unrestricted permutation of raw data; and benthic categories consistently contributing to average similarity within (grey shaded boxes), and dissimilarity between habitats, (unshaded boxes; sim or diss/SD ≥1.5) identified in percentage similarity analysis (SIMPER).

	Staghorn *Acropora*	Branching *Porites*	Massive *Porites*	Mixed	*Pocillopora*	Soft coral
Staghorn *Acropora*	Staghorn *Acropora* Dead coral Soft coral Rubble Sand **Av. Sim: 85.2%**	Branching *Porites* Staghorn *Acropora* Soft coral Sand	Staghorn *Acropora* Massive *Porites* Soft coral Sand	Staghorn *Acropora* Other hard coral Massive *Porites* Sand Other benthos Rubble	Staghorn *Acropora* *Pocillopora* Other hard coral	Staghorn *Acropora* Soft coral Macro-algae Sand
Branching *Porites*	*P* = 0.003	Branching *Porites* Dead coral Sand **Av. Sim: 76.0%**	Branching *Porites* Massive *Porites* Soft coral Sand	Soft coral Sand Other benthos	Branching *Porites* *Pocillopora* Soft coral Other hard coral	Branching *Porites* Soft coral Macro-algae
Massive *Porites*	*P* = 0.003	*P* = 0.001	Massive *Porites* Dead coral Soft coral Sand Rubble Other hard coral **Av. Sim: 76.7%**	Massive *Porites* Other benthos Other hard coral	Massive *Porites* *Pocillopora* Other hard coral Dead coral	Massive *Porites* Soft coral
Mixed	*P* = 0.01	*P* = 0.003	*P* = 0.05	Other hard coral Dead coral Rubble Soft coral Sand Massive *Porites* **Av. Sim: 72.6%**	*Pocillopora* Sand Massive *Porites*	Soft coral Rubble Macro-algae Massive *Porites*
Pocillopora	*P* = 0.001	*P* = 0.002	*P* = 0.001	*P* = 0.002	*Pocillopora* Dead coral Soft coral Rubble **Av. Sim: 68.9%**	*Pocillopora* Sand Massive *Porites*
Soft coral	*P* = 0.004	*P* = 0.001	*P* = 0.001	*P* = 0.001	*P* = 0.002	Soft coral Dead coral Sand **Av. Sim: 73.6%**

Table S5 Percentages of non-overlap between convex hulls shaping fish assemblages at surveyed coral habitats.

	Staghorn *Acropora*	Branching *Porites*	Massive *Porites*	Mixed	*Pocillopora*	Soft coral
Staghorn *Acropora*						
Branching *Porites*	37.17					
Massive *Porites*	40.94	29.53				
Mixed	34.34	20.55	25.95			
Pocillopora	42.39	36.69	34.45	32.86		
Soft coral	36.89	30.85	31.04	25.42	34.78	

Appendix C. Supplemental information for Chapter 4: Mass coral bleaching causes biotic homogenization of reef fish assemblages

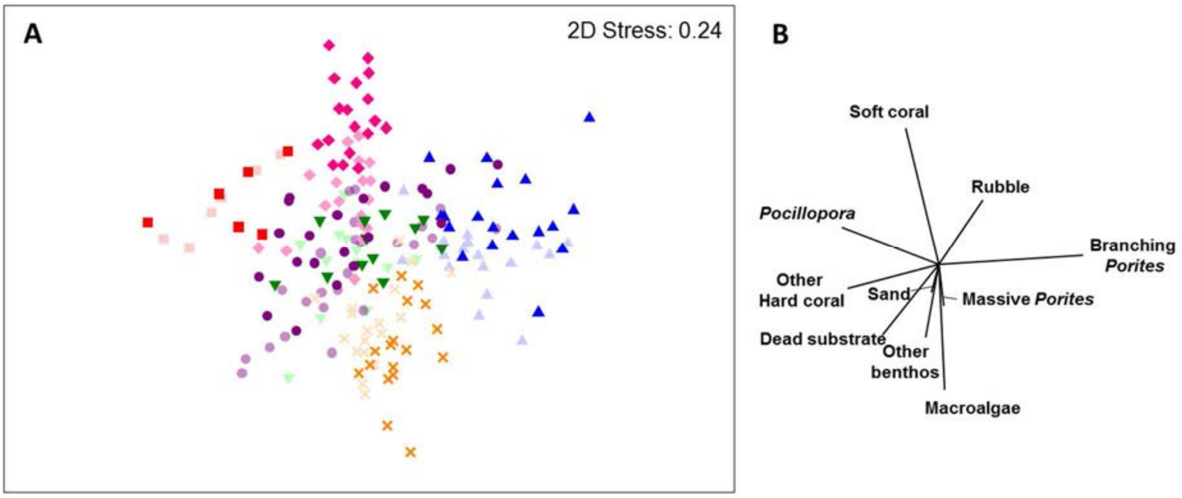

Fig. S1 Non-metric multidimensional scaling of variation in benthic composition among surveyed reefs at Lizard Island, in September 2015 (saturated colour) and October 2016 (paled colour), seven months before and six months after the 2016 bleaching event: (A) Spatial variation in benthic composition of transects on square root transformed data: Data symbols represent habitat types: Branching *Porites* (blue triangle), low coral cover (orange cross), mixed (purple circle), massive *Porites* (green inverted triangle), *Pocillopora* (red square), soft coral (pink diamond); (B) Relative contribution of substratum categories to the observed variation in benthic composition.

Table S1 Fish traits assigned to surveyed species. Trait classification based on mean observed size information and published literature (Wilson et al. 2008; Green et al. 2009; Pratchett et al. 2011; Mouillot et al. 2013), and FishBase (Froese and Pauly 2014). Schooling trait categories abbreviated as follows: Small groups (SmallG); medium groups (MedG); large groups (LargeG).

Species	Observed mean size (TL, cm)	Diet	Mobility	Time of activity	Social grouping	Position in water
Abudefduf bengalensis	≤10	Planktivore	Sedentary	Diurnal	MedG	Bentho-pelagic
Abudefduf sexfasciatus	≤10	Planktivore	Sedentary	Diurnal	MedG	Bentho-pelagic
Abudefduf vaigiensis	≤10	Mixed diet	Sedentary	Diurnal	MedG	Bentho-pelagic
Abudefduf whitleyi	≤10	Planktivore	Sedentary	Diurnal	MedG	Bentho-pelagic
Acanthochromis polyacanthus	≤10	Planktivore	Sedentary	Diurnal	MedG	Benthic
Acanthurus blochii	11-20	Grazer/detritivore	Mobile within reef	Diurnal	SmallG	Benthic
Acanthurus dussumieri	11-20	Grazer/detritivore	Sedentary	Nocturnal	MedG	Bentho-pelagic
Acanthurus grammoptilus	11-20	Grazer/detritivore	Mobile within reef	Diurnal	SmallG	Bentho-pelagic
Acanthurus lineatus	11-20	Mixed diet	Sedentary	Diurnal	Solitary	Bentho-pelagic
Acanthurus nigricauda	11-20	Grazer/detritivore	Mobile within reef	Diurnal	SmallG	Benthic
Acanthurus nigrofuscus	≤10	Grazer/detritivore	Sedentary	Diurnal	SmallG	Benthic
Acanthurus olivaceus	21-30	Grazer/detritivore	Mobile within reef	Diurnal	SmallG	Benthic
Acanthurus xanthopterus	21-30	Grazer/detritivore	Mobile within reef	Diurnal	MedG	Benthic
Amblyglyphidodon curacao	≤10	Planktivore	Sedentary	Diurnal	MedG	Bentho-pelagic
Amblyglyphidodon leucogaster	≤10	Planktivore	Sedentary	Diurnal	MedG	Bentho-pelagic
Amphiprion clarkii	≤10	Planktivore	Sedentary	Diurnal	SmallG	Benthic
Amphiprion melanopus	≤10	Planktivore	Sedentary	Diurnal	SmallG	Benthic
Anampses geographicus	≤10	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Anampses neoguinaicus	11-20	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Apogon compressus	≤10	Planktivore	Sedentary	Nocturnal	MedG	Bentho-pelagic
Apogon cyanosoma	≤10	Planktivore	Sedentary	Nocturnal	MedG	Bentho-pelagic
Aprion virescens	41-50	Piscivore	Mobile across reefs	Both	SmallG	Bentho-pelagic
Archamia zosterophora	≤10	Planktivore	Sedentary	Nocturnal	MedG	Bentho-pelagic
Arothron hispidus	21-30	Mixed diet	Mobile within reef	Diurnal	Solitary	Benthic
Arothron nigropunctatus	11-20	Corallivore	Mobile within reef	Diurnal	Solitary	Benthic
Arothron stellatus	21-30	Mixed diet	Mobile within reef	Diurnal	Solitary	Benthic

