Understanding anthropogenic disturbance on coral reefs through species traits

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The candidate confirms that the work submitted is her own and that appropriate credit has been given where reference has been made to the work of others.

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Abstract

As climate change and local stressors reshape species assemblages, our understanding of ecosystems and how to manage them increasingly centres on their changing function. From the perspective of species traits, knowledge gaps remain around disturbance responses and particularly relationships between different taxa. This thesis explores disturbances on coral reefs through a trait-based lens, and highlights avenues through which these perspectives can inform future management strategies. First, this work investigates how trait-derived groups of fishery target species respond differentially to fishing pressure, discovering that groups sharing similar traits also share responses to fisheries activity. Positing that by extension trait groups also respond similarly to management actions, it proposes a framework for incorporating trait information into conservation decision-making. Next, an analysis of linked trait space distributions between corals and fish finds that they become decoupled following a coral bleaching disturbance, driven by changes in the trait composition of the coral community whilst the fish remained relatively stable. A follow-up study highlights how subsets of the fish assemblage make unique contributions to linked trait space distributions and assesses their importance for detecting habitat structuring across the coral and fish community. Finally, this thesis evaluates long-term changes in the functional composition and cross-taxa relationships between coral and fish assemblages over successive, varied disturbances. It finds fluctuations in the functional diversity of coral and fish communities explained by latitude, shelf position and disturbance history, which are also reflected in changes in shared structuring between coral and fish trait assemblages. The most influential traits in temporal cross-taxa associations indicate that functions such as structural complexity and herbivory are crucial for relationships between coral and fish assemblages. As a whole, this thesis examines how anthropogenic disturbance affects the trait composition of coral reef communities, identifying aspects of resistance and vulnerability that can inform future management approaches.

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Chapter 1. Introduction

Tropical coral reefs are among the most diverse ecosystems on earth and perform several important functions (Woodhead et al., 2019). However, as the impacts of anthropogenic activity continue to escalate, they are increasingly shaped by human social and economic drivers (Williams et al., 2019). Coral reefs are a crucial resource for human populations (Hoegh-Guldberg et al., 2019). They represent an important source of food, income, and are foundational to many societies' cultures and histories (Cinner, 2014). In this context, managers must attempt to halt or reverse ecosystem degradation whilst ensuring that reefs maintain these key services (McLeod et al., 2019).

Against a backdrop of continued anthropogenic driven decline, coral reefs and other vulnerable ecosystems are increasingly viewed from a resilience standpoint (Thompson et al., 2020, Capdevila et al., 2021, McLeod et al., 2021), where maintaining or restoring resilient ecosystems and their functions takes precedence over preserving specific species assemblages (Bellwood et al., 2004, Beyer et al., 2018, Bellwood et al., 2019a, McLeod et al., 2019, McLeod et al., 2021). Trait-based approaches, which define species' ecological roles in a system and the diversity of these roles rather than simply taxonomic species diversity, provide a useful perspective from which to approach resilience, functions and how to manage for them (Capdevila et al., 2021). However, there remain gaps in our understanding of trait community responses to anthropogenic disturbance and how this links with ecosystem functioning (Bellwood et al., 2019a).

1.1 Threats to coral reefs, disturbance responses, and management

Localised disturbances on coral reefs include fishing (Harborne et al., 2018), nutrient pollution and land use change (Reopanichkul et al., 2009, Wooldridge, 2009, Adam et al., 2020), invasive species (Neilson et al., 2018, Benkwitt et al., 2019), and coastal development (Peña-García et al., 2014). What unites these threats is that they can largely be addressed at the local or regional scale (Knowlton and Jackson, 2008). Over time, anthropogenic climate change has overtaken these localised disturbances as the most significant threat to coral reefs globally, leading to declines in coral cover even in areas far from other human pressures (Hughes et al., 2017, Hughes et al., 2018b, Bellwood et al., 2019a). This threat primarily manifests as ocean warming and consequent coral bleaching mortality, though ocean acidification and increased storm frequency and intensity are also climate impacts (McLeod et al., 2013, Vercelloni et al., 2020).

The duration, intensity and frequency of a disturbance will all dictate how it influences an ecosystem and the different communities within it. The duration and intensity of disturbances is used to characterise them as ‘pulse’ (short-term, acute) disturbances, or ‘press’ (long-term, chronic) disturbances. Framing disturbance in this way can be useful for thinking about ecosystem responses and resilience (Scheffer et al., 2001, Anthony et al., 2015), though limitations include considering the cumulative and synergistic impacts of multiple disturbances and their frequency (Bozec and Mumby, 2015). For example, anthropogenic climate change manifests acutely as thermal stress events (which are increasing in frequency and severity), and chronically through ocean acidification (Bozec and Mumby, 2015).

Whether an ecosystem resists, recovers from, or succumbs to a pulse or press disturbance is not uniform (Raj et al., 2021). Heterogeneity in community composition, exposure to stressors and prevailing environmental conditions can all influence how an ecosystem responds to disturbance (Roche et al., 2018). This inherent variability in responses at multiple scales presents opportunities to strategically manage key parts of ecosystems into the future, to preserve overall ecosystem functioning and provision for human subsistence and livelihoods (Roche et al., 2018, McLeod et al., 2021). Interventions can include spatial protection (Emslie et al., 2015), fisheries restrictions (McClanahan et al., 2015), changes in ecosystem use (Purcell et al., 2021), and restoration (Ladd et al., 2018). This type of localised management of course cannot prevent climate impacts (Hughes et al., 2018a, Bruno et al., 2019), and rapid divergence from current climate trajectories remains crucial to protecting reefs. However, managing local stressors to improve resistance and recovery capacity at smaller scales is still an important management tool (McLeod et al., 2019), particularly from a human social-ecological perspective where resources must be maintained to support subsistence, livelihoods, and cultural practices (Cinner, 2014, Anthony et al., 2015). There is increasing acceptance that irreversible climate-driven changes to coral reef distribution and community structure are now largely inevitable, so management must also include a view to preserve underlying mechanisms and functions where possible (Roche et al., 2018).

1.2 Trait-based community ecology

Central to heterogeneity in ecosystem disturbance responses are species traits. Traits are heritable morphological, phenological or physiological characteristics that determine species responses to the environment through reproduction, growth, and survival (Violle et al., 2007, Mouillot et al., 2013). Consequently, they are foundational to our understanding of ecosystem function (Mouillot et al., 2021), which is how energy is stored and transferred through a system (Bellwood et al., 2019b). Because the impacts of a given disturbance are not felt equally throughout a community (Loya et al., 2001, Adler et al., 2014, McLean et al., 2018), species traits provide an important avenue through which to consider these impacts across spatial and temporal gradients (Denis et al., 2017, Henriques et al., 2017, Johannesen et al., 2017, Carturan et al., 2018). Trait community composition determines both the initial sensitivity of a community, and ultimately how it responds, to disturbance (McLean et al., 2019). Uneven mortality, combined with shortening recovery windows, is driving significant community composition changes in corals and the other taxa that associate with them (Graham et al., 2007, Hughes et al., 2018b, Robinson et al., 2019, Magel et al., 2020). For example, bleaching mortality disproportionally impacts coral species with branching, fast growing traits that are key for providing the complex habitats that characterise coral reefs (Hughes et al., 2018b).

Functional, trait-based perspectives therefore have an important role to play in understanding, adapting to and predicting ecosystem change (Laughlin, 2014, Oliver et al., 2015, McLeod et al., 2019). They have been applied to fisheries management and gear restrictions (McClanahan et al., 2015, Mbaru et al., 2019), forecasting change (Beukhof et al., 2019), spatial prioritisation (Grenié et al., 2018), and understanding the spread and impacts of invasive species (Green and Côté, 2014, Givan et al., 2017). They also provide avenues to assess the resilience of functions provided by ecosystems (Bregman et al., 2016, Carturan et al., 2018, Ford et al., 2018, Swenson et al., 2020). Indices that quantify functional diversity (such as functional richness, divergence, and evenness) can detect community changes before they manifest as shifts in taxonomic species richness, and so are an important tool for ecosystem managers (Mouillot et al., 2013, Bates et al., 2014, Henriques et al., 2017). They also enable broad comparisons to be made across sites with different species compositions and in different biogeographic regions (McWilliam et al., 2018, McLean et al., 2021), facilitating working across scales and linking how the environment affects organisms (traits), with communities and ecosystems (De Battisti, 2021).

However, this does not necessarily mean that individual traits map neatly on to specific ecosystem functions (Adler et al., 2014). Ultimately, their usefulness comes down to how well the measured traits represent the functional characteristics of different groups of species in the community (Mouillot et al., 2013). Analyses may therefore be limited or skewed by the selection of traits that are easy to measure, are already included in monitoring efforts, or traits that are simply an inaccurate reflection of the functions that an organism performs (Roche et al., 2018, Bellwood et al., 2019b). Trait choice (and which traits are subsequently omitted) can thus disproportionately influence outcomes and interpretations (Mouillot et al., 2021). Traits are frequently used to explore interspecific variation (including in this thesis), but it is important to acknowledge that traits also vary at the intraspecific level. Fish trophic modes, body sizes and behaviour can vary with life history stage (Villéger et al., 2017), whilst morphological growth forms in corals vary widely within single species (Darling et al., 2012, Dwyer et al., 2014, Villéger et al., 2017).

Coral reefs are ideal systems in which to examine traits in the context of environmental change due to their high levels of biodiversity and because they are undergoing profound alterations with climate change (Hughes et al., 2018a). Coral traits such as growth rate or colony structure dictate the types of habitats and the level of structural complexity on reefs (Darling et al., 2012, Denis et al., 2017), and can inform bleaching vulnerability (Darling et al., 2013, Foden et al., 2013, Mizerek et al., 2018, Zawada et al., 2019). Over successive, increasingly severe disturbances, coral species with vulnerable traits are filtered out of the community, causing changes in ecosystem functioning that has a knock-on effect towards reduced or changed functions in fishes (Darling et al., 2017, Richardson et al., 2018, Tebbett et al., 2021). Fishes with traits that make them dependent on vulnerable corals are thus susceptible to these coral community changes (Graham et al., 2007). Consequently, fish functional structure has also exhibited shifts towards more homogenous, generalist communities because of large-scale coral mortality (Richardson et al., 2018, Stuart-Smith et al., 2018, Stuart-Smith et al., 2021). Traits thus occupy a dual role as indicators of mechanisms that drive community composition, and as predictors of ecosystem processes (including resilience) (Mason and de Bello, 2013).

Coral reef resilience, defined as the ecosystem's ability to resist and recover from disturbance, is therefore determined to a significant extent by disturbance responses, mediated in turn by species traits (McClanahan et al., 2012, Carturan et al., 2018, McLean et al., 2019). Traits can also have direct management applications (Mbaru et al., 2019), though it remains an under-explored area. The ability of traits to detect changes, enable comparisons across complex systems, and simplify measures of diverse species assemblages makes these applications an important avenue for further work (McLean et al., 2021). Traits afford broader insight into the structure of coral reef communities and how they are changing. Specifically, how communities of traits are linked, and how these linkages change in response to disturbances, has not been fully investigated. With corals as major habitat builders, and fish as regulators of several key functions (Mumby and Steneck, 2008), these associations may offer useful insights into disturbance and recovery dynamics on reefs beyond our initial conceptual and taxonomic understanding of these relationships. From there, it is also possible to identify which traits are driving changes in trait community structure, which in turn is useful for informing future management interventions around maintaining functional diversity and resilience (Mouillot et al., 2013, Villéger et al., 2017).

1.3 Aims and objectives

This thesis contributes to the literature on how traits mediate disturbance impacts on coral reefs, and how our understanding of these can be incorporated into management. The primary aim is to consider the changing community structure of Anthropocene coral reefs from a trait-based perspective. It addresses knowledge gaps around the practical applications of the growing body of trait information, how traits are interacting between taxa, and what disturbance impacts look like at different spatial and temporal scales for trait communities and their linkages. I assess both pulse-type stressors (bleaching events) and press-type stressors (fishing) at short (1-4 year) and long (20+ year) timescales. I also go from small-scale explorations of reef community structure to ecosystem-wide assessments. Case studies consist of a less economically developed island state and a larger, more economically developed country.

The objectives of this thesis are to:

Objective 1: *Explore the practical applications of functional traits for management from the perspective of how food fish respond to fishing pressure proxies.*

Fishing pressure is a major driver of coral reef fish community assemblages throughout Micronesia, and trait-based approaches are a presently underutilised opportunity to inform the management of these complex fisheries. I first identify groups of target fish species that share similar traits and evaluate how the biomass of these groups responds to fishing pressure proxies. I find that trait-derived groups of species respond differentially to various indicators of fishing pressure. Second, I present a trait-based adaptive management framework that applies these findings towards how management goals around maintaining functions can be combined with ensuring fisheries can continue to support local populations.

Objective 2: *Assess short-term resilience of coral and fish traits, and associations between them, over a bleaching disturbance.*

Coral bleaching elicits shifts in ecosystem functioning by reorganising species assemblages. How bleaching events affect trait distributions, and crucially, the associations between key taxa that underpin cross-taxon functioning, remains largely unmeasured. This impedes the ability of managers to predict shifts in functions and to target management actions accordingly, to support reef ecosystems and the human populations that depend on them. I quantify changes in trait distributions of coral and fish communities, and measure how associations between these taxa change before and after a coral bleaching event. I show that relationships between coral and fish traits break down post-disturbance, and that this is largely driven by compositional shifts in the coral community whilst the fish remain relatively stable before and after the bleaching disturbance.

Objective 3: *Evaluate the importance of different parts of the functional space for detecting and interpreting patterns in associations between taxa.*

For an understanding of linked coral and fish trait distributions to inform management, it must be clear what current monitoring protocols capture and miss, evaluating whether they are suitable to support increasingly functional and resilience-based management objectives. I use data on site attached, non-target fish species alongside food fish monitoring data to demonstrate how methodological decisions affect our understanding of functional interactions across taxa. I find that detecting relationships between coral and fish traits, and how this is structured across reef habitat types, is dependent on the contributions of site-attached species. This means that managers increasingly prioritising ecosystem functioning goals may need to re-evaluate the suitability of current monitoring programs to informing these objectives.

Objective 4: *Investigate how coral and fish traits change in the long term over multiple disturbances and identify key traits driving change.*

It is important to develop long-term perspectives of how coral and fish trait distributions, and their relationships to each other, are changing in response to a range of anthropogenic disturbances. Here, I identify which traits are driving changes over time in the linked coral-fish trait community, and evaluate how these traits, alongside the broader functional diversity of the community, are mediated by successive disturbance impacts. I find that the temporal functional composition of coral and fish communities is explained by spatial variation in disturbance histories, and that shared structuring between the two taxa fundamentally changes in parts of the study system. Traits that confer structural complexity in corals, and lower trophic modes in fish, are instrumental in driving shared temporal patterns across taxa. This highlights which functions are currently subject to the most change, with implications for future management and conservation decision-making.

Each objective in this thesis is addressed as its own chapter. These chapters are prefaced by this introduction, which provides background information and context for this research, and postfaces with an overarching discussion (Figure 1). This thesis argues that traits exhibit patterns in disturbance responses that (a) show how trait-based approaches can be used to manage coral reef fisheries and (b) demonstrate that relationships between coral and fish assemblages are changing in response to short- and long-term disturbances, largely driven by shifts in coral trait composition and coral-dependent fish species.

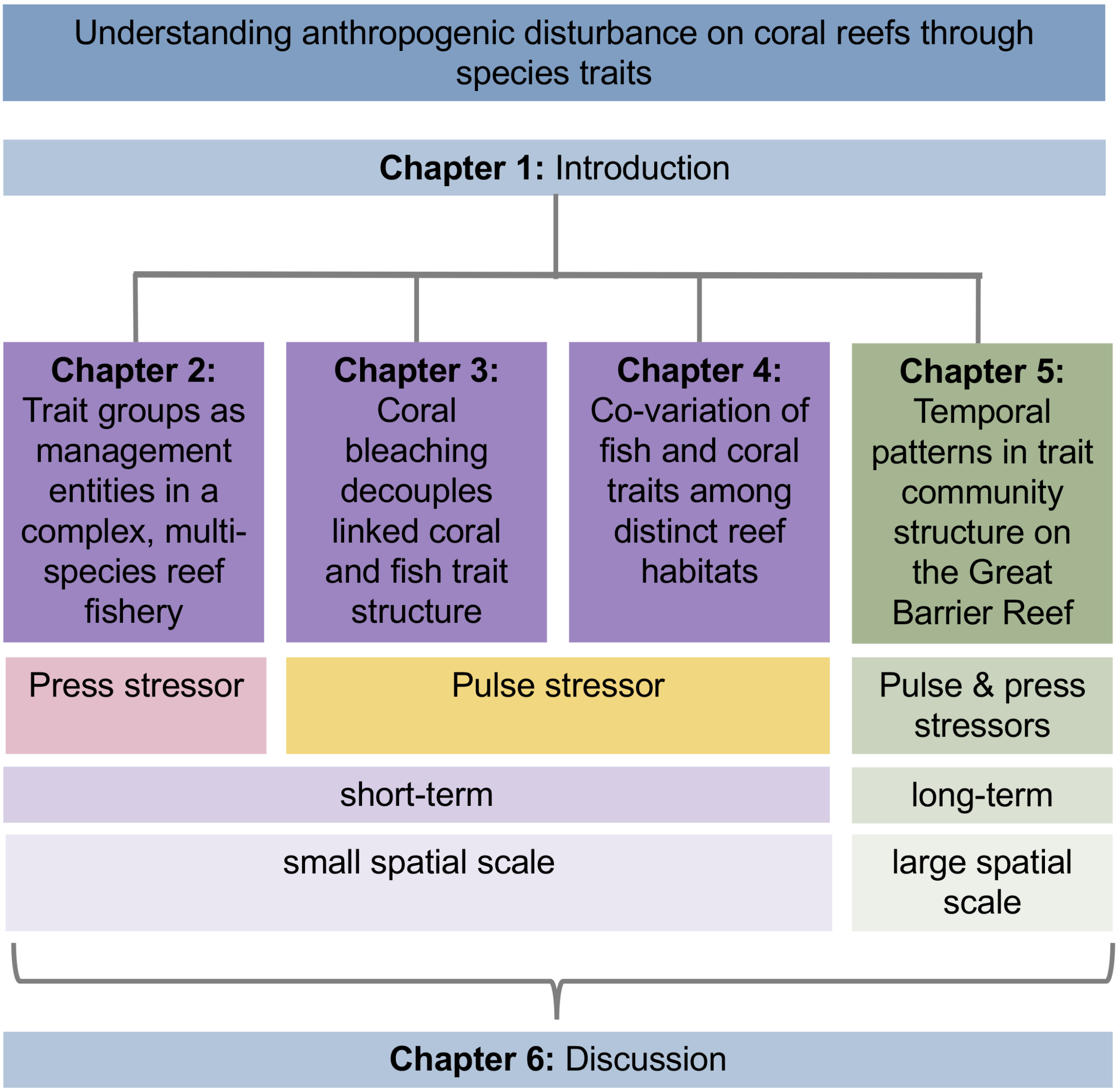

Figure 1. Schematic overview of thesis structure and core themes.

1.3.1 Style note

Chapters 2-5 of this thesis have been written in manuscript format intended for publication. Chapters 2-4 are now in revisions (co-authors, journals, and author contributions listed below). I am the lead author on each, and am responsible for question formulation, study design, data collation and analysis, and writing. The layout of Chapter 4 reflects that it has been submitted as a ‘note’ article. In the text I will use the terms ‘we’ and ‘our’ to acknowledge the contributions of the co-authors. Chapter 5 has not yet been submitted for publication, and so there I use ‘I’.

Chapter 2: Louise Anderson, Peter Houk, Mark G. R. Miller, Javier Cuetos-Bueno, Curtis Graham, Kriskitina Kanemoto, Elizabeth Terk, Elizabeth McLeod, Maria Beger. Accepted, Conservation Biology.

P.H. provided food fish monitoring data and additional guidance with data analysis. M.M. assisted with checking code and interpretations. J.C-B. shared fishing pressure data. C.G., K.K. and E.T. supplied information on dynamite fishing and ensured interpretations remained locally relevant. E.M. provided secondary supervision and M.B. primary supervision. All authors gave critical feedback on earlier drafts.

Chapter 3: Louise Anderson, Matthew McLean, Peter Houk, Curtis Graham, Kriskitina Kanemoto, Elizabeth Terk, Elizabeth McLeod, Maria Beger. In revisions with Marine Ecology Progress Series.

M.Mc. provided additional guidance with data analysis, checking code and interpretations. P.H. shared coral and fish monitoring data. C.G., K.K. and E.T. ensured interpretations remained locally relevant and shared important contextual knowledge. E.M. provided secondary supervision and M.B. primary supervision. All authors gave critical feedback on early drafts.

Chapter 4: Louise Anderson, Matthew McLean, Peter Houk, Curtis Graham, Kriskitina Kanemoto, Elizabeth Terk, Elizabeth McLeod, Maria Beger. In revisions with Coral Reefs.

M.Mc. provided additional guidance with data analysis, checking code and interpretations. P.H. shared coral and fish monitoring data. C.G., K.K. and E.T. ensured interpretations remained locally relevant and shared important contextual knowledge. E.M. provided secondary supervision and M.B. primary supervision. All authors gave critical feedback on early drafts.

Chapter 5: Louise Anderson, Mike Emslie, Maria Beger. Draft only.

M.E. contributed data and M.B. provided supervision.

1.3.2 Statement on data used in this thesis

The non-food fish data used in Chapter 4 are primary data collected myself (with field assistance from Adele Dixon) in July-August 2019 during routine monitoring with the University of Guam and Chuuk Department of Marine Resources. All other data used in this thesis are secondary data contributions from collaborators listed above.

1.4 Study site background information

This thesis focuses on two coral reef regions. The first is Chuuk, in the Federated States of Micronesia (FSM), and the second is Australia's Great Barrier Reef (GBR). Comparatively, Chuuk is a smaller reef area, where humans have greater reliance on marine resources and avenues for protection and management are currently limited. The GBR in contrast is located in a more economically developed country, and is well-monitored and well-resourced for management, providing a useful contrast for examining anthropogenic disturbance on reef trait communities.

1.4.1 Chuuk, Federated States of Micronesia

Chuuk is one of four states in the FSM, located in the Western Pacific. It is made up of several island groups, but most of its population lives within Chuuk Lagoon (Weeks et al., 2017). This is a large lagoon reef system characterised by a wide range of habitats, environmental conditions, and high levels of biodiversity (Figure 2) (Weeks et al., 2017). Marine resources are a central pillar of Chuuk's economy (Weeks et al., 2017) and Chuuk's commercial reef fishery is the largest in Micronesia (Cuetos-Bueno et al., 2018). Reef fisheries are a key part of local cultural identities and are critically important for the ~60% of people that maintain subsistence livelihoods (Weeks et al., 2017). Fisheries in Chuuk are now fully exploited (Rhodes et al., 2011, Cuetos-Bueno et al., 2018), in no small part due to increasing demand-driven exports to nearby Guam, with annual commercial landings valued at approximately USD$ 1.02 million (Cuetos-Bueno et al., 2018). This is a diverse fishery (~132 species) with Serranids, Acanthurids, and Scarids as the three most dominant families in the catch (Cuetos-Bueno et al., 2018).

Consequently, fishing is currently the dominant threat to coral reefs in Micronesia, and regional research largely reflects this (DeMartini et al., 2008, Taylor et al., 2014, Houk et al., 2015). However, the escalating rate and severity of impacts makes anthropogenic climate change an increasingly important consideration (Maynard et al., 2015, Raymundo et al., 2019, Houk et al., 2020), with some evidence pointing towards fishing as eroding overall ecosystem resilience (McLean et al., 2016). Approaches that use species traits have not yet been applied in Chuuk.

During the 2016-17 global coral bleaching event, Chuuk experienced significant coral mortality and subsequent declines in coral cover (Houk et al., 2020). These events are becoming more frequent and more serious as the climate changes (Hughes et al., 2017). Other climate-related disturbances that have impacted Chuuk's coral reefs in recent years include a crown of thorns starfish (COTS) outbreak in 2006, and typhoon Maysak in 2015 (Houk et al., 2016). COTS (*Acanthaster planci*) eat live corals, and during population explosions can cause substantial declines in coral cover (Pratchett et al., 2017), whilst typhoons cause mechanical damage to the reef (Matthews et al., 2019).

Historically, traditional management in Chuuk successfully maintained a sustainable subsistence fishery (Weeks et al., 2017). The linked impacts of colonialism, a growing population, and the transition towards a cash-based economy have eroded these traditional strategies over time (Houk et al., 2016). Nonetheless, practices such as *mechen* (a temporary closure of a fishing area) remain widely used and are an important foundation for current moves towards science-informed management (Weeks et al., 2017). Today, small areas of reef are typically owned and managed by single families (Weeks et al., 2017). Currently, less than 1% of reef habitat is formally protected and managed in Chuuk, though it is in the process of developing a larger network of protected areas to meet its targets under the Micronesia Challenge (Weeks et al., 2017). The Micronesia Challenge is an international agreement (between the Federated States of Micronesia, the Republic of the Marshall Islands, the Republic of Palau, Guam, and the Northern Mariana Islands) to protect 50% of marine resources by 2030 (Remengesau et al., 2006, Houk et al., 2015). To meet this goal, Chuuk is now involved in spatial planning processes for an updated network of MPAs which aims to protect biodiversity and benefit fisheries (Weeks et al., 2017).

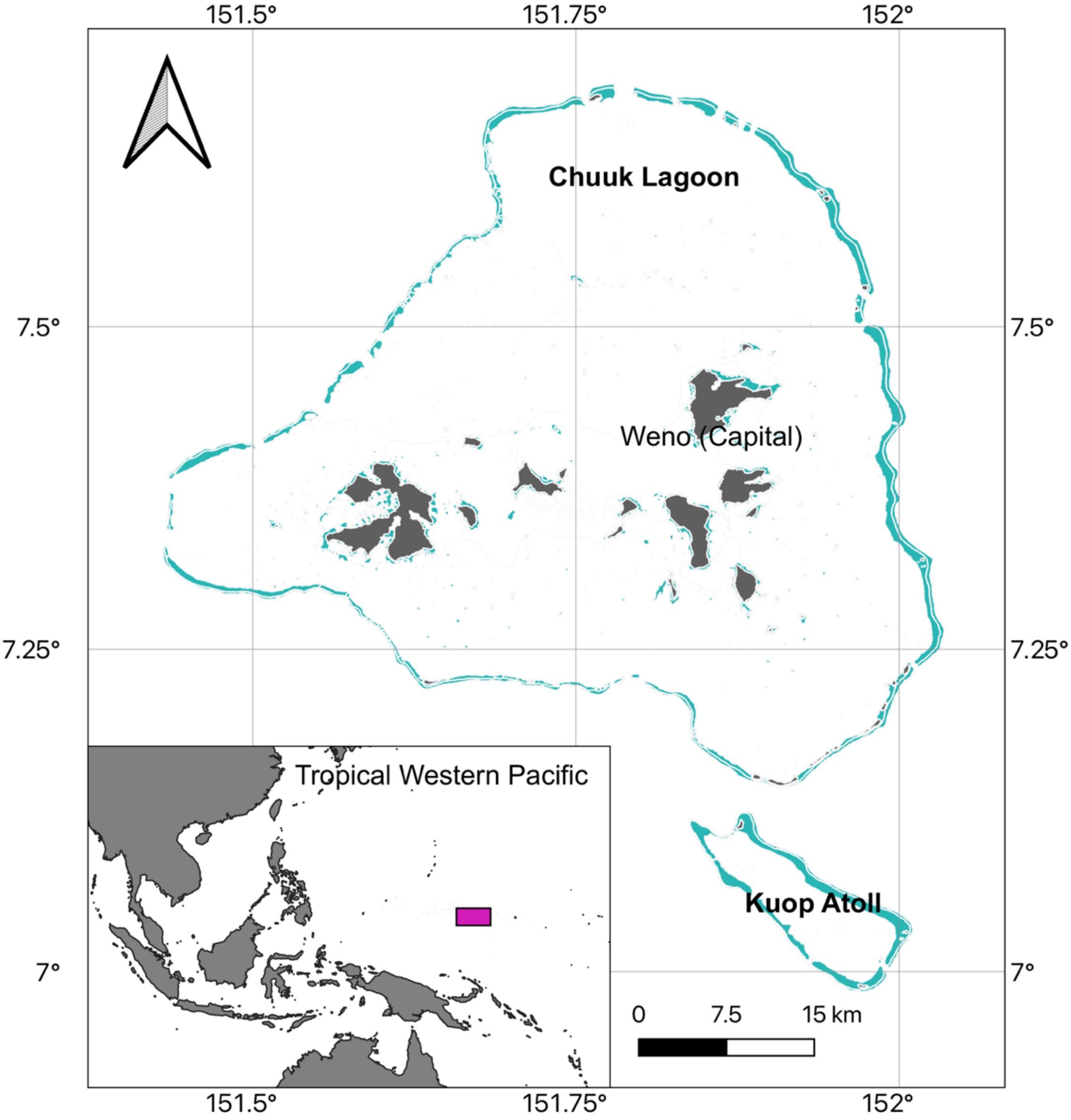

Figure 2. Reef area (blue) of Chuuk Lagoon and Kuop Atoll (UNEP-WCMC, 2018).

1.4.2 The Great Barrier Reef, Australia

The Great Barrier Reef (GBR) is a coral reef system extending 2300km along Australia’s north-east coast (Figure 3) (Emslie et al., 2020). Within this, reefs and their community structure are characterised by their shelf position; those closest to the shore are inshore reefs, those in the middle are mid-shelf reefs, and furthest from shore are outer barrier reefs (Emslie et al., 2020). Shelf position affects the environmental conditions reefs are exposed to, and thus dictates community structuring, though reefs are also subject to strong latitudinal gradients (Emslie et al., 2020).

Due to the combined effects of climate-driven cyclones, crown of thorns (COTS) outbreaks and coral bleaching events, coral cover on the GBR has declined by ~ 50% since monitoring began in 1985 (De'ath et al., 2012), though this varies regionally and among species (Osborne et al., 2011, Sweatman et al., 2011). Responses of fish communities to disturbance are more complex. Some predatory fish remain stable post-disturbance (Emslie et al., 2017), whereas planktivores are particularly vulnerable to habitat degradation (Emslie et al., 2019). Fish communities often exhibit stronger responses to cyclones (which rapidly reduce structural complexity) compared to bleaching and COTS outbreaks where structural complexity remains intact in the short term (Wilson et al., 2006, Emslie et al., 2014, Emslie et al., 2020). Most of these investigations look at fish communities via trophic groups alone, and coral cover is rarely broken down beyond growth forms. Others have also looked explicitly at functions such as herbivory and productivity (Cheal et al., 2013, Streit et al., 2019, Morais et al., 2020, Semmler et al., 2021, Tebbett et al., 2021). To date however, few have taken a multi-taxon, trait-based approach (Richardson et al., 2018).

Assessments of disturbance responses and ecological resilience on the GBR (Maynard et al., 2010, Thompson et al., 2020) have increasingly begun to incorporate species traits (Cheal et al., 2013, Brandl et al., 2016, Mellin et al., 2019, Zawada et al., 2019, McWilliam et al., 2020). Management plans also recognise the need to consider resilience to successive disturbances in future planning (Ainsworth et al., 2016, Bozec et al., 2020), though there remains a gap in terms of how the impact of management is measured (Fraser et al., 2019). The GBR is managed as a marine park, under the authority of the Great Barrier Reef Marine Park Authority (GBRMPA). It was first established in 1983, and over time new sections have been added and greater areas designated as no-take marine reserves (NTMRs) (Emslie et al., 2020). It was re-zoned in 2004 to better reflect the distinctive ecology of different parts of the marine park, bringing the percentage of NTMRs up to 31% (Emslie et al., 2015, Emslie et al., 2020). The GBRMPA also manages the long-term monitoring program (LTMP) for the GBR (Emslie et al., 2020). It is important to recognise the role of Traditional Owner groups in the management of the GBR. Aboriginal and Torres Strait Islander people have been custodians of these ecosystems for thousands of years and maintain strong connections to their land and sea Country. Several of these groups are additionally engaged in co-management with the GBRMPA (GBRMPA, 2021).

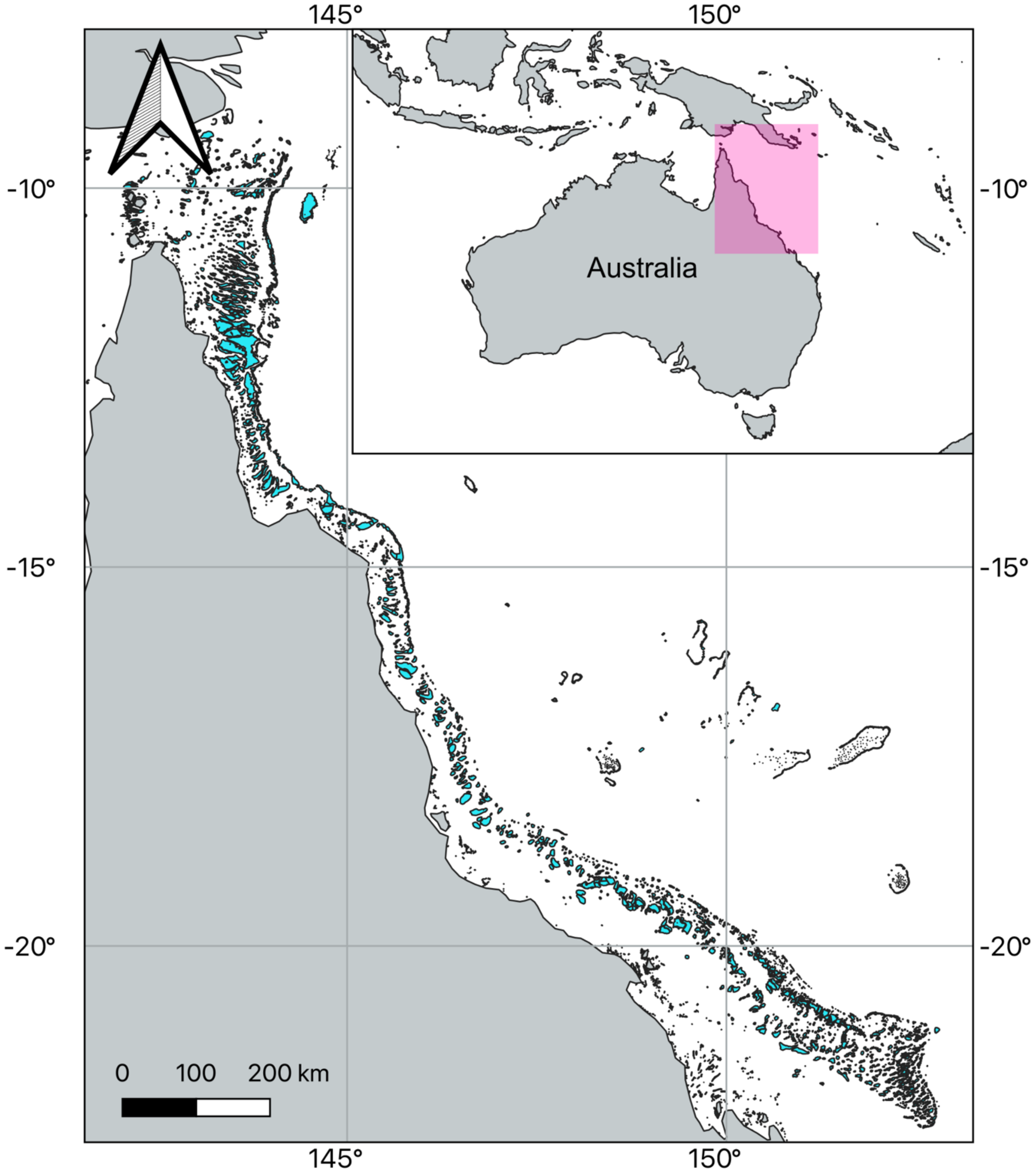

Figure 3. Reef area (blue) of the Great Barrier Reef (UNEP-WCMC, 2018).

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Chapter 2. Trait groups as management entities in a complex, multi-species reef fishery

2.1 Abstract

Localised stressors compound the ongoing climate-driven decline of coral reefs, requiring natural resource managers to work within rapidly shifting paradigms. Trait-based adaptive management (TBAM) is a new framework to help address changing conditions by choosing and implementing management actions specific to species groups that share key traits, vulnerabilities, and management responses. TBAM balances maintenance of functioning ecosystems with provisioning for human subsistence and livelihoods. We first identified trait-based groups of food fish in a Pacific coral reef with hierarchical clustering. Positing that trait-based groups performing comparable functions respond similarly to both stressors and management actions, we ascertained biophysical and socio-economic drivers of trait-group biomass and evaluated their vulnerabilities with generalised additive models. Clustering identified seven trait groups from 131 species. Groups responded to different drivers and displayed divergent vulnerabilities, with human activities emerging as important predictors of community structuring. Biomass of small, solitary reef-associated species increased with distance from key fishing ports, and large, solitary piscivores exhibited a decline in biomass with distance from a port. Group biomass also varied in response to different habitat types, the presence or absence of reported dynamite fishing activity, and wave energy exposure. The differential vulnerabilities of trait groups reveal how food fish community structure is driven by different aspects of resource use and habitat. This inherent variability in the responses of trait-based groups presents opportunities to apply selective trait-based adaptive management strategies for complex, multi-species fisheries. This approach can be widely adjusted to suit local contexts and priorities.

2.2 Introduction

Climate change and local stressors have caused a global deterioration of coral reef ecosystems despite attempts to reduce human impacts and manage for resilience (McLeod et al., 2021). These impacts are reorganising species assemblages and altering ecosystem function, requiring a shift in management approaches (Bellwood et al., 2019a). This need has been acknowledged by researchers and the conservation community, where efforts have pivoted from protecting species and contemporary community types towards maintaining the long-term functioning of rapidly changing environments and species assemblages (Bellwood et al., 2019a, McLeod et al., 2019).

The functions performed by species in an ecosystem are determined by their traits (Mouillot et al., 2013, Kraft et al., 2015). Because the types and abundances of traits are influenced by the environment, a trait-based lens provides an important tool for understanding ecosystem change (Sommer et al., 2014, Henriques et al., 2017, Kim et al., 2019), and for responding to these changes through management (Laughlin et al., 2017). Biotic, abiotic and anthropogenic processes shape the trait combinations present in a community (Villéger et al., 2017), hence species with similar trait combinations and functional roles share potential vulnerability and recovery responses (Dee et al., 2016). Classifying groups of species from their traits can glean new insights in to community structuring (Darling et al., 2012), and we argue that they provide a hitherto underutilised opportunity to inform management in coral reef systems. Functioning reefs and fisheries that maintain human food security and livelihoods are not mutually exclusive (Martin et al., 2017), and management that accounts for species traits and functions can help meet these goals. Building on principles of resilience-based and adaptive management (Anthony et al., 2015, McLeod et al., 2019), we introduce Trait-Based Adaptive Management (TBAM), a practical framework for incorporating emerging trait-based management principles in to managing diverse species assemblages in changing ecosystems.

2.2.1 A trait-based adaptive management framework for coral reefs

Species with similar traits, and by extension, functioning, respond similarly to disturbances. Indeed, disturbances ranging from localised fishing to climate change have the potential to remove entire functional groups from some fish assemblages (Micheli and Halpern, 2005). Functions are thus increasingly used as an avenue to inform management (McLeod et al., 2019), ranging from the impacts of reef degradation (Plass-Johnson et al., 2016), to fisheries (McClanahan et al., 2015, Mbaru et al., 2019) and the role of herbivory (Roff and Mumby, 2012). Consequently, the concept of using functional groups as a management tool is well-established (Bellwood et al., 2004). However, many previously defined functional groups are in fact trophic groups (McClanahan et al., 2015), which are not necessarily consistent between studies (Parravicini et al., 2021). Trophic group is a single trait, and when used alone, presents a limited view of functionality.

In this study we expand beyond using trophic groups to exclusively define functionality and consider how additional traits mediate responses to fishing disturbance. Body size, for example, determines vulnerability to fishing pressure (Stuart-Smith et al., 2013), and aggregation behaviour affects vulnerability to different fishing methods (Plass-Johnson et al., 2016). This information is useful for formulating management strategies and underpins the reasoning behind our proposed trait-based adaptive management framework.

The TBAM framework suggests using functional groups, derived from a wide range of traits, as broad management units in species-rich fisheries (Figure 4). Using traits in management has been advocated for previously, and here we outline a practical approach to implementing those insights. This approach assumes that species within each functional group respond similarly to disturbance impacts and management actions, and so we test that first assumption here. Provided we can accurately assess the vulnerabilities of different groups of species, managing fisheries in this way allows controlled exploitation of more robust groups, and places limits on fishing for more vulnerable groups. This selectivity and flexibility in how fisheries are exploited lends itself well to actions such as gear-based management, additionally informed by species traits (Mbaru et al., 2019). In applying this framework to other systems or contexts, trait choices can conceivably vary depending on management goals, relevant taxa, and available trait information. Trait selection aims to capture a range of traits denoting different aspects of likely function, and so the framework is flexible to including different traits.

Using a coral reef fishery in Chuuk Lagoon, Federated States of Micronesia (FSM) as a case study (Figure A1), we explore whether TBAM is a viable strategy. First, we use species traits to identify key functional groups of food fish (species targeted for sustenance and market sales). We then test how those groups respond to proxies of fishing disturbance and environmental drivers. Finally, we discuss how groups' divergent responses to these drivers can inform targeted management strategies, according to their specific vulnerabilities and the needs and priorities of local communities. We suggest potential management actions, but do not test their efficacy here.

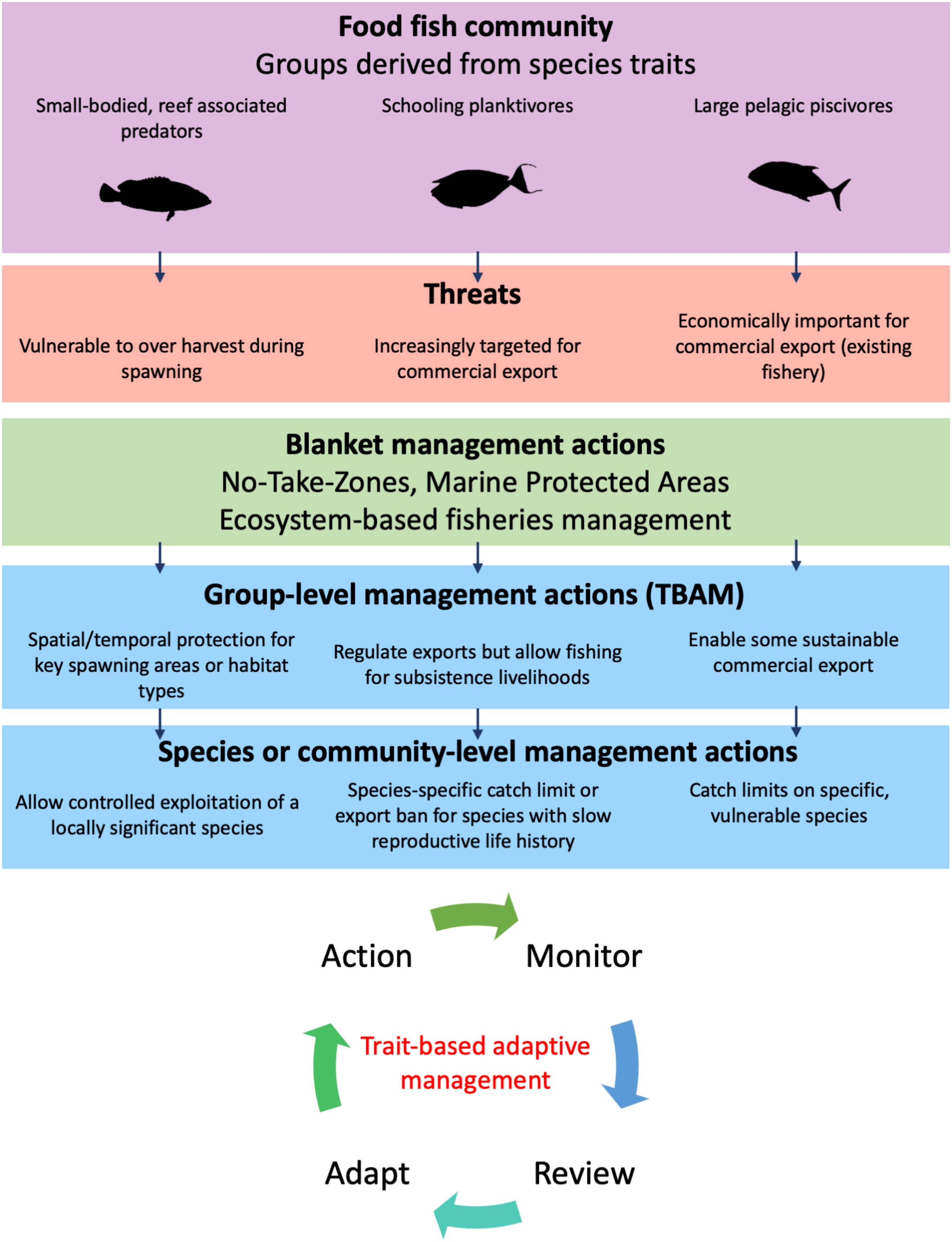

Figure 4. Generalised schematic of the trait-based adaptive management framework, using theoretical trait groups, threats, and management actions.

2.3 Methods

2.3.1 Fish and coral surveys

Food fish biomass data, and coral diversity and cover data were collected from 61 sites throughout Chuuk Lagoon in 2016, representing a variety of reef types, management regimes, geographic areas, and levels of wave exposure. Fish size and abundance was collected using 12 stationary point counts (five metre radius, three minutes) per site, and food fish families identified through landings data on target species (Appendix A2). Habitat types covered outer reefs (outside the lagoon), channel reefs, patch/back reefs (inside the lagoon), and inner reefs (adjacent to islands). See Appendix A3 for full details of survey methods (Houk et al., 2015, Cuetos-Bueno and Hernandez-Ortiz, 2017).