Balistapus undulatus	11-20	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Balistoides viridescens	21-30	Corallivore	Mobile within reef	Diurnal	Solitary	Benthic
Bodianus mesothorax	≤10	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Caesio cuning	≤10	Planktivore	Mobile across reefs	Diurnal	LargeG	Pelagic
Canthigaster amboinensis	≤10	Mixed diet	Sedentary	Diurnal	Solitary	Benthic
Canthigaster solandri	≤10	Mixed diet	Sedentary	Diurnal	Solitary	Benthic
Canthigaster valentini	≤10	Mixed diet	Sedentary	Diurnal	Solitary	Benthic
Caranx ignobilis	>60	Piscivore	Mobile across reefs	Diurnal	Solitary	Pelagic
Caranx melampygus	≤10	Piscivore	Mobile across reefs	Both	SmallG	Pelagic
Centropyge bicolor	≤10	Grazer/detritivore	Sedentary	Diurnal	Pairing	Benthic
Centropyge vrolikii	≤10	Grazer/detritivore	Sedentary	Diurnal	Pairing	Benthic
Cephalopholis cyanostigma	21-30	Mixed diet	Sedentary	Both	Solitary	Benthic
Cephalopholis microprion	≤10	Mixed diet	Sedentary	Both	Solitary	Benthic
Cetoscarus ocellatus	31-40	Excavator	Mobile within reef	Diurnal	SmallG	Benthic
Chaetodon aureofasciatus	≤10	Corallivore	Sedentary	Diurnal	Pairing	Benthic
Chaetodon auriga	≤10	Invertivore	Sedentary	Diurnal	Pairing	Benthic
Chaetodon baronessa	≤10	Corallivore	Sedentary	Diurnal	Pairing	Benthic
Chaetodon citrinellus	≤10	Corallivore	Sedentary	Diurnal	Pairing	Benthic
Chaetodon ephippium	≤10	Invertivore	Sedentary	Diurnal	Pairing	Benthic
Chaetodon kleinii	11-20	Corallivore	Sedentary	Diurnal	Pairing	Bentho-pelagic
Chaetodon lineolatus	≤10	Invertivore	Sedentary	Diurnal	Pairing	Benthic
Chaetodon lunulatus	≤10	Corallivore	Sedentary	Diurnal	Pairing	Benthic
Chaetodon melannotus	≤10	Corallivore	Sedentary	Diurnal	Pairing	Benthic
Chaetodon plebeius	≤10	Corallivore	Sedentary	Diurnal	Pairing	Benthic
Chaetodon rafflesi	11-20	Invertivore	Sedentary	Diurnal	Pairing	Benthic
Chaetodon rainfordi	≤10	Corallivore	Sedentary	Diurnal	Pairing	Benthic
Chaetodon trifascialis	≤10	Corallivore	Sedentary	Diurnal	Pairing	Benthic
Chaetodon vagabundus	≤10	Invertivore	Sedentary	Diurnal	Pairing	Benthic
Cheilinus chlorourus	11-20	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Cheilinus fasciatus	11-20	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Cheilinus trilobatus	≤10	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Cheilinus undulatus	51-60	Mixed diet	Mobile within reef	Diurnal	Solitary	Benthic
Cheilodipterus artus	≤10	Piscivore	Sedentary	Nocturnal	SmallG	Bentho-pelagic
Cheilodipterus macrodon	11-20	Mixed diet	Sedentary	Nocturnal	Solitary	Bentho-pelagic

Cheilodipterus quinquelineatus	≤10	Mixed diet	Sedentary	Nocturnal	SmallG	Bentho-pelagic
Cheiloprion labiatus	≤10	Corallivore	Sedentary	Diurnal	Solitary	Benthic
Chelmon rostratus	≤10	Invertivore	Sedentary	Diurnal	Pairing	Benthic
Chlorurus bleekeri	21-30	Excavator	Mobile within reef	Diurnal	SmallG	Benthic
Chlorurus microrhinos	11-20	Excavator	Mobile within reef	Diurnal	SmallG	Benthic
Chlorurus sordidus	≤10	Excavator	Mobile within reef	Diurnal	SmallG	Benthic
Choerodon anchorago	31-40	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Choerodon fasciatus	11-20	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Choerodon schoenleinii	31-40	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Chromis atripectoralis	≤10	Planktivore	Sedentary	Diurnal	LargeG	Bentho-pelagic
Chromis sp	≤10	Planktivore	Sedentary	Diurnal	MedG	Bentho-pelagic
Chromis ternatensis	≤10	Planktivore	Sedentary	Diurnal	MedG	Bentho-pelagic
Chromis viridis	≤10	Planktivore	Sedentary	Diurnal	LargeG	Bentho-pelagic
Chrysiptera cyanea	≤10	Planktivore	Sedentary	Diurnal	SmallG	Benthic
Chrysiptera flavipinnis	≤10	Planktivore	Sedentary	Diurnal	SmallG	Benthic
Chrysiptera rollandi	≤10	Planktivore	Sedentary	Diurnal	SmallG	Benthic
Coris aygula	≤10	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Coris batuensis	≤10	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Corythoichthys sp	≤10	Invertivore	Sedentary	Diurnal	SmallG	Benthic
Cromileptes altivelis	31-40	Piscivore	Sedentary	Both	Solitary	Benthic
Ctenochaetus binotatus	≤10	Grazer/detritivore	Sedentary	Diurnal	Solitary	Benthic
Ctenochaetus cyanocheilus	≤10	Grazer/detritivore	Sedentary	Diurnal	SmallG	Benthic
Ctenochaetus striatus	≤10	Grazer/detritivore	Sedentary	Diurnal	MedG	Benthic
Dascyllus aruanus	≤10	Planktivore	Sedentary	Diurnal	MedG	Benthic
Dascyllus reticulatus	≤10	Planktivore	Sedentary	Diurnal	MedG	Benthic
Dascyllus trimaculatus	11-20	Planktivore	Sedentary	Diurnal	SmallG	Benthic
Diagramma pictum	21-30	Invertivore	Mobile within reef	Diurnal	MedG	Benthic
Dischistodus melanotus	≤10	Farmer	Sedentary	Diurnal	Solitary	Benthic
Dischistodus perspicillatus	≤10	Farmer	Sedentary	Diurnal	SmallG	Benthic
Dischistodus prosopotaenia	≤10	Farmer	Sedentary	Diurnal	SmallG	Benthic
Dischistodus pseudochrysopoecilus	≤10	Farmer	Sedentary	Diurnal	SmallG	Benthic
Epibulus insidiator	11-20	Piscivore	Mobile within reef	Diurnal	Solitary	Benthic
Epinephelus fasciatus	11-20	Piscivore	Sedentary	Diurnal	LargeG	Benthic
Epinephelus hexagonatus	31-40	Mixed diet	Mobile within reef	Both	Solitary	Benthic

Epinephelus maculatus	21-30	Mixed diet	Mobile within reef	Both	Solitary	Benthic
Epinephelus merra	11-20	Mixed diet	Mobile within reef	Both	Solitary	Benthic
Epinephelus ongus	31-40	Mixed diet	Mobile within reef	Both	Solitary	Benthic
Fistularia commersonii	>60	Piscivore	Sedentary	Diurnal	Pairing	Bentho-pelagic
Gomphosus varius	≤10	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Halichoeres chloropterus	≤10	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Halichoeres hortulanus	≤10	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Halichoeres marginatus	≤10	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Halichoeres melanurus	≤10	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Halichoeres nebulosus	≤10	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Hemigymnus fasciatus	≤10	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Hemigymnus melapterus	≤10	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Heniochus chrysostomus	≤10	Corallivore	Sedentary	Diurnal	Pairing	Benthic
Heniochus varius	≤10	Invertivore	Sedentary	Diurnal	Pairing	Benthic
Hipposcarus longiceps	21-30	Scraper	Mobile within reef	Diurnal	MedG	Benthic
Holocentridae sp	≤10	Mixed diet	Mobile within reef	Nocturnal	Solitary	Bentho-pelagic
Kyphosus cinerascens	11-20	Browser	Mobile across reefs	Diurnal	MedG	Bentho-pelagic
Kyphosus vaigiensis	11-20	Browser	Mobile across reefs	Diurnal	MedG	Bentho-pelagic
Labrichthys unilineatus	≤10	Corallivore	Sedentary	Diurnal	Solitary	Benthic
Labroides dimidiatus	≤10	Invertivore	Sedentary	Diurnal	Pairing	Benthic
Lates calcarifer	51-60	Mixed diet	Mobile within reef	Nocturnal	Solitary	Benthic
Lethrinus nebulosus	11-20	Mixed diet	Mobile across reefs	Nocturnal	MedG	Benthic
Lethrinus obsoletus	21-30	Mixed diet	Mobile within reef	Nocturnal	SmallG	Benthic
Lutjanus bohar	21-30	Piscivore	Mobile within reef	Nocturnal	MedG	Bentho-pelagic
Lutjanus carponotatus	11-20	Mixed diet	Mobile within reef	Nocturnal	MedG	Bentho-pelagic
Lutjanus ehrenbergii	≤10	Mixed diet	Mobile within reef	Both	SmallG	Bentho-pelagic
Lutjanus fulviflamma	21-30	Mixed diet	Mobile within reef	Both	MedG	Bentho-pelagic
Lutjanus fulvus	11-20	Piscivore	Mobile within reef	Both	SmallG	Bentho-pelagic
Lutjanus gibbus	≤10	Piscivore	Mobile within reef	Both	MedG	Benthic
Lutjanus kasmira	≤10	Mixed diet	Mobile within reef	Nocturnal	LargeG	Bentho-pelagic
Lutjanus quinquelineatus	≤10	Mixed diet	Mobile within reef	Nocturnal	LargeG	Bentho-pelagic
Lutjanus russelli	11-20	Piscivore	Mobile within reef	Nocturnal	SmallG	Bentho-pelagic
Macropharyngodon meleagris	11-20	Invertivore	Sedentary	Diurnal	SmallG	Benthic
Monotaxis grandoculis	≤10	Invertivore	Mobile within reef	Nocturnal	Solitary	Bentho-pelagic

Mulloidichthys flavolineatus	21-30	Invertivore	Mobile within reef	Diurnal	MedG	Benthic
Myripristis sp	11-20	Planktivore	Sedentary	Nocturnal	Pairing	Benthic
Naso brevirostris	11-20	Grazer/detritivore	Mobile across reefs	Diurnal	LargeG	Bentho-pelagic
Naso lituratus	21-30	Browser	Mobile within reef	Diurnal	SmallG	Benthic
Naso unicornis	11-20	Browser	Mobile within reef	Diurnal	SmallG	Benthic
Naso vlamingii	11-20	Planktivore	Mobile across reefs	Diurnal	SmallG	Bentho-pelagic
Neoglyphidodon melas	≤10	Corallivore	Sedentary	Diurnal	Solitary	Benthic
Neoglyphidodon nigroris	≤10	Mixed diet	Sedentary	Diurnal	SmallG	Benthic
Neopomacentrus azysron	≤10	Planktivore	Sedentary	Diurnal	LargeG	Bentho-pelagic
Neopomacentrus bankieri	≤10	Planktivore	Sedentary	Diurnal	LargeG	Bentho-pelagic
Neopomacentrus cyanomos	≤10	Planktivore	Sedentary	Diurnal	LargeG	Bentho-pelagic
Oxycheilinus digramma	11-20	Piscivore	Mobile within reef	Diurnal	Solitary	Bentho-pelagic
Parupeneus barberinus	≤10	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Parupeneus ciliatus	11-20	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Parupeneus cyclostomus	11-20	Piscivore	Mobile within reef	Diurnal	Solitary	Benthic
Parupeneus multifasciatus	≤10	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Plagiotremus tapeinosoma	≤10	Mixed diet	Sedentary	Diurnal	Solitary	Benthic
Platax pinnatus	11-20	Mixed diet	Mobile across reefs	Diurnal	MedG	Bentho-pelagic
Plectorhinchus albovittatus	51-60	Mixed diet	Mobile within reef	Diurnal	Solitary	Bentho-pelagic
Plectorhinchus chaetodonoides	31-40	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Plectorhinchus chrysotaenia	31-40	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Plectorhinchus gibbosus	41-50	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Plectorhinchus lineatus	21-30	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Plectroglyphidodon dickii	≤10	Mixed diet	Sedentary	Diurnal	Solitary	Benthic
Plectroglyphidodon lacrymatus	≤10	Farmer	Sedentary	Diurnal	Solitary	Benthic
Plectropomus laevis	31-40	Piscivore	Mobile within reef	Diurnal	Solitary	Benthic
Plectropomus leopardus	21-30	Piscivore	Mobile within reef	Diurnal	Solitary	Benthic
Pomacanthus sexstriatus	21-30	Mixed diet	Sedentary	Diurnal	Solitary	Benthic
Pomacanthus xanthometopon	21-30	Invertivore	Sedentary	Diurnal	Solitary	Benthic
Pomacentrus adelus	≤10	Farmer	Sedentary	Diurnal	SmallG	Benthic
Pomacentrus amboinensis	≤10	Planktivore	Sedentary	Diurnal	MedG	Benthic
Pomacentrus bankanensis	≤10	Farmer	Sedentary	Diurnal	SmallG	Benthic
Pomacentrus brachialis	≤10	Farmer	Sedentary	Diurnal	MedG	Bentho-pelagic
Pomacentrus chrysurus	≤10	Farmer	Sedentary	Diurnal	SmallG	Benthic