2.3.2 Reef fisheries activity

Approximate locations of dynamite fishing were obtained from the Chuuk Department of Marine Resources, with staff sharing experiential knowledge. Nine survey sites fell within these areas and were classed as experiencing dynamite fishing within the last few years. These sites were all located at patch/back and inner reef types.

Total annual landings and the number of fishing trips were derived from landings data based on market surveys conducted during 12 consecutive months (Cuetos-Bueno et al., 2018). These estimates relate to specific fishing areas and are attributed to the nearest ecological survey sites (Appendix A4).

Survey sites were allocated estimates of human population size of the nearest municipality derived from the most recent census (FSM Census, 2010), assuming that proximity to larger populations implies greater fishing pressure (Cinner et al., 2018). Fishing pressure associated with commercial activity was linked to two locations: Weno, where the state capital and airport are located, and Faichuuk, where most commercial fishers live (Figure A1) (Cinner et al., 2018, Cuetos-Bueno et al., 2018). Distance to these markets (km) was calculated with spDistsN1 from the sp package (Pebesma and Bivand, 2005). Mean wave energy estimates (joules/m^2) for each survey site were derived from wind speed, wind direction and fetch length (Jenness and Houk, 2014).

2.3.3 Fish traits and functional groupings

Trait information was compiled from Fishbase (Froese and Pauly, 2019), the literature, and data gaps were imputed for phylogenetically related species based on expert opinion. We selected five traits relating to species’ ecological responses to disturbances and fishing sensitivity, that had good coverage for the species in this study and were a combination of continuous and categorical traits (Weiher et al., 1999). These were maximum length (cm), mean pelagic larval duration (PLD) (days), trophic mode, aggregation type and position in the water column (Table 1). These traits deal with facets of reproductive capacity, life history, feeding ecology and behaviour that link to several ecosystem functions, vulnerability to fishing, habitat preferences, recovery from disturbance and requirements for protection (Table 1).

Table 1. Selected fish traits and justification for inclusion.

Type	Trait	Definition	Justification
Morphological/Life history	Maximum length (Numeric)	Maximum total length (cm) recorded in the species core range.	Important for species sensitivity to predation, thermal resistance, fecundity, extinction risk, and metabolic rates (Graham et al., 2011, Beauchard et al., 2017). Related to vulnerability to size selective fishing (Stuart-Smith et al., 2013, Bellwood et al., 2019b).
Reproductive	Mean pelagic larval duration (PLD) (Numeric)	Theoretical time (days) that a larval fish remains viable in the water column, measured from hatching or spawning.	Associated with range size, recovery following disturbance and dispersal connectivity (Álvarez-Romero et al., 2017, Wilson et al., 2018).
Trophic ecology	Trophic mode (Factor)	Broad diet categories. (Piscivore, predator, planktivore, omnivore, corallivore, herbivore)	Linked to food acquisition, growth requirements, demographics (predator-prey interactions), vulnerability to climate change and nutrient cycling (Graham et al., 2011, Beauchard et al., 2017).

Behaviour	Position in water column (Factor)	Location on reef where species spend the most time. (Pelagic, reef pelagic, upper benthic, benthic, demersal, sub-benthic, sand associated and cnidarian associated	Ties in with motility, foraging, migratory requirements, and dispersal (Stuart-Smith et al., 2013, Beauchard et al., 2017).
Behaviour	Aggregation (Factor, ordered)	Grouping behaviour. (schools, groups, harems, pairs, solitary)	Linked to foraging strategy, vulnerability to predation and different fishing methods (Plass-Johnson et al., 2016).

To identify clusters of similar species based on shared traits, we used average-method hierarchical clustering of a species by traits, cailliez corrected Gower dissimilarity matrix (100 runs) (Hennig, 2018). Seven groups were identified by assessing the relative cluster stabilities of between six and ten groupings (Appendix A5). We also used a generalised boosted regression model, where group is modelled as a function of each of the traits. By sequentially improving model fit using a subset of the traits provided, this identifies which trait best predicts the groupings (1000 iterations) (Darling et al., 2012, Greenwell et al., 2019). Community trait space was visualised with a Principal Coordinate Analysis (PCoA) of the dissimilarity matrix, retaining the first four axes as a reasonable assessment of diversity (Maire et al., 2015). The third and fourth PCoA axes are visualised in Figure A3.

We assessed whether our results were robust to trait choice by comparing our original dissimilarity matrix against matrices with all possible combinations of four out of five of the chosen traits (Mbaru et al., 2019, Mouillot et al., 2021) and used mantel tests to determine that all were strongly correlated with the original distance matrix. We ran separate PCoAs for each trait combination and found they explained similar amounts of variation along their first four axes, excepting was when maximum length was excluded (Table A2). However, there is strong ecological justification for retaining this trait in the analysis (Table 1).

2.3.4 Relationships of trait groups to the environment and fishing pressure proxies

Separate models were constructed for the square-root transformed mean biomass (kg) of each trait group at each site. Generalised additive models (GAMs) with landings (kg), percent coral cover, wave energy (log) (joules/m^2), nearest human population size (log), and distance to fish markets (km) at each site as smooth terms (thin plate regression splines), and reef habitat type (patch/back, inner, channel and outer) and method (spear and dynamite fishing) at each site as categorical terms were constructed (mgcv package) (Table A3) (Wood, 2011). GAMs were selected to avoid assumptions of linearity in relationships, and because they cope well with potential concurvity issues in spatial data. The number of fishing trips was discarded from the models due to high correlation with landings ($r = 0.985$). Square root transformations of biomass were applied to satisfy normality, and all continuous variables standardised by subtracting the mean and dividing by the standard deviation to aid interpreting the models. We applied interaction terms between coral cover and reef type, and wave energy and reef type. Inclusion of interaction terms was determined by whether they better fit the data than the smooth term alone, based on AIC values and visual inspection of residual plots.

2.4 Results

2.4.1 Food fish trait groups and characterisation

We identified seven groups from the 131 recorded fish species that encompass different taxa and trait combinations (Table 2, Figure 5, Table A1). Water column position was the best predictor of the groupings (71.36%), followed by trophic mode (10.24%), mean pelagic larval duration (8.77%), maximum length (7.16%) and aggregation type (2.47%). Trait group six contained one species and one observation for the giant moray *Gymnothorax javanicus* and was excluded from further analysis. We also excluded trait group seven. This was the least stable cluster with the largest number of times dissolved, implying that it was not a ‘true’ grouping, and it contained just three *Myripristis* species (Hennig, 2018). The remaining five groups represent 127 species overall, with group size ranging from 75 to 7 species (Table 2).

Table 2. Trait group characterisation and number of species (n=131) in each. Cluster stability and number of times resolved derived from the clusterboot function (Hennig, 2018), which runs bootstrap iterations to test stability. Clusters are more stable when stability is closer to 1, and those that have been dissolved (do not appear in new bootstrapped iterations) more are less stable.

Group	Cluster stability	no. times dissolved	no. species	Broad characterisation	Example species
1	0.839	8	75	Small body size, mid-range PLD, reef-associated fishes. Mostly upper benthic, some cnidarian associated. Combination of trophic modes and aggregation types (majority are solitary).	*Acanthurus blochii, Balistoides viridescens, Chlororus bleekeri.*
2	0.684	33	29	Solitary benthic predators, with similar PLD and body size ranges to group 1.	*Epinephelus howlandi, Parupeneus barberinus, Sargocentron tiere.*
3	0.910	7	7	Reef pelagic, primarily schooling/grouping planktivores with long PLDs. Contains one reef pelagic predator.	*Acanthurus mata, Naso annulatus, Caranx papuensis.*
4	0.721	17	9	Large, mainly solitary piscivores with short or no PLD. Mostly upper benthic.	*Aphareus furca, Carcharhinus melanopterus, Syphraena barracuda.*
5	0.925	4	7	Large, pelagic, schooling/grouping predators/piscivores.	*Caranx sexfasciatus, Elagatis bipinnulata, Seriola lalandi.*
6	0.640	38	1	Giant moray eel. Large, demersal, solitary predator with a long PLD	*Gymnothorax javanicus.*
7	0.470	64	3	Small, solitary planktivores with longer PLDs. Either sub benthic or cnidarian associated.	*Myripristis adusta, Myripristis berndti, Myripristis kuntee.*

Group one mostly contains small fishes with shorter PLDs that prefer swimming above the reef (upper benthic habitat association) and are found largely solitary or in small groups (Table 2). It is the largest group and contains several trophic modes, largely herbivores and predators. Group two contains 29 species of primarily solitary predators, sharing similar PLDs and body sizes to group one. They are distinguished from similar trophic modes in group one because they occupy a benthic position in the water column. Group three has seven species. They are mainly schooling or grouping, reef pelagic species with the longest PLDs of any of the trait groups. Except for the brassy trevally *Caranx papuensis*, all are planktivorous or herbivorous Acanthurids. Group four is characterised by large-bodied, upper benthic, solitary piscivores with short or no PLD, and includes several shark species. Group five also comprises of high trophic level fish, made up of large, pelagic, and schooling species like *Grammatorcynus bilineatus* (Figure 5).

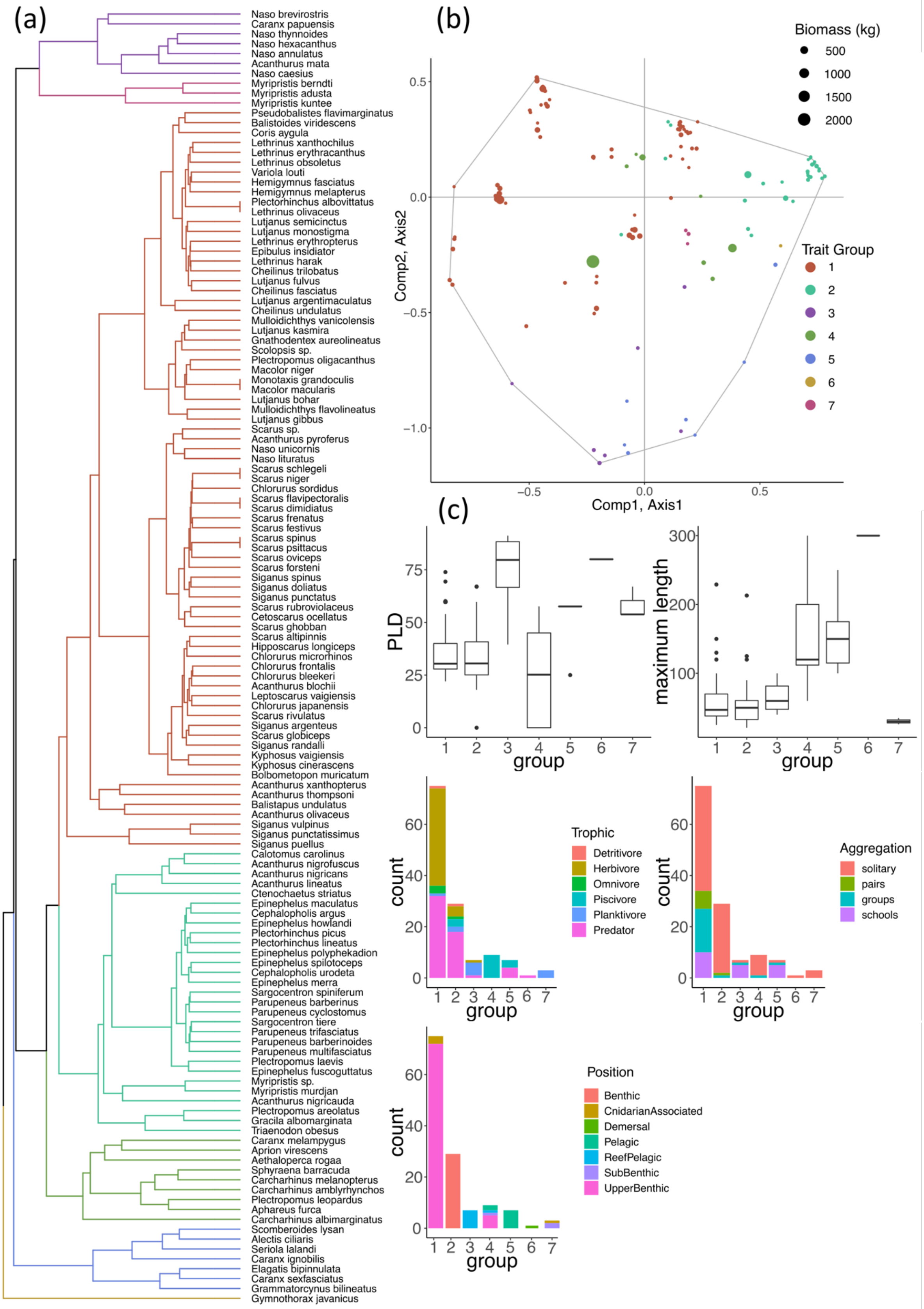
(a)
Naso brevirostris
Caranx papuensis
Naso thynnoides
Naso hexacanthus
Naso annulatus
Acanthurus mata
Naso caesius
Myripristis berndti
Myripristis adusta
Myripristis kuntee
Pseudobalistes flavimarginatus
Balistoides viridescens
Coris aygula
Lethrinus xanthochilus
Lethrinus erythracanthus
Lethrinus obsoletus
Variola louti
Hemigymnus fasciatus
Hemigymnus melapterus
Plectorhinchus albovittatus
Lethrinus olivaceus
Lutjanus semicinctus
Lutjanus monostigma
Lethrinus erythropterus
Epibulus insidiator
Lethrinus harak
Cheilinus trilobatus
Lutjanus fulvus
Cheilinus fasciatus
Lutjanus argentimaculatus
Cheilinus undulatus
Mulloidichthys vanicolensis
Lutjanus kasmira
Gnathodentex aureolineatus
Scolopsis sp.
Plectropomus oligacanthus
Macolor niger
Monotaxis grandoculis
Macolor macularis
Lutjanus bohar
Mulloidichthys flavolineatus
Lutjanus gibbus
Scarus sp.
Acanthurus pyroferus
Naso unicornis
Naso lituratus
Scarus schlegeli
Scarus niger
Chlorurus sordidus
Scarus flavipectoralis
Scarus dimidiatus
Scarus frenatus
Scarus festivus
Scarus spinus
Scarus psittacus
Scarus oviceps
Scarus forsteni
Siganus spinus
Siganus doliatus
Siganus punctatus
Scarus rubroviolaceus
Cetoscarus ocellatus
Scarus ghobban
Scarus altipinnis
Hipposcarus longiceps
Chlorurus microrhinos
Chlorurus frontalis
Chlorurus bleekeri
Acanthurus blochii
Leptoscarus vaigiensis
Chlorurus japanensis
Scarus rivulatus
Siganus argenteus
Scarus globiceps
Siganus randalli
Kyphosus vaigiensis
Kyphosus cinerascens
Bolbometopon muricatum
Acanthurus xanthopterus
Acanthurus thompsoni
Balistapus undulatus
Acanthurus olivaceus
Siganus vulpinus
Siganus punctatissimus
Siganus puellus
Calotomus carolinus
Acanthurus nigrofuscus
Acanthurus nigricans
Acanthurus lineatus
Ctenochaetus striatus
Epinephelus maculatus
Cephalopholis argus
Epinephelus howlandi
Plectorhinchus picus
Plectorhinchus lineatus
Epinephelus polyphekadion
Epinephelus spilotoceps
Cephalopholis urodeta
Epinephelus merra
Sargocentron spiniferum
Parupeneus barberinus
Parupeneus cyclostomus
Sargocentron tiere
Parupeneus trifasciatus
Parupeneus barberinoides
Parupeneus multifasciatus
Plectropomus laevis
Epinephelus fuscoguttatus
Myripristis sp.
Myripristis murdjan
Acanthurus nigricauda
Plectropomus areolatus
Gracila albomarginata
Triaenodon obesus
Caranx melampygus
Aprion virescens
Aethaloperca rogaa
Sphyraena barracuda
Carcharhinus melanopterus
Carcharhinus amblyrhynchos
Plectropomus leopardus
Aphareus furca
Carcharhinus albimarginatus
Scomberoides lysan
Alectis ciliaris
Seriola lalandi
Caranx ignobilis
Elagatis bipinnulata
Caranx sexfasciatus
Grammatorcynus bilineatus
Gymnothorax javanicus
(b)
Biomass (kg)
500
1000
1500
2000
Comp2, Axis2
0.5
0.0
−0.5
−1.0
Comp1, Axis1
−0.5
0.0
0.5
Trait Group
1
2
3
4
5
6
7
(c)
PLD
75
50
25
0
1 2 3 4 5 6 7
group
maximum length
300
200
100
1 2 3 4 5 6 7
group
count
60
40
20
0
1 2 3 4 5 6 7
group
Trophic
Detritivore
Herbivore
Omnivore
Piscivore
Planktivore
Predator
count
60
40
20
0
1 2 3 4 5 6 7
group
Aggregation
solitary
pairs
groups
schools
count
60
40
20
0
1 2 3 4 5 6 7
group
Position
Benthic
CnidarianAssociated
Demersal
Pelagic
ReefPelagic
SubBenthic
UpperBenthic

Figure 5. Characteristics of trait groups of food fishes in Chuuk: (a) Seven trait group clusters based on hierarchical average clustering of the dissimilarity matrix. Branch length is truncated. (b) Principal coordinates analysis (PCoA) representation of food fish community trait space, with point size weighted by overall biomass (kg) observed during 2016 surveys and points coloured by trait group. The first two axes explain 17% of the variation, and the first four axes 28%. Equivalent figure with species labels in Figure A2, plot of axes three and four in Figure A3. (c) Trait variability for (i) mean pelagic larval duration (days), (ii) maximum length (cm), (iii) trophic mode (iv) aggregation behaviour and (v) position in the water column for each of the seven food fish trait groupings.

2.4.2 Drivers of trait group biomass

Trait group biomass is affected by environmental characteristics and proxy fishing activity measures, and groups respond to different drivers (Table 3, Figure 6). Fishing pressure proxies affect biomass of several groups. Human population has a possible positive relationship with biomass for small, solitary benthic predators (group two; $p = 0.058$), but otherwise does not predict biomass. Distance to key markets emerges as having important relationships with biomass in groups one and four. For example, larger solitary upper benthic predators have lower biomass further from Faichuuk (group four; $p = 0.006$), whereas smaller reef-associated species have higher biomass further from both Weno and Faichuuk (group one; $p = 0.006$, $p = 0.038$). Wave energy affects biomass when interacting with reef type. Mean annual landings does not affect biomass of these trait groups (Table 3). The presence or absence of spearfishing (versus dynamite) activity at a site strongly affects biomass of small, solitary benthic predators (group two, $p = 0.006$) and large upper benthic predators (group four, $p < 0.001$). Both tend to have lower biomass at sites where there is just spearfishing occurring (and no reported dynamite fishing activity) (Figure 7).

Reef habitat types emerge as important predictors of biomass for group two ($p = 0.003$) and four ($p = 0.041$) in their own right, additionally interacting with coral cover and wave energy for group two, and with wave energy for group three. Wave energy has a roughly unimodal relationship with biomass at outer reefs for group two's small, solitary benthic predators ($p = 0.028$), and a positive relationship with biomass at inner reefs for group three's schooling planktivores ($p = 0.008$). At patch/back reefs, biomass of group three declines with increasing wave energy ($p = 0.023$). Additionally, the biomass of reef-associated, smaller species in group one increases with increased coral cover ($p = 0.031$) (Table 3).

Table 3. Degrees of freedom (*df*) for parametric terms, effective degrees of freedom (*edf*) for smooth terms, and p-values for GAM smooth, parametric and interaction terms for trait groups (one - five) at each site (n = 61). P-values in bold where p < 0.05. RT – reef type.

	Trait Group		1	2	3	4	5
Parametric terms	Reef Type	df	3	3	3	3	3
		p	0.693	**0.003**	0.132	**0.041**	0.466
	Spear	df	1	1	1	1	1
		p	0.132	**0.006**	0.076	**<0.001**	0.547
	Dynamite	df	1	1	1	1	1
		p	-	-	-	-	-
Smooth terms	Mean annual landings (kg)	edf	1	1	1	1	1
		p	0.158	0.592	0.388	0.661	0.560
	(log) Wave energy (joules/m2)	edf	1	-	-	1	1
		p	0.531	-	-	0.146	0.376
	(log) Population	edf	1	1.755	1	1	1
		p	0.220	0.058	0.541	0.670	0.866
	Coral cover (%)	edf	1	-	1	1	1
		p	**0.031**	-	0.573	0.867	0.945
	Distance from Weno (km)	edf	1	1	1.533	1	1
		p	**0.006**	0.393	0.161	0.265	0.775
	Distance from Faichuuk (km)	edf	1.857	1	1	1	1
		p	**0.038**	0.819	0.911	0.006	0.396
Interaction terms	energy:RT channel	edf	-	1	1.375	-	-
		p	-	0.060	0.668	-	-
	energy:RT inner	edf	-	1.375	1	-	-
		p	-	0.740	**0.008**	-	-
	energy:RT outer	edf	-	1.822	1	-	-
		p	-	**0.030**	0.910	-	-
	energy:RT patch/back	edf	-	1.508	1.515	-	-
		p	-	**0.051**	**0.023**	-	-
	cover:RT channel	edf	-	1	-	-	-
		p	-	0.261	-	-	-
	cover:RT inner	edf	-	1	-	-	-
		p	-	**0.028**	-	-	-
	cover:RT outer	edf	-	1	-	-	-
		p	-	0.188	-	-	-
	cover:RT patch/back	edf	-	1	-	-	-
		p	-	0.812	-	-	-

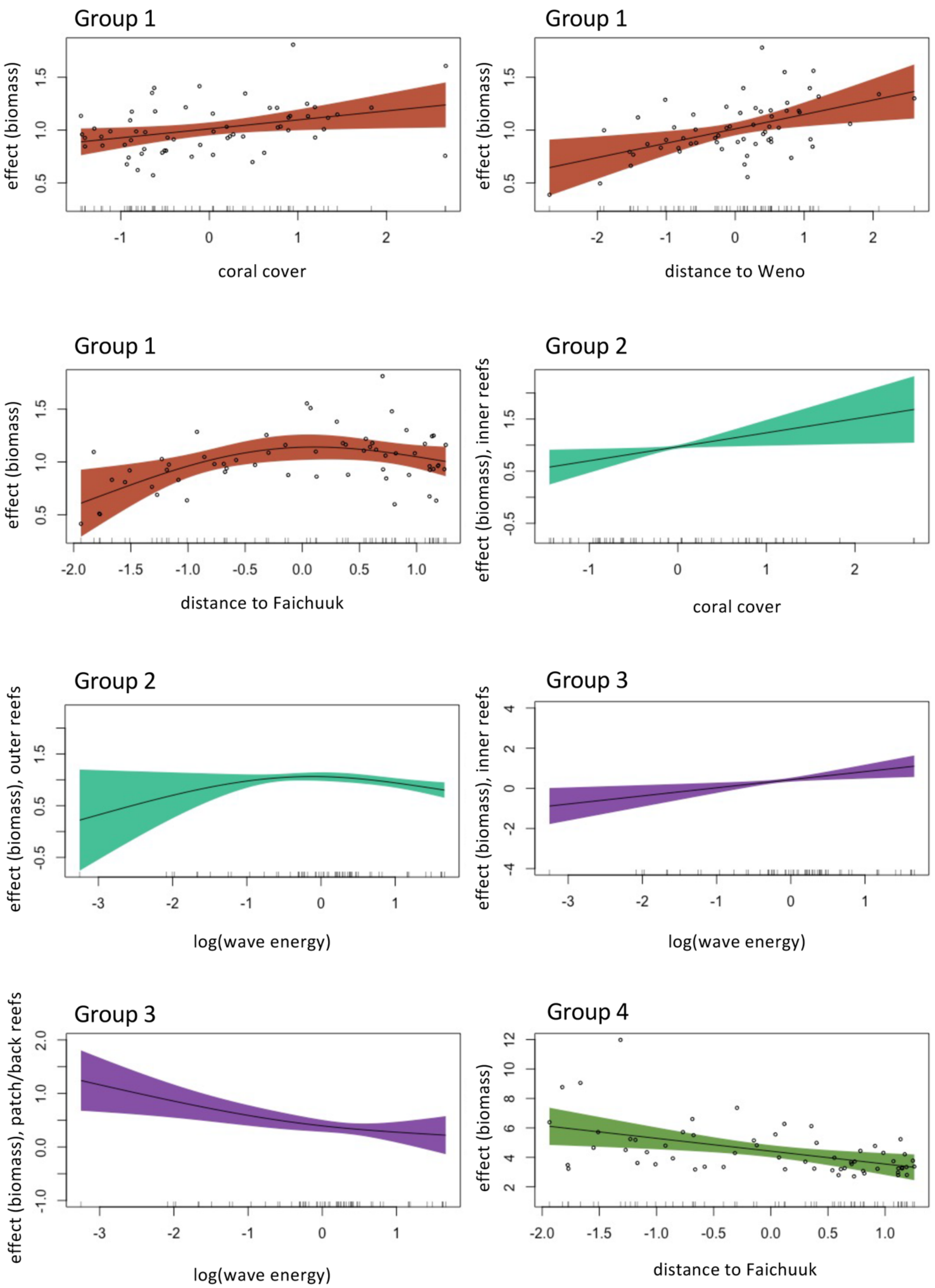

Figure 6. Partial effects plots for continuous variables (smooth terms) of trait group GAMs in group two - four where significance of term $p < 0.05$. Shaded areas are partial model residuals and colours correspond to groupings in Figure 5. Partial effects plots for all terms in each GAM in Figure A4 – A9.

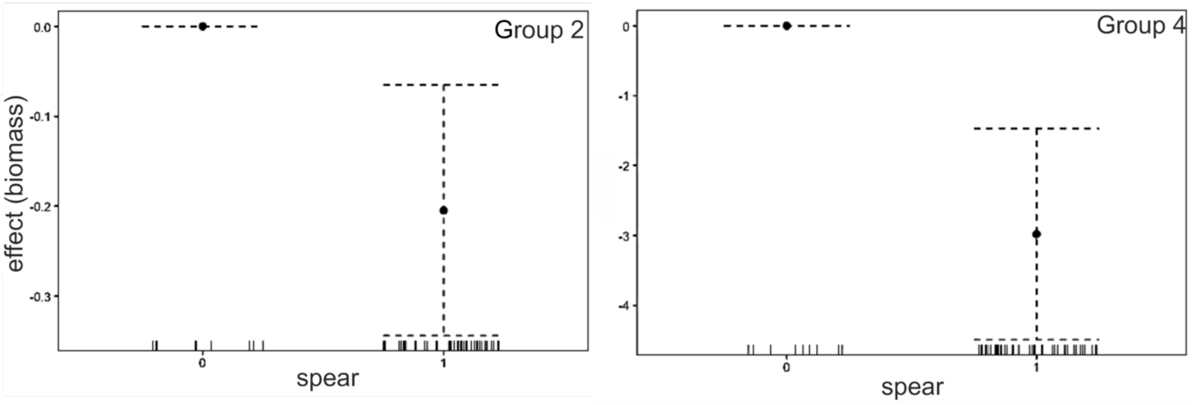

Figure 7. Partial effects of spear and dynamite fishing (dummy coded) for GAMs of trait groups two (left) and four (right) where p-values < 0.05. Partial effect plots for all terms in Figure A4 – A9.

2.5 Discussion

Effective use of the TBAM framework requires that groups of species with similar traits similarly respond to disturbances and management. For a case study of marine food fishes on a Pacific atoll, we demonstrate that trait-based groups indeed show group-specific or variable magnitudes of responses to environmental and human drivers, such as proximity to ports and dominant fishing methods. By extension, trait groups are also likely to respond comparably to group-specific management actions. The TBAM framework thus breaks down a diverse fishery into convenient units that can be prioritised for different management actions, enabling fishing of some groups whilst protecting others.

2.5.1 Functional implications of trait group responses to biophysical and fishing proxy variables

We find that Chuuk's food-fish community subsets in to five stable groups that capture functional roles and exhibit differing relationships with key environmental and socio-economic drivers (Table 4). A multitude of traits characterise these groups, highlighting that traits that relate to a range of ecological function and susceptibility to threats are most appropriate for TBAM, despite the frequent use of trophic mode as a proxy for function in the coral reef literature (McClanahan et al., 2015, Nash et al., 2016, Richardson et al., 2020). Groups are further distinguishable in terms of desirability within the fishery; larger species tend to be targeted for commercial export, and many of the species in group one represent important targets for subsistence fisheries in Micronesia. Fishing methods, habitat types, coral cover, wave energy, and distance to key markets all emerge as important predictors of group biomass. Indeed, many of these also drive total biomass (McClanahan et al., 2015, Cinner et al., 2018), so as subsets of the total assemblage we would expect to see these responses among the trait groups.

Table 4. Overview of functional roles performed by each trait group.

Trait Group	Broad characterisation	Functional implications
1	Small body size, mid-range PLD, reef-associated fishes. Mostly upper benthic, some cnidarian associated. Combination of trophic modes and aggregation types (majority are solitary).	Largest, broadest group. Would likely require further classification for management. Comparatively small body size, association with the reef and shorter PLD characterises them as site-attached species that may be vulnerable to localised disturbances. Species in this group perform functions as grazing herbivores and predators of smaller fish and invertebrates.
2	Solitary benthic predators, with similar PLD and body size ranges to group one.	This group has smaller body sizes than the other predator/piscivore groups. This is an important functional distinction between predators that consume a range of fish and invertebrates, versus piscivores targeting other fishes.
3	Reef pelagic, primarily schooling and grouping planktivores with long PLDs. Contains one reef pelagic predator.	Reef pelagic species. From a functional perspective this is important for nutrient cycling between reefs and pelagic systems. Mainly planktivores or algal browsers (Fox and Bellwood, 2013). *Caranx papuensis* is an incongruous inclusion, but because it shares habitat-uses is potentially vulnerable to the kinds of disturbances that affect the rest of this group.
4	Large, mainly solitary piscivores with short or no PLD. Mostly upper benthic.	Most reef sharks occupy a similar functional role to other large piscivores (Frisch et al., 2016), and so are included in this group.
5	Large, pelagic, schooling/grouping predators/piscivores.	Distinguished from group 4 by pelagic rather than reef-association and

		therefore play different roles in nutrient cycling (Roff et al., 2016).

Small, solitary benthic predators (group two) and larger upper benthic predators (group four) both have a higher biomass at sites where dynamite fishing has occurred. Similar to this finding, greater biomass of high trophic level fish has been associated with fishing disturbance (Graham et al., 2017). Group four contains several shark species, including the grey reef shark *Carcharhinus amblyrhynchos* which has a notably high biomass within the broader fish community (Figure 5b). The higher numbers of sharks at dynamited versus spear-fished sites may supress herbivory and alter ecosystem functioning (Rizzari et al., 2014). The study design does not allow us to parse whether these patterns are an effect of changing behaviour, altered biomass because of disturbance, or an effect of site selection by fishers. The relationship between these species and destructive fishing activity requires further investigation.

Reef associated, short PLD species (group one) have increased biomass with distance from the Weno market and are desirable catch; of the 20 species that collectively make up 75% of the landings in Chuuk (Cuetos-Bueno et al., 2018), 70% are represented by this group, and a further 25% are represented in group two. Body size, more so than trophic level, is a key driver of exploitation in other Micronesian fisheries such as Guam, where smaller species and individuals are making increasing contributions to the overall catch (Houk et al., 2018). Species in groups one and two have smaller maximum body sizes (median 47cm and 50 cm respectively) than all the other groups, and the proportion of these fish in landings suggests that they are fished as other, larger species are depleted.

Estimates of annual landings help to identify unsustainable exploitation, areas of vulnerability, and apparent stability (Cinner et al., 2016, Mbaru et al., 2019). However, mean annual landings do not predict biomass of our trait groups, and landings data at the national level can be unreliable (Pauly and Zeller, 2016). In most island regions, landings already outstrip sustainable levels, and the FSM is considered fully exploited. Landings are thus not necessarily a useful indicator of community dynamics in the context of fisheries that are fully or over-exploited (Harborne et al., 2018).

2.5.2 Applying trait-based adaptive management

These insights have potential to inform management strategies. The TBAM framework is an objective-driven management approach that considers trade-offs in species requirements against the needs and adaptability of fishers. Actions that have been identified as contextually appropriate because they work within existing management structures and traditional strategies include MPA networks with designated areas for commercial versus subsistence fishing, gear, and species-based restrictions (Houk et al., 2016). Trait-based, functional groupings fit particularly well with gear and species or trait group restrictions (Mbaru et al., 2019), and the cumulative effects of different actions can be positive for biomass overall (Melnychuk et al., 2021). Spatial features of human activity (i.e., proximity to key markets), and how they interact with the biomass of different trait groups can inform spatial management such as temporary closures (Figure A10).

For example, our findings indicate that current fishing effort is focused on group one, which contains species that are valued for local consumption in Micronesia (Cuetos-Bueno et al., 2018). Group one is also the largest trait group derived from our clustering. A limitation of this study is that the food fish community is subset from the entire reef fish assemblage. Because these species will inherently share several traits, it is unsurprising that the clustering produces one much larger group, which may also arise when applied to other datasets comprising only of fished species. Larger groups also imply species occupying a broader functional niche compared to specialists in smaller trait groups.

To manage this group using the TBAM framework, actions such as prioritising local subsistence exploitation over commercial export or placing size restrictions on catches could help to maintain biomass and key functions (i.e., herbivory) whilst still enabling some fishing of an important group of species. It may also be practical to have some more targeted management within large trait groups, for example with actions such as widely employed restrictions for parrotfish (Pinheiro et al., 2021), on morphologically similar species (to facilitate communication and enforcement of any restrictions), or even species-specific actions such as bans for *Bolbometopon muricatum* (Roff et al., 2017). The TBAM approach also offers a way to prioritise; in contexts where management resources are limited focusing on one or two large, stable groups with particular importance to the fishery may yield maximum benefits. In contrast, less stable trait groups, and the species within them, will have to be evaluated by managers on a case-by-case basis as to their utility and inclusion in the framework.

It is important to acknowledge that this study does not capture intraspecific trait variability (Villéger et al., 2017). This has implications for interpreting results, such as the role of body size in size-selective fisheries, where targeting of smaller species or earlier life history stages can imply overexploitation of other trait groups. Management decision-making using the TBAM framework needs to be cognisant of this limitation. The exact systems that link different traits to ecosystem function are unknown for reef fishes (Bellwood et al., 2019b) but managing for specific functions could certainly be incorporated under this framework in the future. Incorporating additional traits as the data for them become available would strengthen the groupings. Trait choice invariably influences the outcomes and interpretations of trait-based work (Mouillot et al., 2021), which is why here we have tried to include traits that encompass several possible functional roles and responses to disturbance. Traits that capture productivity, such as size at maturity or generation time, would be good candidates for inclusion in future TBAM frameworks where that information exists (Taylor et al., 2014). Fisheries with reduced biomass can still have relatively high productivity, and the relationship between the two is important for understanding how fisheries are responding to exploitation (Morais et al., 2019).

Ultimately, a balance must be found that minimises impacts to fishers whilst recognising that environmental change may require yield reductions. Decisions must be made in full consultation with affected communities to accommodate local priorities, requiring robust links between local people and management bodies (Jupiter et al., 2014). There is a strong precedent for the trait-based management proposed here in traditional marine resource governance. Examples including adaptive temporary closures and gear restrictions have a long and successful history throughout the Pacific (Cinner and Aswani, 2007), and areas with traditional management remain ‘bright spots’ with high fish biomass (Cinner et al., 2016). Trait groupings could empirically support the ecological component of decision-making processes in traditional governance, government, or NGO-led efforts. Moving forward, we need to test how well trait groups work for fisheries management within the wider context of protecting biodiversity and ecosystem functioning. This includes understanding the interactions between groups and how focusing fishing effort on perceived resilient groups could have repercussions for others. Whether or not the fisheries management proposed under the TBAM approach enables people to meet their subsistence and livelihood needs will also need to be addressed.

This study identifies key trait groups for food fish in Chuuk and illustrates how human resource use patterns are influential drivers of trait structure and function on coral reefs. It shows that groups are differentially affected by both gradients in habitat and fishing proxy measures. The TBAM framework outlined here is a suggestion for how our growing understanding of traits and functions could support management decision-making, incorporating flexibility for different local contexts, the scope to use existing management actions, and to design new ones. These outcomes provide a catalyst to further explore targeted, trait-based adaptive management of key groups of species that transcends biodiversity-based management of coral reefs.

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Chapter 3. Coral bleaching decouples linked coral and fish trait structure

3.1 Abstract

In coral reef systems, increasingly frequent, severe climate change driven disturbances are responsible for declines in vulnerable species, and a reorganisation of assemblages. Whilst these changes will certainly elicit shifts in ecosystem functioning, how trait distributions and cross-taxon interactions are altered remains largely unmeasured, hampering our ability to predict functional shifts and target management actions to maintain reef health and support recovery. We quantify trait distributions and interactions between habitat-engineering corals affected by a coral-bleaching mortality event and associated fished reef fish assemblages. First, we assess changes in the proportional contributions of different traits pre-vs. post-disturbance. We then quantify changes in the trait associations that underpin cross-taxon interactions, and test relationships between coral and fish traits. The coral trait structure shifts over the survey period, but the trait structure of the fish assemblage remains stable. This suggests a simplification of the coral assemblage as vulnerable species disappear, with a move towards disturbance resistant traits. That the fish trait assemblage displays little change could indicate a lagged response, limited reliance on coral habitat, influence of other drivers, or relative resilience. However, when examining traits of both taxa together, we discover that associations between individual coral and fish traits largely break down over time. We find reduced co-structure between the assemblages' trait distributions, altering the associations between taxa. Our study signals weakened associations of fishes with their habitat as coral assemblages degrade with climate change, potentially disrupting the ecosystem functions that support coral reef ecosystem services.

3.2 Introduction

Our understanding of the impacts of bleaching-mediated coral declines on reef species abundances, distributions and functions has expanded rapidly (Adam et al., 2011, Robinson et al., 2019b, Taylor et al., 2019, Morais et al., 2020, Tebbett et al., 2021), yet few studies explicitly examine how functional changes in the coral assemblage (beyond declines in cover) interact with fish functional composition. Rapid anthropogenic change necessitates a shift from biodiversity-based management to managing for functional integrity (Bellwood et al., 2019a, McLeod et al., 2019). Such functional or trait-based management requires knowledge of how functioning changes with both disturbances and management to effectively meet conservation goals and provision for human subsistence and livelihoods. The composition of species traits in a community, and whether they confer vulnerability or resistance to a disturbance, determines community responses to environmental change, and by extension ecosystem function (Mouillot et al., 2013).

Coral bleaching is a thermal stress response that can cause widespread coral mortality (Hughes et al., 2018a). This mortality can lead to changes in associated reef fish abundance and species richness, particularly for species and life history stages that rely heavily on live coral for food or habitat (Wilson et al., 2006, Graham et al., 2007). In the long-term, successive disturbances cause changes in community composition as novel assemblages of resilient species arise, with altered species interactions and ecosystem functions (Graham et al., 2014, Hughes et al., 2018b, Bellwood et al., 2019a). Disturbance impacts are not felt equally throughout a reef. Heterogeneity in responses amongst both coral and fish assemblages is due in part to differences in trait-mediated vulnerability (Foden et al., 2013, Mizerek et al., 2018, Richardson et al., 2018). Functional traits are the heritable morphological, physiological, and behavioural characteristics that determine species' responses to the environment (Violle et al., 2007). For example, coral colony growth form is a morphological trait that influences a species' vulnerability to disturbance (Zawada et al., 2019). Spatial heterogeneity in environmental conditions and habitats drives the traits of the species present in a community and their responses to disturbance (Zinke et al., 2018). As such, the variability of functional traits in species assemblages underpins ecosystem function, i.e., how energy is stored and moves through an ecosystem (Darling et al., 2012, Darling et al., 2013, Carturan et al., 2018, Bellwood et al., 2019b). Thus, traits represent a useful proxy to identify functionally relevant ecosystem trends and responses to stressors (Graham et al., 2014, Bellwood et al., 2019b, Beukhof et al., 2019, McWilliam et al., 2020). We are beginning to parse how traits mediate disturbance responses of corals and reef fish (Plass-Johnson et al., 2016, Richardson et al., 2017b, McLean et al., 2019, Taylor et al., 2019), but do not yet have a holistic view of functional shifts in coral and fish assemblages together (Darling et al., 2017). However, understanding the changing trait community compositions and interactions across taxa is key to anticipating and responding to changes in ecosystem function.

First, we quantify trait distributions between habitat-engineering corals affected by a coral bleaching mortality event and associated reef fishery species using the case of Chuuk, in the Federated States of Micronesia. The most novel aspect of this work is that we also assess changes in the shared co-structure, and direct trait associations between the two assemblages. We assemble the types and abundances of traits present in a reef community to compile a picture of trait-based community structure. Based on species-level coral and fish records from 2016 (pre-bleaching) and 2019 (post-bleaching), we ask: (a) how are coral and fish traits structured across time and environmental regimes (examining reef habitat types and different lagoon areas) and what are the most influential traits driving this structuring, and (b) how are coral and fish traits associated and how have these patterns changed post-disturbance?

3.3. Methods

3.3.1 Study system

Chuuk is a large lagoon system and populous island state in the Federated States of Micronesia (7.4469°N, 151.7473°E) with diverse marine atoll habitats and a varied disturbance history (Houk et al., 2016, Weeks et al., 2017), which includes the 2016-17 global coral bleaching event and associated declines in coral cover (Figure 8). Survey sites represent a variety of reef habitat types, geographic areas, and levels of wave exposure. Habitat types are characterised as outer reefs (outside the lagoon), channel reefs, patch/back reefs (inside the lagoon), and inner reefs (adjacent to islands). We collected data from sites throughout Chuuk Lagoon and nearby Kuop Atoll in 2016 and 2019 (Figure 8), conducting 114 surveys total, with 75 site surveys in 2016 and 39 in 2019. 38 sites were surveyed in both years. The 39 sites surveyed in 2019 are a representative sample of the 2019 sites and reef types (Table B1).

3.3.2 Fish and coral surveys

Diversity and abundance data for reef fisheries target (food) fish species and scleractinian corals were obtained from the Micronesia Challenge monitoring program (Houk et al., 2015). This program’s focus on food fish reflects local monitoring priorities. Informed by landings data, food fishes are defined as species that people consume and sell locally from the reef (Houk et al., 2015), including Acanthurids, Scarids, Serranids, Carangids, Labrids, Lethrinids, Lutjanids, Balistoidids, Kyphosids, Mullids, Holocentrids and Carcharhinids. Sites were at 3-5m depth at inner reef sites or 6-8m at channel, outer and patch reefs sites (Figure 8) (Houk et al., 2015, Houk et al., 2016). Fish species abundance was recorded with 12 stationary point counts (SPCs) (5 metre radius, 3 minutes) per site, with counts equally spaced across five 50m transects (approximately every 20m). SPCs are appropriate for the species counted here, and they offer good replication and statistical power for the scale of this monitoring effort (Houk and van Woesik, 2013). Coral species and cover were collected with ten 1m^2 quadrats per site placed along the same transects. Total % coral cover at each site was calculated from the summed % coverage of all the species present at a given site (Houk et al., 2015). Species accumulation curves confirmed sufficient sites for our analysis (*vegan*) (Figure B1) (Gotelli and Colwell, 2001). Species names were checked against the World Register for Marine species (WoRMS) (*worrms)* before assembling trait data (Horton et al., 2017, Chamberlain, 2019).

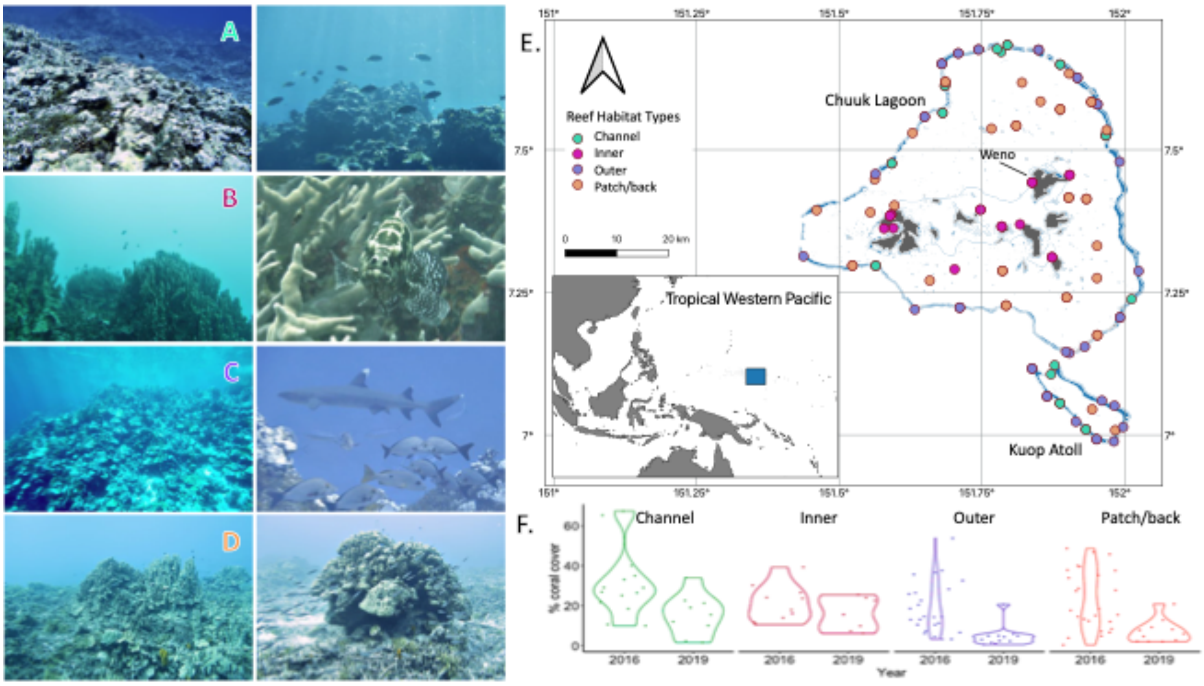


Figure 8. Reef habitat types listed as (a) channel reefs, (b) inner reefs, (c) Outer reefs and (d) patch/back reefs. Photos taken in 2019 (post-bleaching). (e) Map of Chuuk Lagoon (North) and Kuop Atoll (South) in the FSM, Tropical Western Pacific. 114 sites total, 75 surveyed in 2016 and 39 in 2019, 38 sites surveyed in both years (Table B1) (UNEP-WCMC, 2018). (f) % coral cover changes at each reef type (Wilcoxon rank sum test: channel (p=0.018), inner (p=0.187), outer (p<0.001), patch (p=0.002)).