Pomacentrus grammorhynchus	≤10	Farmer	Sedentary	Diurnal	SmallG	Benthic
Pomacentrus lepidogenys	≤10	Planktivore	Sedentary	Diurnal	SmallG	Benthic
Pomacentrus moluccensis	≤10	Planktivore	Sedentary	Diurnal	MedG	Benthic
Pomacentrus nagasakiensis	≤10	Planktivore	Sedentary	Diurnal	SmallG	Benthic
Pomacentrus reidi	≤10	Mixed diet	Sedentary	Diurnal	SmallG	Benthic
Pomacentrus simsiang	≤10	Mixed diet	Sedentary	Diurnal	SmallG	Benthic
Pomacentrus tripunctatus	≤10	Mixed diet	Sedentary	Diurnal	SmallG	Benthic
Pomacentrus wardi	≤10	Farmer	Sedentary	Diurnal	SmallG	Benthic
Premnas biaculeatus	≤10	Planktivore	Sedentary	Diurnal	SmallG	Benthic
Priacanthus hamrur	31-40	Mixed diet	Mobile within reef	Nocturnal	SmallG	Bentho-pelagic
Pseudocheilinus evanidus	≤10	Invertivore	Sedentary	Diurnal	Solitary	Benthic
Ptereleotris evides	≤10	Planktivore	Sedentary	Diurnal	SmallG	Benthic
Pterocaesio marri	≤10	Planktivore	Mobile across reefs	Diurnal	LargeG	Pelagic
Sargocentron spiniferum	21-30	Mixed diet	Mobile within reef	Nocturnal	Solitary	Bentho-pelagic
Scarus altipinnis	11-20	Scraper	Mobile within reef	Diurnal	LargeG	Benthic
Scarus chameleon	21-30	Scraper	Mobile within reef	Diurnal	Solitary	Benthic
Scarus dimidiatus	≤10	Scraper	Mobile within reef	Diurnal	SmallG	Benthic
Scarus flavipectoralis	21-30	Scraper	Mobile within reef	Diurnal	Solitary	Benthic
Scarus frenatus	21-30	Scraper	Mobile within reef	Diurnal	Solitary	Benthic
Scarus ghobban	11-20	Scraper	Mobile within reef	Diurnal	SmallG	Benthic
Scarus globiceps	11-20	Scraper	Mobile within reef	Diurnal	Solitary	Benthic
Scarus niger	21-30	Scraper	Mobile within reef	Diurnal	Solitary	Benthic
Scarus oviceps	21-30	Scraper	Mobile within reef	Diurnal	Solitary	Benthic
Scarus psittacus	21-30	Scraper	Mobile within reef	Diurnal	MedG	Benthic
Scarus rivulatus	11-20	Scraper	Mobile within reef	Diurnal	MedG	Benthic
Scarus schlegeli	21-30	Scraper	Mobile within reef	Diurnal	MedG	Benthic
Scarus sp	≤10	Scraper	Mobile within reef	Diurnal	SmallG	Benthic
Scarus spinus	11-20	Scraper	Mobile within reef	Diurnal	Solitary	Benthic
Scolopsis bilineata	≤10	Invertivore	Mobile within reef	Diurnal	Solitary	Benthic
Scolopsis lineata	≤10	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Scolopsis margaritifer	≤10	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Scolopsis monogramma	11-20	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Scorpaenopsis sp	≤10	Mixed diet	Sedentary	Diurnal	Solitary	Benthic
Siganus corallinus	≤10	Grazer/detritivore	Mobile within reef	Diurnal	Pairing	Benthic

Siganus doliatus	≤10	Grazer/detritivore	Mobile within reef	Diurnal	Pairing	Benthic
Siganus lineatus	≤10	Grazer/detritivore	Mobile across reefs	Nocturnal	MedG	Benthic
Siganus puellus	≤10	Grazer/detritivore	Mobile within reef	Diurnal	Pairing	Benthic
Siganus punctatissimus	11-20	Grazer/detritivore	Mobile within reef	Diurnal	Pairing	Benthic
Siganus punctatus	11-20	Grazer/detritivore	Mobile within reef	Diurnal	Pairing	Benthic
Siganus sp	≤10	Grazer/detritivore	Mobile within reef	Diurnal	Pairing	Benthic
Siganus vulpinus	11-20	Grazer/detritivore	Mobile within reef	Diurnal	Pairing	Benthic
Sphaeramia nematoptera	≤10	Invertivore	Sedentary	Nocturnal	MedG	Bentho-pelagic
Stegastes apicalis	≤10	Farmer	Sedentary	Diurnal	SmallG	Benthic
Stegastes fasciolatus	≤10	Farmer	Sedentary	Diurnal	SmallG	Benthic
Stegastes nigricans	≤10	Farmer	Sedentary	Diurnal	MedG	Benthic
Stethojulis bandanensis	≤10	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Stethojulis interrupta	≤10	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Sufflamen chrysopterum	11-20	Invertivore	Sedentary	Diurnal	Solitary	Benthic
Thalassoma hardwicke	≤10	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Thalassoma jansenii	≤10	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Thalassoma lunare	≤10	Invertivore	Mobile within reef	Diurnal	SmallG	Benthic
Zanclus cornutus	≤10	Mixed diet	Mobile within reef	Diurnal	SmallG	Benthic
Zebrasoma scopas	≤10	Grazer/detritivore	Mobile within reef	Diurnal	SmallG	Benthic
Zebrasoma velifer	≤10	Grazer/detritivore	Mobile within reef	Diurnal	Pairing	Benthic
Zoramia fragilis	≤10	Planktivore	Sedentary	Nocturnal	LargeG	Bentho-pelagic

Table S2 One-way PERMANOVA pairwise comparisons of benthic composition among coral habitats in September 2015. Comparisons based on Bray-Curtis similarities of unrestricted permutation of raw data (>7750 permutations). Benthic variables consistently contributing to average similarity within (sim/SD >4; grey shaded boxes), and dissimilarity between habitats (unshaded boxes; diss/SD >2), identified in one-way SIMPER are listed.

	Branching *Porites*	Low coral cover	Massive *Porites*	Mixed	*Pocillopora*	Soft coral
Branching *Porites*	Branching *Porites* Dead substrate **Av.sim. 74.85%**	Branching *Porites* Macroalgae **Av.dissim. 43.96%**	Branching *Porites* Massive *Porites* **Av.dissim. 38.15%**	Branching *Porites* **Av.dissim. 38.19%**	Branching *Porites* *Pocillopora* **Av.dissim. 50.41%**	Branching *Porites* Soft coral **Av.dissim. 46.08%**
Low coral cover	***P* = 0.0001**	Dead substrate **Av.sim. 76.90%**	Macroalgae Massive *Porites* **Av.dissim. 38.20%**	Macroalgae **Av.dissim. 38.63%**	Macroalgae *Pocillopora* **Av.dissim. 45.61%**	Macroalgae Soft coral **Av.dissim. 44.20%**
Massive *Porites*	***P* = 0.0001**	***P* = 0.0001**	Massive *Porites* Dead substrate Soft coral **Av.sim. 79.73%**	**Av.dissim. 28.21%**	Massive *Porites* *Pocillopora* **Av.dissim. 42.85%**	Massive *Porites* Soft coral **Av.dissim. 36.21%**
Mixed	***P* = 0.0001**	***P* = 0.0001**	***P* = 0.0002**	Dead substrate **Av.sim. 72.23%**	*Pocillopora* **Av.dissim. 38.60%**	Soft coral **Av.dissim. 36.39%**
Pocillopora	***P* = 0.0001**	***P* = 0.0001**	***P* = 0.0002**	***P* = 0.0001**	*Pocillopora* Dead substrate Soft coral **Av.sim. 80.08%**	Soft coral *Pocillopora* **Av.dissim. 43.38%**
Soft coral	***P* = 0.0001**	***P* = 0.0001**	***P* = 0.0001**	***P* = 0.0001**	***P* = 0.0001**	Soft coral Dead substrate Rubble **Av.sim. 81.01%**

Table S3 Mean ± SE benthic cover of surveyed habitats, before (September 2015) and after (October 2016) the 2016 bleaching event.

Habitat	Period	Total coral cover (%)	Dominant coral taxa or substratum (degraded habitat)	Proportion of total coral cover (%)	Proportion of total substrate (%)
Branching *Porites*	Sept-15	57.13 ± 2.79	Branching *Porites*	78.03 ± 4.83	44.26 ± 3.39
	Oct-16	42.08 ± 2.30 ***		73.07 ± 5.30	31.48 ± 3.06
Low coral cover	Sept-15	10.46 ± 1.80	Dead substrate and macroalgae	66.29 ± 2.74	62.30 ± 2.74
	Oct-16	14.63 ± 1.87 *		57.78 ± 2.25	57.78 ± 2.25
Massive *Porites*	Sept-15	49.37 ± 2.81	Massive *Porites*	51.47 ± 4.55	26.04 ± 3.03
	Oct-16	46.60 ± 3.19		63.01 ± 5.55	30.90 ± 4.13
Mixed	Sept-15	46.63 ± 3.07	n/a	-	-
	Oct-16	29.03 ± 2.43 ***		-	-
Pocillopora	Sept-15	39.31 ± 6.01	*Pocillopora*	62.89 ± 4.15	24.72 ± 3.95
	Oct-16	35.83 ± 3.41		75.25 ± 6.27	26.53 ± 2.63
Soft coral	Sept-15	59.49 ± 1.93	Soft coral	90.05 ± 2.02	53.98 ± 2.64
	Oct-16	28.56 ± 2.65 ***		71.64 ± 5.54	21.76 ± 3.00

* Asterisks indicate the habitats where there was significant change in total coral cover (*, $P \leq 0.05$; **, $P < 0.01$; ***, $P < 0.001$).

Table S4 Percentage of coral taxa observed within colour saturation categories during April 2016 (and October 2016 shown in brackets), the bleaching event at Lizard Island.

Coral taxa (and growth form variation)	**Bleached (1-2)**	**Mid-range (3)**	**Saturated (4-6)**
Acropora (bottlebrush)	**100**	(100*)	
Acropora (bushy)	**100**	(100*)	
Acropora (corymbose)	**76** (50)	24 (17*)	(33)
Acropora (digitate)	**67**	(33*)	33* (67)
Acropora (staghorn)	**79** (17)	18 (75)	3* (8*)
Astreopora	**75** (67)	25* (33*)	
Aveopora			**100**
Coeloseris	**100**	(83)	(17*)
Cyphastrea		**100*** (100*)	
Diploastrea		3*	97 (100)
Echinopora (branching)	**55** (57)	15 (39)	30 (4*)
Echinopora (plate/columnar)	**52** (18)	36 (35)	12 (48)
Favia	**67** (33)	8* (33)	25 (33)
Favites	**55** (100)	18	27
Fungia	27 (5)	33 (24)	**40** (71)
Galaxea	**70** (23)	(15)	30 (62)
Goniastrea	**85** (33)	10 (50)	5* (17)
Goniopora	**53** (38)	23 (24)	23 (38)
Heliopora	2 (30)	36 (34)	**62** (36)
Hydnophora	**60** (100*)		40
Isis			**100*** (100*)
Isopora	**75**	25* (100*)	
Leptastrea			**100***
Leptoseris	(75)		
Lobophyllia	18 (11*)	**65** (56)	18 (33)
Lobophyton	**76** (27)	24 (39)	<1 (35)
Merulina	**52** (14)	30 (69)	17 (17)
Montastrea	**80** (20*)	20* (60)	(20*)
Montipora	**57** (42)	34 (51)	9 (7)
Pachyseris	**100** (11*)	(78)	(11*)
Pavona	23 (46)	**38** (38)	**38** (15)
Pectina	**100***	(67)	(33*)
Physogyra	**100***		
Platygyra	**43** (40)	29 (20*)	29 (40)
Pocillopora (branching)	**58** (15)	11 (76)	30 (8)
Porites (branching)	45 (79)	**50** (17)	6 (3)
Porites (encrusting)	24 (67)	**76** (17*)	(17*)
Porites (massive)	**44** (29)	33 (44)	23 (27)
Porites (submassive)	13 (18)	**70** (57)	17 (24)
Psammacora	28 (17)	**56** (30)	17 (52)
Sarcophyton	47 (11)	**52** (61)	1 (28)
Seriatopora	**100**	(50*)	(50*)
Sinularia	**80** (16)	19 (57)	(27)
Soft coral other	**73** (7*)	(13)	27 (80)
Stylophora	**100** (50*)	(50*)	
Symphyllia		**100*** (50)	(50)
Turbinaria	18	**65** (100)	18

* Asterisks indicate where only one observation was made during the respective survey period (April or October 2016).

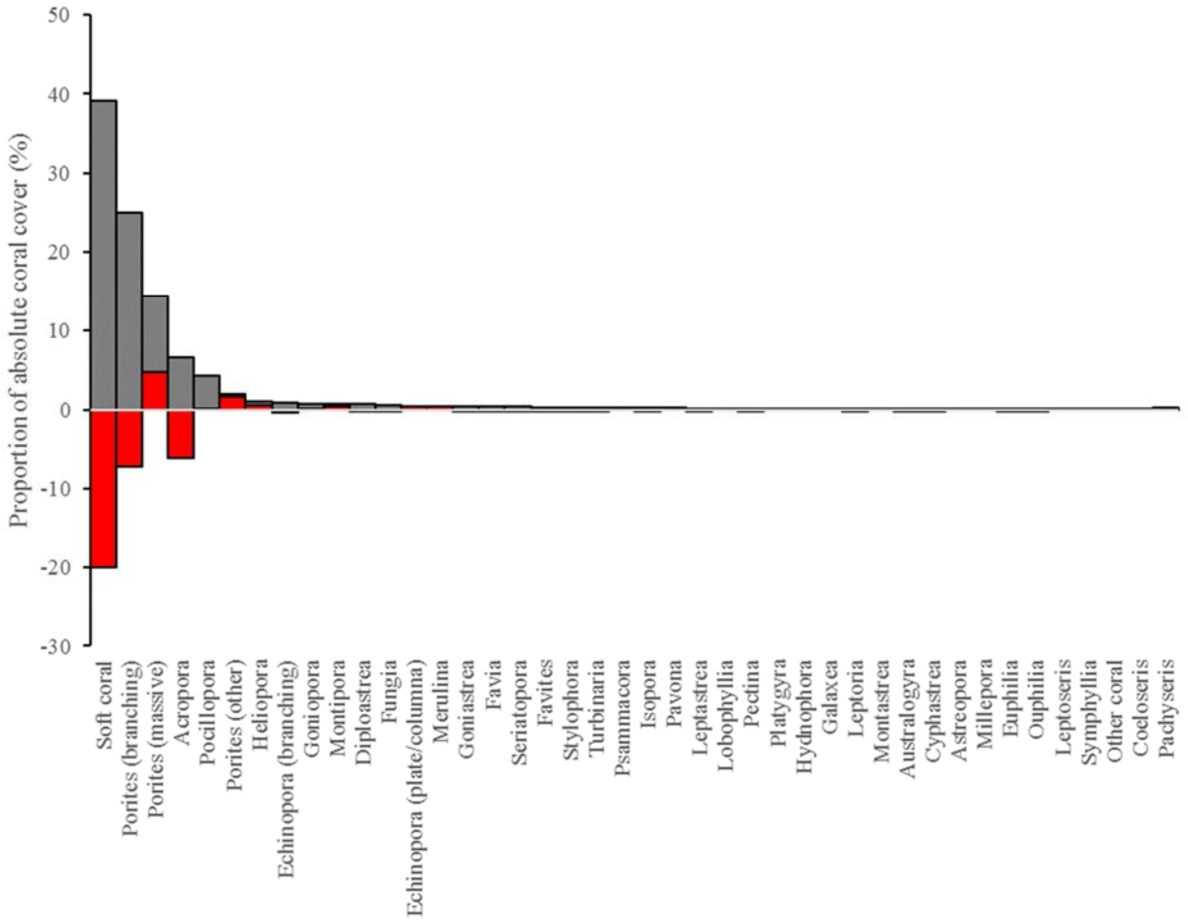

Fig. S2 Percentage of coral taxa as a proportion of total coral cover in September 2015 (grey bars), and the change in cover by October 2016 (red bars).