3.3.3 Species traits

Trait choice ultimately influences the findings and interpretations of any given analysis (Hadj-Hammou et al., 2021). We used species traits to broadly characterise the functional structure of fish and coral assemblages, and thus selected a combination of categorical and continuous traits that feasibly link to several processes and functions (Table 5), are widely used in other assessments, and have good coverage for the species represented in this study.

Fish traits were assembled from Fishbase (Froese and Pauly, 2019), the wider literature, and gaps were imputed for phylogenetically-related species using expert opinion. No fish species were excluded due to a lack of trait information. Coral traits were derived from The Coral Trait Database and bleaching vulnerability assessments (Foden et al., 2013, Madin et al., 2016a, Madin et al., 2016b). In some cases, multiple species identifications were synonymised. Where this occurred, they were condensed into totals under the single current species name. Where feasible, missing traits were imputed for phylogenetically-related species, as trait information was not always available (Table B2). Due to limited trait information for several coral species, those with more than two trait values missing were excluded from this analysis (85% of species retained (187/221)).

Intraspecific trait variability is beyond the scope of this study; though it is important to note, especially for corals, that there can be a high degree of phenotypic plasticity within populations and species (Darling et al., 2012, Villéger et al., 2017). The localised scale of this study helps to minimise this issue. It should also be noted that functional differences between adult and juvenile fish are not considered in this study.

Table 5. Definitions and justification for selected coral and fish traits.

	Trait	Definition	Abbreviations	Justification
Coral	Growth Form (Factor) - Morphological	The typical morphology of a species (Veron and Stafford-Smith, 2000). (branching closed, branching open, columnar, corymbose, digitate, encrusting, encrusting long uprights, hispidose, laminar, massive, submassive, tables/plates)	br_close br_open col corymb digit enc enc_up hisp lam mas submas tab_plate	Key predictor of function for corals (Denis et al., 2017). Affect life history strategies and population dynamics (Darling et al., 2012). Complex morphologies are important for reef structural complexity, indicating disturbance vulnerability (Carturan et al., 2018, Zawada et al., 2019) and are important habitats for other reef species (Darling et al., 2017).
	Larval Development Mode (Factor) - Reproductive	Brooders: Internal fertilisation, colonies release planular larvae. Spawners: Broadcast release of gametes. Fertilisation and development of planulae happens in water column.	brood spawn	Role in life history strategies and population dynamics (Darling et al., 2012). Brooded larvae settle more rapidly on more diverse substrates but have a higher post-settlement mortality rate (Carturan et al., 2018). Brooding assemblages suggestive of more disturbed habitats (Darling et al., 2017).
	Growth rate (mm/yr)	Rate of yearly extension.	GR	Indicative of life history strategies and

	(Numeric) - Physiological			population dynamics (Darling et al., 2012), habitat provisioning for other reef species (Darling et al., 2017) and recovery capacity (Carturan et al., 2018).
	Bleaching Susceptibility (Factor) - Physiological	Overall climate vulnerability (high or low) derived from assessments of sensitivity, adaptability and exposure for each species (Foden et al., 2013) (susceptible, resistant).	resistant suscept	Makes distinctions between families where traits such as growth form and growth rate do not predict vulnerability to bleaching events (Mizerek et al., 2018).
	Maximum Depth (m) (Numeric) - Ecological	Maximum observed depth	DL	Affect life history strategies and population dynamics (Darling et al., 2012), important for understanding type of habitat available to other species.
Fish	Maximum Length (cm) (Numeric) – Life history	Maximum length (cm) recorded in the species core range.	max_length	Important for species sensitivity to predation, thermal resistance, fecundity, extinction risk, and metabolic rates (Graham et al., 2011, Beauchard et al., 2017). Related to a species’ vulnerability to size selective fishing methods (Stuart-Smith et al., 2013, Bellwood et al., 2019b).
	Maximum Depth (m) (Numeric) - Ecological	Maximum depth, either observed or from expert opinion.	D_max	Depth is a key environmental filter for reef fish assemblages (Bridge et al., 2016).
	Mean pelagic larval duration (days) (Numeric) – Life history	Theoretical amount of time (days) that a larval fish can remain viable in the water column, measured	PLD	Associated with range size, recovery following disturbance and dispersal connectivity (Lester and Ruttenberg, 2005, Wilson et al., 2018).

		from hatching or spawning.		
	Trophic mode (Factor) – Feeding ecology	Indicates broad diet categories of species. (Piscivore, predator, planktivore, omnivore, detritivore, herbivore)	pisciv predator planktiv omniv detrit herbiv	Linked to food acquisition, growth requirements, demographics (predator-prey interactions), vulnerability to climate change and nutrient cycling (Graham et al., 2011, Beauchard et al., 2017).
	Position in the water column (Factor) - Behaviour	Location on reef where species spend most of their time. (Pelagic, reef pelagic, upper benthic, benthic, demersal, sub-benthic, cnidarian associated)	pelagic reef_pel upper_ben benthic demersal sub_ben cnid_ass	Ties in with motility, foraging, migratory requirements, and dispersal (Stuart-Smith et al., 2013, Beauchard et al., 2017).
	Aggregation (ordered factor) - Behaviour	Grouping behaviour. (schools, groups, pairs, solitary)	groups pairs school solitary	Linked to foraging strategy, vulnerability to predation and different fishing methods (Plass-Johnson et al., 2016).

3.3.4 Analysis

Data analysis was performed in R version 4.0.3 (R Development Core Team, 2019), with RStudio version 1.0.153 and the packages *vegan* (Oksanen et al., 2019), *FD* (Laliberté and Legendre, 2010, Laliberté et al., 2014), and *ade4* (Dray and Dufour, 2007).

To analyse broad differences in assemblage structure across time and environmental regimes, we calculated community-weighted means (CWM) as the percent contribution of a trait to the community assemblage (*FD*) (Garnier et al., 2004, Kleyer et al., 2012, Denis et al., 2017) with log-transformed abundance data for corals and fishes and dummy-coded categorical traits. Abundances were transformed to help mediate the effects of the most common species. Trait structure of coral and fish assemblages across both survey years were assessed with a scaled principal component analysis (PCA) of the CWM. PERMANOVA (permutations = 999, fixed factors: reef type, year, island) with SIMPER analysis on the CWMs with Euclidean distance were used to test for differences between reef types, survey years, and survey areas (Chuuk vs. Kuop) (*vegan*), including interactions between these variables and testing for marginal effects between them. The top 25% of PCA loadings were extracted for corals and fishes to identify the most influential traits driving overall structuring in each assemblage. As a comparison, we also ran equivalent PCAs and PERMANOVAs on the abundance data alone (Table B3, Figure B2).

Associations between coral and fish traits were explored using an RLQ and fourth corner analysis for 2016 and 2019 separately. Here, we subset our data to only the 38 survey sites that were visited in both years. RLQ analysis is an ordination method across three tables (R - environmental variables, L - species abundances, Q - species traits) that summarises the shared structure between these tables (*ade4*) (Mouillot et al., 2013, Dray et al., 2014). To look at shared structuring between coral traits and the fish assemblage, we treated the corals as the environment for the fishes, so our R table was the coral CWM, L was the log-transformed fish species abundances and Q was the fish trait table. The fourth corner analysis is a complement to the RLQ, and the fourth corner refers to the matrix of interaction coefficients between the environment (coral cwm) and fish traits. We used this to test for bivariate associations between each coral-fish trait in both 2016 and 2019 (Brown et al., 2014, Dray et al., 2014). We also examined whether the results were sensitive to potential spatial autocorrelation using Moran spectral randomisation constraints on the fourth corner analysis, which revealed similar results to the standard analysis detailed here (Figure B3) (Wagner and Dray, 2015, McLean et al., 2018).

3.4 Results

3.4.1 Characterising the trait structure of coral and fish assemblages

PERMANOVAs of the coral CWMs reveal that trait structuring varies strongly across reef types and survey areas, with a lesser effect across years. Similarly, there is clear structuring of the fish assemblage across reef types and survey areas, but no clear differences between 2016 and 2019 (Table 6, Figure 9). In contrast, the analysis of the abundance data alone does find significant changes in species composition between the two years (Table B3, Figure B2). The top 25% of PCA loadings from the coral CWM identify digitate growth form, growth rate, maximum depth, brooding and spawning traits as the most influential traits overall. For fishes respectively, the most influential traits are maximum depth, herbivorous trophic mode, schooling, maximum length, and pelagic water column position traits.

Table 6. PERMANOVAs for corals and fishes. Model: scaled log CWM ~ reef type * year * area. Number of permutations = 999. Euclidean distance matrix (Marginal effects of interactions p > 0.05). Dark shaded cells where p<0.05.

	Factor	R2	F	*p*
Corals	Reef Type	0.147	6.586	< 0.001
	Year	0.026	3.510	0.002
	Area	0.030	4.043	< 0.001
	Reef Type:Year:Area	0.007	0.948	0.461
Fishes	Reef Type	0.106	4.483	< 0.001
	Year	0.014	1.825	0.063
	Area	0.024	3.043	0.004
	Reef Type:Year:Area	0.008	0.993	0.465

While the multivariate methods applied to community weighted mean trait values used here are a common approach for examining community structure (Kleyer et al., 2012), mean trait values are simplistic and do not capture trait variation within communities. We therefore validated our results by examining patterns in spatial beta diversity (Chao et al., 2019). We found very little year-to-year change in fish trait communities, with an average dissimilarity of 0.045 between each site in 2016 and 2019 (Table B4). We did find evidence of a slight redistribution of spatial beta diversity, with some site pairs displaying higher or lower dissimilarity in 2019 than in 2016, however these differences were minor, and among-site beta diversity remained low in both years (2016 mean = 0.059, 2019 mean = 0.060) (Table B5). As expected, the corals do show some year-to-year change in the coral assemblage, with an average dissimilarity of 0.194 between each site in 2016 and 2019 (Table B4). Among-site diversity was also higher for corals (2016 mean = 0.231, 2019 mean = 0.196) (Table B5).

SIMPER analysis indicates that the most influential coral traits driving dissimilarity between reef habitat types are bleaching susceptibility, growth forms (particularly massive, encrusting, and digitate forms) and depth limits. Larval development mode is also important for dissimilarity between patch/back and channel vs. outer reef types (Table B6). For the fish traits, trophic modes, water column position and aggregation types are the key drivers of dissimilarity between reef types. Pelagic larval duration (PLD) is relevant for differences between patch/back and channel vs. outer reefs, and maximum length and depth are important for distinguishing patch/back reefs from other habitat types (Table B6). Differences in the coral assemblage between 2016 and 2019 are driven by bleaching susceptibility, growth rate, growth forms (encrusting, digitate, massive, and branching closed) and depth limits (Table B7). Chuuk Lagoon and Kuop Atoll also exhibit key differences in their trait structuring for corals and fish. For fishes, variation in the trait structure was explained by differences in maximum depth and length, trophic mode, aggregation type and water column position traits. Kuop contains predator and piscivore trophic groups, as well as grouping aggregations and higher maximum length traits (Figure 9). Dissimilarity in the coral assemblage is driven by growth form, lower depth limits, and larval development mode traits. Dissimilarity in the fish assemblage is driven by PLD, herbivore and piscivore trophic modes, water column position, grouping aggregations and maximum depth traits (Table B8).

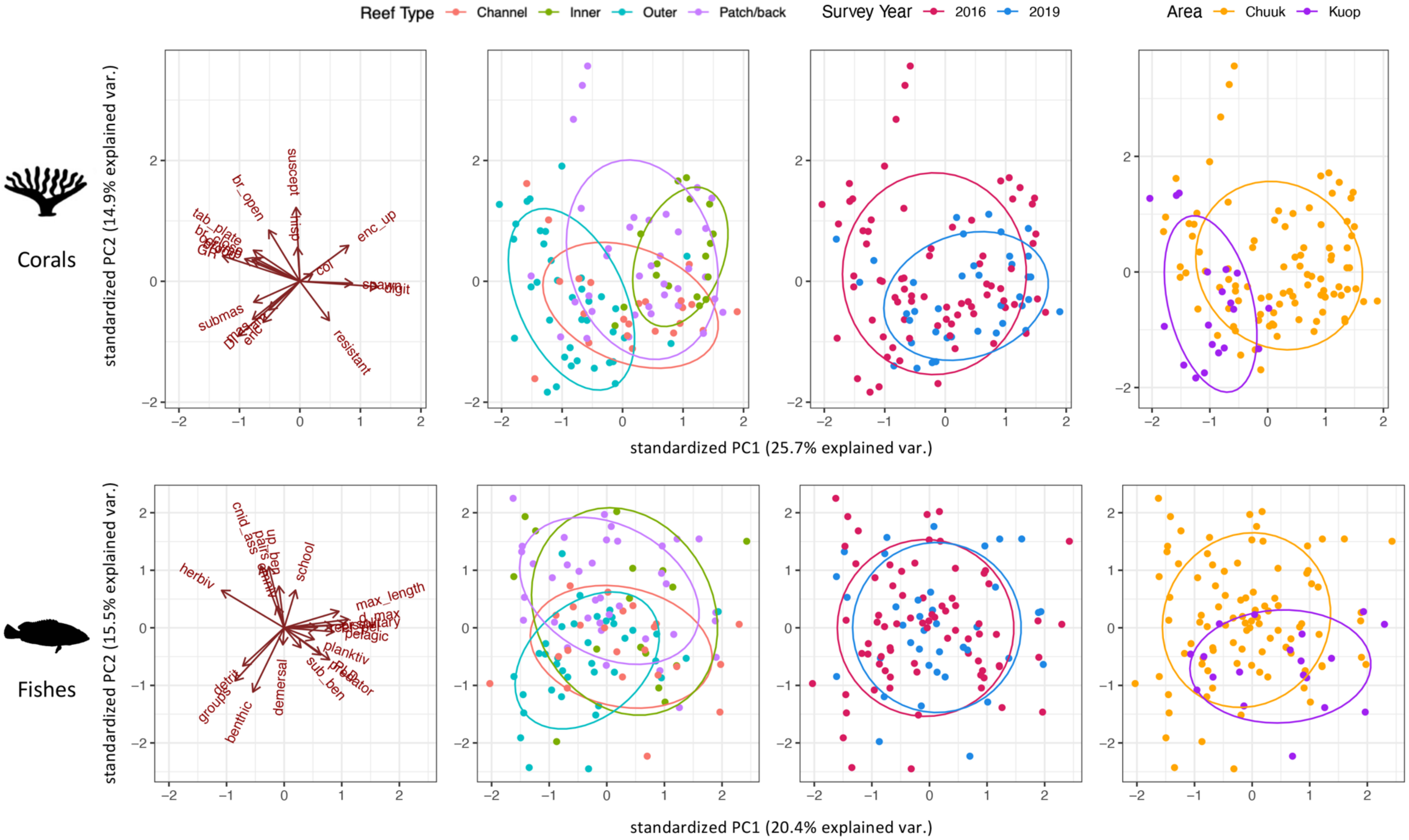


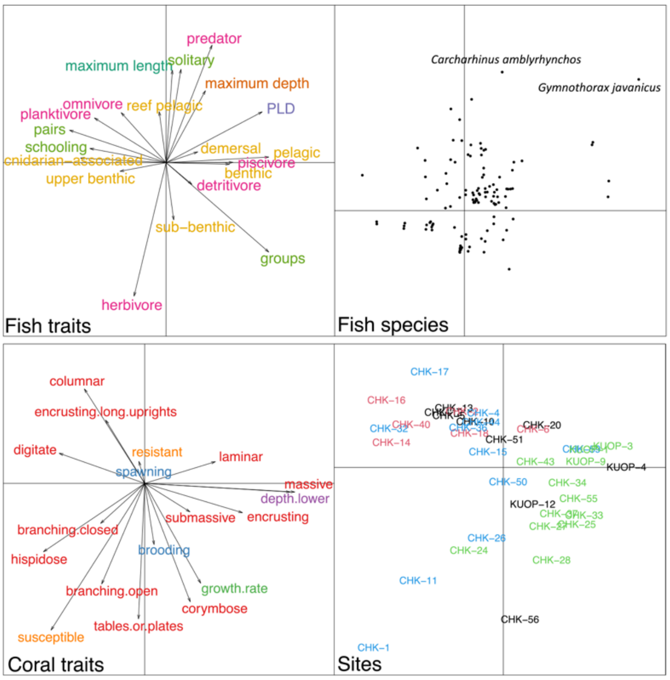
Figure 9. Principal component analysis (PCA) of coral (top row) and fish (bottom row) CWMs (log-transformed abundance), with ellipses for reef type, survey year and atoll (Chuuk or Kuop). Trait names abbreviated (see Table 5).

3.4.2 Associations between coral and fish traits

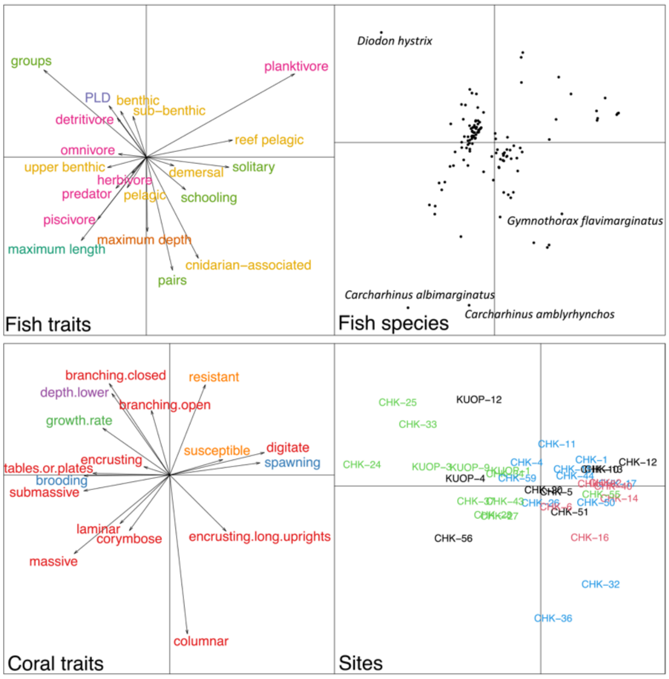
The first two axes of the 2016 RLQ explain approximately 73% of the variation between the three tables (see % total co-inertia) (Table B9). Together, models two and four of the permutation test confirm that there is shared structuring between the coral CWM (R, environment), fish abundance (L, log-transformed abundance) and the fish traits (Q) in 2016 (permutation test model 2, p = 0.014, nperm = 999, permutation test model 4, p = 0.011, nperm = 999), and that fish species composition is affected by both fish and coral (environment) traits (Dray et al., 2014). In 2019, the first two axes of the RLQ explain approximately 70% of the variation (Table S9), and the permutation test suggests that while there may be some association between the fish species composition (L) and the corals (R) (permutation test model 2, p = 0.049, nperm = 999), the fish species composition is not correlated with the fish traits (Q) (permutation test model 4, p = 0.105, nperm = 999).

In 2016, pelagic, benthic/upper benthic, piscivorous and cnidarian-associated fishes align closely along the 1st RLQ axis (x), with herbivore and predator levels of the trophic group trait driving differences along the second (y) (Figure 10). There are key outliers in the fish assemblage composition with substantial trait differences. These species include sharks, moray eels and in 2019 the porcupinefish *Diodon hystrix*. For the coral traits, massive growth forms and lower depth limits explain variation differences along the 1st axis, with bleaching susceptibility/resistance (and associated growth forms) driving the variation along the second axis (Figure 10). In 2019, the same species outliers are present in the fish assemblage, and there are less obvious differences among the sites. Reef pelagic and solitary traits define the variation in fish traits along the first axis, and maximum depth along the second. Coral trait structure is defined by reproductive mode and growth forms along the x axis, and on the second (y) axis is most influenced by columnar growth forms.

Fourth corner analysis of 2016 and 2019 reveals several associations between coral and fish traits. There were fewer correlations between traits in 2019 (11 correlations) versus in 2016 (20 correlations). The only correlations carried over from 2016 are between predatory fish and bleaching susceptible corals (Figure 11).

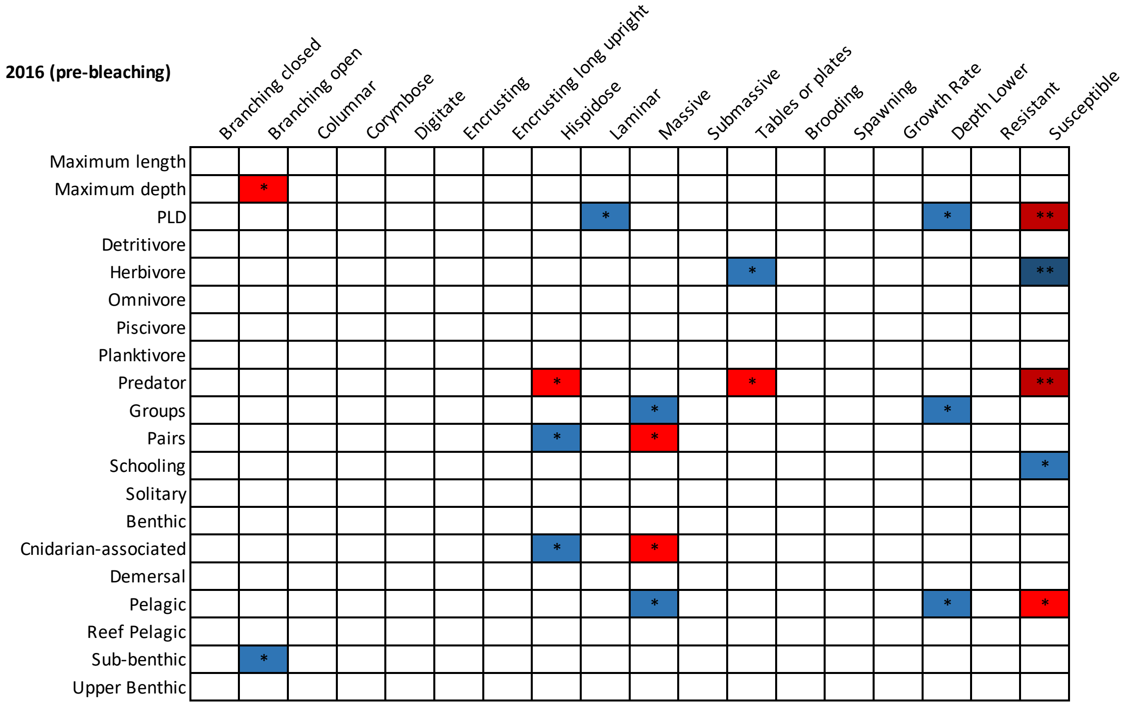


2016 (pre-bleaching)



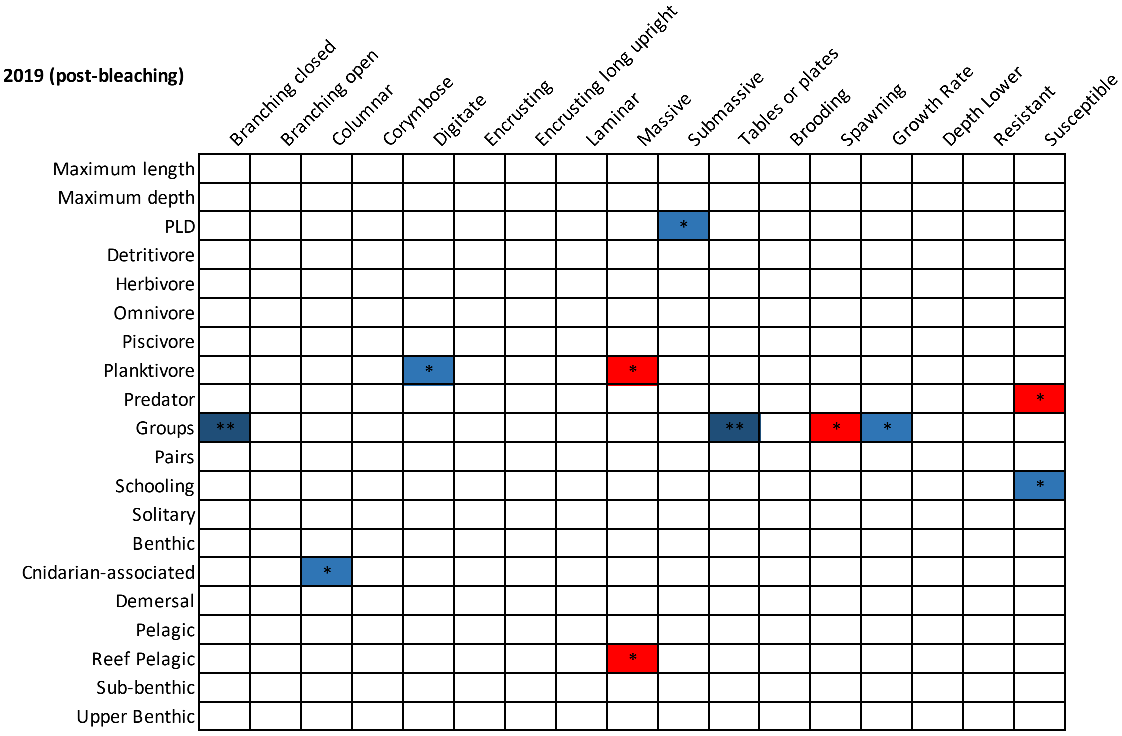
2019 (post-bleaching)

Figure 10. Shared co-structure between the environment (R, in this case coral trait CWM), fish abundance (L – log abundance) and fish trait (Q) tables in RLQ analysis for 2016 (left) and 2019 (right) from scaled trait CWMs. Top row in each year is the fish trait (left) and species (right) structure. Bottom row is coral trait structure (left) and sites (right). Fish and coral traits are coloured by trait category (ex. coral growth forms in red). Sites coloured by habitat types; patch/back (blue), inner (red), channel (black) and outer (green) reefs.



2016 (pre-bleaching)

	Branching closed	Branching open	Columnar	Corymbose	Digitate	Encrusting	Encrusting long upright	Hispidose	Laminar	Massive	Submassive	Tables or plates	Brooding	Spawning	Growth Rate	Depth Lower	Resistant	Susceptible
Maximum length																		
Maximum depth		🟥 *																
PLD									🟦 *							🟦 *		🟥 **
Detritivore																		
Herbivore												🟦 *						🟦 **
Omnivore																		
Piscivore																		
Planktivore																		
Predator								🟥 *				🟥 *						🟥 **
Groups										🟦 *						🟦 *		
Pairs								🟦 *		🟥 *								
Schooling																		🟦 *
Solitary																		
Benthic																		
Cnidarian-associated								🟦 *		🟥 *								
Demersal																		
Pelagic										🟦 *						🟦 *		🟥 *
Reef Pelagic																		
Sub-benthic		🟦 *																
Upper Benthic																		



2019 (post-bleaching)

	Branching closed	Branching open	Columnar	Corymbose	Digitate	Encrusting	Encrusting long upright	Laminar	Massive	Submassive	Tables or plates	Brooding	Spawning	Growth Rate	Depth Lower	Resistant	Susceptible
Maximum length																	
Maximum depth																	
PLD										🟦 *							
Detritivore																	
Herbivore																	
Omnivore																	
Piscivore																	
Planktivore					🟦 *				🟥 *								
Predator																	🟥 *
Groups	🟦 **										🟦 **		🟥 *	🟦 *			
Pairs																	
Schooling																	🟦 *
Solitary																	
Benthic																	
Cnidarian-associated			🟦 *														
Demersal																	
Pelagic																	
Reef Pelagic									🟥 *								
Sub-benthic																	
Upper Benthic																	

Figure 11. Fourth corner analysis of associations between coral (horizontal) and fish (vertical) traits from scaled, log-transformed community-weighted mean values in 2016 (top) and 2019 (bottom). Blue denotes a positive relationship, and red a negative one, with significance level given by asterisks (* $p < 0.05$, ** $p \leq 0.01$) and shaded accordingly.

3.5 Discussion

Disturbance-driven changes in species assemblages may cause a loss of key functions that define coral reefs and uphold ecosystem services (Morais et al., 2020, Tebbett et al., 2021). Our findings characterise a reef community that has undergone significant changes in trait structure, and by extension likely shifts in functioning over time. Strikingly, shared structuring between coral and fish traits is reduced from 2016 to 2019, and there are fewer direct associations between the two trait assemblages in 2019, lessening the extent of trait-based functional associations between fishes and corals.

Despite clear environmental differences in the trait assemblages of corals and fish at different reef habitats and atolls within the survey area, only the coral assemblage exhibits a change in trait space from 2016 to 2019 with a shift towards traits that suggest resilience, such as fast-recovering digitate growth forms and disturbance-resistant massive growth forms (Darling et al., 2012, Mizerek et al., 2018). We also detected some year-to-year variation in functional beta diversity over this period, and the decline in mean site-site dissimilarity also implies that the coral functional assemblage has become more homogenous (Table B4, B5). The study period encompasses a global coral bleaching event, which caused widespread declines in coral cover and shifts in community composition both in Micronesia and globally (Figure 8) (Eakin et al., 2019, Raymundo et al., 2019, Houk et al., 2020b). The disturbance-mediated reorganisation of traits and how they associate with each other will shape the functional effects of climate-driven disturbances on coral reefs.

In contrast, the fish trait assemblage exhibits no such changes from 2016 to 2019 (Figure 9) and is accompanied by low year-to-year variation in functional beta diversity (Table S4). Post-bleaching, herbivore biomass and abundance tends to increase (Adam et al., 2011, Robinson et al., 2019a, Taylor et al., 2019), and populations of food fish specifically are broadly maintained (Robinson et al., 2019b). Documented changes in fish assemblages tend to instead come from declines in coral or habitat dependent species (Stuart-Smith et al., 2018, Morais et al., 2020). From 2016-2019, the food fish biomass on Micronesian coral reefs nearly doubled, was consistent across major trophic groups and was proportional to the pre-disturbance state (Houk et al., 2020a), reflecting the minimal functional changes for food fish seen in this study.

Rapid recovery of fish biomass following the 2016 bleaching event has been documented elsewhere in the Pacific, where recovery trajectories were also influenced by gradients of human activity (Magel et al., 2020). Careful management of the fishery could thus supply certain commercial, and subsistence needs despite the loss of coral functional diversity (Martin et al., 2017, Robinson et al., 2019b).

The temporal stability of the fish assemblage could be interpreted as independence of trait structure from the corals, at least for the food fish species surveyed here. However, there were some changes in the species composition (Table B3, Figure B2), implying a level of functional redundancy in the trait assemblage. Importantly, our analysis focuses on a subset of fishes that are targeted by reef fisheries, though there is evidence elsewhere for declines in coral-dependent species despite an overall recovery or even increase in fish biomass (Brandl et al., 2016, Magel et al., 2020). The full impacts of coral bleaching on fish assemblages are likely felt within the smaller, coral-dependent, cryptobenthic and non-food fish species that are not counted in this methodology but still play a critical role in ecosystem function (Richardson et al., 2018, Stuart-Smith et al., 2018, Brandl et al., 2019, Wilson et al., 2019, Stuart-Smith et al., 2021).

While coral trait structure was primarily environment and disturbance-driven over this period, the fish assemblage may be subject to factors that mask these environmental drivers to some extent. Fishing is a dominant use of reef resources across Micronesia (Harborne et al., 2018), and it is possible that fishing pressure drives fish trait structure more than habitat integrity (Houk et al., 2015). As such, our pre-bleaching fisheries fish assemblage may already have been shaped by fishing pressure, as Chuuk has some of the highest levels of fishing impact in the Western Pacific after Guam (Cuetos-Bueno et al., 2018, Harborne et al., 2018). The idea that fisheries play a key role in structuring is further supported by differences in the fish assemblage between Chuuk Lagoon and Kuop Atoll, which could potentially be explained by gradients in human access. Kuop is further from human population centres and key markets, which are all within Chuuk Lagoon. Fisheries cause functional and assemblage structure changes through targeting larger fish and predators (DeMartini et al., 2008, Sandin et al., 2008, Martin et al., 2017, Zgliczynski and Sandin, 2017). That the Kuop fish assemblage contains larger body size and higher trophic level traits suggests that this area experiences reduced fishing pressure and is consistent with Chuuk's size selective fishery (Cuetos-Bueno et al., 2018). An alternative explanation could be that variation in hard coral cover drives these differences (Russ et al., 2021). However, Kuop had lower mean percentage coral cover compared to Chuuk in both survey years (Chuuk in 2016: 24.1%, 2019: 11.1%. Kuop in 2016: 17.7%, 2019: 1.47%), which does not support the positive association between coral cover and large predators and piscivores observed in Russ et al. 2021.

Our most novel finding is the loss of shared structuring between the two trait assemblages over time. The coral traits (CWM), fish abundances and fish traits have linked patterns in trait space distributions across sites in 2016. Variability in fish functional assemblages is mediated by reef structural complexity, creating environmental filtering that is determined by coral traits (Denis et al., 2017, Richardson et al., 2017a). However, this broke down by 2019, with weak evidence for shared structuring between the coral and fish traits. This reveals that the coral and fish trait assemblages have dissociated following the bleaching, probably as a consequence of coral shifts away from vulnerable traits post-bleaching that we identified in the initial PCA (Figure 9). That surveys were only conducted in 2016 and 2019 is an important limitation of this work. Future work should include additional time points prior to a disturbance to confirm that linked coral-fish trait associations are relatively stable pre-bleaching. More broadly, as the rate and severity of disturbances on coral reefs increases, monitoring programs may have to reassess whether current protocols adequately capture these impacts. Similarly, the potentially distortive impact of fishing on trait assemblages means that conducting this analysis in no-take zones would improve our understanding of these interactions.

Fourth corner analysis of associations between coral and fish traits in 2016 versus 2019 underscores the reduction of shared structuring and indicates a reorganisation of trait linkages. Few of the 2016 associations are preserved in to 2019 and several new associations are detected. For example, positive associations between herbivores and tabular/plating and bleaching susceptible corals are lost in 2019, whereas negative associations between predators and bleaching-susceptible corals are maintained. Planktivorous fishes in contrast have more detectable associations with coral traits in 2019. The reasons for these new associations are not obvious. They may simply be more easily detectable once other associations are lost, or indeed be newly arisen from changing proportions of different traits in the coral and fish assemblages. In the case of the new associations between corals and planktivorous fish, it is worth noting that the planktivores have greater loading in determining trait structure in 2019 (Figure 10).

In 2019, fish with grouping aggregation types have positive associations with complex coral morphologies (branching closed and tables/plates) with high growth rates (Figure 11). Fish with this trait include a number of *Acanthurus* and parrotfish (*Bolbometopon muricatum*, *Scarus* and *Chlorurus*) species. These associations highlight two key ecosystem functions: complex habitat provisioning by corals (Rogers et al., 2014), and herbivory by fish (Richardson et al., 2020, Tebbett et al., 2021). Except for *B. muricatum*, the grouping herbivores identified here are grazers (which includes cropping, excavating and scraping mechanisms) (Richardson et al., 2020), and are important for facilitating coral recovery processes (Bellwood et al., 2004). The associations indicate that these functions are linked, in that grouping fish performing herbivory are associated with complex coral habitat. In 2016 herbivores were associated with tabular/plating and bleaching susceptible corals and this link with more complex morphologies is at least in part maintained through the associations of the grouping fish species. Among the grouping species are some upper benthic predators (i.e. *Macolor niger)* and their association with complex coral morphologies also reflects preferred habitat (Kerry and Bellwood, 2015). Shifting associations point towards potential changes in the spatial distribution of habitat provisioning, herbivory, and predator functions post-disturbance, which has implications for how spatial prioritisation and fisheries management may be adapted to changing reefscapes. Losing these associations, whether through declines in complex coral habitat or in associated fishes may result in reduced or absent functions.

Our study has some limitations that are inherent to examining complex functional changes over time. First, we cannot confirm causality between the bleaching event and functional changes shown here, and other impacts (i.e., dynamite fishing, storms) may have played a role in the changes observed. However, widespread bleaching occurred in Chuuk in 2016, and it is reasonable to attribute the declines in coral cover to this bleaching event and subsequent functional shifts as an extension of this impact. Second, though comprehensive across the survey area, the relatively small spatial scale of this study requires a degree of caution in interpreting results, particularly as they relate to high trophic-level feeding traits which can appear much more influential at small scales (Heenan et al., 2020). Also, intrinsic to functional trait studies are the limitations of trait choice, and the opacity of the link between traits and functions in reef ecosystems (Bellwood et al., 2019b). Here, we report trait assemblage changes and associations across a single ‘pulse’ disturbance event. Future work should incorporate longer-term perspectives to better understand how the functional structure of reefs is changing, particularly in the context of reduced recovery windows (Hughes et al., 2018a). Finally, while this study focuses on the relationships between coral and fish traits, other taxa that characterise reef habitats (i.e., macroalgae) will no doubt also form an important part of the picture.

This study depicts a coral reef area that has undergone significant changes. We show that there is clear environmental structuring of coral trait structure and that to some extent this is reflected in the fish. However, the shifts in coral traits over the study period were not mirrored by a similar response in the fish trait assemblage, highlighting their relative resistance to bleaching disturbance. We illustrate that linked trait space distributions between corals and fish have been reduced as the coral trait structure changes, and that this has loosened and restructured links between the two taxa. Under a regime of escalating frequency and severity of climate impacts, we expect reefs to become increasingly generalist in trait structure, particularly for corals and fish species that directly rely on them. Recovery potential persists however, if local stressors can be managed and current climate trajectories averted.

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Chapter 4. Co-variation of fish and coral traits among distinct reef habitats

4.1 Abstract

Escalating climate impacts on coral reefs are increasingly shifting management goals from preserving biodiversity towards maintaining ecosystem functions. Morphological and ecological species traits can help assess functions within reef communities beyond taxonomic identities alone. However, our limited understanding of trait-based interactions between fishes and corals, and whether they are captured by current monitoring practices, hampers management of function. Here, we use a trait-based framework combined with co-inertia analyses to test whether the spatial distribution of traits co-varies across different habitats in corals and fishes, and test whether different components of the reef fish community (fisheries specific vs. site-attached species) display distinct patterns in this regard. We reveal that our ability to detect associations and shared spatial patterns between coral and fish traits relies on monitoring site-attached species in addition to fisheries target species. We thus highlight the unique contributions of different parts of the fish community to the overall trait structure, and the importance of considering monitoring protocols when drawing conclusions about traits and ecosystem functioning.

4.2 Introduction

On coral reefs, functions of habitat-building corals are linked to those performed by fishes and other associated species through processes that include herbivory (Darling et al., 2017, Richardson et al., 2020), predation (Hempson et al., 2018), and habitat provisioning (Rogers et al., 2014). Traits offer insight into functions performed by groups of species across spatial, temporal and disturbance gradients (McLean et al., 2019, Pecuchet et al., 2020), and have applications in management, conservation prioritisation, restoration and forecasting change (Laughlin et al., 2017, Grenié et al., 2018, Beukhof et al., 2019). A detailed understanding of trait-based composition of communities at relevant scales can thus guide decision-making in fisheries management, invasive species management, and spatial conservation (Givan et al., 2017, Mbaru et al., 2019, McLean et al., 2019). Fundamental to these applications is effective monitoring, but it is unclear whether current programs can effectively support decision-making on maintaining reef function.

Non-random trait filtering can be observed among reef habitats, but also across disturbances including climate-driven heatwaves (Richardson et al., 2018). In the latter, coral loss through bleaching-induced mortality affects the structure of fish communities, with planktivore, corallivore and small-bodied fishes particularly vulnerable (Brandl et al., 2016) and herbivore abundances typically increasing after coral loss (Robinson et al., 2019). Clearly, morphological traits in the coral community shape fish assemblages through providing complex habitat (Darling et al., 2017), and disturbance-driven functional shifts in corals can affect fish trait structure (Richardson et al., 2018). However, cross-taxon associations between different trait combinations are rarely evaluated, despite the importance of linked functioning across habitat-building corals and associated fishes.

Here, we explore linked spatial community trait structure of corals and fishes across reef habitats. As survey methods, trait selection, and trait availability all impact the results and interpretations of trait-based work (Hadj-Hammou et al., 2021), we quantify how trait-based metrics of coral-fish community structure vary with inclusion of specific fish species. Some monitoring programs focus on fisheries target (food fish) species (Andrew et al., 2011, Houk et al., 2015, Muller-Karanassos et al., 2021). Here, we highlight the role that site attached, non-target fish play in detecting associations between coral and fish trait structure and how this varies across habitats, even on reefs that are subject to frequent disturbance.

4.3 Methods

In 2019, we surveyed 39 sites on outer, channel, patch/back and inner reefs at Chuuk Lagoon and Kuop Atoll in Chuuk State, Federated States of Micronesia (Houk et al., 2015) (Figure 12). Coral bleaching occurred in 2016, causing significant declines in coral cover, particularly at outer reefs. Fish diversity and abundance was recorded with 12 stationary point counts per site (SPCs) (five metre radius, three minutes), distributed evenly across five 50m transects. Previous monitoring focused on food fish families (Houk et al., 2015), while in 2019, we also recorded all non-cryptic, site-attached families. Coral species and colony diameter were recorded with ten 1m^2 quadrats per site placed along the fish transects (Houk et al., 2015).

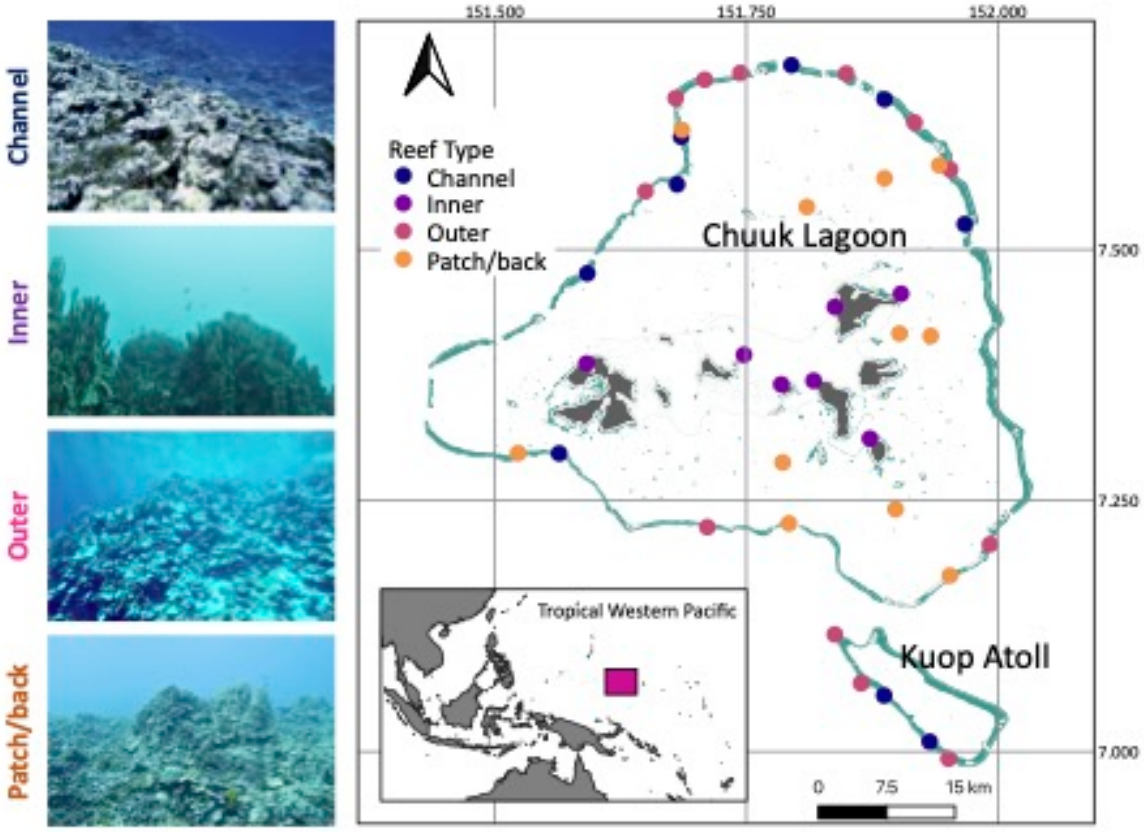

Figure 12. Chuuk Lagoon and Kuop Atoll survey sites and habitat types (UNEP-WCMC, 2018).

To characterise co-occurring coral and fish assemblages, we compiled trait information related to species' ecology, morphology, and life history. Coral traits selected were growth form, larval development mode, growth rate, lower depth limit and bleaching susceptibility traits derived from The Coral Trait Database and bleaching vulnerability assessments (Foden et al., 2013, Madin et al., 2016). Selected fish traits were maximum length, maximum water depth, pelagic larval duration (PLD), trophic mode, aggregation type and water column position, assembled from Fishbase (Froese and Pauly, 2019) and the literature (Table C1). Where feasible, gaps were imputed within genera using the mean of available trait values (continuous) or the dominant trait (categorical) (Taugourdeau et al., 2014).

All analyses were conducted in R (Appendix C1). We built separate fish and coral trait spaces with Principal Coordinate Analyses (PCoA) on Gower dissimilarity matrices.

Fish trait spaces were calculated for all species, site-attached species, and food species. We calculated community weighted mean (CWM) values for coral and fish communities from trait tables and log-transformed abundance data (to moderate the effects of extremely abundant species). CWM measures the contribution of each trait to the overall community at each site, weighted by species abundances (Garnier et al., 2004). To characterise the trait community across habitats, we ran an indicator species analysis on the CWMs (hereafter indicator trait analysis) (Dufrêne and Legendre, 1997), to identify traits that were significantly associated with specific reef habitats. We evaluated covariation and identified shared patterns between the coral and fish trait communities (CWMs) with two co-inertia analyses. Co-inertia analysis is a flexible multivariate method for examining the shared structure of a pair of data tables (Dray et al., 2003). The first included the whole fish community, whilst the second excluded site-attached fish in order to explore if detecting shared structuring was dependent on these species. Permutation tests (n=999) for each co-inertia tested the strength of shared structuring, summarised by a p-value and RV coefficient (0-1, values closer to one indicate stronger correlation between communities).