Table S5 Planned comparisons (effect sizes and 95% confidence intervals; CI) of coral cover and fish assemblage responses to the 2016-bleaching event (September 2015 vs October 2016) among distinct reef habitats, using contrast analyses of linear mixed effects models.

Response	Habitat	Period contrast	Lower CI	Upper CI	Test statistic	*df*	*P*
Total coral cover	**Branching *Porites***	**-15.049**	**-21.725**	**-8.373**	**-4.44**	**265**	**<0.001**
	Low coral cover	4.166	-2.510	10.842	1.23	265	0.22
	Mixed coral	**-17.875**	**-23.882**	**-11.867**	**-5.86**	**265**	**<0.001**
	Massive *Porites*	-2.776	-10.952	5.400	-0.67	265	0.50
	Pocillopora	-3.473	-15.036	8.089	-0.59	265	0.55
	Soft coral	**-30.927**	**-37.603**	**-24.251**	**-9.12**	**265**	**<0.001**
Fish species richness	**Branching *Porites***	**0.879**	**0.775**	**0.996**	**-2.03**	**266**	**0.04**
	Low coral cover	1.054	0.920	1.209	0.76	266	0.44
	Mixed coral	0.903	0.810	1.006	-1.87	266	0.06
	Massive *Porites*	0.899	0.768	1.053	-1.32	266	0.19
	Pocillopora	**0.793**	**0.648**	**0.972**	**-2.25**	**266**	**0.02**
	Soft coral	1.013	0.891	1.151	0.20	266	0.85
Total fish abundance	Branching *Porites*	0.769	0.584	1.014	-1.87	265	0.06
	Low coral cover	1.206	0.911	1.600	1.32	265	0.19
	Mixed coral	0.802	0.624	1.030	-1.74	265	0.08
	Massive *Porites*	1.120	0.798	1.573	0.66	265	0.51
	Pocillopora	0.703	0.436	1.134	-1.45	265	0.15
	Soft coral	**1.597**	**1.210**	**2.108**	**3.32**	**265**	**<0.001**
Functional richness	Branching *Porites*	-0.048	-0.117	0.021	-1.36	265	0.18
	Low coral cover	0.020	-0.049	0.089	0.56	265	0.58
	Mixed coral	-0.041	-0.104	0.021	-1.31	265	0.19
	Massive *Porites*	-0.001	-0.086	0.084	-0.02	265	0.98
	Pocillopora	**-0.135**	**-0.255**	**-0.015**	**-2.22**	**265**	**0.03**
	Soft coral	-0.026	-0.095	0.043	-0.73	265	0.47
Functional dispersion	**Branching *Porites***	**0.047**	**0.018**	**0.077**	**3.14**	**265**	**0.002**
	Low coral cover	**-0.046**	**-0.075**	**-0.016**	**-3.04**	**265**	**0.003**
	Mixed coral	0.008	-0.019	0.034	0.56	265	0.58
	Massive *Porites*	-0.026	-0.062	0.010	-1.41	265	0.16
	Pocillopora	-0.010	-0.061	0.041	-0.40	265	0.69
	Soft coral	-0.021	-0.050	0.008	-1.40	265	0.16
Functional originality	**Branching *Porites***	**0.062**	**0.024**	**0.099**	**3.24**	**260**	**0.001**
	Low coral cover	0.007	-0.019	0.033	0.53	260	0.60
	Mixed coral	0.022	-0.006	0.049	1.53	260	0.13
	Massive *Porites*	-0.001	-0.035	0.034	-0.03	260	0.97
	Pocillopora	0.013	-0.014	0.041	0.97	260	0.33
	Soft coral	0.011	-0.027	0.049	0.56	260	0.57

Table S6 Mean ± SE fish assemblage species richness (number of species), total abundance, and fish functional diversity indices for each coral habitat.

Habitat	Period	Fish species richness	Total fish abundance	Functional richness	Functional dispersion	Functional originality
Branching *Porites*	Sept-15	29.33 ± 1.14	1016.61 ± 127.80	0.36 ± 0.03	0.26 ± 0.01	0.08 ± 0.01
	April-16	31.83 ± 1.32	1436.06 ± 248.83	0.36 ± 0.02	0.29 ± 0.01	0.12 ± 0.02
	Oct-16	25.78 ± 1.25	748.33 ± 61.81	0.31 ± 0.04	0.31 ± 0.01	0.14 ± 0.01
Low coral cover	Sept-15	22.44 ± 1.31	295.06 ± 68.06	0.21 ± 0.03	0.32 ± 0.01	0.14 ± 0.01
	April-16	28.44 ± 1.34	534.50 ± 63.26	0.30 ± 0.02	0.29 ± 0.01	0.13 ± 0.01
	Oct-16	23.67 ± 1.30	336.89 ± 31.83	0.23 ± 0.02	0.27 ± 0.01	0.15 ± 0.01
Massive *Porites*	Sept-15	27.33 ± 1.96	401.17 ± 34.34	0.28 ± 0.03	0.31 ± 0.01	0.12 ± 0.01
	April-16	24.75 ± 1.30	629.25 ± 73.47	0.27 ± 0.03	0.28 ± 0.01	0.11 ± 0.01
	Oct-16	24.58 ± 1.56	456.67 ± 55.10	0.28 ± 0.04	0.28 ± 0.01	0.11 ± 0.01
Mixed	Sept-15	31.10 ± 1.46	693.43 ± 71.14	0.36 ± 0.03	0.29 ± 0.01	0.13 ± 0.01
	April-16	36.96 ± 1.48	1100.04 ± 89.40	0.41 ± 0.02	0.29 ± 0.01	0.09 ± 0.01
	Oct-16	28.46 ± 1.61	575.67 ± 53.88	0.32 ± 0.03	0.30 ± 0.01	0.14 ± 0.01
Pocillopora	Sept-15	35.50 ± 3.47	885.33 ± 119.67	0.31 ± 0.04	0.25 ± 0.03	0.04 ± 0.01
	April-16	34.50 ± 1.38	953.67 ± 184.56	0.24 ± 0.03	0.27 ± 0.02	0.06 ± 0.01
	Oct-16	28.17 ± 1.25	622.67 ± 81.67	0.17 ± 0.04	0.24 ± 0.02	0.05 ± 0.01
Soft coral	Sept-15	26.11 ± 1.25	336.61 ± 21.57	0.30 ± 0.03	0.34 ± 0.01	0.14 ± 0.01
	April-16	27.78 ± 1.23	882.61 ± 152.04	0.28 ± 0.02	0.29 ± 0.01	0.10 ± 0.01
	Oct-16	26.44 ± 1.28	562.94 ± 72.24	0.28 ± 0.03	0.31 ± 0.01	0.15 ± 0.02

Table S7 Top candidate models selected to describe fish assemblage response variables with explanatory variables period, habitat, and total coral cover (%). Asterisks indicate models with the fewest degrees of freedom considered most parsimonious. Models are ranked by Akaike's information criteria (AICc), with all models within ΔAICc < 2 of the top ranked model. The relative weight of evidence for each model is indicated by Akaike weight (wAICc), and the variables present in each model are indicated with an X. The relative importance of each variable based on the sum of Akaike weights of the models in which the variable is present.