4.4 Results and Discussion

Coral trait space in Chuuk Lagoon is generally homogenously populated, with the exception of several functionally unique taxa, mostly containing brooding corals with branching or encrusting morphologies (i.e., *Isopora palifera*) (Figure 13). There is considerable trait space overlap between food versus site-attached fish, but both make unique contributions to the trait space. For the food fish, these are large piscivores (i.e., *Macolor macularis*), and for the site-attached fish are small, reef associated species (i.e., *Chaetodon ornatissimus*) (Figure 13). The distinct contributions of functionally unique species could indicate candidates for focused monitoring and protection under a trait-based management strategy (McLean et al., 2021). We would expect to see further expansion of the trait space if cryptobenthic fishes were included (Brandl et al., 2019).

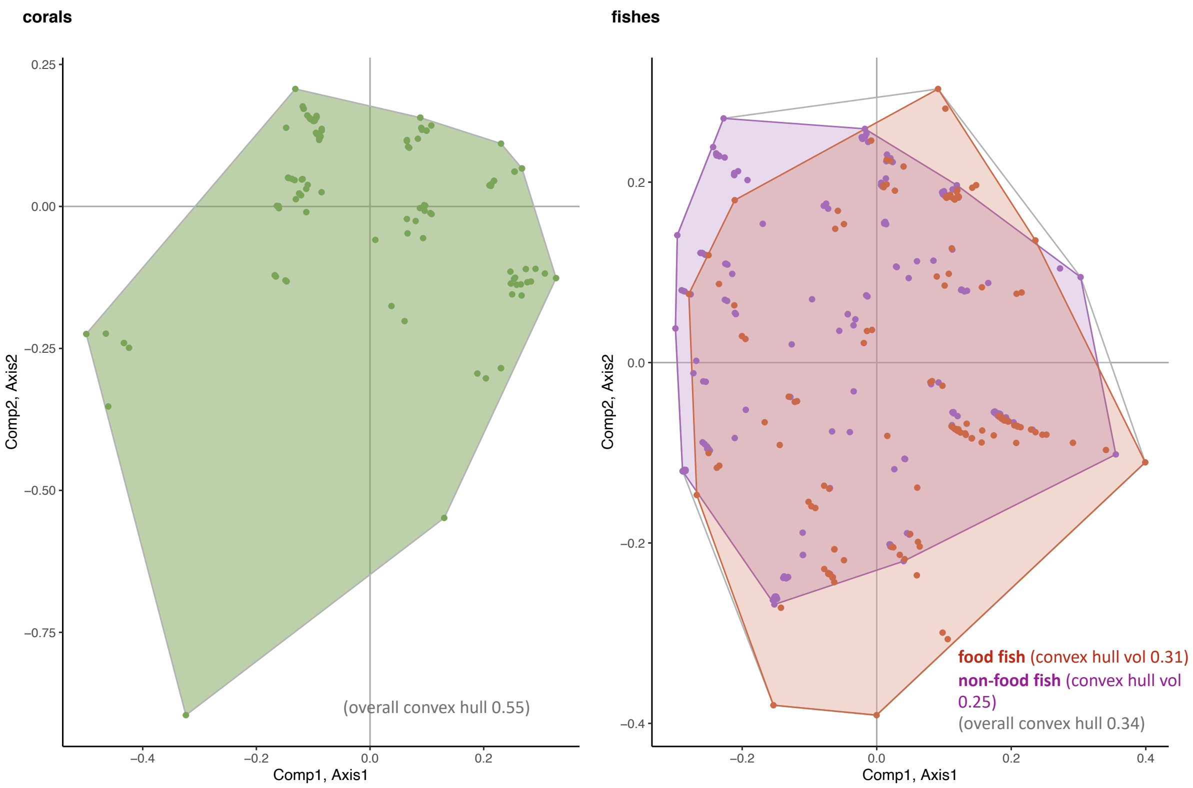

Figure 13. PCoAs of coral and fish trait space. First two axes describe approximately 48.42% of the coral variation, and 37.45% of the fish. Red convex hull (right) denotes food-fish and purple for non-food fish (Table C2). Grey line denotes entire trait space. See Figure C1 for equivalent with species labels.

Different habitats support assemblages characterised by different traits for both corals and fishes (Table 7). For example, outer reefs host encrusting and sub-massive coral growth forms with greater depth limits that populate the steep drop-offs. The prevalence of sub-massive and encrusting growth forms at outer reefs is probably a reflection of Chuuk's disturbance history, including past bleaching events and cyclones (Houk et al., 2016). These disturbances disproportionately reduce branching, fast growing traits that might otherwise inhabit outer reef sites (Mellin et al., 2019). Contrastingly, inner and patch/back reefs are characterised by encrusting, long upright growth forms, alluding to the high coral cover of species like *Porites rus* on shallow, inner and patch reefs in Chuuk (Figure 12). Broadly, this portrays a post-bleaching coral community that may become increasingly representative of reefs globally as the climate changes (Alvarez-Filip et al., 2013, Hughes et al., 2018). For fishes, traits primarily held by site-attached fish species (i.e., harem aggregations, sand-associated positions) are important in characterising the spatial composition of the reef (Table 7).

This highlights their role in community structuring, and so the contribution of site attached species should clearly be incorporated into future trait-based analyses in Chuuk.

Table 7. Indicator trait analysis of log-transformed CWM for corals and fish with p-values <0.05 (permutations = 999) (GF = Growth Form). Reported results for maximum two combined habitat types.

	Habitat	Trait	stat	p
Corals	Outer	GF submassive	0.601	<0.001
		Depth Lower	0.547	0.009
		GF encrusting	0.539	0.006
	Inner + Patch/back	GF encrusting long uprights	0.462	0.015
Fishes	Channel	Position sub-benthic	0.606	<0.001
	Inner	Position demersal	0.764	<0.001
		Position sand associated	0.628	<0.001
	Outer	Trophic detritivore	0.442	0.028
	Channel + Outer	Aggregation solitary	0.629	<0.001
	Outer + Patch/back	Aggregation harems	0.472	0.018

Co-inertia between fish and coral trait communities are stronger when all fishes are included in the analysis (p<0.001), compared to only food fishes (p=0.049) (Figure 14). The traits most important for driving variation within the co-inertia differ slightly for each approach (Figure C3). Fish and coral communities are organised roughly by reef types with a few outliers that are retained in the food fish community co-inertia analysis. There is clearer structuring across reef types when site-attached species are included, with sites more clustered without them. In line with prior evidence (Darling et al., 2017), these results highlight that including a wide range of species when discerning functional relationships across taxa is crucial, particularly as functionally distinct species may support vulnerable functions (Mouillot et al., 2013), that might otherwise be overlooked in monitoring and management efforts.

Monitoring in Chuuk is presently focused on food fish, reflecting local management priorities and the fact that fishing is the primary driver of fish assemblages in this region (Houk et al., 2015, Harborne et al., 2018). However, as climate disturbances become more frequent it may be necessary to expand monitoring to capture the wider fish community (not just food fish) in a way that is still practical and affordable. This is because climate driven changes in coral functional diversity and associated changes in dependent fish species may also have long-term implications for food fish as a resource. We illustrate that trait-based perspectives must be accompanied by careful assessment of parts of the community that are excluded by sampling design.

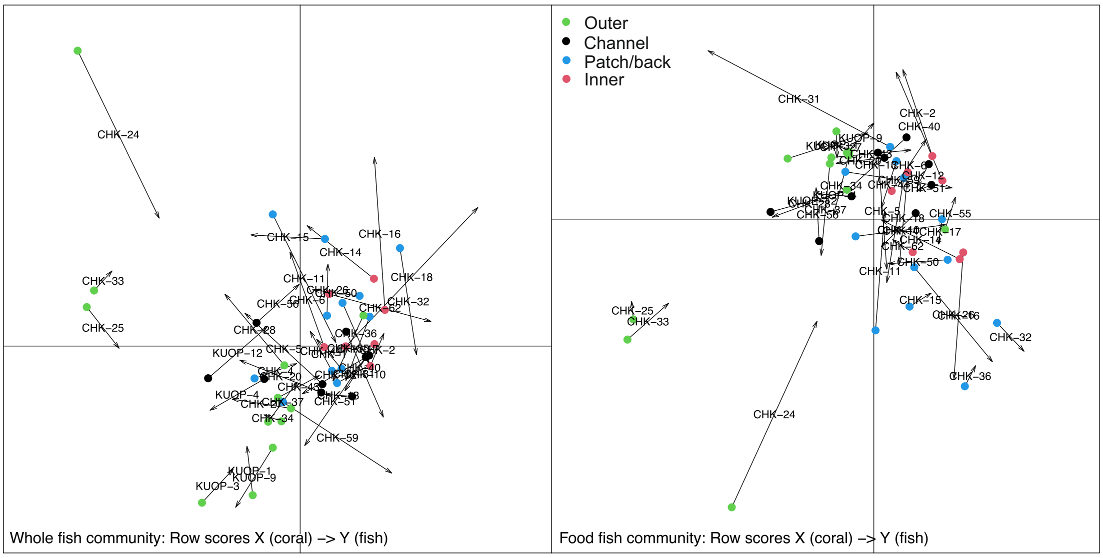

Figure 14. Coinertia of the whole fish and coral community (left, RV = 0.294, p<0.001, reps = 999, 73.95% variation described in 1st two axes) and the coral community with food fish only (right, RV = 0.249, p = 0.049, reps = 999, 65.98% variation described in 1st two axes). Sites coloured by reef habitat. Beginning of each arrow is position of the site described by coral CWM, and end is the fish CWM.

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Chapter 5. Temporal patterns in trait community structure on the Great Barrier Reef

5.1 Abstract

Escalating climate impacts are profoundly changing species assemblages, and by extension how ecosystems function. The types and abundances of functional traits present in a community mediate response to and recovery from disturbance. On coral reefs, temporal functional relationships across taxa and which traits are most influential in this structuring are not well known, which ultimately restricts managers' ability to maintain ecosystem functioning. This study examines how disturbances (cyclones, coral bleaching, and crown of thorns (COTS) outbreaks) drive long-term fluctuations in trait composition of coral and fish assemblages on the Great Barrier Reef (GBR) over the past three decades. It examines temporal changes in shared structuring between the two taxa and identifies which traits are most influential in driving change. Different parts of the GBR exhibit different temporal patterns in functional diversity, explained by varying latitudes, shelf positions and disturbance histories. The impacts of increasing sea temperatures are overtaking cyclones and COTS as the main driver of functional change. While spatial protection status does not affect long-term changes in coral assemblages, it helps to maintain fish functional diversity. Shared structuring between coral and fish trait assemblages fundamentally changes in the Northern GBR. Coral traits that confer structural complexity drive most of the temporal functional variability in the fish and are particularly associated with lower trophic group traits. This study finds that loss or transformation of some functions are likely well underway despite exemplary management efforts. These findings highlight potential avenues for management prioritisation, but also emphasise that maintaining present functioning on coral reefs will require rapid diversion from current climate trajectories.

5.2 Introduction

Coral reef ecosystems are transforming due the combined impacts of localised stressors and escalating climate change, where reduced recovery windows between disturbances threaten resilience (Hughes et al., 2017). In this context, ecosystem managers must increasingly prioritise managing for resilience and maintaining ecosystem functions, rather than necessarily retaining, or returning to pre-disturbance assemblages (McLeod et al., 2019, McLeod et al., 2021). An understanding of ecosystem function, underpinned by the composition and abundances of species traits in a community, forms an important part of how managers will navigate the Anthropocene (Bellwood et al., 2019a). Elucidating how traits respond across successive disturbances, particularly in terms of relationships between taxa, remains an understudied aspect of understanding changing functions on coral reefs (McLeod et al., 2019). This knowledge may help managers with prioritising vulnerable traits and maintaining overall functioning, even as the species performing specific ecosystem functions may change (Laughlin et al., 2017).

The cumulative impacts of different stressors on coral reefs have profound implications for community assemblages, species distributions and ecosystem functioning over time (Bellwood et al., 2019a). Crucially, disturbance impacts are not felt uniformly throughout a system. Instead, the trait composition of assemblages prior to disturbance, and whether those traits confer resistance or vulnerability, mediates first how initial impacts are felt and then determines recovery potential (McLean et al., 2018). Resilient communities can return to or maintain similar composition and function over time, whilst others undergo shifts towards different community structure and function (Anthony et al., 2015). Because species traits, rather than their taxonomic identity, determines responses to environmental change, functional and trait-based approaches offer a more process-oriented understanding of how communities are changing in response to successive disturbances (Pecuchet et al., 2020).

Measuring functional change is important for anticipating and responding to disturbance impacts in threatened ecosystems such as coral reefs, and a suite of indices are used to quantify this (Mouillot et al., 2013). These broad measures of functional diversity are enhanced by trait-based perspectives, providing valuable insight for linking consequences of environmental change to altered ecosystem function (Mouillot et al., 2013). Traits are heritable physiological, morphological, and behavioural characteristics of species that dictate responses to the environment (Violle et al., 2007). Accordingly, they also regulate responses to disturbance and by extension, ecosystem functioning (Mouillot et al., 2013). Globally, we are increasingly turning towards looking at functional community dynamics to inform predictions and responses to rapidly changing Anthropocene ecosystems (Beukhof et al., 2019, Pecuchet et al., 2020).

In the context of coral reef ecosystems, such approaches have shown that traits mediate coral susceptibility to disturbance (Zawada et al., 2019), recovery processes, and the delivery of structural complexity as a key function that in turn shapes fish assemblages (Emslie et al., 2014, Richardson et al., 2017a, Bierwagen et al., 2018, Morais et al., 2020). Fish tend to exhibit relative stability, but increasing homogeneity of functional assemblages post-disturbance (Brandl et al., 2016, Richardson et al., 2018), leading to changes in the delivery of functions such as productivity (Morais et al., 2020, Tebbett et al., 2021). Herbivory is a crucial function for reef recovery processes. How this is delivered is determined by species traits (Brandl and Bellwood, 2014, Marshell and Mumby, 2015, Streit et al., 2019, Semmler et al., 2021) and has also changed with successive disturbances (Cheal et al., 2013, Stuart-Smith et al., 2018, Richardson et al., 2020). Species traits are thus shaping communities' responses to disturbance, but which traits are most influential, whether traits are retained over time, and how this varies across taxa are largely unknown for coral reefs. Corals are essential habitat builders, and their functioning is tightly linked with associated fish assemblages (Darling et al., 2017), so it is important to understand how these interactions can shape community responses to disturbance (Richardson et al., 2017b). How this plays out on coral reefs and what this means for resilience, particularly over longer time scales is not well understood (Stuart-Smith et al., 2018). Identifying how different traits have responded over time can help us to understand and anticipate the impacts of successive disturbances as they become more frequent, with implications for management and conservation (McLean et al., 2019).

In this study I ask:

i. How does functional diversity in coral and fish communities change over time, and what are the role of disturbances in driving these temporal dynamics?
ii. How do species traits influence any shared patterns and associations in the temporal changes of coral and fish communities?

5.3 Methods

5.3.1 Study site

The Great Barrier Reef (GBR) on the north-east Australian coast, is a 2300km-long coral reef system with a varied disturbance history (Emslie et al., 2020). It also has a comparatively long record of management and monitoring, which makes a valuable contribution to our understanding of coral reef ecology, successive disturbance impacts and management interventions (Williamson et al., 2014, Hughes et al., 2018b, Stuart-Smith et al., 2018, Fraser et al., 2019, Mellin et al., 2019a, Zawada et al., 2019, Emslie et al., 2020). The GBR has influential environmental gradients across latitude and reef shelf positions that affect the community structure of taxa including scleractinian corals and fishes (Emslie et al., 2020). These gradients accordingly also have implications for ecosystem functions. Herbivores, for example, have higher abundances, functional diversity and redundancy at offshore compared to inshore reefs (Cheal et al., 2013).

Spatial variability in disturbance history is also an important factor influencing community composition, particularly for corals (Graham et al., 2014, Hughes et al., 2017, Mellin et al., 2019a). Disturbances on the GBR include short term pulse stressors such as storms that have clear physical impacts, longer term outbreaks of COTS, or coral bleaching (Emslie et al., 2020). Hard coral cover has declined substantially since monitoring began, attributed to cyclones, COTS, freshwater runoff and coral bleaching (De'ath et al., 2012, Maynard et al., 2016), whilst the resilience of these communities to disturbance is also affected by water quality (Mellin et al., 2019a). Indeed, the largest declines in coral cover and complexity correlate with declines in fish abundance and diversity, with coral dependent species (I.e., Chaetodontidae) particularly vulnerable (Emslie et al., 2014). Coral bleaching events, for example, have not only altered coral communities (Hughes et al., 2017), but have also caused profound changes in the trophic structure of fish communities (Stuart-Smith et al., 2018).

To explore temporal patterns in functional diversity and cross-taxa relationships, I used 27 years (1995-2021) of long-term monitoring data from the Australian Institute of Marine Science's (AIMS) Long-Term Monitoring Program (LTMP), excluding a small number of sites that had only fish or coral surveys, or were very recent additions to the monitoring program. 93 individual reefs were monitored with 3 sites at each reef. Sites are categorised by their shelf position, management area (hereafter characterised as the North, Mid, and Southern GBR), and whether they are in a fished area or no-take zone (NTZ) (Figure 15) (Table D1) (Great Barrier Reef Marine Park Authority, 2004, Emslie et al., 2020). At each site, monitoring was conducted along five 50m fixed transects. Benthic cover, including scleractinian coral cover and diversity, was collected using 50 photographs at around one-metre intervals per transect. Forty of these were randomly selected and assessed using five fixed points per photograph (Jonker et al., 2008, Emslie et al., 2020). Non-cryptic fish species were also counted on each of the five transects. Larger mobile fishes were counted using 5m wide belt transects. Damselfishes (Pomacentridae) were counted separately on a 1m wide transect (Emslie et al., 2020).

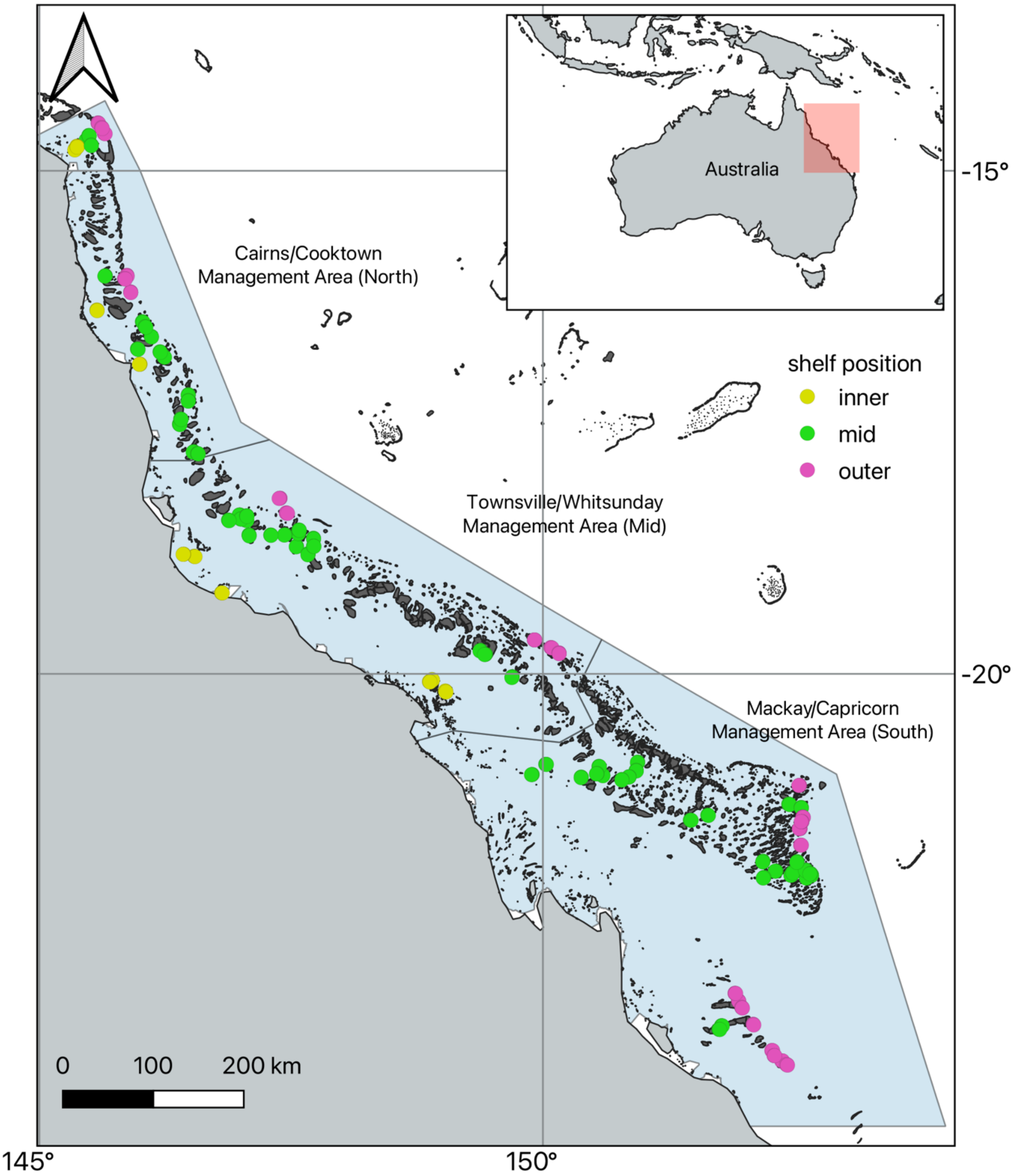


Figure 15. The Great Barrier Reef (GBR), with survey sites and shelf position. Management Zones in blue (Great Barrier Reef Marine Park Authority, 2004, UNEP-WCMC, 2018).

5.3.2 Species traits and disturbance histories

To broadly characterise functional structure, behavioural, morphological and life history traits relating to different processes and functions were assembled for both the coral and fish communities, using a combination of continuous and categorical traits (Table D2, Table D3). Prior to assembling trait data, species names were checked against the World Register for Marine Species (WoRMS) (R package *worrms*) (Horton et al., 2017, Chamberlain, 2019). The coral traits were colony growth form, larval development mode, growth rate, depth lower and maximum corallite width. These were derived from the Coral Trait database (Madin et al., 2016). The fish traits used were maximum length, mean pelagic larval duration, trophic mode, aggregation type, position in the water column, spawning mode and species generalisation index (SGI). Fish traits were derived from Fishbase (Froese and Pauly, 2019) and the broader literature. SGI was obtained from (Stuart-Smith et al., 2021). For both taxa, gaps were imputed for phylogenetically related species using expert opinion and calculating averages of numeric traits within a genus where possible (Taugourdeau et al., 2014, McWilliam et al., 2020). Species where information for more than two traits was missing were excluded from the analysis. Fish had 100% trait coverage with no exclusions, and corals had 85% trait coverage.

The disturbance history of each site was characterised using modelled annual estimates of cyclone exposure, COTS outbreaks and heat stress exposure from 1995-2018 (Matthews et al., 2019). Heat stress is presented as maximum Degree Heating Weeks (DHW). Cyclone exposure is the number of hours that each grid cell was exposed to damaging wind speeds and wave heights (Puotinen et al., 2016, Matthews et al., 2019). Mean annual estimates of COTS densities were derived from manta tow data collected by the AIMS LTMP (Matthews et al., 2019).

5.3.3 Data analysis

All analyses were performed in R (R Core Team, 2020) with RStudio (RStudio Team, 2016) using ggplot2, ade4, FD and mgcv packages (Dray and Dufour, 2007, Laliberté et al., 2014, Wickham, 2016, Pedersen et al., 2019).

Temporal patterns in functional diversity and the role of disturbance

To explore the temporal dynamics of coral and fish trait communities in response to major disturbances, I modelled key species and functional diversity metrics for coral and fish against the disturbance history parameters from 1995 – 2018 using generalised additive models (GAMs) (Pedersen et al., 2019). GAMs were selected because they are good for modelling non-linear relationships, particularly over time, and cope well with the autocorrelation issues that can arise with spatial data. All GAMs were run with a Gaussian distribution for continuous data and a restricted maximum likelihood (REML) estimation (Pedersen et al., 2019).

The indices for the response variable are species diversity, functional richness, and Rao's quadratic entropy (RaoQ) for each survey year. I use species richness here as a comparison with two other measures of diversity that use functional traits. The first is functional richness, the volume of multidimensional functional space occupied by species in a community, which is useful for detecting shifts in ecosystem function (Mouillot et al., 2013). Complementary to this is RaoQ, a broad measure of functional diversity that accounts for both the relative abundance of different species in the community and their functional differences (Botta-Dukát, 2005). Hence if the abundances, but not overall composition of species and their traits changes, RaoQ can detect changes where an overall estimate of functional volume or number of species would not. From an ecological standpoint, these provide a broad overview of functional changes over time.

I included latitude and longitude as interacting smooth terms to account for the spatial structure in the data, and shelf position as a factor smooth (bs = fs) for the year smooth term. This approach recognises that shelf position is an important part of the data structure, but because it is a known driver of community organisation is not the focus of this study. Model structure was as follows:

Index ~ s(lat, lon) + s(year, shelf) + s(DHW) + s(COTS) + s(cyc) + fishing

where index refers to either species richness, functional richness, or RaoQ. DHW is the maximum degree heating weeks per year, COTS is a density estimate for *A. planci* per year and cyc is cyclone exposure per year (Matthews et al., 2019). Fishing is a factor variable, with each site either categorised as fished or NTZ depending on its zoning status (Table D1). Model fit was evaluated using gam.check() (*mgcv*) and visual inspections of the diagnostics plots.

To visualise how disturbances manifest across the entire trait community in recovery trajectories, I ran scaled Principal Component Analyses (PCAs) on the log-transformed abundance-weighted trait community weighted means (CWMs) across the entire community of corals and fish from 1995-2021, split by taxa and latitudinal zones (*prcomp*). The CWM is an abundance-weighted measure of the average trait values at each site in each year (Garnier et al., 2004, Kleyer et al., 2012). I then selected representative years from the beginning of monitoring (1995), at key points post-disturbance (2003, after the 1998 and 2002 bleaching events), after a period of recovery (2013) and contemporary (2021) trait community composition. This PCA is intended purely as a broad visualisation, and so the first two axes only are shown. In all cases, these explain most of the variance (Figure D1).

Shared temporal structuring between coral and fish trait communities, key driving traits and associations between taxa

To ascertain how the coral and fish trait communities are interacting over time, I carried out an RLQ with fourth corner analysis for the Northern, Mid, and Southern GBR sections from 1995-2021. RLQ analysis is an ordination method across three tables (R - environmental variables, L - species abundances, Q - species traits) that summarises the shared structure between these tables (Dray and Dufour, 2007, Mouillot et al., 2013, Dray et al., 2014). Here, I used the coral community as the environment, so R was the average coral community weighted mean (CWM) across all sites in each year, L was log-transformed mean fish species abundances at each site in each year, and Q was the fish trait table (Beukhof et al., 2019). To look explicitly at the importance of specific traits, I additionally identified the four most influential coral traits driving structuring in each RLQ ordination (North, Mid and South) from a Pearson correlation of each trait with the first and second RLQ axes.

Each RLQ for the North, Mid and Southern GBR sections is accompanied by a fourth corner analysis, which tests for bivariate association between each coral and fish trait (Dray et al., 2014). Given the strong effects of latitude and shelf position, I used a more conservative version of the fourth corner analysis (Moran spectral randomisation constraints) that helps to account for spatial autocorrelation in the data (Wagner and Dray, 2015, McLean et al., 2018).

5.4 Results

How does functional diversity in coral and fish communities change over time, and what is the role of disturbances in driving these temporal dynamics?

Over time, species richness, functional richness, and functional diversity (RaoQ) fluctuate across the GBR, exhibiting different patterns in different latitudinal zones. RaoQ is a broad index of functional diversity that accounts for both the relative abundances of species in a community, and how different they are from each other based on their traits (Botta-Dukát, 2005), thus providing a useful overall metric of change. Coral communities in all latitudes exhibit a distinct decline between the late 1990’s and early 2000’s (Figure 16), though this is least pronounced at outer reefs in the mid GBR. Beyond that, different zones follow different trajectories. For the fish community, functional diversity clearly varies across shelf position, with outer reefs having the highest levels of functional diversity across the GBR, followed by mid and inner reefs (Figure 16).

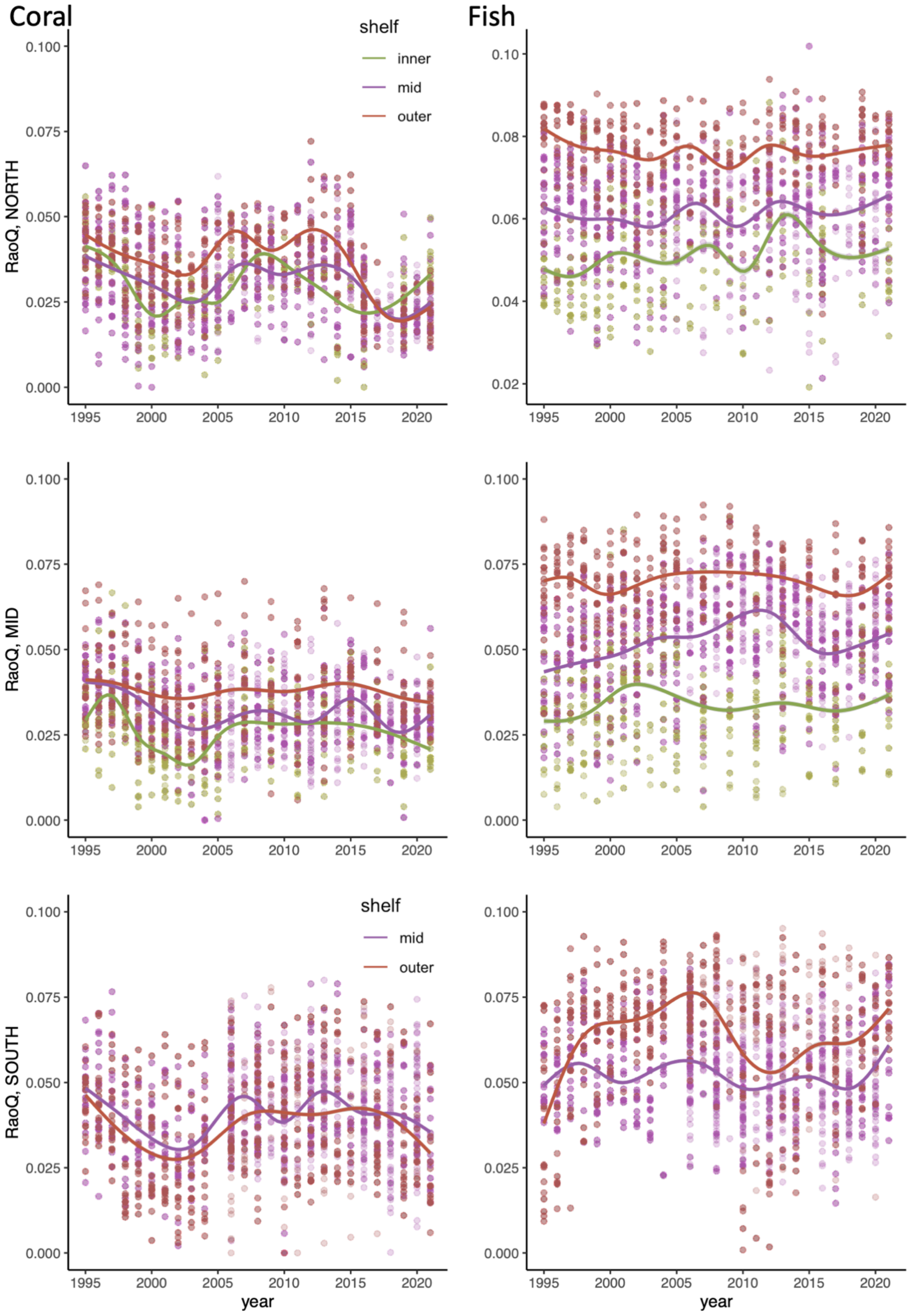


Figure 16. Functional diversity (RaoQ) of fish (right) and coral (left) communities between 1995 and 2021 on the North, Mid and Southern GBR, visualised with a GAM smooth.

In addition to these cross-shelf temporal patterns, all three indices have clear latitudinal structuring and are differentially influenced by disturbance (Table 8). For coral communities across the GBR, these disturbance predictors explain more variation in species richness and RaoQ than they do the overall functional richness. In the Mid-GBR, there is a subset of inner reefs with substantially lower species richness, functional richness, and functional diversity in both coral and fish assemblages that means comparatively these models fit less well than in the North and Southern sections.

Maximum DHW emerges as an important driver of coral community structure in the North and South, where species richness and RaoQ have a negative relationship with DHWs, but not in the Mid-section. However, the Mid-GBR is the only section where the protection status of an area has a possible bearing on coral functional richness and RaoQ, with slightly lower indices for both in NTZs. In the North, the main disturbances driving coral functional community structure are DHW and cyclone intensity, with COTS playing a lesser role. These changes manifest broadly as declines in species or functional richness and diversity, though relationships are variable between indices, and few are strictly linear. In the mid-GBR, COTS have a negative relationship with general functional diversity, whereas DHW and cyclone impacts do not have an effect. DHW emerges again as an important driver of declines in species richness and RaoQ in the southern GBR.

Fish communities in the Northern GBR share similar responses to the corals. Broadly, DHW remains an important driver of community structure, with COTS, cyclones and fishing having smaller, more variable effects. In the Mid-GBR they are shaped by DHW even as the corals are less affected. Whether a site is a NTZ or is fished affects the functional richness of Mid and Southern GBR fish communities, with higher functional richness in NTZs in these areas.

Table 8. GAM results for key functional diversity metrics of coral and fish taxa over time, modelled against disturbances on the GBR.

			Species richness		Functional richness		Functional diversity (RaoQ)	
			edf/df	p	edf/df	p	edf/df	p
North Coral	Smooth	Lat, lon	22.251	<0.001	15.885	<0.001	23.044	<0.001
	Factor Smooth	Year, shelf	21.594	<0.001	15.723	<0.001	16.940	<0.001
	Smooth	DHW	6.601	<0.001	4.212	0.038	5.567	<0.001
		COTS	6.610	<0.001	2.046	0.348	5.781	0.014
		Cyclone	7.456	<0.001	1.662	0.137	4.735	<0.001
	Parametric	Fishing	1	0.507	1	0.024	1	0.931
Mid Coral	Smooth	Lat, lon	24.971	<0.001	13.468	<0.001	22.116	<0.001
	Factor Smooth	Year, shelf	22.349	<0.001	18.910	<0.001	13.281	<0.001
		DHW	1.003	0.784	1.370	0.136	4.360	0.079
		COTS	2.862	0.042	2.505	0.343	1.001	<0.001
		Cyclone	1.001	0.535	1.811	0.318	1.004	0.596
	Parametric	Fishing	1	0.176	1	0.031	1	0.051
South Coral	Smooth	Lat, lon	25.695	<0.001	21.171	<0.001	23.920	<0.001
	Factor Smooth	Year, shelf	14.133	<0.001	14.596	<0.001	13.046	<0.001
		DHW	1.002	0.002	1.000	0.530	1.015	<0.001
		COTS	3.853	0.004	2.680	0.360	3.368	0.185
		Cyclone	1.157	0.735	1.000	0.008	1.000	0.391
	Parametric	Fishing	1	0.555	1	0.915	1	0.372
North Fish	Smooth	Lat, lon	17.648	<0.001	21.415	<0.001	23.726	<0.001
	Factor Smooth	Year, shelf	8.676	<0.001	6.217	<0.001	2.992	<0.001
		DHW	3.822	<0.001	3.687	0.004	5.862	0.004
		COTS	1.666	0.003	1.341	0.053	4.445	0.014
		Cyclone	2.710	0.001	1.40	0.232	4.310	<0.001
	Parametric	Fishing	1	0.122	1	0.158	1	0.527
Mid Fish	Smooth	Lat, lon	25.350	<0.001	20.875	<0.001	23.710	<0.001
	Factor Smooth	Year, shelf	5.693	<0.001	5.558	0.001	11.416	<0.001
		DHW	1.002	0.012	1.000	0.007	4.296	<0.001
		COTS	2.129	0.064	1.421	0.264	1.007	0.621
		Cyclone	1.002	0.266	1.000	0.013	1.001	0.093
	Parametric	Fishing	1	0.584	1	0.014	1	0.478
South Fish	Smooth	Lat, lon	26.013	<0.001	24.641	<0.001	24.795	<0.001
	Factor Smooth	Year, shelf	11.417	<0.001	10.283	<0.001	11.898	<0.001
		DHW	1.001	<0.001	1.000	0.243	1.003	0.081
		COTS	1.944	0.352	2.319	0.027	2.415	0.083
		Cyclone	1.728	0.499	1.187	0.671	1.439	0.373
	Parametric	Fishing	1	0.013	1	<0.001	1	0.334

The overall abundance weighted (CWM) trait spaces of fish and coral communities, assembled across the entire study period, have a differing broad structure between latitudinal sections on the GBR. Over time, there are clear changes in the trait space of corals. In the Northern GBR, coral trait space shrinks and then expands during recovery, but to a distinctly different trait composition with lower depths and spawning species as more of the trait space. The Mid-GBR retains a core trait composition, but nonetheless also exhibits changes in trait structure across time. The Southern GBR has a very small trait space in 1995, which expands over time before starting to shrink again in 2021 (Figure 17).

The fish also exhibit different trajectories in the trait space in different sections of the GBR. In the Northern section, the trait space contracts and then expands, to a slightly larger trait space occupying a similar position before and after the contraction in 2003. The Mid-GBR exhibits a similar pattern, contracting away from the cnidarian-associated part of the trait space in 2003. The Southern GBR is the most variable, expanding towards and away from the part of the trait space driven by benthic and omnivore fish traits (Figure 18). The first two PCA axes describe more of the variation in the trait community than the corals (Figure 17, Figure 18). Combined, the first two PCA axes describe the greatest proportion of the variation across both taxa, and so these axes only are displayed (Figure 17, Figure 18, Figure D1). For comparison, the trait space derived from the transformed abundance data was also run as a PCA. For the corals, observations to genus level only drove most of the variation along the first two PCA axes, with *Acropora, Pocillopora and Montipora* and *Porites* species. the most influential in the trait space. For the fish, specific Pomacentrids were most influential by virtue of their overall abundance in the fish assemblages and characterised reefs by shelf position (i.e., Yellowtail demoiselle *Neopomacentrus azysron*) (Figure D2, Figure D3) (Wilson et al., 2009).

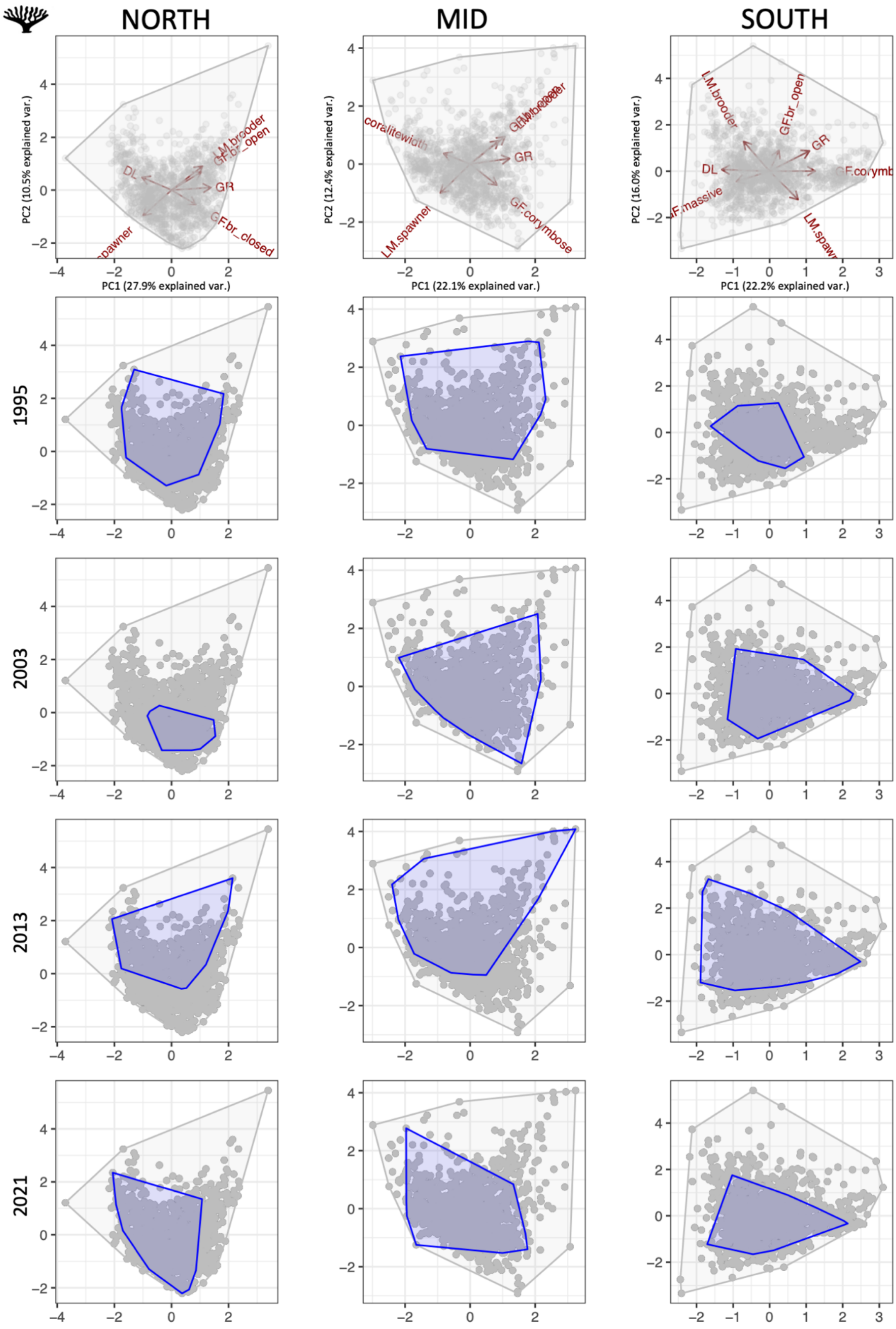


Figure 17. Coral trait space (CWM) derived from the first two PCA axes (North – 38.4%, Mid – 34.5%, South – 38.2%) across the North, Mid and Southern GBR in 1995, 2003, 2013 and 2021. Top row is global trait space (all sites, all years) and shaded plots (blue) are trait space of single year. Four most influential traits from PCA axes 1 and 2 shown only.

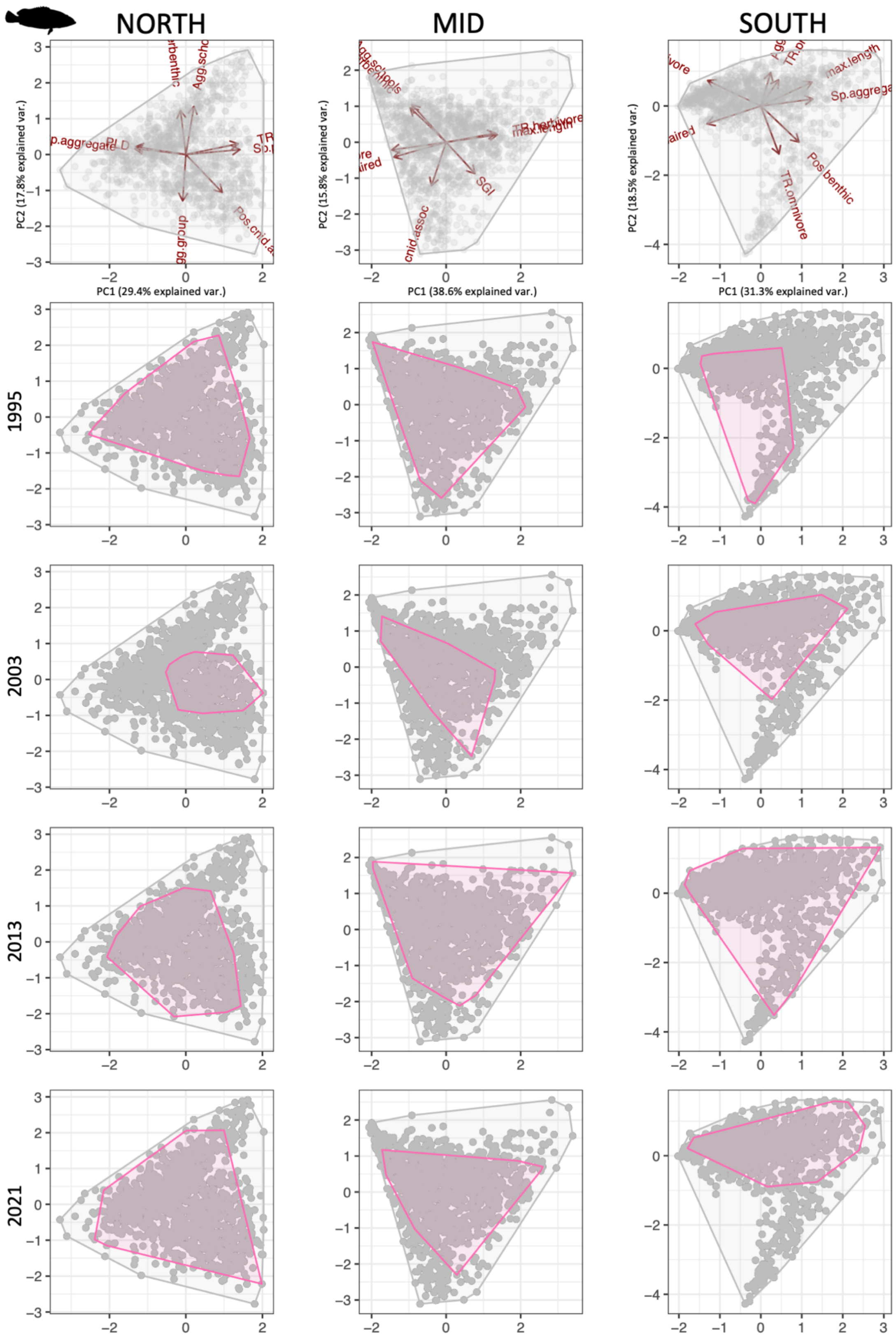


Figure 18. Fish trait space (CWM) derived from the first two PCA axes (North – 47.2%, Mid – 54.4%, South – 49.8%) across the North, Mid and Southern GBR in 1995, 2003, 2013 and 2021. Top row is global trait space (all sites, all years) and shaded plots (pink) are trait space of single year. Four most influential traits from PCA axes 1 and 2 shown only.

How do species traits influence any shared patterns and associations in the temporal changes of coral and fish communities?

There is clear shared temporal structuring between the coral and fish trait communities in all three latitudinal zones. The shared trait space distributions between coral and fish communities shift towards a distinctly different space, indicating that functional relationships between the two communities have changed over time (Figure 19). This is most apparent in the Northern GBR, where the first two RLQ axes explain 91.48 % of the variation. The Mid and Southern reef sections fluctuate more within the ordination space, and the first two axes explain 96.98 % and 94.14 % of the variation respectively (Table D4) (Figure 19). The contributions of each trait to the coral community (CWM) over time clearly influences fish species composition at all three latitudinal zones (permutation test model 2, n = 999, p < 0.001 in North, Mid and Southern GBR). Additionally, the changing composition of fish traits over time also affects fish species assemblages, though this is weaker in the Southern GBR (permutation test model 4, n = 999, p <0.001 North and Mid, p = 0.008 Southern GBR) (Table D4)(Dray et al., 2014).

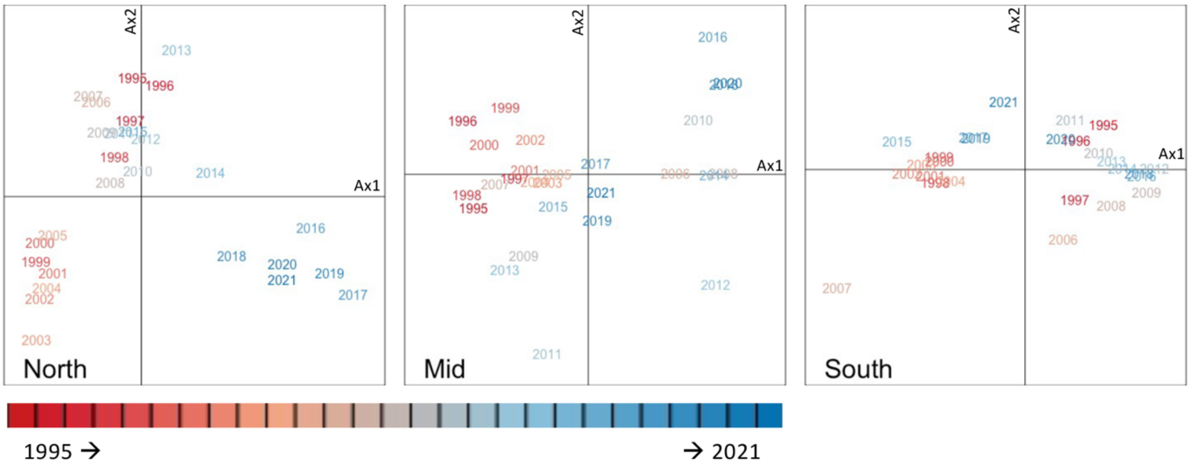


Figure 19. Shifts in shared coral-fish trait structuring over time (RLQ row coordinates) in the North, Mid and Southern GBR (Colour scheme: red = 1995, blue = 2021).

In the Northern section, the most influential coral traits (identified based on Pearson correlation with the first two RLQ axes) are columnar growth forms (corr = 0.780) and brooding larval development mode (corr = -0.764) along the first RLQ axis and encrusting long upright (corr = 0.810) and corymbose (corr = -0.563) growth forms along the second (Figure 20). The CWM of columnar growth forms increases slightly over time, and brooding corals stay relatively stable until declining around 2013. The CWM of encrusting long upright corals declines in the early 2000’s, whilst corymbose corals exhibit the opposite pattern (Figure 21). In the Mid-GBR, the most influential coral traits are branching closed (corr = 0.786) and laminar (corr = -0.957) growth forms along the first RLQ axis, and growth rates (corr = 0.844) and corallite width (corr = -0.568) along the second (Figure 20). The CWM of laminar growth forms steadily declines over the study period, whilst corallite width remains stable and branching closed growth forms and coral growth rates fluctuate through time (Figure 21). In the Southern GBR, the most influential traits along the first RLQ axis are depth lower (corr = 0.974) and corymbose (corr = -0.850) growth forms, and along the second axis encrusting (corr = 0.516) and branching open (corr = -0.761) growth forms are most influential (Figure 20). The CWM of branching corals declines over time in the Southern GBR, whilst the corymbose corals increase (Figure 21). Across all latitudinal zones, correlation with the RLQ axes does not necessarily correspond with the most abundant traits across the whole study period (Figure D4 - D6).

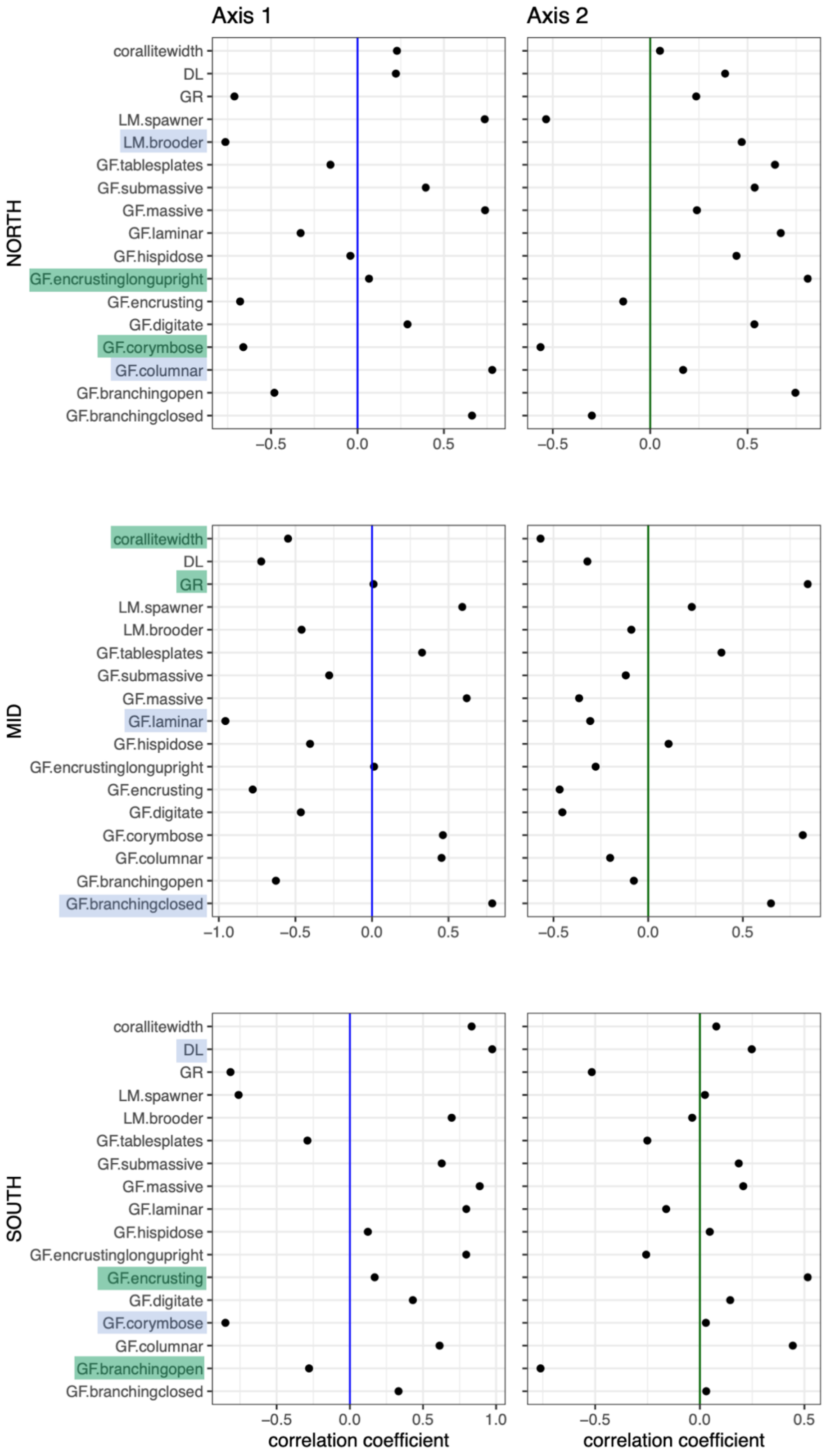


Figure 20. Pearson correlation of coral traits with the first and second RLQ axes in the North, Mid and Southern GBR. Highlighted traits are the most influential, where correlation is closest to 1/-1 along axis 1 (blue) and axis 2 (green). GF: Growth form. LM: Larval development mode.

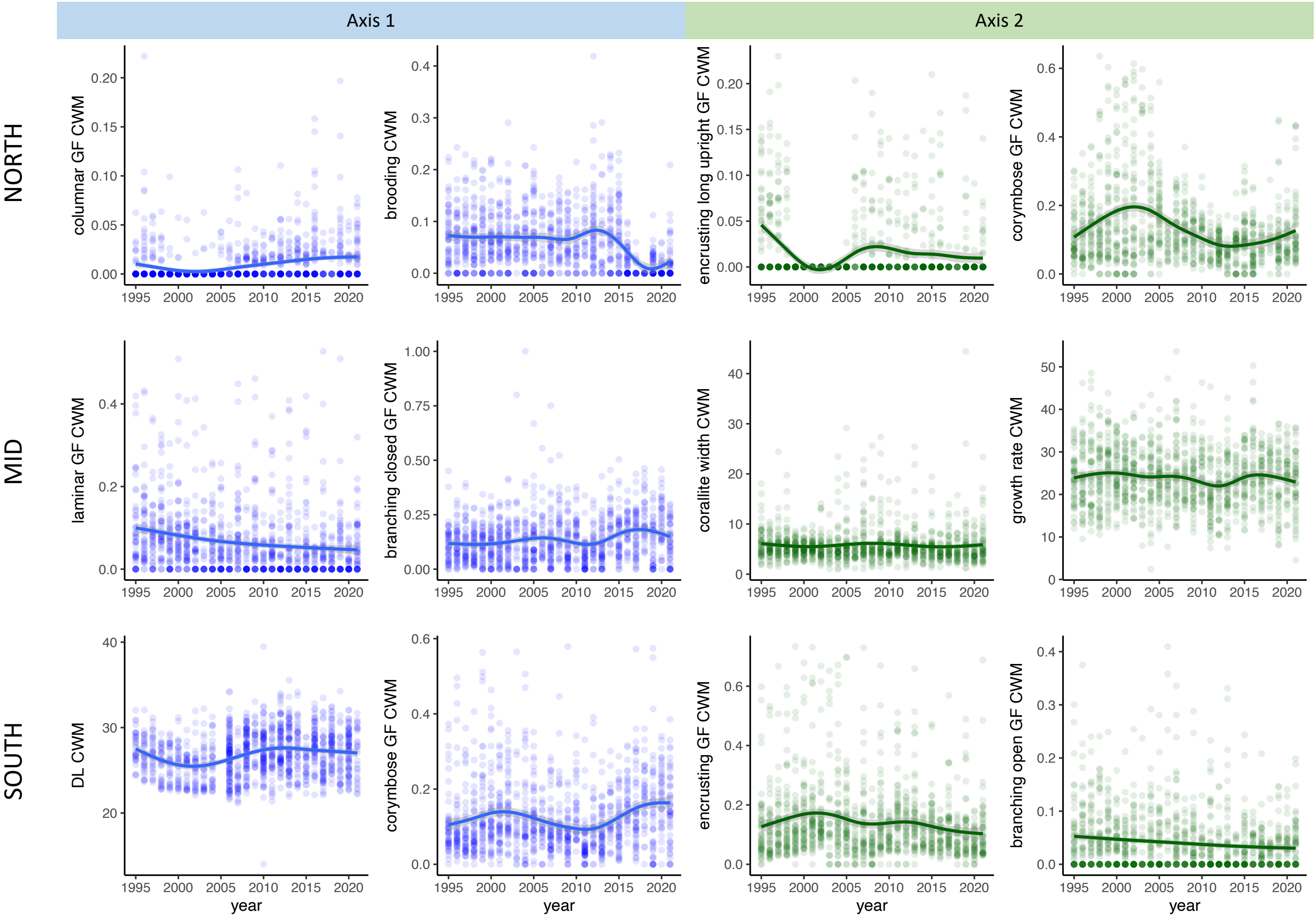
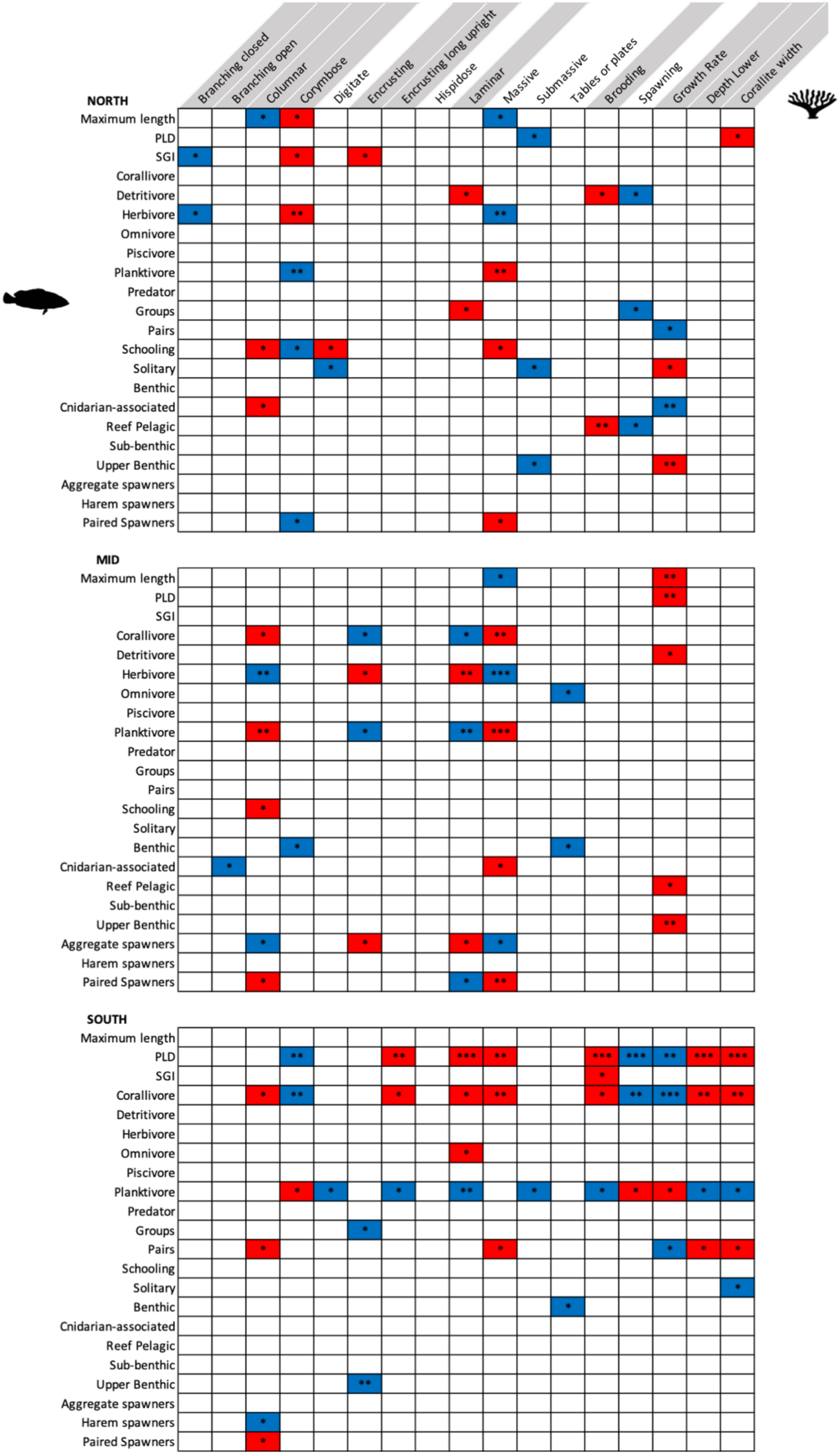


Figure 21. CWM of most influential coral traits over time in the North, Mid and Southern GBR (blue – RLQ axis 1, green – RLQ axis 2), visualised with fitted GAM smooths (CWM ~ time) and 95% confidence intervals. GF: growth form, DL: Depth lower, CWM: Community-weighted mean.

The middle section of the GBR has the lowest number of associations between coral and fish traits over time (31), followed by the Northern GBR (36). The Southern part of the GBR has the highest number of associations (42) overall. In the Northern GBR, columnar growth forms are positively correlated with larger fish lengths, but negatively correlated with schooling and cnidarian associated fish over time. Brooding corals are negatively associated with detritivores and reef pelagic fish. Despite being an important trait explaining structuring along the RLQ, the encrusting long upright trait does not have any associations with any fish traits detected. Corymbose growth forms are positively associated with planktivorous, schooling and paired spawning fish traits, and negatively with body size, SGI and herbivore traits. Corymbose, massive and brooding coral traits have particularly strong associations with the fish trait community (Figure 22). The contribution of planktivores to the trait community composition declines over time whilst the contribution of herbivores increases (Figure 23).

In the Mid-GBR, branching closed coral growth forms do not have any detectable associations with specific fish traits despite being important drivers over time. There are also no direct associations detected between corallite width and any of the fish traits. Laminar growth forms are positively associated with corallivore, planktivore and paired spawning traits, and negatively with herbivores and aggregate spawners. These patterns contrast with the associations with massive coral growth forms. High coral growth rates are negatively associated with fish maximum length and PLD, and detritivore, reef pelagic and upper benthic fish traits. Fish trophic modes, mainly corallivores, herbivores and planktivores have particularly clear associations with the coral traits over time (Figure 22). The CWM of planktivorous fishes declines in the Mid-GBR before beginning to recover around 2012, whilst the contribution of herbivores to the trait community exhibits an opposing pattern (Figure 23).

In the Southern GBR, fish that are corallivores, and those with longer PLDs, have distinct, very similar patterns of associations with the coral traits over time. Both are positively associated with corymbose, spawning corals and high growth rates. They are negatively associated with laminar, massive, and encrusting long upright growth forms, higher depth limits and corallite width. Planktivorous fish broadly show the opposing pattern with many of the same coral traits, though the associations here are less strong (Figure 22). The CWM of planktivores over this time remains stable, whilst the CWM of corallivores declines (Figure 23). Across all latitudinal zones, planktivorous trophic modes make the greatest contribution to the fish community (CWM, abundance weighted), followed by herbivores. In the Southern GBR, omnivores also make a sizeable contribution. Many of the higher trophic modes remain stable over time and are present in much lower proportions (Figure 23).



NORTH

	Branching closed	Branching open	Columnar	Corymbose	Digitate	Encrusting	Encrusting long upright	Hispidose	Laminar	Massive	Submassive	Tables or plates	Brooding	Spawning	Growth Rate	Depth Lower	Corallite width
Maximum length			🟦 *	🟥 *						🟦 *							
PLD											🟦 *						🟥 *
SGI	🟦 *			🟥 *		🟥 *											
Corallivore																	
Detritivore									🟥 *				🟥 *	🟦 *			
Herbivore	🟦 *			🟥 **						🟦 **							
Omnivore																	
Piscivore																	
Planktivore				🟦 **						🟥 **							
Predator																	
Groups									🟥 *					🟦 *			
Pairs															🟦 *		
Schooling			🟥 *	🟦 *	🟥 *					🟥 *							
Solitary					🟦 *						🟦 *				🟥 *		
Benthic																	
Cnidarian-associated			🟥 *												🟦 **		
Reef Pelagic													🟥 **	🟦 *			
Sub-benthic																	
Upper Benthic											🟦 *				🟥 **		
Aggregate spawners																	
Harem spawners																	
Paired Spawners				🟦 *						🟥 *							

MID

	Branching closed	Branching open	Columnar	Corymbose	Digitate	Encrusting	Encrusting long upright	Hispidose	Laminar	Massive	Submassive	Tables or plates	Brooding	Spawning	Growth Rate	Depth Lower	Corallite width
Maximum length										🟦 *					🟥 **		
PLD															🟥 **		
SGI																	
Corallivore			🟥 *			🟦 *			🟦 *	🟥 **							
Detritivore															🟥 *		
Herbivore			🟦 **			🟥 *			🟥 **	🟦 ***							
Omnivore												🟦 *					
Piscivore																	
Planktivore			🟥 **			🟦 *			🟦 **	🟥 ***							
Predator																	
Groups																	
Pairs																	
Schooling			🟥 *														
Solitary																	
Benthic				🟦 *								🟦 *					
Cnidarian-associated		🟦 *								🟥 *							
Reef Pelagic															🟥 *		
Sub-benthic																	
Upper Benthic															🟥 **		
Aggregate spawners			🟦 *			🟥 *			🟥 *	🟦 *							
Harem spawners																	
Paired Spawners			🟥 *						🟦 *	🟥 **							

SOUTH

	Branching closed	Branching open	Columnar	Corymbose	Digitate	Encrusting	Encrusting long upright	Hispidose	Laminar	Massive	Submassive	Tables or plates	Brooding	Spawning	Growth Rate	Depth Lower	Corallite width
Maximum length																	
PLD				🟦 **			🟥 **		🟥 ***	🟥 **			🟥 ***	🟦 ***	🟦 **	🟥 ***	🟥 ***
SGI													🟥 *				
Corallivore			🟥 *	🟦 **			🟥 *		🟥 *	🟥 **			🟥 *	🟦 **	🟦 ***	🟥 **	🟥 **
Detritivore																	
Herbivore																	
Omnivore									🟥 *								
Piscivore																	
Planktivore				🟥 *	🟦 *		🟦 *		🟦 **		🟦 *		🟦 *	🟥 *	🟥 *	🟦 *	🟦 *
Predator																	
Groups						🟦 *											
Pairs			🟥 *							🟥 *					🟦 *	🟥 *	🟥 *
Schooling																	
Solitary																	🟦 *
Benthic												🟦 *					
Cnidarian-associated																	
Reef Pelagic																	
Sub-benthic																	
Upper Benthic						🟦 **											
Aggregate spawners																	
Harem spawners			🟦 *														
Paired Spawners			🟥 *														

Figure 22. Fourth corner analyses (constrained, nrepet = 999) for bivariate relationships between coral and fish traits in the North, Mid and Southern GBR. Blue = positive associations. Red = negative associations. Shaded coral traits are influential drivers in RLQ. Cut-off point p<0.05 (*, p <0.05, **, p<0.01, *** p<0.001).

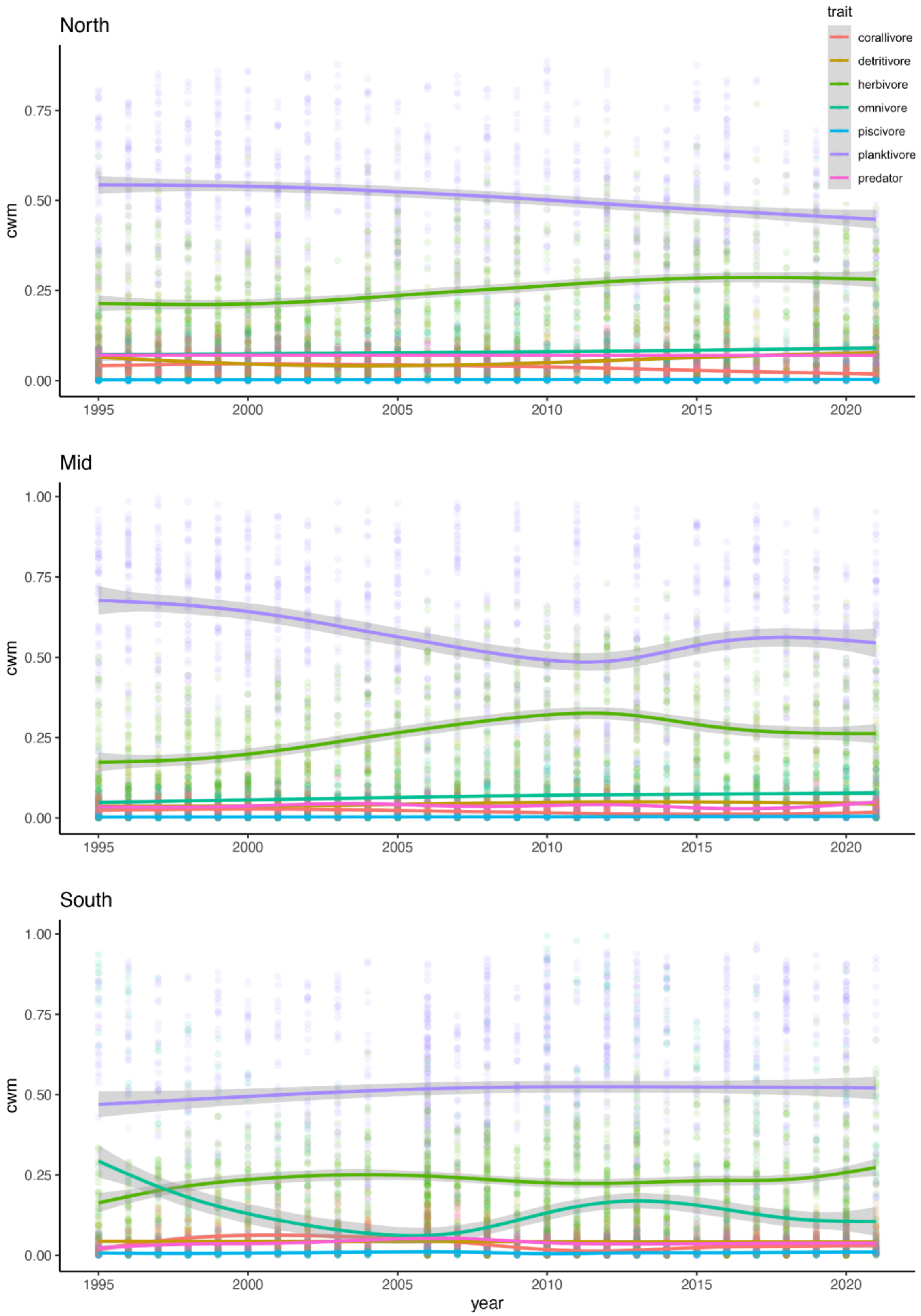


Figure 23. CWM of fish trophic modes over time in the North, Mid and Southern GBR, 1995 - 2021. GAM smooths (CWM ~ time) and 95% confidence intervals.

5.5 Discussion

In this study, I first asked how functional diversity in coral and fish communities changes over time, exploring the role of disturbance histories in driving these temporal dynamics. I found that DHW, COTS and cyclones all emerge as important predictors of different aspects of coral functional diversity, though DHW is the strongest driver and the presence of a NTZ does not play a clear role. Fish exhibit similar responses, but the presence of an NTZ correlates with increased functional richness in the Southern GBR. Second, I examined the influence of species traits in any shared community structuring patterns between corals and fish. I find that over time, coral and fish trait communities have clear shared structuring across the GBR, with coral growth forms and growth rates emerging as important drivers of this. These shared patterns between trait assemblages are further reflected in the 4th corner analysis, with several coral growth forms consistently correlating with key fish trophic modes. Most notably, the Northern GBR undergoes a substantial shift in cross-taxa community trait structuring that has been maintained since 2016, which has significant implications for the resilience of this ecosystem and its continued functioning.

How does functional diversity in coral and fish communities change over time, and what is the role of disturbances in driving these temporal dynamics?

In common with findings of coral and fish taxonomic community structuring on the GBR (Emslie et al., 2020), spatial gradients in latitude and shelf position are key determinants of how the functional diversity of coral and fish communities are structured (Table 8). It is crucial to keep in mind that latitude and shelf position are additionally very important for functional community structuring. Disturbance histories have varying levels of influence depending on the latitudinal section in question, an expected result given the geographically constrained impacts of cyclones, coral bleaching and COTS outbreaks on the GBR (Matthews et al., 2019). For example, the Northern GBR coral assemblage was most impacted in the 2016 bleaching event, but Mid and Southern reefs experienced more bleaching in the 2002 and 1998 events respectively (Hughes et al., 2017). Strikingly, declines in coral functional diversity in the Northern GBR were well underway prior to 2016, and coincide with when Cyclone Yasi made landfall in 2011, which caused extensive structural damage to the reef within the cyclone track (Beeden et al., 2015). Despite early signs of recovery (Beeden et al., 2015), functional diversity in the Northern GBR did not recover between the cyclone and the bleaching event in 2016 at this scale, though it is important to acknowledge there are significant differences in recovery trajectories depending on shelf position (Figure 16) (Mellin et al., 2019b). This is supported by other findings from the region where reassembly of trait space following disturbance has been limited (McWilliam et al., 2020).

These broad patterns are supported by shifts in the overall coral functional structure (CWM trait space), where the Northern GBR shrinks and then returns to a different and broader trait space over time, implying recovery of some sites but not others (Figure 17). DHW additionally takes on the most significant role in driving community structuring in the Northern section. Throughout the GBR, cyclones and COTS outbreaks had previously been more influential drivers of coral assemblages (De'ath et al., 2012, Beeden et al., 2015), but this result suggests that climate-related increases in DHW are overtaking these other disturbances in terms of impact. For all latitudinal sections, the disturbances used in these models explain more variation in species richness and Rao than they do the overall functional richness. This means that whilst there is disturbance-driven turnover in terms of species, their abundances and how this affects functional diversity, it has not yet translated into clear effect on the overall functional richness. This result suggests some functional redundancy in the corals and additionally highlights the importance of considering multiple indices of functional and species diversity in assessing disturbance impacts (Mouillot et al., 2013).

Overall, the clear impacts of disturbance and variability of functional diversity in the coral assemblage was also apparent in the fish. In the Northern GBR, the fish trait space exhibits a similar contraction and subsequent expansion to the corals (Figure 18). The return to a similar fish trait space after the 1998 and 2002 bleaching events is indicative of some resilience, defined as returning to a similar structure and function (McClanahan et al., 2012). Whilst the level of protection did not have strong effects on the coral assemblage over time, the presence of a NTZ in the Southern GBR conferred higher fish functional and species richness (Table 8). This broadly supports the concept that protected areas are effective for specific groups of fish (Williamson et al., 2014, Emslie et al., 2015, Emslie et al., 2017), but that they do not confer protection to a benthic community experiencing escalating climate impacts (Hughes et al., 2018a). However, functional diversity and redundancy in fish assemblages may facilitate recovery processes in corals (Nash et al., 2016), and so spatial protection for the fish community is still an important part of how managers maintain overall ecosystem function.

How do species traits influence any shared patterns and associations in the temporal changes of coral and fish communities?

This study identifies clear shared patterns in the temporal structuring of coral and fish communities on the GBR. The Mid and Southern GBR fluctuate over the ordination space during the survey period, but the Northern section switches much more decisively towards a different structure between the coral and fish traits, coinciding with the combined impacts of Cyclone Yasi in 2011 and the 2016 coral beaching event (Figure 19). Corals are known to shape fish assemblages (Darling et al., 2017, Richardson et al., 2018, Richardson et al., 2020), but here I show that this is maintained over large spatial and temporal scales and link this shared structuring to specific functional traits. There is a slightly weaker relationship between fish traits and overall fish species assemblages over time in the Southern GBR, which suggest that other factors may have additional influence. This may be a feature of disturbance history or environmental gradients, or that the role of spatial protection identified in the GAMs is substantially influencing the species composition of fish assemblages in this area (Emslie et al., 2015).

The most influential coral traits identified in the RLQ analysis afford insight into how coral trait composition, and its effect on the fish assemblage, are changing over time. Most of these are growth form traits, and those influential growth forms are those that confer structural complexity, indicating their particular importance for how fish assemblages are structured over time. For example, in the Northern GBR, encrusting long upright and corymbose growth forms are most influential in explaining structuring along the RLQ axis, and exhibit contrasting temporal trends in the CWM values (Figure 20, Figure 21). The corymbose corals in this study are all fast-growing *Acropora* species that have been characterised as having ‘competitive’ life history strategies in that they tend to dominate assemblages, particularly on outer shelf reefs (Darling et al., 2012). They are vulnerable to disturbance, but their fast growth means they can also characterise recovering assemblages (Darling et al., 2012, McWilliam et al., 2020). In contrast, encrusting long upright growth forms include species such as the stress-tolerant *Porites cylindrica*, which are more dominant on inner reefs, but are also a key provider of structural complexity (Hoadley et al., 2021). This is important because more complex growth forms are also more broadly susceptible to bleaching disturbances and mechanical damage from extreme weather (Zawada et al., 2019), which given their clear associations with parts of the fish assemblage means there are likely long-term implications for overall functioning across both taxa (Emslie et al., 2017, Robinson et al., 2019a, Robinson et al., 2019b). It should be noted however that some of the CWMs of the most influential coral traits remain stable over time (Figure 21). These may be important in structuring the fish community precisely because they do not fluctuate drastically. Corallite width is one such stable trait that is related to functions such as nutrient capture, suggesting that this reef function is maintained over time, whilst others such as habitat provisioning are not (McWilliam et al., 2020).

The fourth corner analysis affords further insight into the temporal relationships between coral and fish trait assemblages. In the Northern GBR, corymbose growth forms are positively associated with schooling, paired spawning fish traits and negatively with large body sizes, high SGI and herbivorous fish (Figure 22). Instead, massive coral growth forms correlate positively with larger body sizes and herbivorous fish traits. High SGI means that a species is found across a greater percentage of available habitat space and is therefore more generalist (Stuart-Smith et al., 2021), which suggests that corymbose growth forms (fast-growing *Acropora* species) host fish with more specialised ecological niches, whilst the larger herbivores associated with massive growth forms are more generalist. Massive corals are less likely to be impacted by bleaching (Zawada et al., 2019), and increased herbivore biomass has been documented elsewhere on disturbed reefs (Robinson et al., 2019a, Robinson et al., 2019b, Taylor et al., 2019).

In the Mid-GBR, there are clear associations related to specific fish trophic modes. Corallivore and planktivore traits share positive associations with encrusting and laminar coral growth forms, and negative ones with massive and columnar growth forms whilst herbivorous fish exhibit the opposite pattern (Figure 22). This further supports findings from the Northern GBR, where herbivores are associating with growth forms that are more suggestive of a disturbed reef environment (Zawada et al., 2019) and are broadly indicative of habitat selection by fish species that share specific traits. Interestingly, in the Southern GBR planktivore and corallivore fish traits do not share the same associations and instead have opposing patterns. Higher fish trophic groups do not have any detectable associations with particular coral traits. This may indicate that these species are not as directly dependent on the coral community (Emslie et al., 2017), though the abundance weighting of the CWMs (and their relatively lower abundances) may also inform this result. Overall, the fourth corner analysis shows that coral traits associated with structural complexity are correlated specifically with planktivore, corallivore, schooling and cnidarian associated fish species, which suggests that these parts of the fish assemblage will be most vulnerable as climate impacts escalate (Ceccarelli et al., 2016, Richardson et al., 2018, Magel et al., 2020).

There are some important aspects of functional diversity that are beyond the scope of this study, but that represent important avenues for future work. The first is intraspecific trait variability. The trait values used here are estimated constants, but there will be variation in these values shaped by environmental gradients and anthropogenic activity. Further, there are functional differences between adult and juvenile fishes that cannot be addressed here (Villéger et al., 2017). Secondly, whilst CWMs are a useful indicator of community trait structure that enables clear temporal assessments (Kleyer et al., 2012), they do not capture trait variation within communities that can be addressed in the future by incorporating functional beta diversity (Chao et al., 2019). Additionally, whilst I have broadly connected traits used here to likely functions using the wider literature, there is currently limited evidence to mechanistically link traits to specific functions (Bellwood et al., 2019b). Finally, this is a large-scale, broad overview of functional changes on the GBR and we would expect to find deviations and different patterns at the more local level that will inform an important part of our understanding (McWilliam et al., 2020).

This study finds that disturbance history drives trait community structure, with a general shift away from vulnerable coral traits. Fished or NTZ status on the GBR confers little or no protection to coral trait assemblages but does for the fish, primarily in the Southern GBR. Functionally diverse fish communities might promote future recovery of corals and should be protected, but managers must continue to be clear about the limitations of spatial protection in the context of rapid environmental change. The Northern GBR undergoes a distinct shift in relationships between coral and fish assemblages, while the Mid and South fluctuate between states. Shared temporal structuring between coral and fish functional assemblages is characterised by specific associations between coral and fish traits. However, not all traits are equally important in these cross-taxa relationships and not all of them are changing over time, which could help to prioritise key traits for monitoring and inform management responses.

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Chapter 6. Discussion

6.1 Revisiting aims and objectives

Coral reefs are transforming under the impacts of successive anthropogenic disturbances, threatening ecosystem services and biodiversity (Hughes et al., 2018). In this context of rapid change, it is crucial to understand the impacts of disturbance on functional assemblages and direct these findings towards improved management and conservation (Bellwood et al., 2019a, McLeod et al., 2021). The aim of this thesis has been to explore the changing community structure of Anthropocene coral reefs from the perspective of species traits. Throughout, I have approached this aim at different spatial and temporal scales, incorporated different management contexts and considered the impacts of different types of disturbance. I have found that as anthropogenic disturbance shapes the trait composition of coral and fish communities, it also drives changes in shared structuring. These findings have implications for understanding coral reef resilience and function, informing future management and conservation.

Objective 1: *Explore the practical applications of functional traits for management from the perspective of how food fish respond to fishing pressure proxies.*

In Chapter 2, I consider potential practical applications of species traits to the management of coral reef fisheries. First, I demonstrate that groups of species derived from shared traits have differing responses to several environmental and socio-economic variables that act as proxies for chronic fishing pressure. I use this finding to highlight how traits can support management decision-making in diverse coral reef fisheries where species specific and blanket spatial approaches are not always practical.

Objective 2: *Assess short-term resilience of coral and fish traits, and associations between them, over a bleaching disturbance.*

In Chapter 3, I illustrate that coral bleaching causes the decoupling of linked coral and fish trait distributions, driven by changes in the trait community composition (and altered functioning) of the coral community. In contrast, I show that the trait community composition of food fish remained stable over the course of this pulse disturbance event.

Objective 3: *Evaluate the importance of different parts of the functional space for detecting and interpreting patterns in associations between taxa.*

In Chapter 4, I assess the unique contributions of different parts of the fish assemblage to overall trait structure, and quantify how this informs our understanding of cross-taxa relationships. I show how our assessment of traits and community assemblages is shaped by chosen monitoring methods, highlighting that whilst managers are increasingly incorporating functionality into management objectives, existing monitoring protocols are not necessarily suitable to meet them.

Objective 4: *Investigate how coral and fish traits change in the long-term over multiple disturbances and identify key traits driving change.*

Finally in Chapter 5, I combine the themes of previous chapters to take a long-term view of the impacts of successive disturbances on coral reefs. I show that disturbance history plays an important role in how trait communities are structured and that some parts of the study area undergo notable shifts in their relationships between taxa. I identify traits that drive these changes and link them to likely shifts in ecosystem functioning, highlighting the provisioning of structural complexity and herbivory processes as key functions undergoing change at the ecosystem level.

Together, the studies outlined here strengthen our understanding of how coral and fish traits filter across environmental and disturbance gradients, examining the short and long-term consequences of different types of anthropogenic activity on the trait structure and likely function of coral reef communities. Crucially, it shows how linked trait space distributions between different taxa form an important part of the story, and identifies management, conservation, and monitoring applications of these findings.

6.2 Research evidence and impacts

6.2.1 Trait-based disturbance responses

Throughout this thesis, I illustrate how trait-based assessments of coral reef community disturbance responses can provide insight beyond looking at species assemblages alone. In Chapter 2, I show that food fish communities break down into broad functional groups based on shared traits, and that some of these groups are less affected by fishing pressure (a chronic, press-type disturbance) than others, at least at the scale and level of pressure captured in this study. This result links to similar work finding that traits can dictate fishing resistance or vulnerability (Henriques et al., 2014). Reef-pelagic, schooling planktivores (mainly Acanthurids) were one such resistant group that can play an important functional role as algal grazers (Marshell and Mumby, 2015). These findings highlight how trophic modes, whilst they are undoubtedly a useful indicator of function, alone do not necessarily capture the full breadth of functional roles (Mihalitsis and Bellwood, 2021, Semmler et al., 2021).

Given that traits mediate disturbance responses, those that indicate either resistance or vulnerability to a specific disturbance are particularly interesting in the context of resilience (Carturan et al., 2018). Chapters 3 and 5 both find that coral traits reduced post-disturbance are what would be expected, with a loss of the complex morphologies that dominate shallow coral assemblages but are vulnerable to mechanical damage from cyclones and coral bleaching mortality (Hughes et al., 2018, Zawada et al., 2019). Instead, coral traits associated with resistance (such as massive growth forms) (Zawada et al., 2019) or recovery (high growth rates) become more important for overall structuring and the coral assemblage becomes more homogenous (McLean et al., 2016). With respect to fish assemblages, traits that suggest vulnerability to bleaching are those that indicate a reliance on coral habitat, such as small bodied, corallivorous species. In contrast, traits that make a species vulnerable to fishing impacts are very different (i.e. large body size) (McLean et al., 2016). It is important to remember that the traits that indicate vulnerability in many fish species will also apply to juvenile life history stages of many others. While that challenge is not addressed in this thesis, it does mean that long-term impacts of disturbances to corals are likely to be felt by a much larger part of the fish assemblage (Fontoura et al., 2019).

A further focus of this thesis is the relationships between coral and fish traits and their shared responses to disturbances. In Chapter 3, I first demonstrate the importance of cross-taxon approaches to understanding traits and functions in the context of disturbance. Shifts in the trait structure of the coral assemblage are not reflected in the food fish but cause reduced shared structuring even though one taxon appears more resistant than the other. This uneven disturbance response is in common with findings from other parts of the world (Robinson et al., 2019, Taylor et al., 2019), and in the long-term may have negative implications for continued ecosystem functioning on coral reefs as trophic structure is altered. In Chapter 4, I illustrate how different parts of the fish assemblage make unique contributions to the trait space, and that small, site-attached, non-target species are key to detecting relationships between coral and fish traits and overall habitat structuring. The species excluded from monitoring due to methodological choices can have important functional roles (Brandl et al., 2019), which means that monitoring efforts must consider whether current methodologies are adequate to inform increasingly trait-based and functional management goals.

Within these shared disturbance responses, many of the most influential traits highlight the known links between complex coral habitat and herbivory (particularly grazers) (Darling et al., 2017, Santano et al., 2021). In this thesis, I show the importance of these traits in driving shared structural changes between coral and fish functional traits at different scales (Chapter 3, Chapter 5). It is also notable that these functional relationships between corals and fish are with lower fish trophic levels. Functions performed by fish in higher trophic groups, such as nutrient cycling through piscivory, appear to be more resistant to disturbances that affect corals (Emslie et al., 2017). This renders some functions more immediately vulnerable to climate change than others, affecting recovery capacity and future responses to climate disturbance.

6.2.2 Management implications

This thesis explores the management applications of trait-based approaches most explicitly in Chapter 2, which includes a proposed framework for managing coral reef fisheries. Trait-based management solutions for fisheries, and for coral reefs in particular, are in their infancy (Koutsidi et al., 2016, Mbaru et al., 2019), while an understanding of traits and functions is increasingly part of a manager’s toolkit (McLeod et al., 2021). The trait-based adaptive management (TBAM) framework offers a new avenue to incorporate our growing understanding of species traits, and the importance of maintaining ecosystem function, with the needs of fishers. By simplifying diverse target assemblages into groups of species that respond similarly to disturbance, it offers a framework through which fishers can target robust groups and prioritise management of others according to local priorities. Applying this framework is designed to support management decisions at the local government level, though it could also feasibly be used to empirically support traditional governance structures where appropriate. Using functional traits rather than focusing on specific species also means it can be adapted to suit a multitude of different locations and contexts. A crucial next step will be to test whether the differential responses to disturbance found here correspond to differential management responses, and whether these findings hold across different locations.

In addition to Chapter 2’s framework, findings in other sections of this thesis also have implications for management. The relative stability of food fish over a pulse bleaching disturbance in Chapter 3 reflects other findings where food fish biomass can remain stable or even increase post-disturbance, suggesting that fisheries could be sustainably managed to provision for human needs even as coral reefs change (Robinson et al., 2019). In Chuuk, this gives clear impetus for managing the coral reef fishery in to the future in order to meet human needs in spite of ecosystem change. The dissociation between coral and fish traits found in Chapter 3 additionally indicates changes in the spatial delivery of linked functions between the two taxa. This has implications for how spatial protection, in the form of marine protected areas (MPAs) and no-take zones (NTZs) are delivered, indicating that the spatial extent of these kinds of management tools will need to become much more flexible in the future, similar to how they will have to accommodate species range shifts (Cashion et al., 2020). Rotating and temporary closures used by traditional governance systems in the Pacific and globally provide a crucial precedent for how this might be implemented. In Chapter 5, I found that the presence of NTZs maintained higher fish functional diversity over time than reefs that were not protected. From a functional perspective, this finding reiterates the fact that NTZs are useful for maintaining parts of the fish assemblage, but that they do not offer protection to corals and closely associated fish species in the face of escalating climate impacts (Emslie et al., 2015, Hughes et al., 2017, Lowe et al., 2019). It also demonstrates that NTZs have an important role to play in maintaining coral reef fisheries, even if they cannot protect coral communities affected by climate change. With regards to monitoring, the contributions of different parts of the fish community illustrated in Chapter 4 show that monitoring efforts and the decision-making they support must evaluate what aspects of functionality current reef health assessment programs can reliably address.