Response	Model rank	AICc	*df*	logLik	ΔAICc	wAICc	Period	Habitat	Period: Habitat	Coral cover (%)
Species richness	1	1813.14	19	-886.13	0.00	0.31	X	X	X	
	2	1813.66	9	-897.50	0.53	0.23	X	X		
	3	1814.37	10	-896.78	1.24	0.16	X	X		X
	4	1814.54	20	-885.68	1.41	0.15	X	X	X	X
	5 *	**1814.66**	**4**	**-903.26**	**1.53**	**0.14**	**X**			
					Relative importance		1.00	0.86	0.46	0.32
Total abundance	1	4010.27	21	-1982.38	0.00	0.65	X	X	X	X
	2	**4011.51**	**20**	**-1984.16**	**1.24**	**0.35**	**X**	**X**	**X**	
					Relative importance		1.00	1.00	1.00	0.65
Functional richness	1	-429.36	6	220.83	0.00	0.46	X			X
	2 *	**-428.91**	**5**	**219.56**	**0.45**	**0.37**	**X**			
	3	-427.44	10	224.12	1.92	0.18	X	X		
					Relative importance		1.00	0.18	NA	0.46
Functional dispersion	**1 ***	**-924.57**	**20**	**483.87**	**0.00**	**0.72**	**X**	**X**	**X**	
	2	-922.71	21	484.11	1.86	0.28	X	X	X	X
					Relative importance		1.00	1.00	1.00	0.28
Functional originality	1	-872.61	20	457.90	0.00	0.34	X	X	X	
	2 *	**-872.15**	**10**	**446.48**	**0.46**	**0.27**	**X**	**X**		
	3	-871.91	21	458.71	0.71	0.24	X	X	X	X
	4	-870.79	11	446.88	1.82	0.14	X	X		X
					Relative importance		1.00	1.00	0.59	0.38

Appendix D. Supplemental information for Chapter 5: Differential response of key ecosystem processes to coral composition

Table S1 Surveyed species mean observed body-size categories, nominal diet groups (Green et al. 2009), and length-weight (L-W) references used to calculate biomass of surveyed fish species.

Species	Body-size (TL; cm)	Diet group	L-W reference
Acanthurus blochii	9-12	Grazer/detritivore	Letourneur et al. 1998
Acanthurus dussumieri	9-12	Grazer/detritivore	Letourneur et al. 1998
Acanthurus grammoptilus	5-8	Grazer/detritivore	Froese et al. 2013
Acanthurus lineatus	17-20	Mixed diet	Froese and Pauly 2014
Acanthurus nigricauda	13-16	Grazer/detritivore	Froese and Pauly 2014
Acanthurus nigrofuscus	13-16	Grazer/detritivore	Froese and Pauly 2014
Acanthurus olivaceus	9-12	Grazer/detritivore	Froese and Pauly 2014
Canthigaster amboinensis	9-12	Mixed diet	Froese et al. 2013
Canthigaster solandri	≤4	Mixed diet	Froese and Pauly 2014
Cetoscarus ocellatus	41-44	Excavator	Froese and Pauly 2014
Chlorurus bleekeri	29-32	Excavator	Froese and Pauly 2014
Chlorurus microrhinos	9-12	Excavator	Froese and Pauly 2014
Chlorurus sordidus	9-12	Excavator	Froese and Pauly 2014
Ctenochaetus binotatus	5-8	Grazer/detritivore	Letourneur et al. 1998
Ctenochaetus striatus	5-8	Grazer/detritivore	Froese and Pauly 2014
Dischistodus melanotus	≤4	Farmer	Froese and Pauly 2014
Dischistodus perspicillatus	≤4	Farmer	Froese et al. 2013
Dischistodus prosopotaenia	≤4	Farmer	Froese et al. 2013
Dischistodus pseudochrysopoecilus	≤4	Farmer	Froese et al. 2013
Hipposcarus longiceps	33-36	Scraper	Froese and Pauly 2014
Kyphosus vaigiensis	9-12	Browser	Froese and Pauly 2014
Naso brevirostris	9-12	Grazer/detritivore	Letourneur et al. 1998
Naso lituratus	37-40	Browser	Froese and Pauly 2014
Naso unicornis	25-28	Browser	Froese and Pauly 2014
Neoglyphidodon nigroris	≤4	Mixed diet	Froese et al. 2013
Plectroglyphidodon lacrymatus	≤4	Farmer	Froese et al. 2013
Pomacanthus sexstriatus	21-24	Mixed diet	Froese and Pauly 2014
Pomacentrus adelus	≤4	Farmer	Froese et al. 2013
Pomacentrus brachialis	≤4	Farmer	Froese and Pauly 2014
Pomacentrus chrysurus	≤4	Farmer	Froese et al. 2013
Pomacentrus grammorhynchus	≤4	Farmer	Froese et al. 2013
Pomacentrus reidi	≤4	Mixed diet	Froese et al. 2013
Pomacentrus simsiang	≤4	Mixed diet	Froese et al. 2013
Pomacentrus wardi	≤4	Farmer	Froese et al. 2013
Scarus altipinnis	5-8	Scraper	Froese and Pauly 2014
Scarus dimidiatus	21-24	Scraper	Froese et al. 2013
Scarus flavipectoralis	13-16	Scraper	Froese et al. 2013
Scarus frenatus	29-32	Scraper	Froese and Pauly 2014

Scarus ghobban	33-36	Scraper	Froese and Pauly 2014
Scarus globiceps	21-24	Scraper	Froese and Pauly 2014
Scarus niger	13-16	Scraper	Froese et al. 2013
Scarus oviceps	17-20	Scraper	Froese and Pauly 2014
Scarus psittacus	13-16	Scraper	Froese and Pauly 2014
Scarus rivulatus	13-16	Scraper	Froese and Pauly 2014
Scarus schlegeli	29-32	Scraper	Froese and Pauly 2014
Scarus sp	≤4	Scraper	Kulbicki et al. 2005
Scarus spinus	25-28	Scraper	Froese et al. 2013
Siganus corallinus	5-8	Grazer/detritivore	Hoey et al. 2013
Siganus doliatus	5-8	Grazer/detritivore	Hoey et al. 2013
Siganus puellus	13-16	Grazer/detritivore	Froese and Pauly 2014
Siganus punctatissimus	13-16	Grazer/detritivore	Hoey et al. 2013
Siganus punctatus	13-16	Grazer/detritivore	Froese and Pauly 2014
Siganus sp	≤4	Grazer/detritivore	Froese et al. 2013
Siganus vulpinus	5-8	Grazer/detritivore	Froese and Pauly 2014
Stegastes apicalis	≤4	Farmer	Froese et al. 2013
Stegastes nigricans	≤4	Farmer	Froese and Pauly 2014
Zanclus cornutus	5-8	Mixed diet	Froese et al. 2013
Zebrasoma scopas	5-8	Grazer/detritivore	Froese and Pauly 2014
Zebrasoma velifer	≤4	Grazer/detritivore	Letourneur et al. 1998

Table S2 Pairwise comparisons (with 95% confidence intervals: CI) among habitats, of linear mixed effects models of benthic composition and herbivorous fish assemblages structure. (Habitats: BP, branching *Porites*; Mix, mixed coral; SC, soft coral).