Beyond addressing the ecological uncertainties associated with how traits and functions can be incorporated into management, any management changes that arise must meaningfully include, or ideally be led by, local communities. Addressing the historical exclusion of local communities in many conservation and management initiatives is an ongoing process. In the context of the coral reef regions discussed in this thesis, improving these inequalities in Australia relates to how Traditional Owners are engaged in reef management alongside the Great Barrier Reef Marine Park Authority (GBRMPA) (Dale et al., 2016). In Chuuk, this applies to the development and implementation of an integrated protected area network as part of the Micronesia challenge (Weeks et al., 2017). How management decision-making for protecting coral reef biodiversity and ecosystem functioning is made to be an inclusive and just process is integral to the success of current and future management actions (Bennett et al., 2021).

In many ways, the trait-based approaches used in this thesis lend a utilitarian view of conservation and management, framing the need to better protect coral reefs around maintaining ecosystem function and services, and providing for human needs. This raises a tension with conservation instead motivated and informed by the intrinsic value of ecosystems and the species within them. Viewing ecosystems in terms of the services and functions they perform represents a useful tool for communicating their importance and for prioritising management, though it also risks undervaluing aspects of ecosystems and communities depending on their contribution to overall function. In contrast, conservation motivated by intrinsic value is easy to advocate for from a moral perspective. However, aspects of this conservation tradition can be criticised for viewing humans as somehow separate from the ecosystems they inhabit, which has been widely used to justify harm caused by excluding humans from areas in the name of conservation (Kashwan et al., 2021). An awareness of the weaknesses of these differing perspectives is important for moving forward with more equitable and effective conservation. Ideally, conservation draws on our human desire to do what is right, whilst using tools that make the case for protecting ecosystems and species and enable sustainable use.

6.2.3 Limitations and future directions

There are currently several key limitations within trait-based research that hinder the progress of the field and how it can translate into effective coral reef management (Bellwood et al., 2019b). These include trait choice, trait data availability, and explicitly linking traits to specific ecosystem functions. In terms of trait choice, the robustness of coral and fish community trait spaces to trait omission can be quite low (Mouillot et al., 2021), meaning that the choices of which traits to include or exclude can significantly affect results and interpretations (Hadj-Hammou et al., 2021). The available trait information in the literature and in data repositories is variable in terms of quality, regional coverage, and intraspecific trait variability, and lags what is available for taxa such as terrestrial plants (Mouillot et al., 2021). To counter issues with lack of trait data, different infilling approaches have been applied, however this also creates inconsistencies among studies (Taugourdeau et al., 2014, Kim et al., 2018). These limitations are all likely to improve as the field advances, and best-practice guidelines are increasingly available (Mouillot et al., 2021). Finally, fully tested links between traits and functions are not currently available for coral reefs (Bellwood et al., 2019b). Trait based approaches include an enormous variety of methods and applications that urgently need standardising, and recent work has gone some way towards setting systems of best practice which should be accounted for in future work (Mouillot et al., 2021). Therefore, whilst these approaches can offer unique insights in to reef communities and how they are changing, there remain several key gaps that provide important avenues for future work.

In producing this thesis, I have deepened my awareness of the limitations of trait-based approaches, and expanded my appreciation for how and where they can be most useful. At their best, traits are carefully chosen to reflect the research question and scale of the study, which can range from large biogeographic comparisons (McWilliam et al., 2018) to local-scale attempts to inform management (Mbaru et al., 2019). With experience, I have become more discerning of which traits to include and how to incorporate sensitivity analyses in order to best answer the question at hand. Recent guidance on best practice for creating trait spaces will also inform future work.

To implement the TBAM framework outlined in Chapter 2, it will first be necessary to explicitly test how different management actions, not just the impacts of fishing activity, affect the trait groups identified. More broadly, work is also needed on the practical applications of traits before they can feasibly be applied to coral reef management and how they inform better stewardship of rapidly changing ecosystems. These applications have been advocated for in terrestrial systems (Laughlin et al., 2017), and in fisheries (Barnett et al., 2019), but uses on coral reefs are particularly under-explored (Mbaru et al., 2019). With respect to the findings of relative food-fish stability in Chapter 3, long-term work is urgently needed on this and other coral reef fisheries to determine if the apparent resistance of these species to bleaching disturbance represents a viable long-term resource that can continue to support the subsistence and livelihood needs of human populations that are dependent on coral reefs. In Chapter 4, I find that site-attached species make unique contributions to the fish trait space and are crucial for detecting habitat structuring and trait relationships with the coral assemblage. This means that conclusions about traits and implications for ecosystem functioning must be particularly clear on what is omitted through study design. Next, broadening our understanding of trait relationships on reefs beyond corals and fish to include other taxa will be necessary to fully understand how things are changing. We have seen the short-term (Chapter 3) and long-term (Chapter 5) impacts of anthropogenic disturbances on coral and fish communities, and their relationships to each other, but the impacts of disturbance are likely to extend beyond fish and corals (e.g. molluscs) (Floyd et al., 2020) and monitoring of such other taxa is important to fully understand functional relationships on coral reefs.

6.3 Concluding remarks

Coral reef ecosystems are likely to change significantly in the coming decades given the dearth of meaningful efforts to address climate change. To manage reefs and inform reef users and the public globally, it is important to understand how communities and their associated functions are changing, so that they can be better protected and people who rely on these ecosystems can continue to meet their needs. Trait based approaches have enormous potential to help us navigate the changing reefs of the Anthropocene, though there remain large knowledge gaps.

This thesis has examined the impacts of disturbances, from localised fishing pressure to global coral bleaching events, on the trait structure of reef communities. It has explored potential routes to applying what we know about traits to the management of coral reef fisheries and considers how monitoring may need to adapt to these new questions and focuses. Hearteningly, there appear to be aspects of resilience that may enable the people that directly rely on reef ecosystems to continue to use them, though the extent to which this remains to be true depends on our collective societal choices in the coming decades.

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List of Abbreviations

AIC	Akaike information criterion
AIMS	Australian Institute of Marine Science
COTS	Crown of thorns starfish
CWM	Community weighted mean
DHW	Degree heating weeks
FSM	Federated States of Micronesia
GAM	Generalised additive model
GBR	Great Barrier Reef
GBRMPA	Great Barrier Reef Marine Park Authority
LTMP	Long-term monitoring program
MPA	Marine protected area
NGO	Non-governmental organisation
NTMR	No-take marine reserve
NTZ	No-take zone
PCA	Principal component analysis
PCoA	Principal coordinate analysis
PERMANOVA	Permutational multivariate analysis of variance
PLD	Pelagic larval duration
RaoQ	Rao’s quadratic entropy
REML	Restricted maximum likelihood
SGI	Species generalisation index
SIMPER	Similarity of percentages
SPC	Stationary point count
TBAM	Trait-based adaptive management

Appendix A. Trait groups as management entities in a complex, multi-species reef fishery

A1. Study location

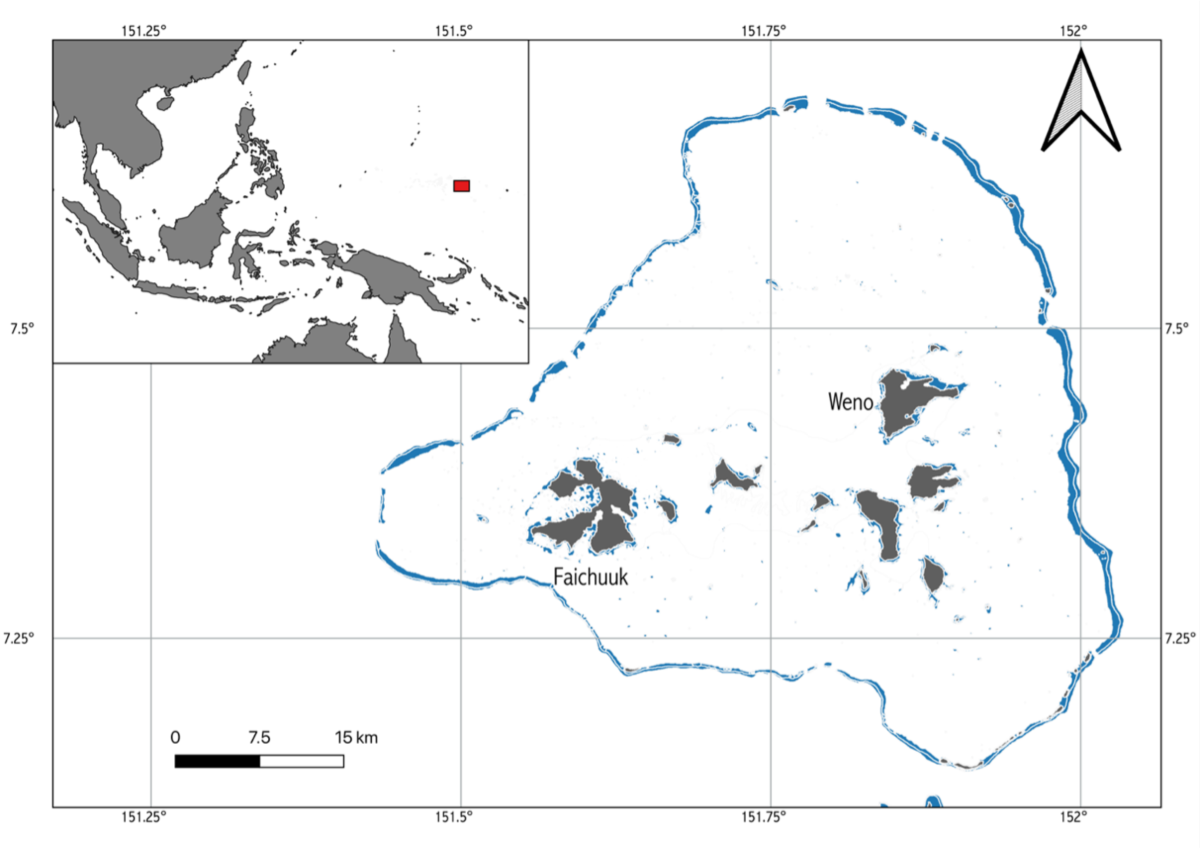

Figure A1. Chuuk Lagoon reef area (blue) and key islands (grey) inset with location in the tropical Western Pacific (Houk et al., 2015, UNEP-WCMC, 2018).

A2. List of food fish families

Acanthuridae, Scaridae, Serranidae, Carangidae, Labridae, Lethrinidae, Lutjanidae, Balistidae, Kyphosidae, Mullidae, Holocentridae and Carcharhinidae

A3. Fish and coral survey details

Food fish species abundance and size were recorded with 12 stationary point counts per site, equally spaced across five 50m transects (Houk et al., 2015, Houk et al., 2016), at 3-5m (inner reefs) or 6-8m depth (channel, outer and patch reefs). It is important to note therefore that habitat type is confounded with depth at shallow inner reef surveys. At each station, species and size were documented for all food fish within a 5m radius over three minutes. Fish sizes were binned in to 5cm groupings and converted to biomass with local-length weight coefficients where possible (Cuetos-Bueno and Hernandez-Ortiz, 2017), from other regional sources when not available for Chuuk (Houk et al., 2017), or from Fishbase (Froese and Pauly, 2019). Coral surveys consisted of ten 1m^2 quadrats per site placed across the five transects. Colonies were identified and diameter recorded for all corals in the quadrat, and percent cover calculated for each site (Houk et al., 2015).

A4. Calculation of landings data

Total annual landings and the number of fishing trips were estimated by multiplying mean daily landings, means landings frequency, and operational weeks of fishing from the daily purchase records of 13 fish markets, and fisher interviews. Geographical distribution of landings was determined using catch location recorded during interviews (Cuetos-Bueno et al., 2018). We used these catch locations to attribute landings data to the nearest food-fish survey sites (metres).

A5. Food fish trait groupings

To identify clusters of similar species based on shared traits, we assembled a Gower dissimilarity matrix with a cailliez correction (for non-euclidean distances) from the traits (Laliberté and Legendre, 2010). We used a 2-norm quality criterion to establish the best clustering method (cl_dissimilarity in package clue) (Hornik, 2005, Maire et al., 2015), and carried out hierarchical average clustering of the dissimilarity matrix to create a dendrogram of the trait-based proximity of different species (*hclust*) (R Development Core Team, 2019). Multiple cut-off heights were run to produce between six and ten groups, with the final cut-off height for eight trait groups decided based on expert opinion and assessments of cluster stability (clusterboot in package *fpc*) (Hennig, 2018). The relative importance of each trait in clustering was calculated with a boosted regression tree (1000 iterations) (gbm in package *gbm*) (Darling et al., 2012, Greenwell et al., 2019).

Table A1. Trait groups and species present in each (n = 131).

Group	Species List
1	*Acanthurus blochii, Acanthurus olivaceus, Acanthurus pyroferus, Acanthurus thompsoni, Acanthurus xanthopterus, Balistapus undulatus, Balistoides viridescens, Bolbometopon muricatum, Cetoscarus ocellatus, Cheilinus fasciatus, Cheilinus trilobatus, Cheilinus undulatus, Chlorurus bleekeri, Chlorurus frontalis, Chlorurus japanensis, Chlorurus microrhinos, Chlorurus sordidus, Coris aygula, Epibulus insidiator, Gnathodentex aureolineatus, Hemigymnus fasciatus, Hemigymnus melapterus, Hipposcarus longiceps, Kyphosus cinerascens, Kyphosus vaigiensis, Leptoscarus vaigiensis, Lethrinus erythracanthus, Lethrinus erythropterus, Lethrinus harak, Lethrinus obsoletus, Lethrinus olivaceus, Lethrinus xanthochilus, Lutjanus argentimaculatus, Lutjanus bohar, Lutjanus fulvus, Lutjanus gibbus, Lutjanus kasmira, Lutjanus monostigma, Lutjanus semicinctus, Macolor macularis, Macolor niger, Monotaxis grandoculis, Mulloidichthys flavolineatus, Mulloidichthys vanicolensis, Naso lituratus, Naso unicornis, Plectorhinchus albovittatus, Plectropomus oligacanthus, Pseudobalistes flavimarginatus, Scarus altipinnis, Scarus dimidiatus, Scarus festivus, Scarus flavipectoralis, Scarus forsteni, Scarus frenatus, Scarus ghobban, Scarus globiceps, Scarus niger, Scarus oviceps, Scarus Psittacus, Scarus rivulatus, Scarus rubroviolaceus, Scarus schlegeli, Scarus sp., Scarus spinus, Scolopsis sp., Siganus argenteus, Siganus doliatus, Siganus puellus, Siganus punctatissimus, Siganus punctatus, Siganus randalli, Siganus spinus, Siganus vulpinus, Variola louti*
2	*Acanthurus lineatus, Acanthurus nigricans, Acanthurus nigricauda, Acanthurus nigrofuscus, Calotomus carolinus, Cephalopholis argus, Cephalopholis urodeta, Ctenochaetus striatus, Epinephelus fuscoguttatus, Epinephelus howlandi, Epinephelus maculatus, Epinephelus merra, Epinephelus polyphekadion, Epinephelus spilotoceps, Gracila albomarginata, Myripristis murdjan, Myripristis sp., Parupeneus barberinoides, Parupeneus barberinus, Parupeneus cyclostomus, Parupeneus multifasciatus, Parupeneus trifasciatus, Plectorhinchus*

	lineatus, Plectorhinchus picus, Plectropomus areolatus, Plectropomus laevis, Sargocentron spiniferum, Sargocentron tiere, Triaenodon obesus
3	*Acanthurus mata, Caranx papuensis, Naso annulatus, Naso brevirostris, Naso caesius, Naso hexacanthus, Naso thynnoides*
4	*Aethaloperca rogaa, Aphareus furca, Aprion virescens, Caranx melampygus, Carcharhinus albimarginatus, Carcharhinus amblyrhynchos, Carcharhinus melanopterus, Plectropomus leopardus, Sphyraena barracuda*
5	*Alectis ciliaris, Caranx ignobilis, Caranx sexfasciatus, Elagatis bipinnulata, Grammatorcynus bilineatus, Scomberoides lysan, Seriola lalandi*
6	*Gymnothorax javanicus*
7	*Myripristis adusta, Myripristis berndti, Myripristis kuntee*

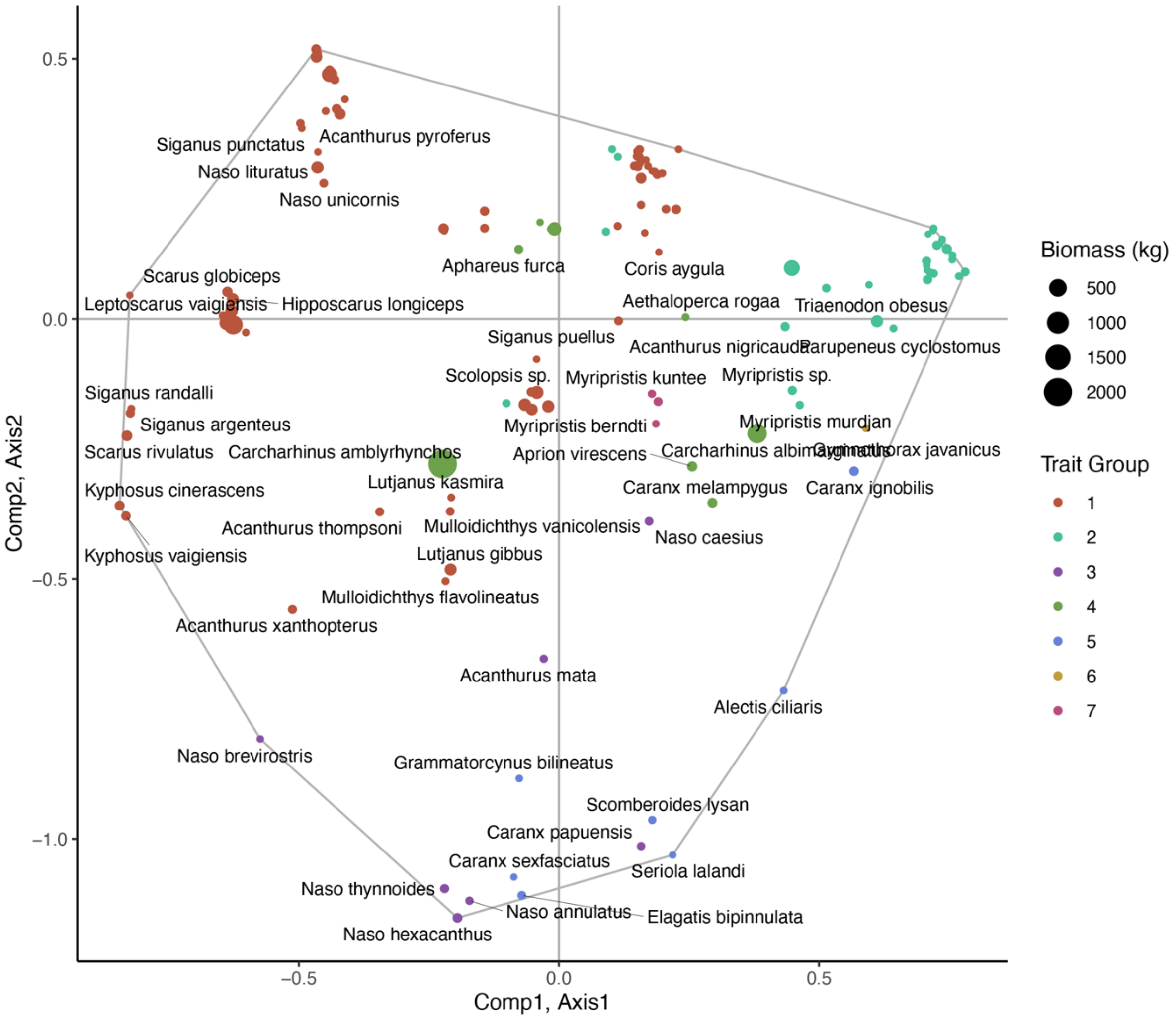

Figure A2. PCoA of food fish community trait space, with species labels (some excluded for readability). Explains approx. 17.27 % of the variation.

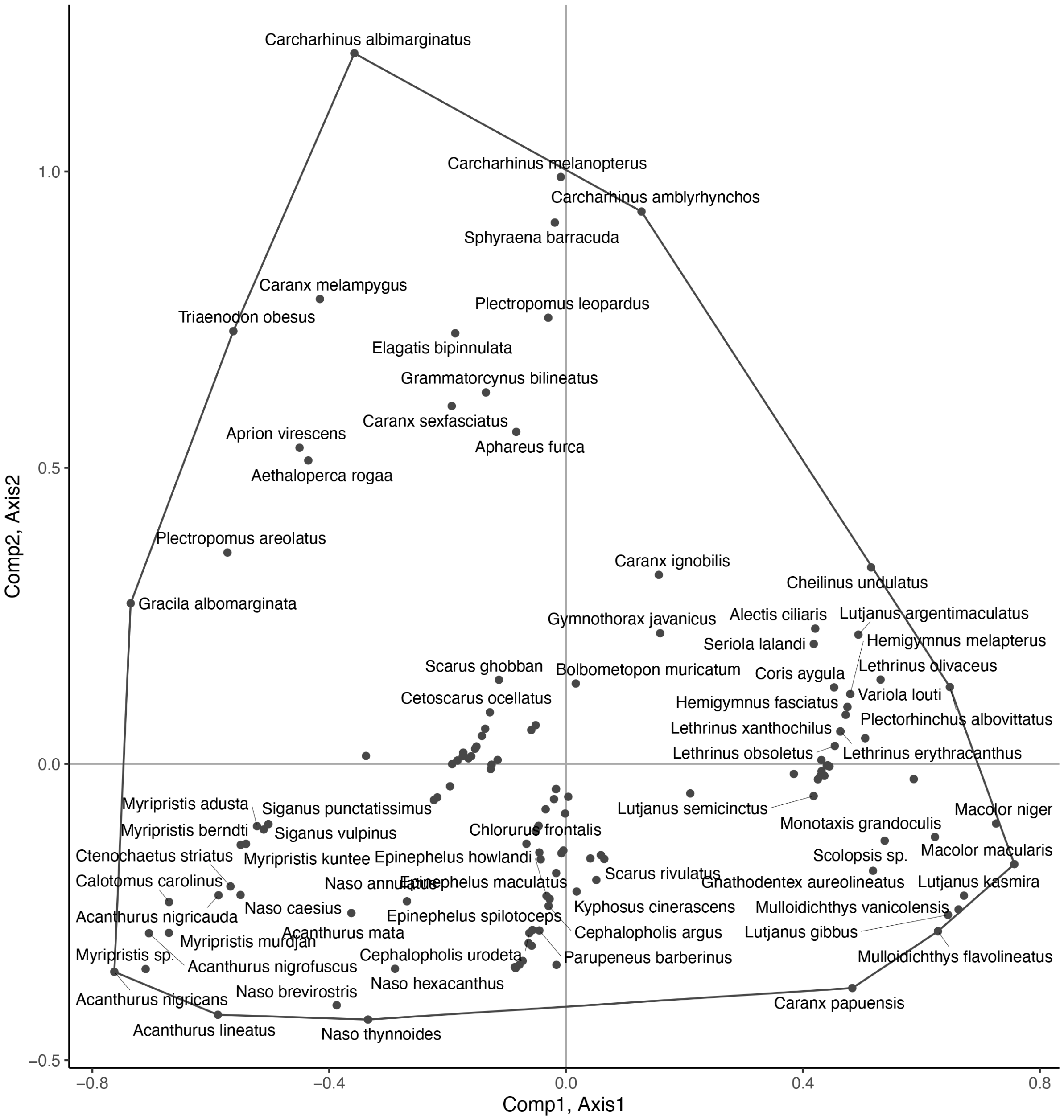

Figure A3. 3rd and 4th axes of food fish community trait space (explains approx. 11.16% of variation).

Table A2. Mantel test results and PCoA variance for each possible combination of four out of five selected traits (Legendre et al., 2005).

Traits	Mantel Statistic	Mantel significance	PCoA variance (4 axes)
All traits	-	-	29%
2 (- position)	0.843	0.001	25%
3 (- aggregation)	0.846	0.001	32%
4 (- trophic)	0.777	0.001	26%
5 (- PLD)	0.985	0.001	29%
6 (- max length)	0.687	0.001	50%

A6. Food fish trait group GAMs

Table A3. Minimum adequate generalised additive model (GAM) structure for each trait group at each site (n=61). Each GAM was initially constructed with three knots (*k*) for each smooth term and further determined with REML smoothing parameter estimation method. Interaction terms between coral cover and reef type, and wave energy and reef type, were included if they improved fit (determined by Akaike Information Criterion and diagnostic plots) Wave energy and population were log-transformed.

Group	Model Formula
1	sqrt(mean biomass) ~ s(landings, k = 3) + s(logWave, k = 3) + s(logPop, k = 3) + s(cover, k = 3) + s(market, k = 3) + s(market, k = 3) + s(market2, k = 3) + reeftype + spear + dynamite
2	sqrt(mean biomass) ~ s(landings, k = 3) + s(logWave, by = reeftype, k = 3) + s(logPop, k = 3) + s(cover, by = reeftype, k = 3) + s(market, k = 3) + s(market, k = 3) + s(market2, k = 3) + reeftype + spear + dynamite
3	sqrt(mean biomass) ~ s(landings, k = 3) + s(logWave, by = reeftype, k = 3) + s(logPop, k = 3) + s(cover, k = 3) + s(market, k = 3) + s(market, k = 3) + s(market2, k = 3) + reeftype + spear + dynamite
4	sqrt(mean biomass) ~ s(landings, k = 3) + s(logWave, k = 3) + s(logPop, k = 3) + s(cover, k = 3) + s(market, k = 3) + s(market, k = 3) + s(market2, k = 3) + reeftype + spear + dynamite
5	sqrt(mean biomass) ~ s(landings, k = 3) + s(logWave, by = reeftype, k = 3) + s(logPop, k = 3) + s(cover, k = 3) + s(market, k = 3) + s(market, k = 3) + s(market2, k = 3) + reeftype + spear + dynamite

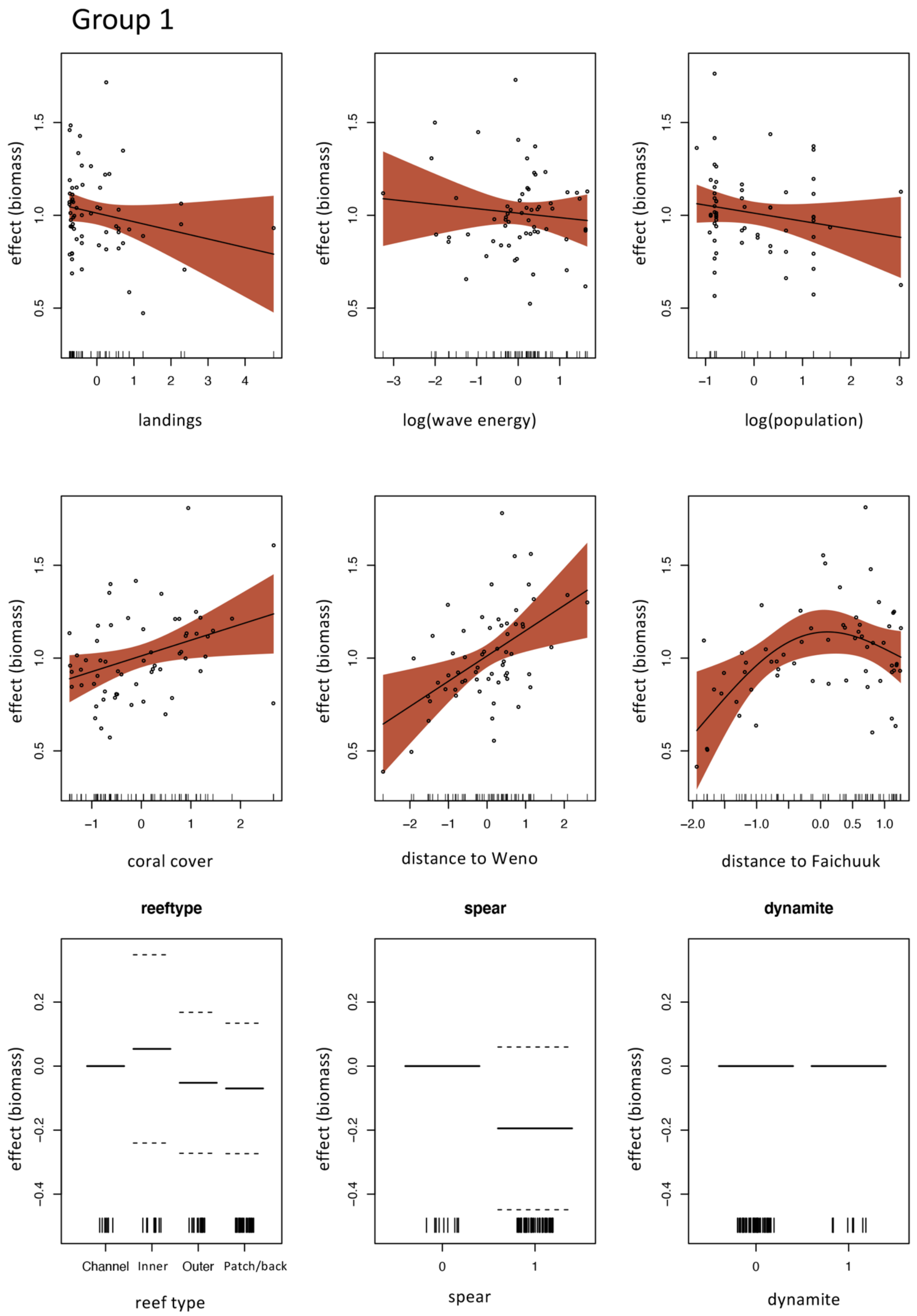

Figure A4. Partial effects plots for all terms of GAM for trait group one: Smaller, reef-associated, and mainly solitary species.

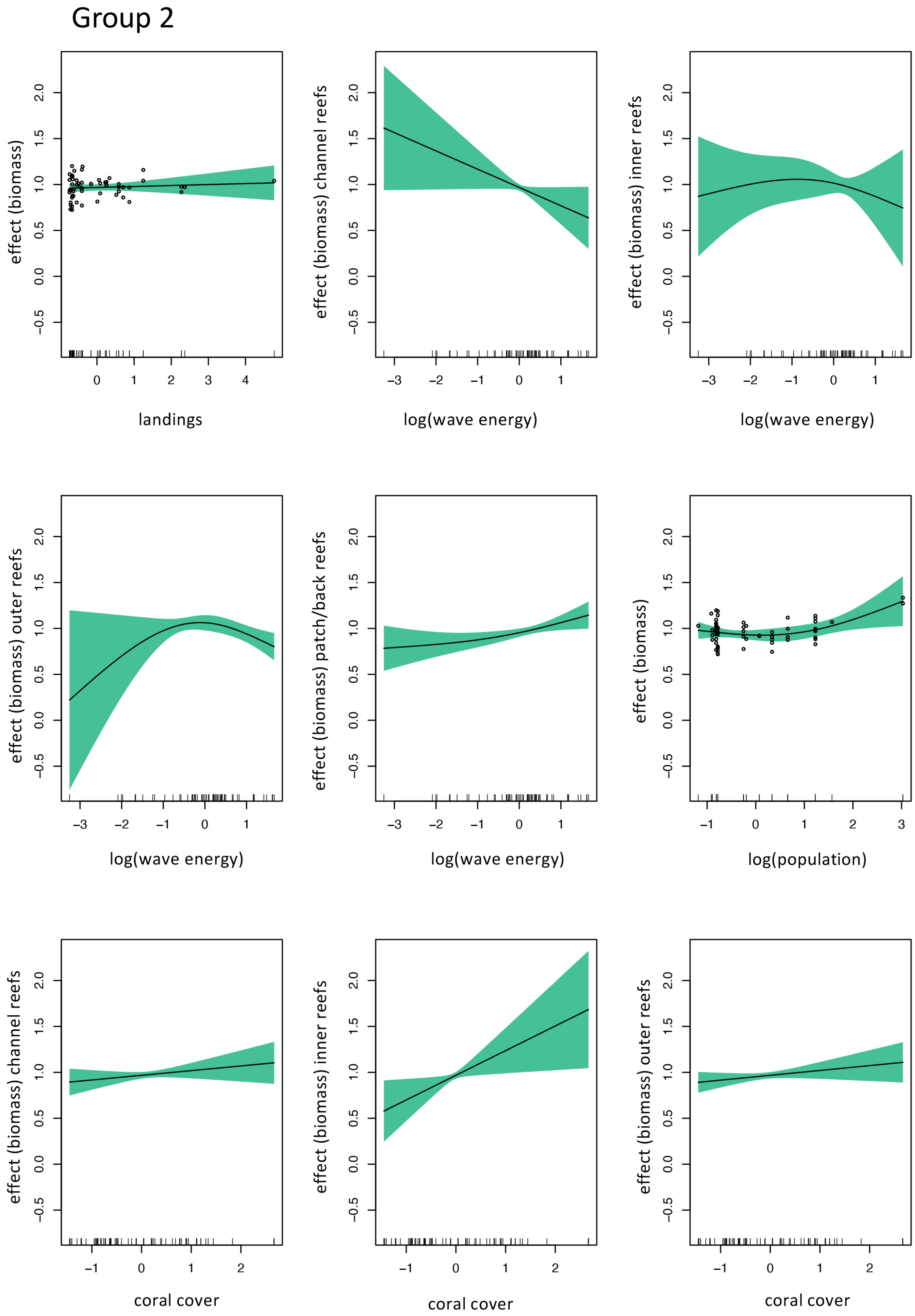

Figure A5. Partial effects plots (1 of 2) for all terms of GAM for trait group two: smaller, solitary benthic predators.

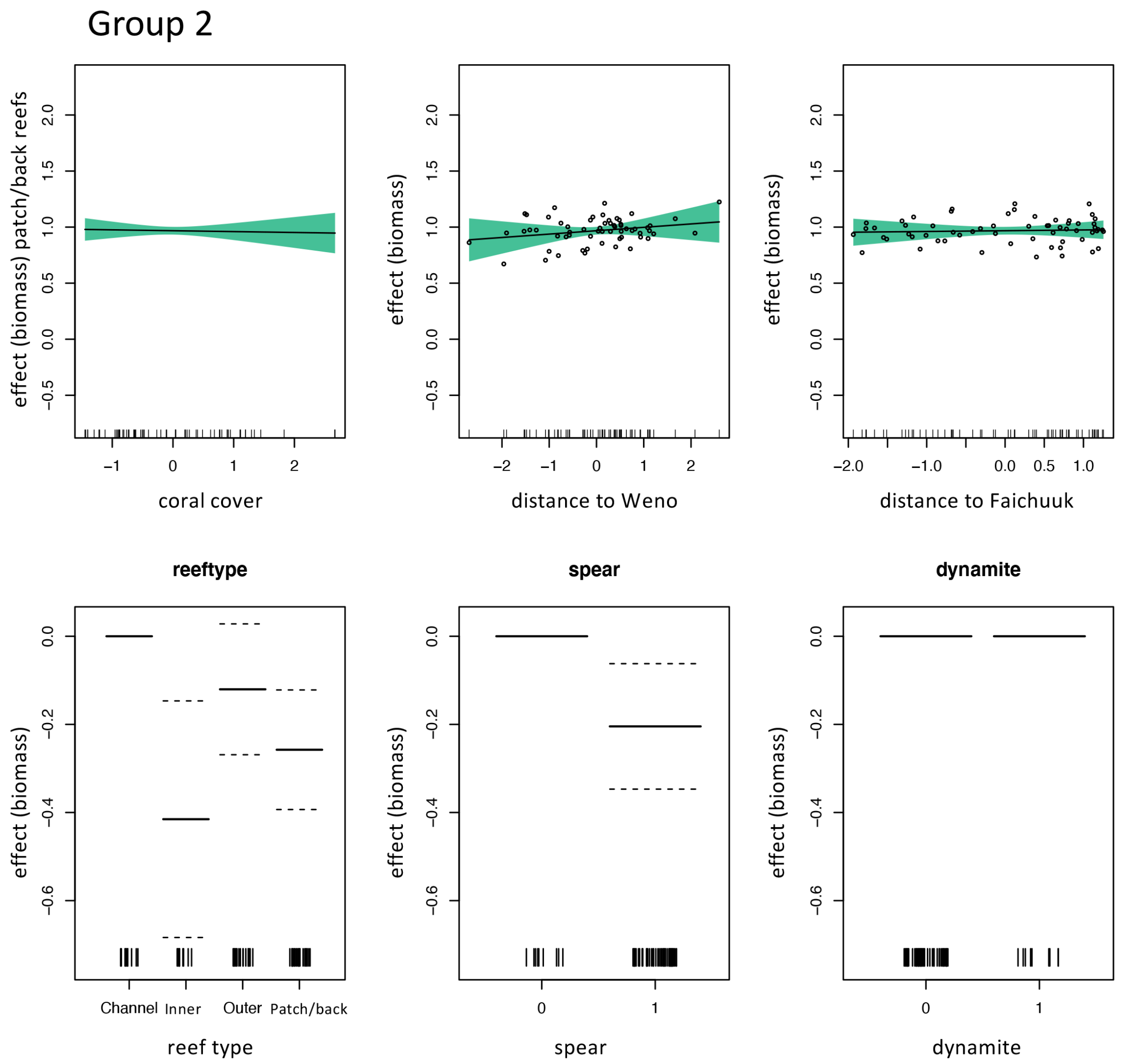

Figure A6. Partial effects plots (2 of 2) for all terms of GAM for trait group two: smaller, solitary benthic predators.

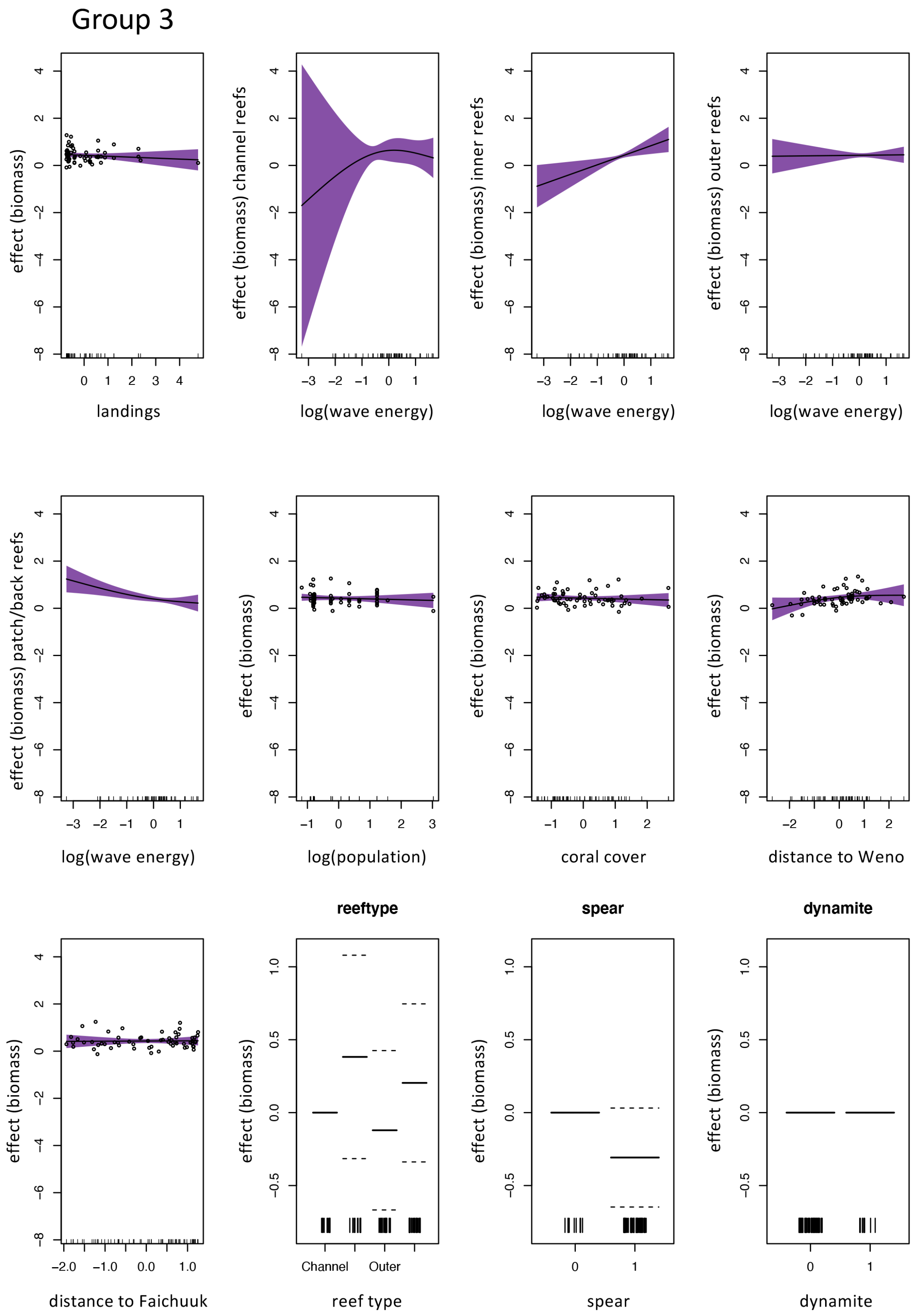

Figure A7. Partial effects plots for all terms of GAM for trait group three: reef pelagic, schooling/grouping planktivores.

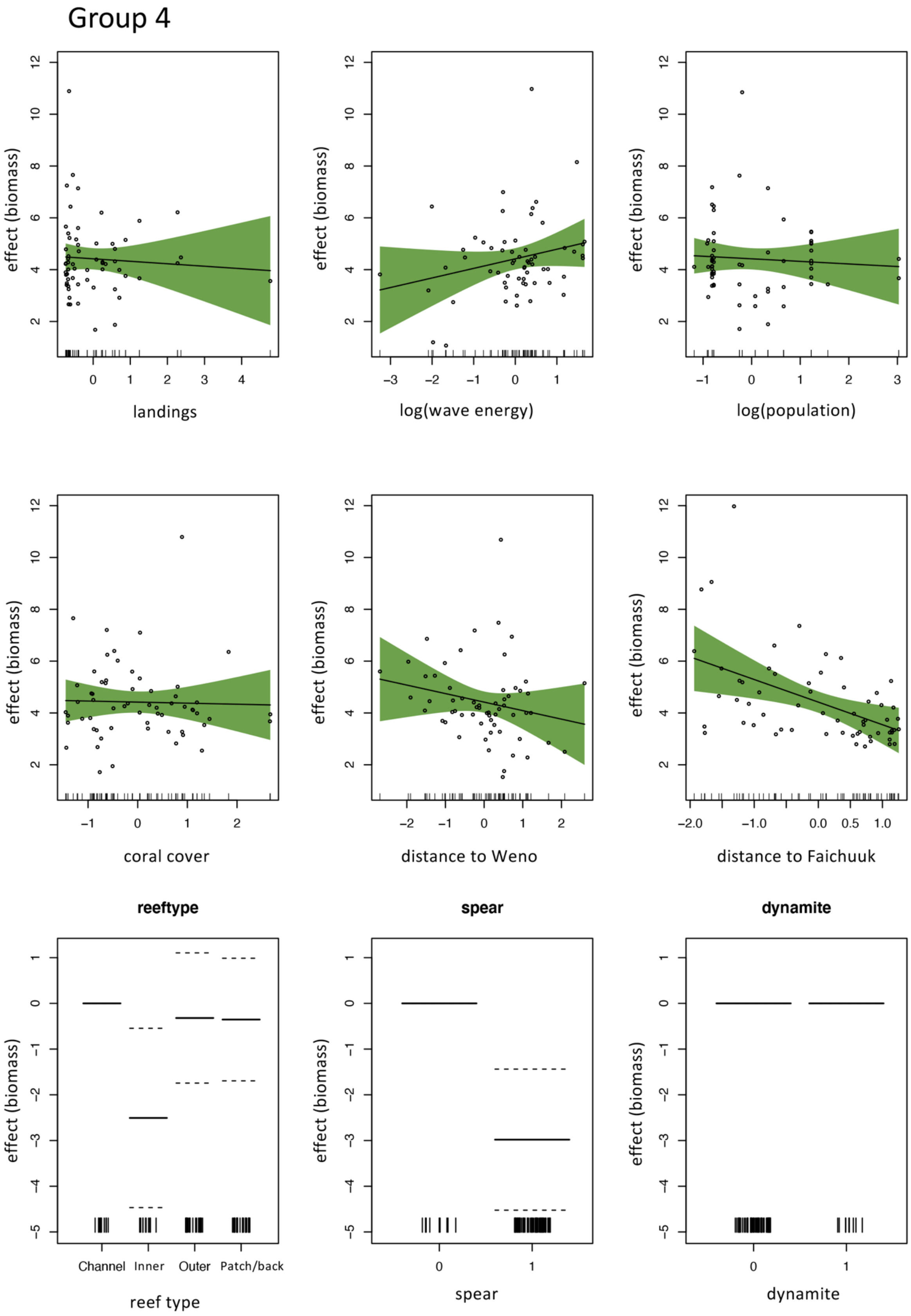

Figure A8. Partial effects plots for all terms of GAM for trait group four: large, solitary upper benthic predators.

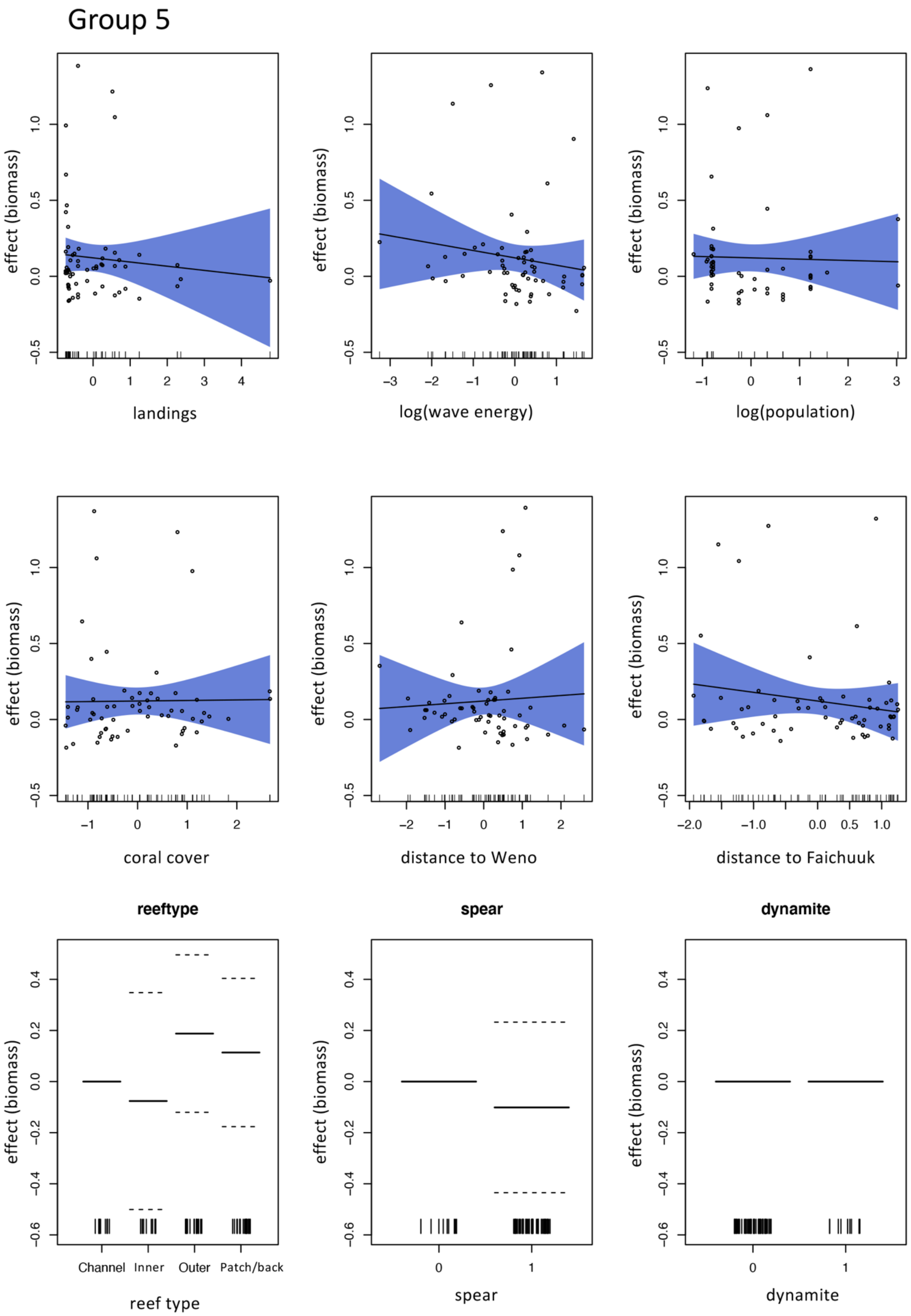

Figure A9. Partial effects plots for all terms of GAM for trait group five: large, pelagic schooling and grouping predators and piscivores.

A7. TBAM in Chuuk

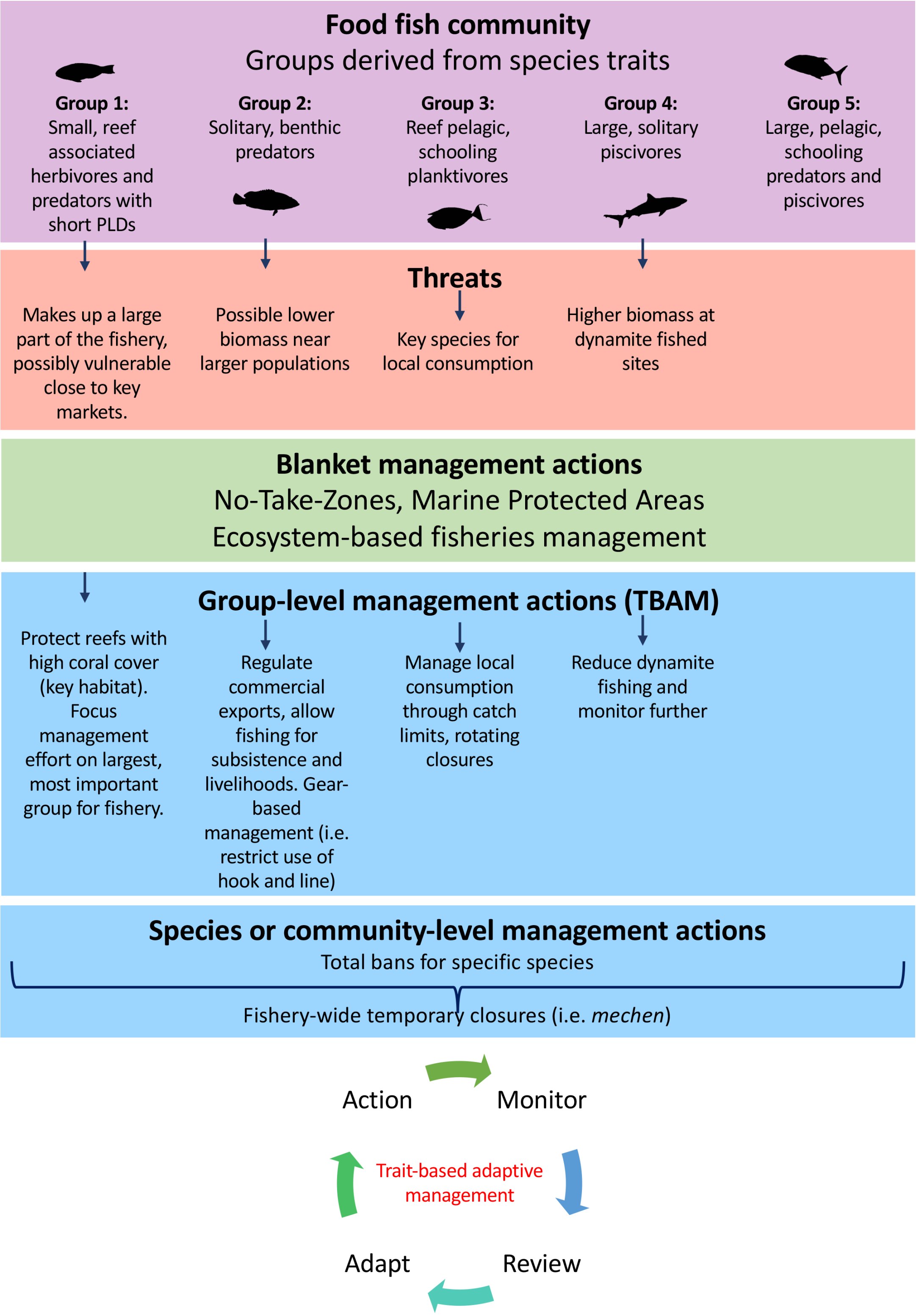

Figure A10. Schematic of trait based adaptive management for coral reef fisheries populated by the Chuuk food fish trait groups. Actions are broad suggestions based on the outcome of this study to demonstrate how TBAM could work in practice, rather than prescriptive recommendations.

References Appendix A

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Appendix B. Coral bleaching decouples linked coral and fish trait structure

B1. Study design

Table B1. Summary of reef types represented by site surveys in 2016 and 2019.

Reef Type	Count 2016 (n = 75)	Percentage 2016	Count 2019 (n = 39)	Percentage 2019
Channel	14	18.67 %	9	23.08 %
Patch	26	34.67 %	11	28.21 %
Inner	10	13.33 %	7	17.95 %
Outer	25	33.33 %	12	30.76 %

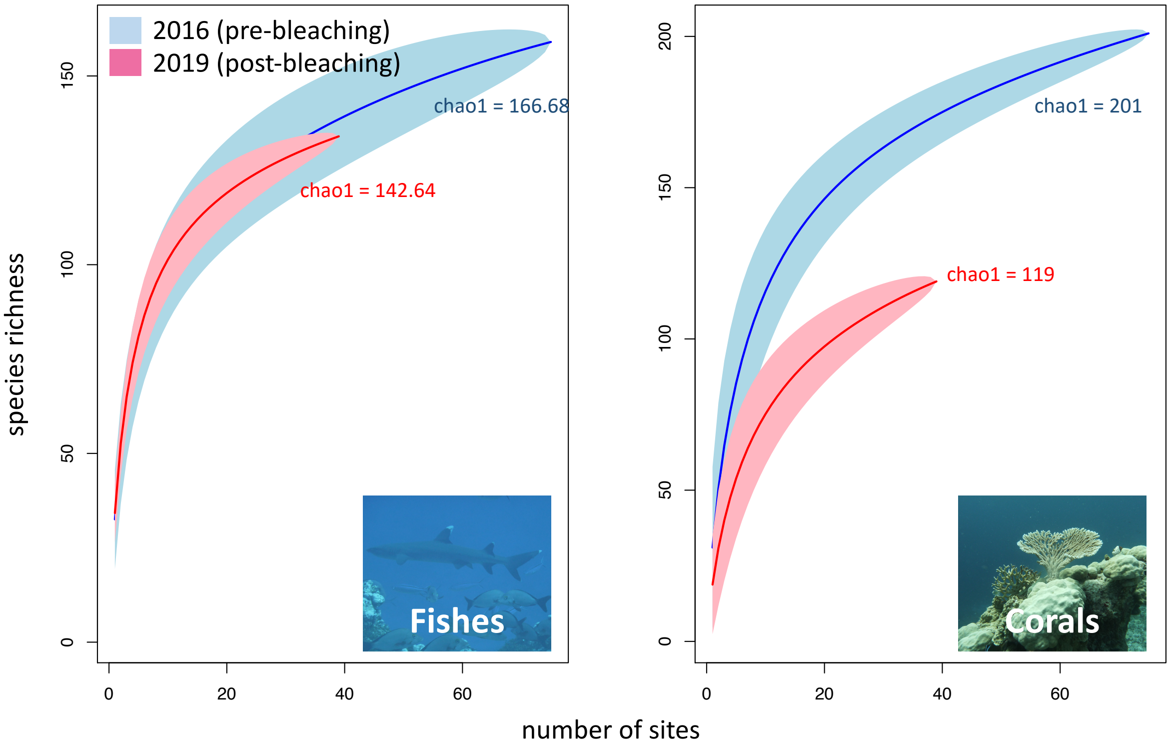


Figure B1. Species accumulation curves for fish (left) and coral (right) communities sampled in 2016 (75 sites, blue) and 2019 (39 sites, red). Curves show the expected (mean) species richness and labelled Chao 1 species richness values (Chao, 1984, Vavrek, 2011).

Table B2. Number of species and trait coverage for coral (187 species) and fish (161 species) assemblages.

	Trait	Number of species covered	% trait coverage
Corals	Growth Form	184	98.41
	Larval Development Mode	177	94.65
	Growth rate (mm/yr^{-1})	67	35.83
	Bleaching Susceptibility	102	54.55
	Maximum Depth (m)	187	100.00
Fish	Maximum Length (cm)	161	100.00
	Maximum Depth (m)	159	98.76
	Mean pelagic larval duration (days)	150	93.17
	Trophic Mode	160	100.00
	Position in the water column	161	100.00

B2. Coral and fish abundances

Table B3. PERMANOVAs for coral and fish assemblage abundances. Model: log abundance ~ reef type * year * area. Number of permutations = 999. (Marginal effects of interactions p > 0.05).

	Factor	R2	F	*p*
Corals	Reef Type	0.153	7.146	< 0.001
	Year	0.047	6.895	< 0.001
	Area	0.029	4.258	<0.001
	Reef Type:Year:Area	0.008	1.148	0.281
Fishes	Reef Type	0.146	6.563	< 0.001
	Year	0.023	3.118	< 0.001
	Area	0.019	2.603	0.002
	Reef Type:Year:Area	0.005	0.621	0.906

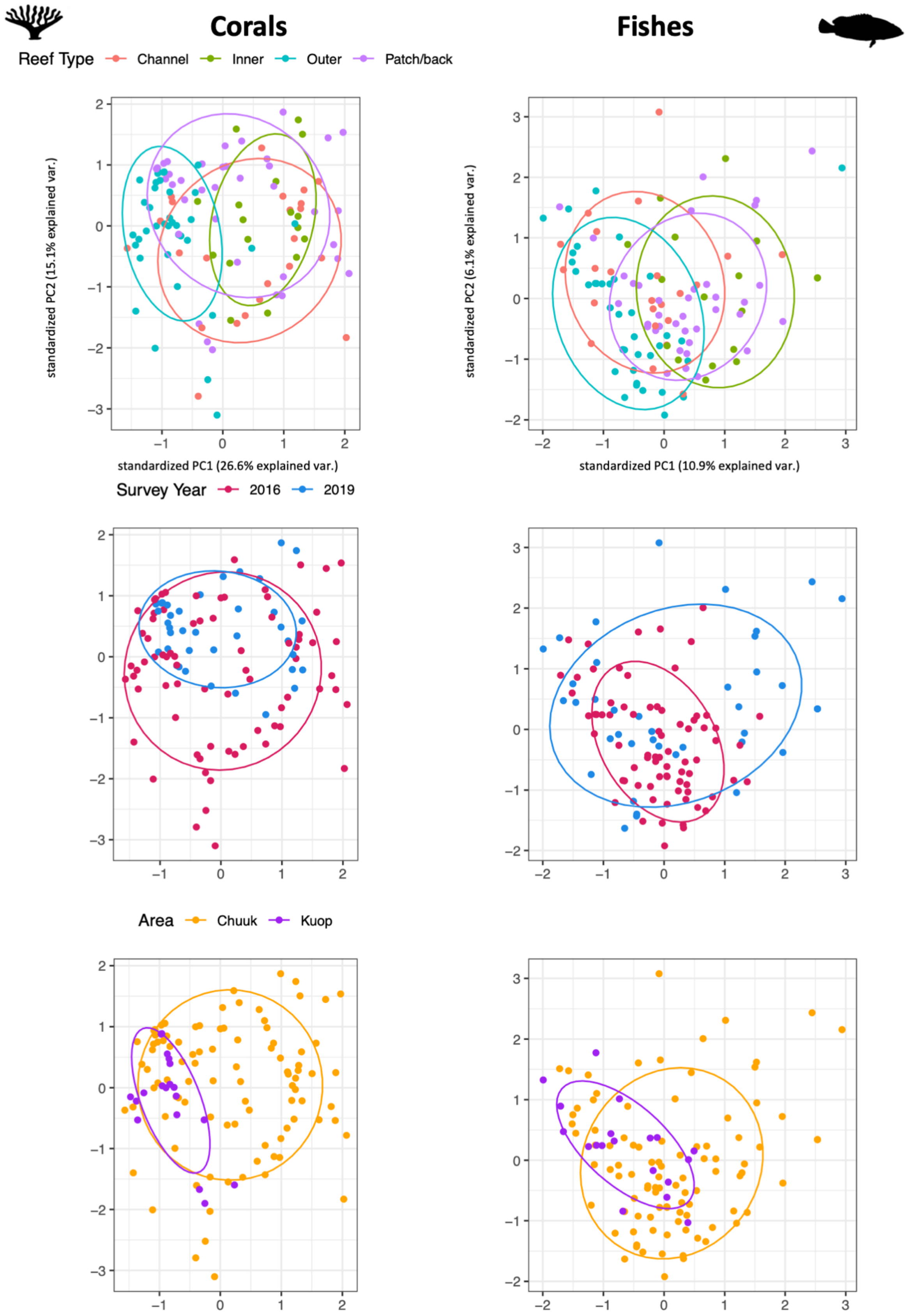


Figure B2. Principal component analysis (PCA) of coral (left) and fishes (right) log-transformed abundances, with ellipses for reef type, survey year and atoll (Chuuk or Kuop).

B3. Functional beta diversity

Table B4. Summary of year – to year change in functional beta diversity of coral and fish assemblages, 2016 – 2019.

	Min.	1st quartile	Median	Mean	3rd quartile	Max.
Coral	0.010	0.040	0.151	0.194	0.289	0.821
Fish	0.007	0.017	0.037	0.045	0.069	0.110

Table B5. Summary of among-site functional beta diversity of coral and fish assemblages in 2016 and 2019.

	Min.	1st quartile	Median	Mean	3rd quartile	Max.
Coral 2016	0.005	0.096	0.180	0.231	0.302	0.960
Coral 2019	0.001	0.069	0.141	0.196	0.300	0.712
Fish 2016	0.002	0.035	0.052	0.059	0.074	0.196
Fish 2019	0.004	0.036	0.058	0.060	0.083	0.137

B4. Results of SIMPER analyses

Table B6. Summary of SIMPER results for comparing the CWMs of corals and fishes across different reef types, and cumulative (%) contribution of each trait to within-group similarity (50% cut-off). Abbreviations: BL = bleaching, GF = growth form, TR = trophic, Pos = position in water column, Agg = aggregation, PLD = pelagic larval duration.

	Contrast	Trait	Contribution (%)	Cumulative Contribution (%)
Coral	patch/back vs. channel	BL susceptible	8.15	8.15
		GF digitate	7.98	16.13
		BL resistant	7.87	24.00
		Growth Rate	7.17	31.17
		Depth Lower	6.83	38.00
		GF branching closed	6.15	44.15
		GF encrusting long uprights	6.12	50.27
	patch/back vs. inner	GF encrusting long uprights	9.65	9.56
		BL susceptible	8.92	18.48
		BL resistant	8.33	26.81
		GF digitate	7.72	34.53
		Depth Lower	7.70	42.23
		Growth Rate	7.26	49.49
		GF massive	6.93	56.42
	patch/back vs. outer	GF massive	7.04	7.04
		Depth Lower	6.55	13.59
		Growth Rate	6.54	20.13
		GF encrusting	6.36	26.49

		BL susceptible	6.32	32.81
		larval mode spawner	6.02	38.83
		GF submassive	5.94	44.77
		larval mode brooder	5.92	50.69
	channel vs. inner	GF encrusting long uprights	9.67	9.67
		Depth Lower	8.93	18.60
		BL resistant	8.74	27.34
		GF digitate	8.11	35.45
		GF massive	7.72	43.17
		BL susceptible	7.57	50.74
	channel vs. outer	Growth Rate	7.78	7.78
		GF digitate	7.65	15.43
		GF massive	7.62	23.05
		GF corymbose	7.40	30.45
		larval mode brooder	7.11	37.56
		GF submassive	7.04	44.60
		GF laminar	7.02	51.62
	inner vs. outer	Depth Lower	8.41	8.41
		GF massive	7.87	16.28
		GF encrusting long uprights	7.46	23.74
		GF encrusting	7.43	31.17
		Growth Rate	7.26	38.43
		GF digitate	6.77	45.20
		GF laminar	6.00	51.20
Fish	patch/back vs. channel	Max Depth	5.96	5.96
		TR herbivore	5.83	11.79
		Pos benthic	5.74	17.53
		TR piscivore	5.71	23.24
		Pos reef pelagic	5.69	28.93
		Pos sub-benthic	5.62	34.55
		Agg pairs	5.58	40.13
		TR planktivore	5.47	45.60
		Max Length	5.40	51.00
	patch/back vs. inner	Agg schools	6.35	6.35
		Pos cnidarian associated	6.21	12.56
		TR predator	6.07	18.63
		Agg pairs	6.00	24.63
		Pos upper benthic	5.87	30.50
		TR herbivore	5.85	36.35
		Max Length	5.55	41.90
		Pos reef pelagic	5.31	47.21
		Max Depth	5.30	52.51
	patch/back vs. outer	Agg solitary	6.50	6.50
		Pos benthic	5.93	12.43
		Pos cnidarian associated	5.92	18.35
		TR omnivore	5.76	24.11
		Agg pairs	5.72	29.83
		TR detritivore	5.55	35.38

		Max Length	5.39	40.77
		PLD	5.33	46.10
		Agg groups	5.27	51.37
	channel vs. inner	Agg schools	6.93	6.93
		Pos upper benthic	5.90	12.83
		Agg solitary	5.85	18.68
		Agg pairs	5.76	24.44
		TR piscivore	5.40	29.84
		TR herbivore	5.28	35.12
		Agg groups	5.21	40.33
		TR predator	5.21	45.54
		Pos benthic	5.14	50.68
	channel vs. outer	TR detritivore	6.52	6.52
		Agg groups	6.18	12.70
		Pos sub benthic	6.10	18.80
		TR planktivore	5.88	24.68
		TR herbivore	5.74	30.42
		TR piscivore	5.60	36.02
		PLD	5.48	41.50
		Pos benthic	5.46	46.96
		Pos upper benthic	5.38	52.34
	inner vs. outer	Agg solitary	7.85	7.85
		Agg schools	7.31	15.16
		Agg pairs	5.90	21.06
		Pos upper benthic	5.55	26.61
		TR detritivore	5.51	32.12
		TR predator	5.45	37.57
		TR herbivore	5.40	42.97
		Agg groups	5.28	48.25
		Pos cnidarian asscociated	5.18	53.43

Table B7. Summary of SIMPER results comparing the CWMs of corals and fishes between 2016 and 2019, with cumulative (%) contribution of each trait to within-group similarity (50% cut-off). Abbreviations: BL = bleaching, GF = growth form, TR = trophic, Pos = position in water column, Agg = aggregation, PLD = pelagic larval duration.

2016:2019	**Trait**	**Contribution (%)**	**Cumulative Contribution (%)**
Coral	BL resistant	7.17	7.17
	Growth Rate	7.12	14.29
	GF encrusting	7.04	21.33
	GF digitate	7.02	28.35
	GF massive	6.90	35.25
	Depth Lower	6.88	42.13
	BL susceptible	6.87	49.00
	GF branching closed	5.87	54.87

Fish	Pos reef pelagic	5.65	5.65
	TR planktivore	5.56	11.21
	Agg schools	5.47	16.68
	Pos upper benthic	5.42	22.10
	Max Length	5.41	27.51
	PLD	5.38	32.89
	Agg groups	5.37	38.26
	TR predator	5.36	43.62
	Agg solitary	5.34	48.96
	TR omnivore	5.32	54.28

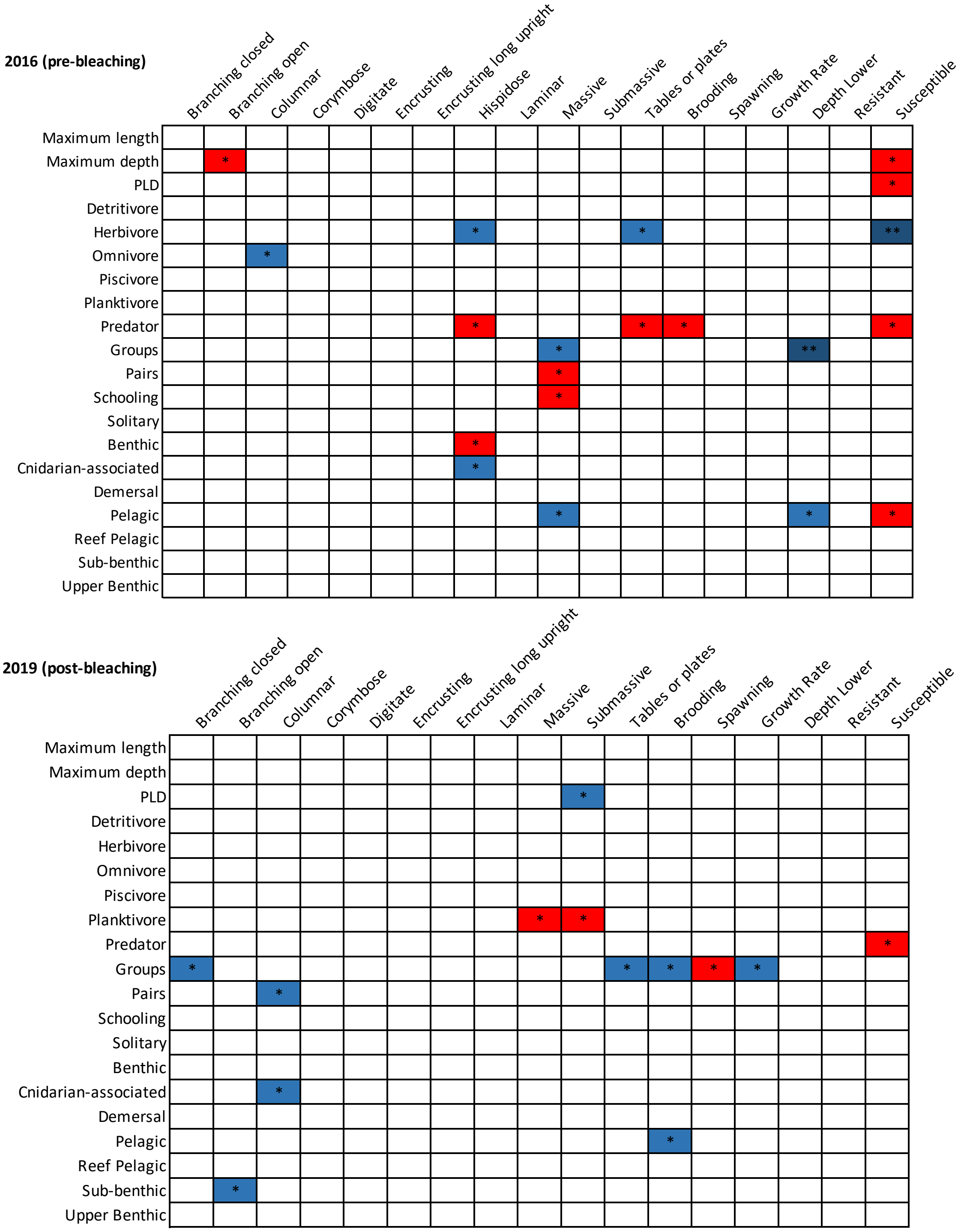
Table B8. Summary of SIMPER results for comparing the CWMs of corals and fishes between Chuuk Lagoon and Kuop Atoll, with cumulative (%) contribution of each trait to within-group similarity (50% cut-off). Abbreviations: BL = bleaching, GF = growth form, TR = trophic, Pos = position in water column, Agg = aggregation, PLD = pelagic larval duration.

Chuuk:Kuop	Trait	Contribution (%)	Cumulative Contribution (%)
Coral	GF encrusting	8.15	8.15
	Depth Lower	8.12	16.27
	GF submassive	7.21	23.48
	larval mode brooder	7.06	30.54
	GF corymbose	6.85	37.39
	GF laminar	6.74	44.13
	larval mode spawner	6.58	50.71
Fish	PLD	6.43	6.43
	TR herbivore	5.72	12.15
	TR piscivore	5.64	17.79
	Pos benthic	5.49	23.28
	Pos upper benthic	5.48	28.76
	Pos pelagic	5.48	34.24
	Agg groups	5.41	39.65
	Pos cnidarian associated	5.24	44.89
	Max Depth	5.21	50.10

B5. RLQ and fourth corner analyses

Table B9. Summary of the 2016 and 2019 RLQ analyses for Axes 1 and 2. Lists eigenvalues, % total co-inertia, and the ratio of inertia and coinertia for the three data matrices R (environment – coral CWM), L (fish traits) and Q (fish species abundance).

	2016		2019	
	Axis 1	Axis 2	Axis 1	Axis 2
eigenvalues decomposition	0.195	0.094	0.225	0.055
% total co-inertia	48.969	23.667	55.489	13.721
inertia and co-inertia R (env - coral)	0.844	0.838	0.835	0.768
inertia and co-inertia Q (fish trait)	0.720	0.752	0.656	0.729
correlation L (fish spp)	0.317	0.277	0.298	0.282



2016 (pre-bleaching)

	Branching closed	Branching open	Columnar	Corymbose	Digitate	Encrusting	Encrusting long upright	Hispidose	Laminar	Massive	Submassive	Tables or plates	Brooding	Spawning	Growth Rate	Depth Lower	Resistant	Susceptible
Maximum length																		
Maximum depth		🟥 *																🟥 *
PLD																		🟥 *
Detritivore																		
Herbivore								🟦 *				🟦 *						🟦 **
Omnivore			🟦 *															
Piscivore																		
Planktivore																		
Predator								🟥 *				🟥 *	🟥 *					🟥 *
Groups										🟦 *						🟦 **		
Pairs										🟥 *								
Schooling										🟥 *								
Solitary																		
Benthic								🟥 *										
Cnidarian-associated								🟦 *										
Demersal																		
Pelagic										🟦 *						🟦 *		🟥 *
Reef Pelagic																		
Sub-benthic																		
Upper Benthic																		

2019 (post-bleaching)

	Branching closed	Branching open	Columnar	Corymbose	Digitate	Encrusting	Encrusting long upright	Laminar	Massive	Submassive	Tables or plates	Brooding	Spawning	Growth Rate	Depth Lower	Resistant	Susceptible
Maximum length																	
Maximum depth																	
PLD										🟦 *							
Detritivore																	
Herbivore																	
Omnivore																	
Piscivore																	
Planktivore									🟥 *	🟥 *							
Predator																	🟥 *
Groups	🟦 *										🟦 *	🟦 *	🟥 *	🟦 *			
Pairs			🟦 *														
Schooling																	
Solitary																	
Benthic																	
Cnidarian-associated			🟦 *														
Demersal																	
Pelagic												🟦 *					
Reef Pelagic																	
Sub-benthic		🟦 *															
Upper Benthic																	

Figure B3. Fourth corner analysis of associations between coral (horizontal) and fish (vertical) traits from scaled, log-transformed community-weighted mean values in 2016 (top) and 2019 (bottom), adjusting to account for spatial autocorrelation. This figure is included to show core result (fewer associations in 2019) does not change when this correction is applied. Blue denotes a positive relationship, and red a negative one. *p<0.05, ** p<0.01.

References Appendix B

Chao, A. 1984. Nonparametric Estimation of the Number of Classes in a Population. *Scandinavian Journal of Statistics,* 11**,** 265-270.

Vavrek, M. J. 2011. fossil: palaeoecological and palaeogeographical analysis tools. *Palaeontologia Electronica,* 14**,** 1T.

Appendix C. Co-variation of fish and coral traits among distinct reef habitats

C1. Details of software and packages for analysis

Analysis was conducted in R version 4.0.3 (R Core Team, 2020) with (RStudio Team, 2016) using *ggplot2, indicspecies, vegan, ade4* and *FD* packages (Dray and Dufour, 2007, De Caceres and Legendre, 2009, Laliberté et al., 2014, Wickham, 2016, Oksanen et al., 2019).

C2. Selected traits

Table C1. Coral and fish traits, their types and definitions.

	Trait	Category	Type	Definition
Coral	Growth form	Morphological	Factor	The typical morphology of a species (Veron and Stafford-Smith, 2000). (branching closed, branching open, columnar, corymbose, digitate, encrusting, encrusting long uprights, hispidose, laminar, massive, submassive, tables/plates)
	Larval development mode	Reproductive	Factor	Brooders: Internal fertilisation, colonies release planular larvae. Spawners: Broadcast release of gametes. Fertilisation and development of planulae happens in water column.
	Growth rate (mm/yr)	Physiological	Numeric	Rate of yearly extension.
	Lower depth limit (m)	Ecological	Numeric	Maximum observed depth.
	Coral bleaching susceptibility	Physiological	Factor	Overall vulnerability to thermal stress (high or low) derived from assessments of sensitivity, adaptability and exposure for each species (Foden et al., 2013) (susceptible, resistant).
Fish	Maximum length (cm)	Morphological	Numeric	Maximum total length (cm) recorded in the species core range.
	Maximum depth (m)	Ecological	Numeric	Maximum depth, either observed or from expert opinion.
	Mean pelagic larval duration (PLD)	Reproductive	Numeric	Theoretical amount of time (days) that a larval fish can remain viable in the water column, measured from

				hatching or spawning.
	Trophic mode	Feeding ecology	Factor	Broad diet categories. (Piscivore, predator, planktivore, omnivore, detritivore, herbivore)
	Aggregation type	Behaviour	Factor (ordered)	Grouping behaviour. (schools, groups, pairs, solitary)
	Position in the water column	Behaviour	Factor	Location on reef where species spend most of their time. (Pelagic, reef pelagic, upper benthic, benthic, demersal, sub-benthic, cnidarian associated)

C3. Food versus non-food fish

Table C2. Species list and categorisation as food or non-food fish (n = 324).

Species	Category
Abudefduf sexfasciatus	other
Abudefduf vaigiensis	other
Acanthurus blochii	food
Acanthurus lineatus	food
Acanthurus maculiceps	food
Acanthurus mata	food
Acanthurus nigricans	food
Acanthurus nigricauda	food
Acanthurus nigrofuscus	food
Acanthurus olivaceus	food
Acanthurus thompsoni	food
Acanthurus triostegus	food
Acanthurus xanthopterus	food
Aethaloperca rogaa	food
Aetobatus narinari	other
Amblyeleotris sp.	other
Amblyglyphidodon aureus	other
Amblyglyphidodon curacao	other
Amblyglyphidodon leucogaster	other
Amblygobius nocturnus	other
Amphiprion chrysopterus	other
Amphiprion clarkii	other
Amphiprion melanopus	other
Amphiprion perideraion	other
Amphiprion sp.	other
Anampses geographicus	other
Anampses melanurus	other

Anampses meleagrides	other
Anampses twistii	other
Aphareus furca	food
Apolemichthys trimaculatus	other
Aprion virescens	food
Arothron nigropunctatus	other
Aulostomus chinensis	other
Balistapus undulatus	food
Balistoides conspicillum	food
Bodianus axillaris	other
Bodianus diana	other
Bodianus mesothorax	other
Bryaninops natans	other
Caesio caerulaurea	other
Caesio teres	other
Calotomus carolinus	food
Canthigaster amboinensis	other
Canthigaster janthinoptera	other
Canthigaster solandri	other
Canthigaster valentini	other
Carangoides plagiotaenia	food
Caranx lugubris	food
Caranx melampygus	food
Caranx papuensis	food
Carcharhinus albimarginatus	food
Carcharhinus amblyrhynchos	food
Carcharhinus melanopterus	food
Centropyge bicolor	other
Centropyge bispinosa	other
Centropyge flavissima	other
Centropyge heraldi	other
Centropyge loriculus	other
Centropyge vrolikii	other
Cephalopholis argus	food
Cephalopholis urodeta	food
Cetoscarus bicolor	food
Chaetodon auriga	other
Chaetodon bennetti	other
Chaetodon citrinellus	other
Chaetodon ephippium	other
Chaetodon kleinii	other
Chaetodon lunula	other

Chaetodon lunulatus	other
Chaetodon melannotus	other
Chaetodon mertensii	other
Chaetodon ornatissimus	other
Chaetodon punctatofasciatus	other
Chaetodon reticulatus	other
Chaetodon trifascialis	other
Chaetodon ulietensis	other
Chaetodon unimaculatus	other
Chaetodon vagabundus	other
Cheilinus fasciatus	food
Cheilinus trilobatus	food
Cheilinus undulatus	food
Cheilodipterus artus	other
Cheilodipterus isostigmus	other
Cheilodipterus macrodon	other
Cheilodipterus quinquelineatus	other
Chlorurus bleekeri	food
Chlorurus frontalis	food
Chlorurus japanensis	food
Chlorurus microrhinos	food
Chlorurus sordidus	food
Chromis acares	other
Chromis alpha	other
Chromis amboinensis	other
Chromis atripectoralis	other
Chromis atripes	other
Chromis caudalis	other
Chromis delta	other
Chromis lepidolepis	other
Chromis margaritifer	other
Chromis ternatensis	other
Chromis viridis	other
Chromis xanthochira	other
Chromis xanthura	other
Chrysiptera biocellata	other
Chrysiptera brownriggii	other
Chrysiptera glauca	other
Chrysiptera traceyi	other
Cirrhilabrus katherinae	other
Cirrhilabrus luteovittatus	other
Cirripectes variolosus	other

Coris aygula	food
Coris batuensis	food
Coris dorsomacula	food
Coris gaimard	food
Corythoichthys intestinalis	other
Ctenochaetus binotatus	other
Ctenochaetus cyanocheilus	food
Ctenochaetus flavicauda	food
Ctenochaetus striatus	food
Ctenogobiops feroculus	other
Ctenogobiops spp.	other
Dascyllus aruanus	other
Dascyllus reticulatus	other
Dascyllus trimaculatus	other
Diodon hystrix	other
Echeneis naucrates	food
Ecsenius bandanus	food
Ecsenius bicolor	food
Elagatis bipinnulata	food
Epibulus insidiator	food
Epinephelus fuscoguttatus	food
Epinephelus howlandi	food
Epinephelus maculatus	food
Epinephelus merra	food
Epinephelus tauvina	food
Eviota sebreei	other
Eviota sp.	other
Forcipiger flavissimus	other
Forcipiger longirostris	other
Fusigobius signipinnis	other
Gnathanodon speciosus	food
Gnathodentex aureolineatus	food
Gnatholepis cauerensis	other
Gnatholepis sp.	other
Gomphosus varius	other
Gracila albomarginata	food
Grammatorcynus bilineatus	food
Gunnellichthys pleurotaenia	other
Gymnothorax flavimarginatus	other
Halichoeres biocellatus	other
Halichoeres chrysus	other
Halichoeres hortulanus	other

Halichoeres marginatus	other
Halichoeres melanurus	other
Halichoeres richmondi	other
Hemigymnus fasciatus	food
Hemigymnus melapterus	food
Hemitaurichthys polylepis	other
Heniochus acuminatus	other
Heniochus chrysostomus	other
Heniochus monoceros	other
Heniochus singularius	other
Heniochus varius	other
Hipposcarus longiceps	food
Hoplolatilus cuniculus	other
Istigobius rigilius	other
Koumansetta hectori	other
Koumansetta rainfordi	other
Kyphosus cinerascens	food
Kyphosus vaigiensis	food
Labrichthys unilineatus	other
Labroides bicolor	other
Labroides dimidiatus	other
Labroides pectoralis	other
Labropsis micronesica	other
Labropsis xanthonota	other
Lethrinus erythracanthus	food
Lethrinus erythropterus	food
Lethrinus harak	food
Lethrinus olivaceus	food
Lethrinus xanthochilus	food
Lutjanus argentimaculatus	food
Lutjanus bohar	food
Lutjanus fulvus	food
Lutjanus gibbus	food
Lutjanus kasmira	food
Lutjanus monostigma	food
Lutjanus semicinctus	food
Macolor macularis	food
Macolor niger	food
Macropharyngodon meleagris	other
Malacanthus brevirostris	other
Malacanthus latovittatus	other
Meiacanthus atrodorsalis	other

Melichthys vidua	food
Monotaxis grandoculis	food
Mulloidichthys vanicolensis	food
Myripristis adusta	food
Myripristis amaena	food
Myripristis berndti	food
Myripristis murdjan	food
Myripristis sp.	food
Naso annulatus	food
Naso brevirostris	food
Naso caesius	food
Naso hexacanthus	food
Naso lituratus	food
Naso thynnoides	food
Naso unicornis	food
Naso vlamingii	food
Nectamia bandanensis	other
Nemateleotris magnifica	other
Odonus niger	food
Ostorhinchus nigrofasciatus	other
Ostorhinchus novemfasciatus	other
Oxycheilinus arenatus	other
Oxycheilinus digramma	other
Oxycheilinus unifasciatus	other
Paracirrhites arcatus	other
Paracirrhites forsteri	other
Parapercis clathrata	other
Parapercis sp.	other
Parupeneus barberinoides	food
Parupeneus barberinus	food
Parupeneus cyclostomus	food
Parupeneus multifasciatus	food
Parupeneus trifasciatus	food
Pempheris oualensis	other
Pentapodus caninus	other
Plagiotremus laudandus	other
Plagiotremus rhinorhynchos	other
Plagiotremus tapeinosoma	other
Platax orbicularis	other
Platax teira	other
Plectorhinchus albovittatus	food
Plectorhinchus lineatus	food

Plectorhinchus vittatus	food
Plectroglyphidodon dickii	other
Plectroglyphidodon johnstonianus	other
Plectroglyphidodon lacrymatus	other
Plectropomus areolatus	food
Plectropomus laevis	food
Plectropomus leopardus	food
Plectropomus oligacanthus	food
Pomacanthus imperator	other
Pomacanthus xanthometopon	other
Pomacentrus bipunctatus	other
Pomacentrus coelestis	other
Pomacentrus grammorhynchus	other
Pomacentrus pavo	other
Pomacentrus sp.	other
Pomacentrus vaiuli	other
Pomachromis exilis	other
Pseudanthias bartlettorum	other
Pseudanthias pascalus	other
Pseudobalistes flavimarginatus	food
Pseudocheilinus evanidus	other
Pseudocheilinus hexataenia	other
Pteragogus cryptus	other
Ptereleotris evides	other
Ptereleotris heteroptera	other
Pterocaesio marri	other
Pterocaesio tessellata	other
Pterocaesio tile	other
Pterocaesio trilineata	other
Pygoplites diacanthus	other
Salarias fasciatus	other
Sargocentron spiniferum	food
Sargocentron tiere	food
Scarus altipinnis	food
Scarus dimidiatus	food
Scarus festivus	food
Scarus flavipectoralis	food
Scarus forsteni	food
Scarus frenatus	food
Scarus ghobban	food
Scarus globiceps	food

Scarus niger	food
Scarus oviceps	food
Scarus psittacus	food
Scarus rivulatus	food
Scarus rubroviolaceus	food
Scarus schlegeli	food
Scarus spinus	food
Scarus tricolor	food
Scolopsis lineata	food
Scomberomorus commerson	other
Siganus argenteus	food
Siganus doliatus	food
Siganus puellus	food
Siganus punctatissimus	food
Siganus punctatus	food
Siganus vulpinus	food
Sphaeramia nematoptera	other
Stegastes fasciolatus	other
Stegastes nigricans	other
Stethojulis bandanensis	other
Stethojulis strigiventer	other
Stethojulis trilineata	other
Sufflamen bursa	food
Sufflamen chrysopterum	food
Sufflamen fraenatum	food
Synodus dermatogenys	other
Synodus variegatus	other
Thalassoma amblycephalum	other
Thalassoma hardwicke	other
Thalassoma jansenii	other
Thalassoma lunare	other
Thalassoma lutescens	other
Thalassoma purpureum	other
Thalassoma quinquevittatum	other
Thalassoma trilobatum	other
Triaenodon obesus	food
Valenciennea muralis	other
Valenciennea sexguttata	other
Valenciennea strigata	other
Variola louti	food
Xanthichthys auromarginatus	food
Zanclus cornutus	other

Zebrasoma flavescens	other
Zebrasoma scopas	other
Zebrasoma velifer	other
Zoramia fragilis	other

C4. Ordinations of coral and fish assemblages

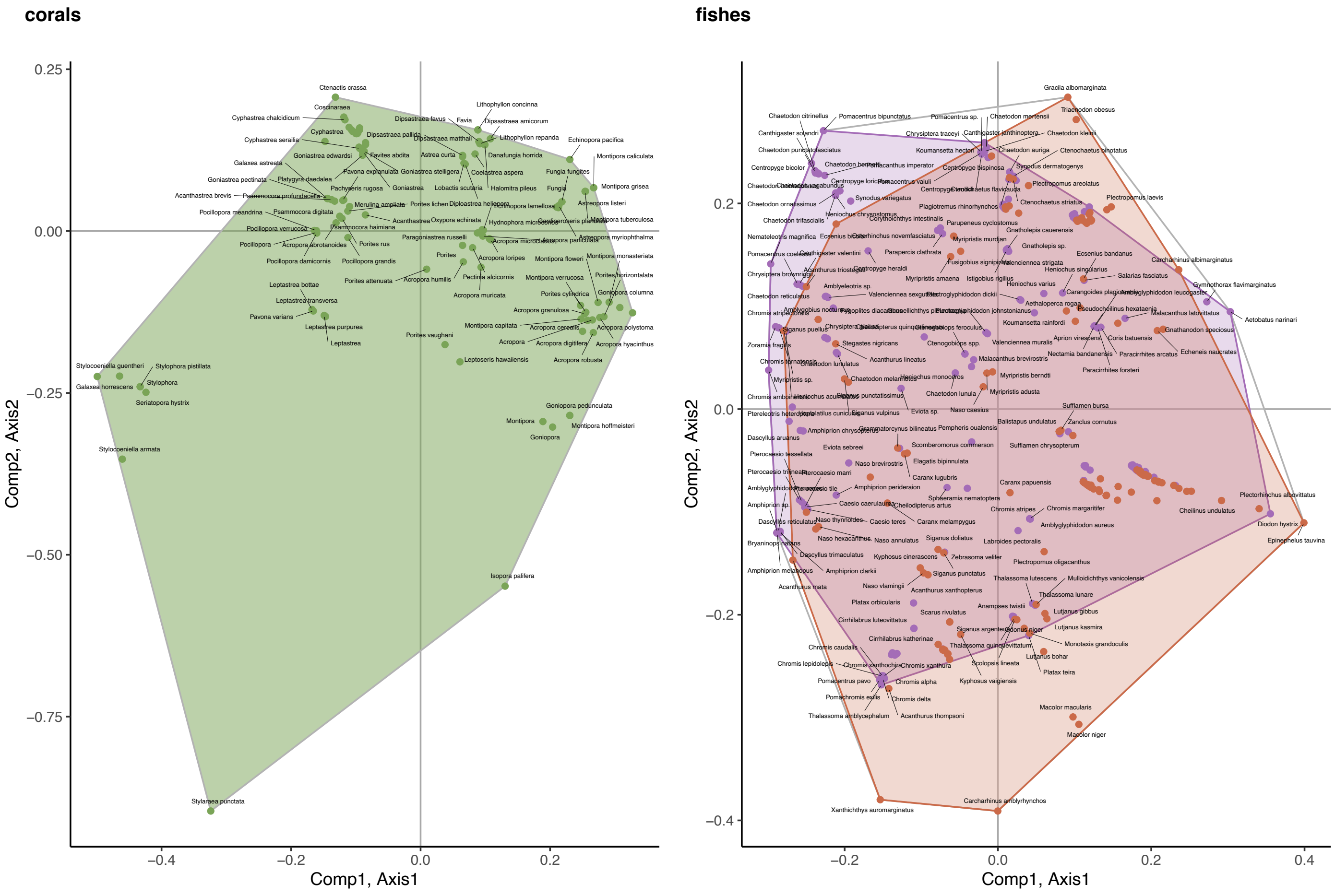


Figure C1. PCoAs of coral and fish community trait space (axes 1 and 2). Equivalent to Figure 2 in main text but includes species names.