Response	Habitat contrast	Contrast estimate	Lower CI	Upper CI	Test stat	*df*	*P* (Tukey)
Total coral cover (hard and soft; %)	**BP > Mix**	**-16.57**	**-27.48**	**-5.67**	**-3.05**	**2, 6**	**0.01**
	BP vs SC	-10.60	-21.51	0.31	-1.95	2, 6	0.12
	Mix vs SC	5.97	-4.94	16.88	1.10	2, 6	0.51
Total bleached coral cover (hard and soft; %)	BP vs Mix	-4.31	-13.39	4.78	-0.95	2, 6	0.61
	BP vs SC	5.46	-3.62	14.54	1.21	2, 6	0.45
	Mix vs SC	9.77	0.69	18.85	2.16	2, 6	0.08
Total dead coral & algae (turf and macroalgae %)	**BP < Mix**	**17.22**	**3.09**	**31.36**	**2.45**	**2, 6**	**0.04**
	BP vs SC	7.69	-6.45	21.82	1.09	2, 6	0.52
	Mix vs SC	-9.54	-23.67	4.60	-1.36	2, 6	0.36
Total macroalgae cover (%)	BP vs Mix	-0.56	-1.89	0.78	-0.83	2, 6	0.64
	BP vs SC	-0.97	-2.07	0.13	-1.77	2, 6	0.17
	Mix vs SC	-0.42	-1.31	0.48	-0.94	2, 6	0.61
Herbivore species richness	BP vs Mix	1.23	1.00	1.52	1.98	2, 6	0.12
	BP vs SC	0.88	0.70	1.10	-1.16	2, 6	0.48
	Mix > SC	**0.71**	**0.58**	**0.89**	**-3.12**	**2, 6**	**0.01**
Total herbivore abundance	**BP < Mix**	**1.68**	**1.12**	**2.53**	**2.59**	**2, 6**	**0.03**
	BP vs SC	0.99	0.66	1.48	-0.06	2, 6	1.00
	Mix > SC	**0.59**	**0.39**	**0.88**	**-2.64**	**2, 6**	**0.02**
Total herbivore biomass (log transformed; kg ha^{-1})	BP vs Mix	0.74	-0.13	1.62	1.70	2, 6	0.20
	BP vs SC	-0.35	-1.23	0.53	-0.81	2, 6	0.70
	Mix > SC	**-1.09**	**-1.97**	**-0.22**	**-2.51**	**2, 6**	**0.03**

Table S3 Pairwise comparisons (with 95% confidence intervals: CI) of diet groups and functionally dominant species biomass (log transformed, kg ha^{-1}) surveyed with UVC among habitats. (Habitats: BP, branching *Porites*; Mix, mixed coral; SC, soft coral).

Log biomass (kg ha^{-1})	Habitat contrast	Contrast estimate	Lower CI	Upper CI	Test stat	*P* (Tukey)
Browsers	BP vs Mix	-0.60	-1.41	0.21	-1.60	0.24
	BP vs SC	-0.79	-1.89	0.31	-1.54	0.27
	Mix vs SC	-0.19	-1.28	0.91	-0.36	0.93
Excavators	BP vs Mix	-0.17	-1.26	0.92	-0.31	0.95
	BP vs SC	0.12	-1.55	1.31	-0.17	0.98
	Mix vs SC	0.05	-1.34	1.44	0.07	1.00
Scrapers	BP vs Mix	0.20	-0.86	1.25	0.37	0.93
	BP vs SC	-0.41	-1.52	0.70	-0.73	0.75
	Mix vs SC	-0.61	-1.66	0.45	-1.14	0.49
Grazers and detritivores	BP vs Mix	0.22	-0.47	0.91	0.63	0.80
	BP vs SC	-0.17	-0.87	0.53	-0.48	0.88
	Mix vs SC	-0.39	-0.96	0.18	-1.35	0.37
Farmers	BP vs Mix	0.33	-0.30	0.96	1.02	0.56
	BP vs SC	-0.04	-0.67	0.60	-0.11	0.99
	Mix vs SC	-0.36	-0.99	0.26	-1.15	0.49
Omnivorous herbivores	BP vs Mix	0.21	-0.40	0.82	0.69	0.77
	BP > SC	**-0.68**	**-1.14**	**-0.22**	**-2.95**	**0.01**
	Mix > SC	**-0.89**	**-1.50**	**-0.28**	**-2.89**	**0.01**
Naso brevirostris	BP vs Mix	-0.32	-10.86	10.23	-0.13	0.99
	BP vs SC	-0.41	-11.51	10.70	-0.16	0.99
	Mix vs SC	-0.09	-10.63	10.46	-0.04	1.00
Pomacanthus sexstriatus	BP vs Mix	0.11	-0.99	1.20	0.21	0.83
Siganus doliatus	BP vs Mix	0.06	-2.07	2.19	0.06	1.00
	BP vs SC	-0.35	-2.37	1.67	-0.36	0.93
	Mix vs SC	-0.41	-2.23	1.41	-0.47	0.89

Table S4 Pairwise comparisons (with 95% confidence intervals: CI) of productivity, assay change and macroalgal assay bite rates among habitats. (Habitats: BP, branching *Porites*; Mix, mixed coral; SC, soft coral).

Response	Contrasts	Contrast estimate	Lower CI	Upper CI	Test stat	*P* (Tukey)
Productivity (turf height, mm)	BP vs Mix	-0.19	-0.86	0.47	-0.58	0.83
	BP vs SC	-0.59	-1.25	0.08	-1.78	0.18
	Mix vs SC	-0.40	-1.06	0.27	-1.20	0.45
Turf removal: assay height (mm) loss	**Caged < exposed**	**-0.79**	**0.21**	**1.38**	**2.71**	**0.01**
	BP > SC	**2.11**	**0.73**	**3.50**	**3.04**	**0.003**
Laurencia removal: Assay wet weight (g) loss	BP: caged vs exposed	1.67	-2.00	5.34	0.90	0.37
	Mix: caged vs exposed	**13.41**	**6.38**	**20.44**	**3.77**	**<0.001**
	SC: caged vs exposed	**9.54**	**4.22**	**14.86**	**3.54**	**0.001**
Total mass-standardised bites^{-h}	Mix vs BP	26.58	1.21	584.12	2.08	0.09
	SC > BP	**53.93**	**2.34**	**1242.43**	**2.50**	**0.03**
	SC vs Mix	2.03	0.10	43.17	0.45	0.89
Naso brevirostris mass-standardised bites^{-h}	SC vs Mix	-1.69	-4.46	1.09	-1.20	0.23
Naso vlamingii mass-standardised bites^{-h}	SC vs Mix	-1.49	-3.81	0.83	-1.31	0.19
Pomacanthus sexstriatus mass-standardised bites^{-h}	Mix vs BP	0.32	-0.70	1.33	0.64	0.80
	SC vs BP	0.03	-1.03	1.08	0.05	1.00
	SC vs Mix	-0.29	-1.19	0.61	-0.66	0.79
Siganus doliatus mass-standardised bites^{-h}	SC vs Mix	-0.05	-0.59	0.49	-0.20	0.85
‘Other species’ (< 5% of total) mass-standardised bites^{-h}	Mix vs BP	1.28	-0.11	2.67	1.82	0.16
	SC vs BP	0.95	-0.67	2.57	0.15	0.48
	SC vs Mix	-0.33	-1.87	1.21	-0.43	0.91

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Appendix E: Publications arising from thesis

Richardson LE, Graham NA, Hoey AS (2017). Cross-scale habitat structure driven by coral species composition on tropical reefs. *Scientific Reports* 7(1), 7557. DOI: 10.1038/s41598-017-08109-4

Richardson LE, Graham NA, Pratchett MS, Hoey AS (2017). Structural complexity mediates functional structure of reef fish assemblages among coral habitats. *Environmental Biology of Fishes* 100(3), 193-207. DOI: 10.1007/s10641-016-0571-0

Richardson LE, Graham NA, Pratchett MS, Eurich J, Hoey AS (2018) Mass coral bleaching causes biotic homogenization of reef fish assemblages. *Global Change Biology*. DOI: 10.1111/gcb.14119