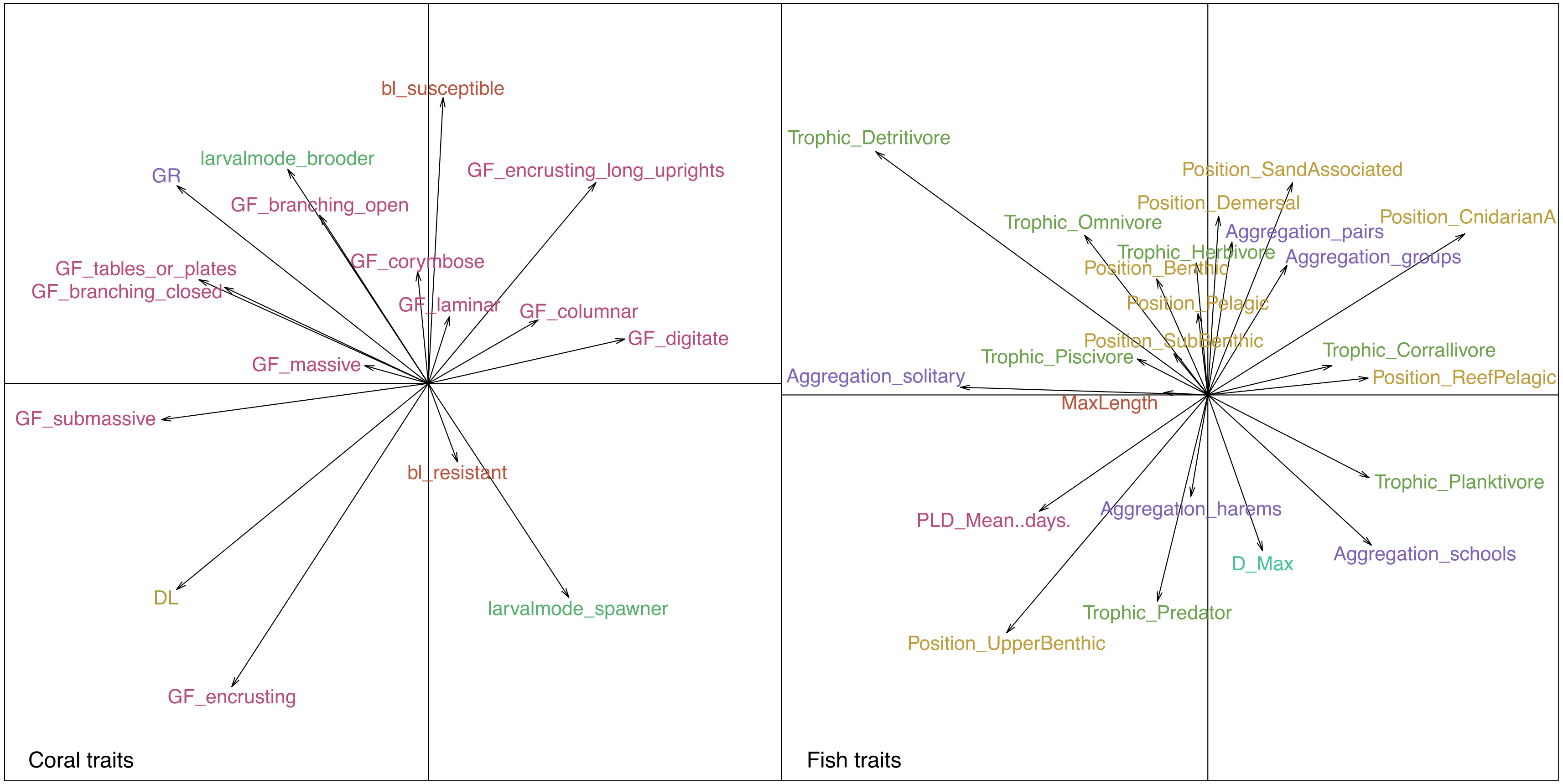


Figure C2. Canonical plots for coral (left) and fish (right) trait communities throughout Chuuk in 2019. Labels are colour coded by trait category (i.e., trophic modes in fish). Abbreviations: GR – growth rate, bl – bleaching, GF – growth form, DL – depth lower, PLD – pelagic larval duration. Arrows show associations between coral and fish traits.

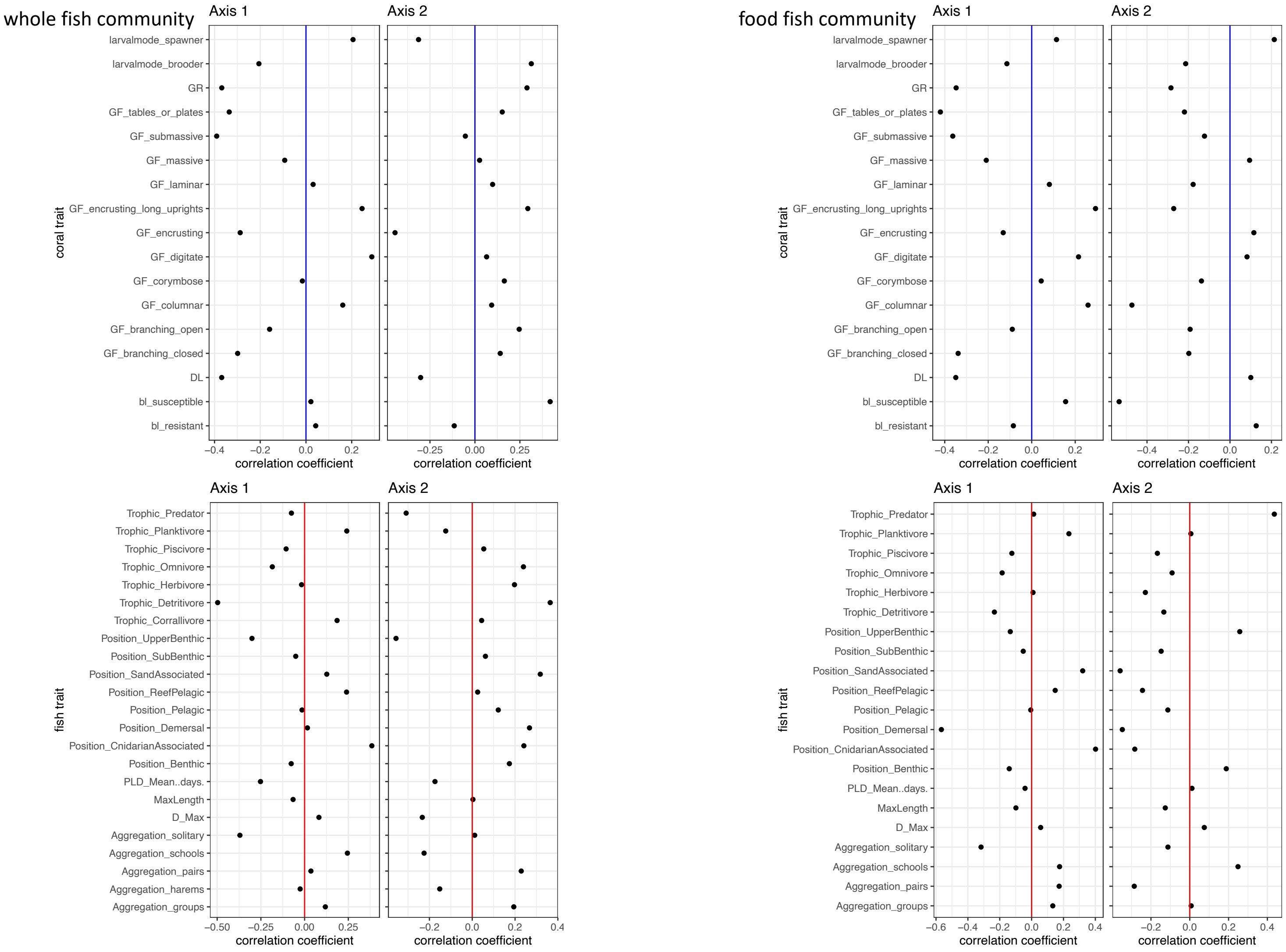


Figure C3. Axis loadings of coral and fish traits in the coinertia analysis for the whole fish community (left) and food fish community (right) throughout Chuuk in 2019.

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Appendix D. Changing trait community structure on the Great Barrier Reef

D1. GBRMPA zoning

Table D1. Details of factor classification of sites (n = 279) as fished (50.18%) or no-take-zone (NTZ) (49.82%) in disturbance models (Great Barrier Reef Marine Park Authority, 2004).

Name	Restrictions	NTZ/fished	No. sites
Buffer zone	Trolling for pelagic fish species is allowed. All other extractive activities including bottom fishing and spearfishing are prohibited.	Fished	2
Conservation Park Zone	Most extractive activities allowed, with additional restrictions for fishing.	Fished	30
Habitat Protection Zone	Trawling not permitted. Activities including spear and line fishing, netting allowed with some restrictions.	Fished	108
Marine National Park Zone	'No-take' area and extractive activities like fishing or collecting are not allowed without a permit.	NTZ	116
Preservation Zone	'No go' area. No access without written permission and extractive activities prohibited.	NTZ	10
Scientific Research Zone	For non-researchers, these are like Marine National Park Zones, where only non-extractive activities (i.e., swimming, snorkeling, and diving) are allowed without permission.	NTZ	13

D2. Coral and fish traits

Table D2. Selected coral traits, definitions, and summary of function.

Trait	Definition	Reef function
Growth form (factor)	Typical species morphology (Veron and Stafford-Smith, 2000).	Structural complexity, habitat provision, life history strategy (LHS), population dynamics (Darling et al., 2012, Darling et al., 2017, Denis et al., 2017, Carturan et al., 2018, Zawada et al., 2019).
Larval development mode (factor)	Mode of larval development. Can be brooder (internal	Connectivity, recovery, LHS and population dynamics (Darling et al., 2012, Darling et

	fertilisation, colonies release planular larvae) or spawner (broadcast release of gametes, fertilisation and development occurs in water column).	al., 2017, Carturan et al., 2018, Hughes et al., 2018).
Growth rate (mm/yr) (numeric)	Rate of yearly extension	Accretion, recovery, habitat provisioning (Darling et al., 2012, Darling et al., 2017, Carturan et al., 2018, Hughes et al., 2018, McWilliam et al., 2020).
Depth lower (m) (numeric)	Maximum observed depth	LHS, population dynamics (Darling et al., 2012).
Maximum corallite width (mm) (numeric)	Typical maximum corallite width, axial corallite width or valley size.	Filter feeding and nutrient capture (Hughes et al., 2018, McWilliam et al., 2020).

Table D3. Selected fish traits, definitions, and summary of function.

Trait	Definition	Reef function
Maximum length (cm) (numeric)	Maximum length recorded in core range	Predation vulnerability, fecundity, thermal resistance, metabolic rates, extinction risk (Graham et al., 2011, Beauchard et al., 2017).
Mean pelagic larval duration (PLD) (days) (numeric)	Theoretical time larval fish remains viable in water column from hatching/spawning.	Connectivity, recovery (Lester and Ruttenberg, 2005, Wilson et al., 2018).
Trophic mode (factor)	Broad diet categories	Nutrient cycling, demographics (Graham et al., 2011, Beauchard et al., 2017).
Aggregation type (factor - ordered)	Grouping behaviour	Foraging, predation vulnerability (Plass-Johnson et al., 2016).
Position in the water column (factor)	Where on a reef species spends most of its time	Foraging, dispersal, motility (Stuart-Smith et al., 2013, Beauchard et al., 2017).
Spawning mode (factor)	Type of spawning behaviour	Life history strategy and population dynamics (Villéger et al., 2017).
Species Generalisation Index (SGI) (numeric)	Estimation of niche breadth. From Stuart-Smith et al. 2021.	Habitat association, disturbance vulnerability (Stuart-Smith et al., 2021).

D3. Ordinations of coral and fish assemblages

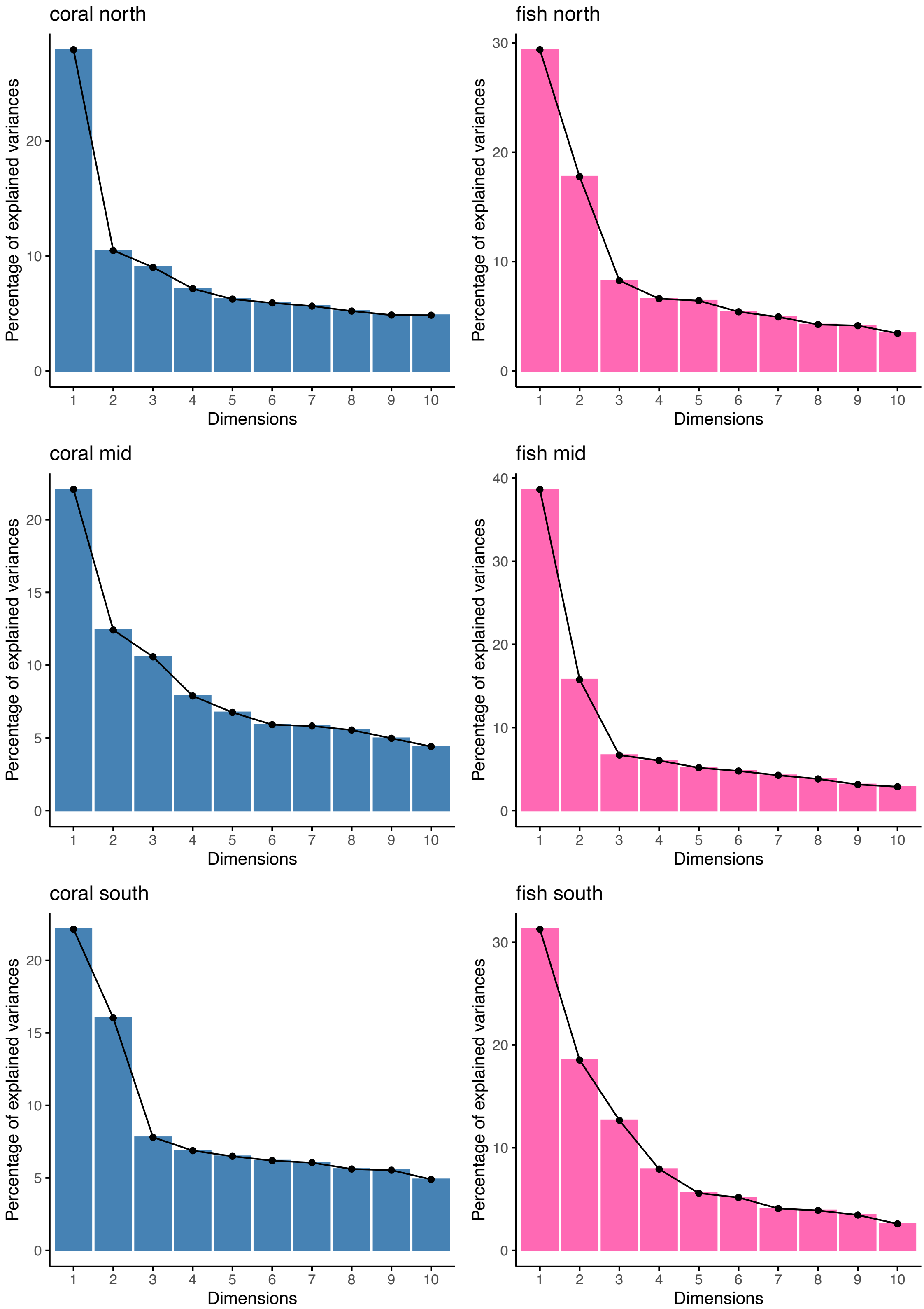

Figure D1. Screeplot of eigenvalues (percentage variance explained by each principal component) for each coral and fish PCA of community-weighted means.

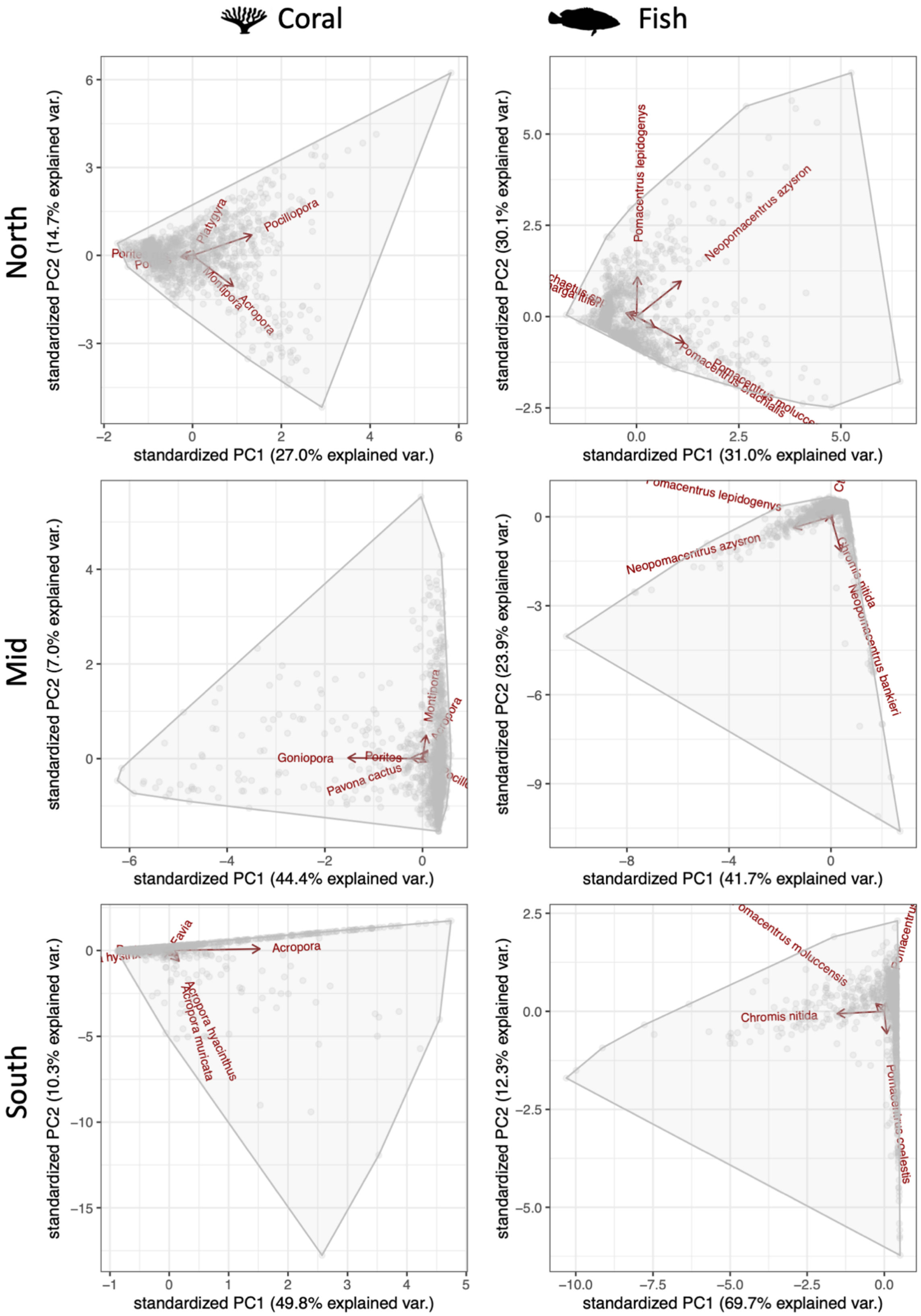

Figure D2. PCA (first two axes) of log-transformed coral and fish abundances across the North, Mid and Southern GBR. Four most influential genera/species from PCA axes 1 and 2 shown only.

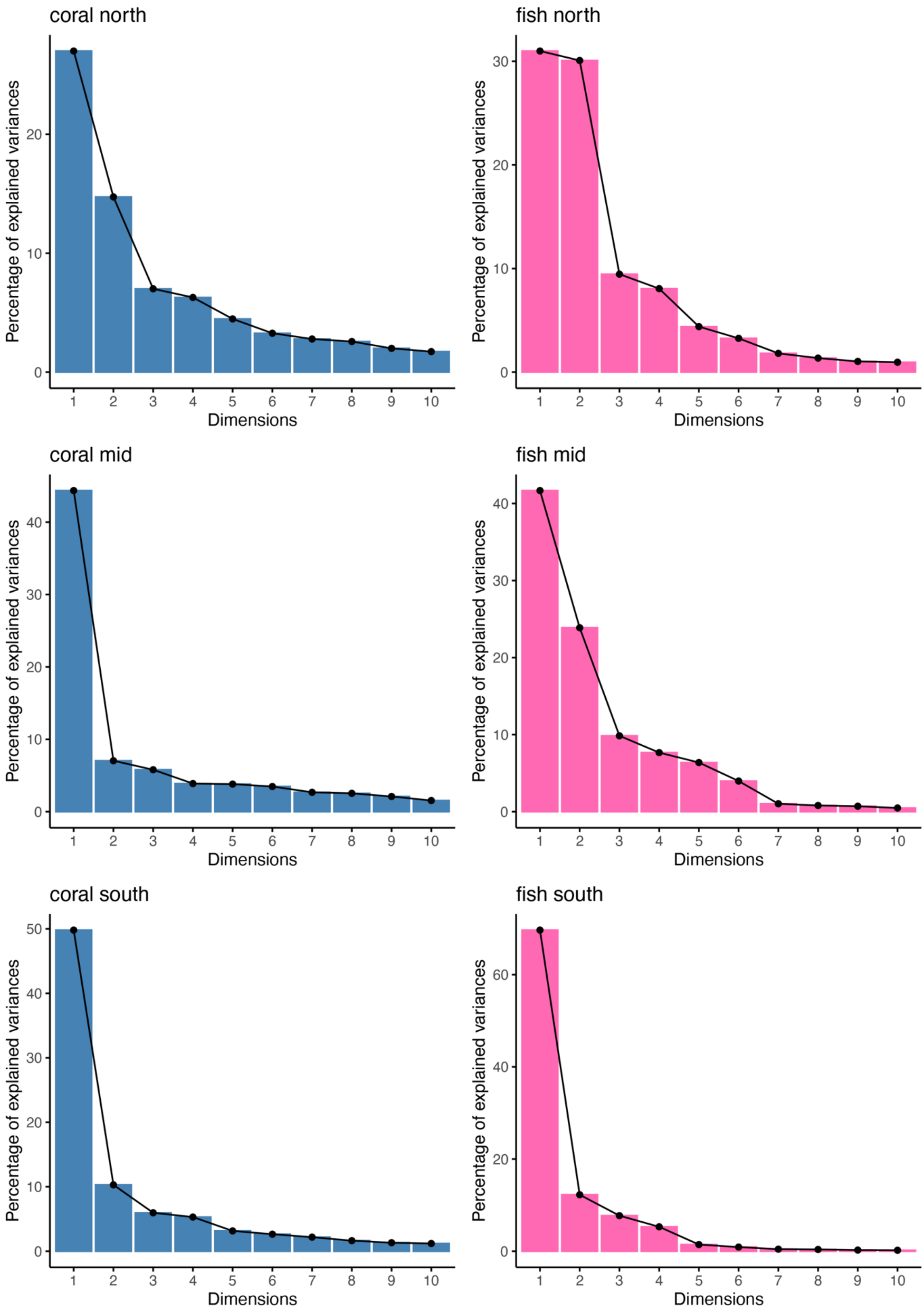

Figure D3. Screeplot of eigenvalues (percentage variance explained by each principal component) for each coral and fish abundance PCA.

Table D4. Summary of the north, mid and south RLQ analyses for Axes 1 and 2. Lists eigenvalues, % total co-inertia (variance explained), and the ratio of inertia and coinertia for the three data matrices R (environment – mean coral CWM/year), L (fish traits) and Q (mean fish species abundance/year). Permutation tests n = 999.

	NORTH		MID		SOUTH	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
eigenvalues decomposition	0.086	0.007	0.196	0.014	0.156	0.009
% total co-inertia (var. explained)	84.442	7.035	90.425	6.557	89.257	4.882
inertia & co-inertia R (env - coral)	4.577	8.120	4.929	7.365	7.221	8.474
inertia and co-inertia Q (fish trait)	2.744	4.770	2.335	4.873	1.816	4.015
correlation L (fish spp)	0.083	0.032	0.130	0.048	0.109	0.056
Permutation test model 2	p<0.001		p<0.001		p<0.001	
Permutation test model 4	p<0.001		p<0.001		p=0.008	

D4. Coral and fish community weighted mean visualisations

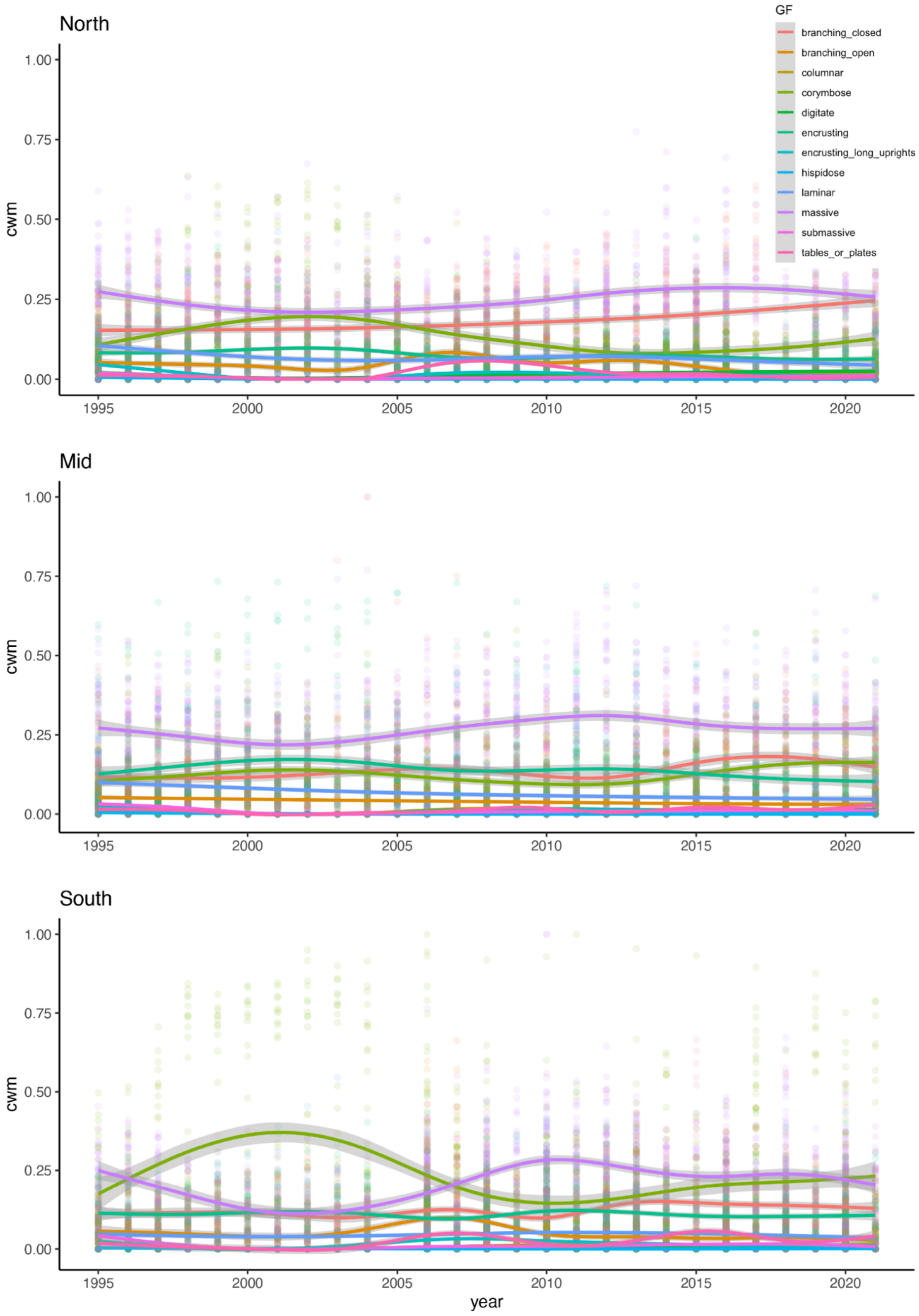

Figure D4. Distribution of CWM of coral growth forms visualised with GAM smooths in the North, Mid and Southern GBR, 1995 – 2021.

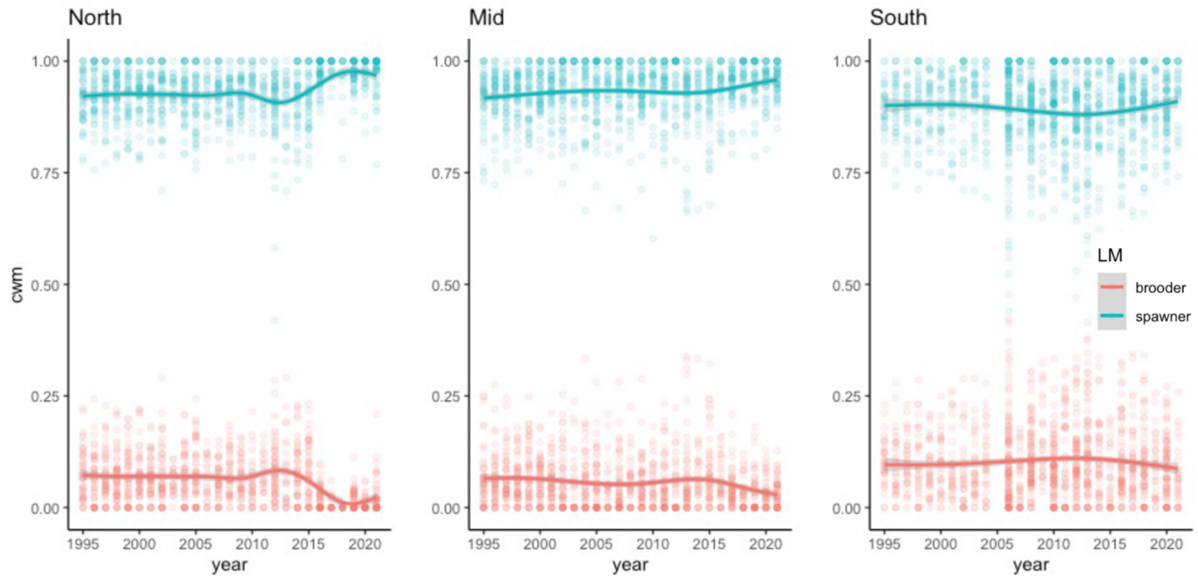

Figure D5. Distribution of coral larval development mode (brooding or spawning) visualised with GAM smooths in the North, Mid and Southern GBR, 1995 – 2021.

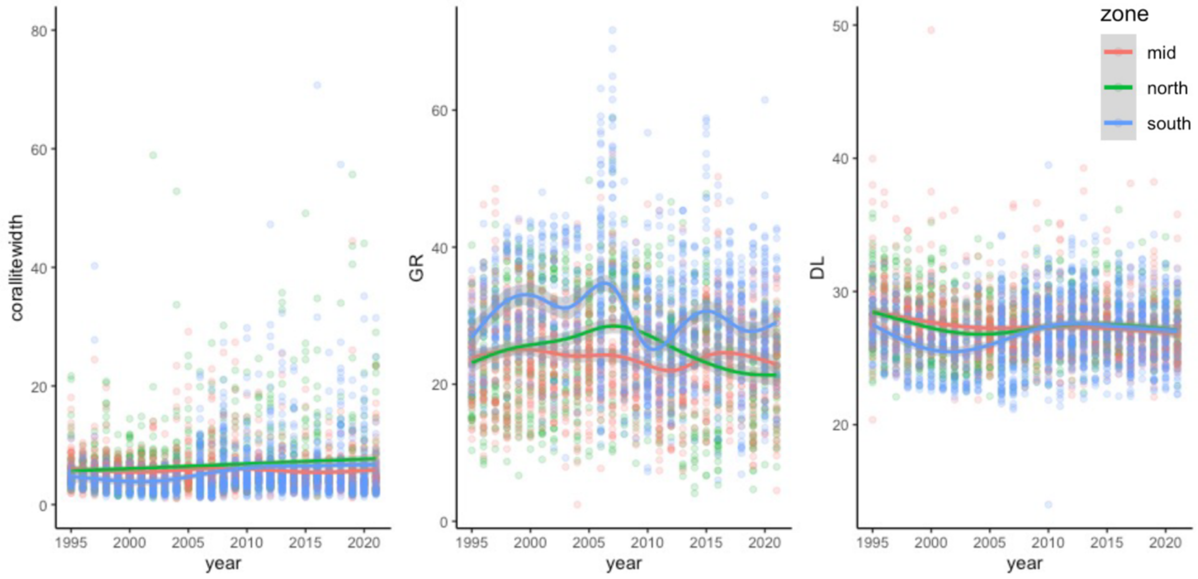

Figure D6. Distribution of continuous coral trait CWMs (corallite width, growth rate (GR) and depth lower (DL)) visualised with GAM smooths in the North, Mid and Southern GBR, 1995 – 2021.

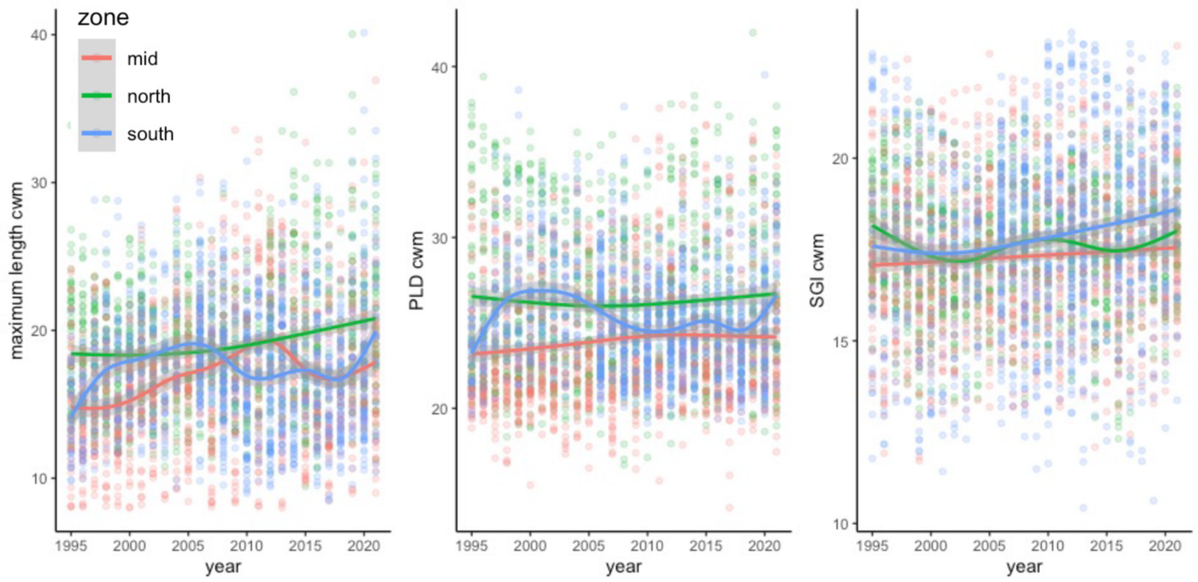

Figure D7. Distribution of continuous fish trait CWMs maximum length, pelagic larval duration (PLD) and species generalisation index (SGI) visualised with GAM smooths in the North, Mid and Southern GBR, 1995 – 2021.

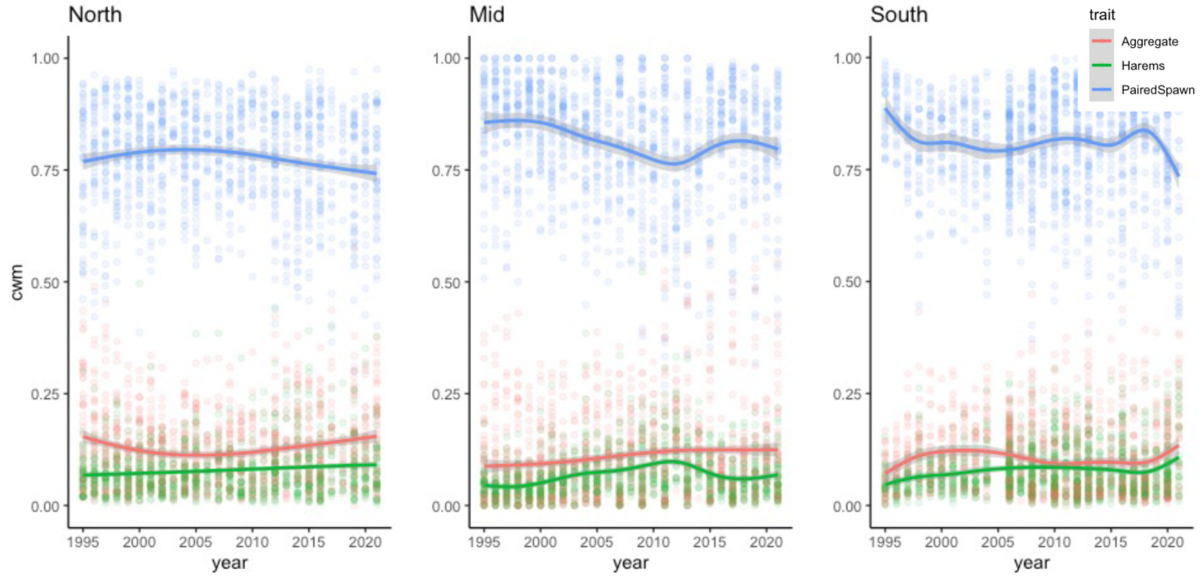

Figure D8. Distribution of CWM of fish spawning modes visualised with GAM smooths in the North, Mid and Southern GBR, 1995 – 2021.

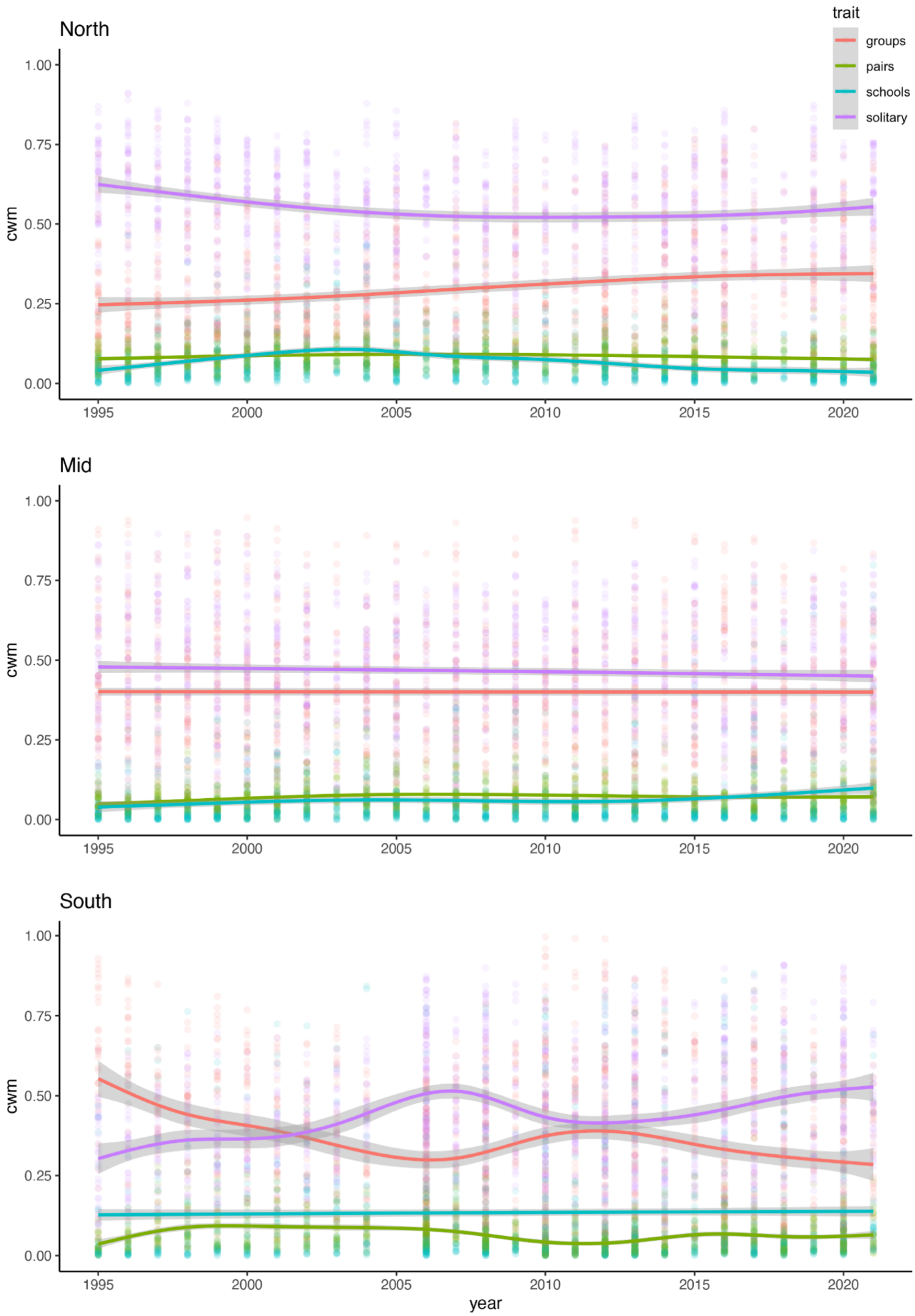

Figure D9. Distribution of CWM of fish aggregation types visualised with GAM smooths in the North, Mid and Southern GBR, 1995 – 2021.

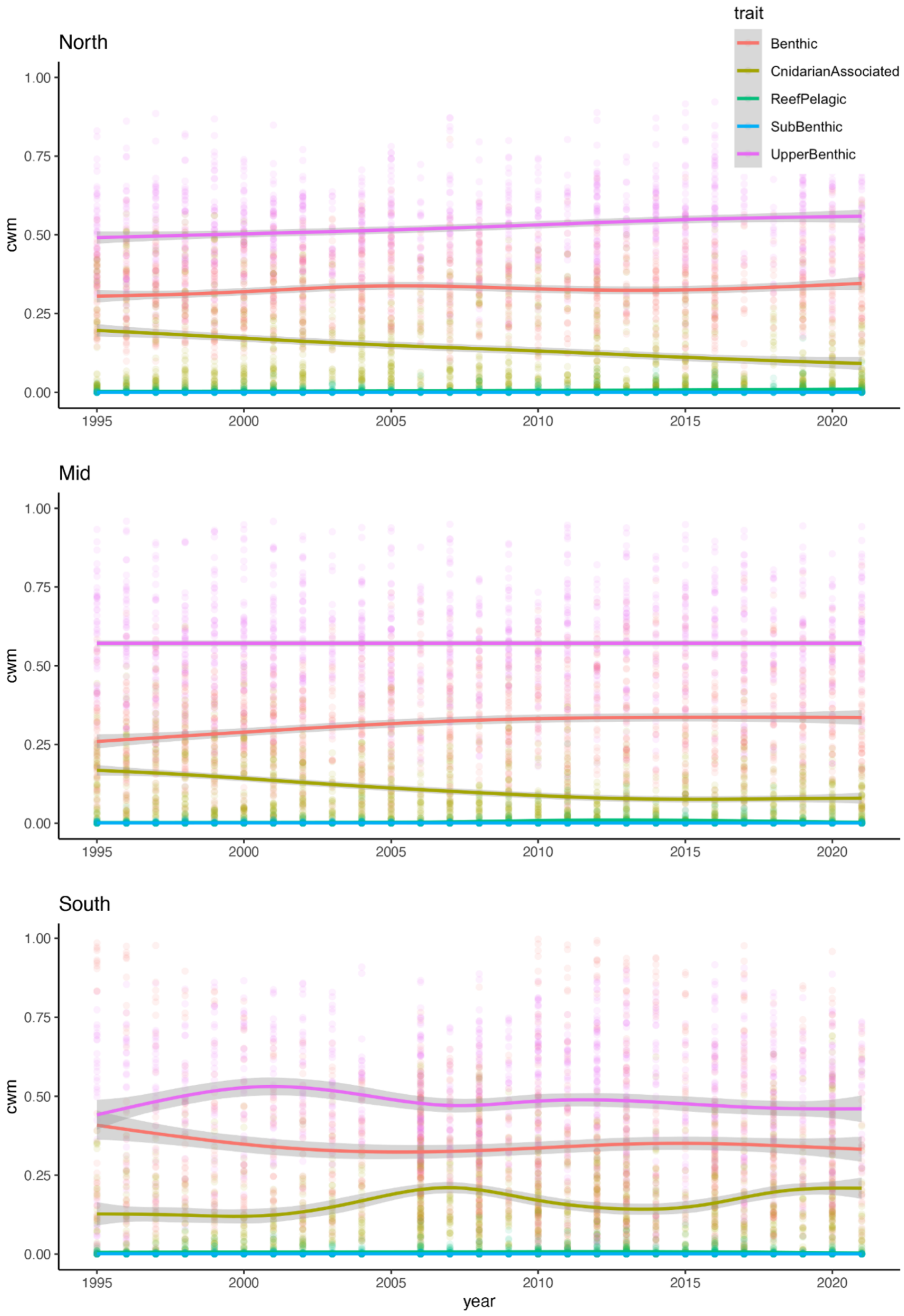

Figure D10. Distribution of CWM of fish water column positions visualised with GAM smooths in the North, Mid and Southern GBR, 1995 – 2021.

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