Functional dynamics of coral reef fish in marine protected areas

Thesis submitted by

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Abstract

Coral reefs are diverse ecosystems that provide services to millions of people around the world. However, these ecosystems are rapidly transforming in the age of the Anthropocene. In this thesis, I explore how a trait-based approach can be used as a methodological tool to understand and conserve coral reef ecosystems through prioritising ecosystem functioning. In **Chapter 1**, I systematically review the literature on coral reef fish traits through a response-and-effect framework. I identify where there is evidence linking traits to disturbances, management actions, and ecosystem processes, and where there are gaps in the literature. In **Chapter 2**, I use traits identified through my review of the literature to look at functional changes over time in no-take marine reserves in Kenya. I demonstrate that over 44 years of protection, both abundance and biomass increase, and the functional trait space of the fish communities within the reserves is novel and not stabilising. In **Chapter 3**, I expand on my work from Chapter 2, where I used surveys conducted by the same individual over multiple decades, to explore more participatory ways to monitor fish communities and biomass trends across a proposed Transboundary Conservation Area between Kenya and Tanzania. I find that fish traps can be used as a participatory monitoring tool to detect trends across a gradient of protection from fishing, and video transects can provide relatively precise biomass estimates and serve as an opportunity for collective learning. Finally, in **Chapter 4**, I shift to looking at traits on a global scale and apply phylogenetic models to predict the fecundity of 831 coral reef fish species. I then look at global drivers of site-level fecundity and demonstrate the positive impact of marine protection on the fecundity of important fisheries species. Overall, this thesis adds to a necessary diversity of tools needed to conserve coral reef functioning in the Anthropocene.

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General introduction

1. Coral reef ecosystems in the Anthropocene

People have shaped - and been shaped by - ecosystems for thousands of years (Ellis *et al.*, 2021). However, global systems of harmful extraction have resulted in climate breakdown and the accelerated degradation of the world's ecosystems (Naeem *et al.*, 2012). Proposals have been made to recognise the start of a new geologic time unit, the Anthropocene, defined by the signature of human activity on the Earth, beginning around the 1950s (Waters *et al.*, 2016). The Anthropocene serves as a lens through which we can interpret interdependent social and ecological systems. The term is often used to capture planetary change, feedbacks between humans and the natural world, and drastic shifts in planetary functioning (Malhi, 2017). In the Anthropocene, humans are dominant evolutionary forces, causing change that is possibly resulting in a sixth mass extinction and extreme declines in biodiversity (Pievani, 2014; McGill *et al.*, 2015).

Coral reefs are some of the most biodiverse ecosystems in the world and provide essential goods and services to millions of people (Teh *et al.*, 2013; Kurien, 2015). However, coral reefs in the Anthropocene are different to the coral reefs of the past (Williams and Graham, 2019). Climate change, pollution, and fishing are some of the main proximal drivers of reef degradation (Hughes *et al.*, 2017a). These stressors can interact and lead to shifts in the functioning and service provision of reefs (Williams and Graham, 2019; Côté *et al.*, 2016). Globally, there has been a decline in the capacity of reefs to provide a range of ecosystem services (Eddy *et al.*, 2021), as well as the simultaneous emergence of novel ecosystem services (Woodhead *et al.*, 2019). A new "functionalist" conservation paradigm advocates for the protection of the ocean to achieve multiple integrated social and ecological goals that prioritise ecosystem functioning and service provision over the preservation of historical ecological compositions (Sala *et al.*, 2021; Cinner *et al.*, 2020; Graham *et al.*, 2014; Jepson, 2013).

2. Ecosystem functions and functional traits

Jax and Setälä (2005) discuss the importance of establishing what exactly is meant when ecologists refer to an ecosystem "function". They identify four common uses for the word in ecology - functions as: processes, roles, services, or the functioning of a system. Jax and Setälä (2005) argue that the first definition is the most practical and can be used interchangeably with the word “process”, or in fact, to describe a collection of processes with the term “ecosystem functioning”. Similarly, Bellwood et al. (2019) propose an operational definition for function, “the movement or storage of energy or material”. I adopt this definition and use the terms “function” and “process” interchangeably in this thesis.

Relatively few studies have quantified functioning as the rate of ecosystem processes (Cheng *et al.*, 2019). Rather, functional traits have frequently been used as a proxy for ecosystem functioning (De Bello *et al.*, 2010). Functional traits have classically been defined as “morpho-physio-phenological traits which impact fitness indirectly via their effects on growth, reproduction and survival, the three components of individual performance” (Violle *et al.*, 2007). While this definition focuses on individual performance, it has been argued that functional traits can integrate across scales, where individual intraspecific traits affect species-level traits, which affect community and population-level traits (Fontana *et al.*, 2021). In the response-and-effect framework, functional traits can be categorised as “response traits”, if they respond to environmental changes, and “effect traits”, if they affect ecosystem processes. While only indirectly capturing ecological processes, effect traits are more available in literature compilations and therefore can be applied to datasets retrospectively (McLean *et al.*, 2019a).

The application of trait-based functional ecology to coral reef ecosystems is still in its nascent stages (Bellwood *et al.*, 2019b). The launch of the Coral Trait Database in 2016 (Madin *et al.*, 2016a) was a milestone to consolidate the use of coral traits, much like the publication of the first terrestrial plant functional trait handbook (Pérez-Harguindeguy *et al.*, 2013), or the terrestrial invertebrate functional trait handbook (Moretti et al., 2017). Similarly, for coral reef fish, several crucial review papers and projects have begun to provide direction around which traits could be measured consistently, what is meant by the term ecosystem functioning, and what a novel functional approach might look like (Kublicki, 2010; Villéger *et al.*, 2017; Bellwood *et al.*, 2019b; Woodhead *et al.*, 2019; Quimbayo *et al.*, 2021). However, there is no central database for coral reef fish traits, and we lack a clear understanding of where there is evidence in the literature linking environmental change to response traits and effect traits to ecosystem processes.

One of the key goals in functional ecology is building our capacity to measure and accurately estimate important functional traits to predict how environmental change is likely to affect ecosystem functioning. Important paired ecosystem processes occurring on the reef include: bioerosion and calcium carbonate production, herbivory and primary production, predation and secondary production, and nutrient uptake and nutrient excretion (Brandl *et al.*, 2019). In addition to individual traits being mechanistically linked to ecosystem processes, Biodiversity-Ecosystem-Functioning (BEF) Theory proposes that ecosystem functioning increases with biodiversity (Srivastava and Vellend, 2005; Lefcheck, 2021; Duffy *et al.*, 2016). Moreover, biomass can be enhanced and predicted by high levels of biodiversity (Duffy *et al.*, 2016; Lefcheck, 2021). For example, Benkwitt et al. (2020) demonstrate that reef fish biodiversity mitigates against multiple stressors (a heatwave and invasive rats) on the Chagos Archipelago, a remote MPA, and positively influences two ecosystem functions: biomass and productivity. Like species diversity, there are many components to functional diversity (e.g., richness, evenness, dispersion). However, functional diversity can broadly be defined as the diversity of traits or trait combinations (functional entities), or, as the distribution of species in a multidimensional functional space, where axes are constructed based on traits (Mouillot *et al.*, 2013). Functional space, therefore, represents the extent to which a community contains the traits and trait-combinations needed for a range of ecosystem functions (D'Agata *et al.*, 2016). Functional diversity, especially when integrated with phylogenetic diversity, can be a good predictor of ecosystem functioning (Flynn *et al.*, 2011; Floeter *et al.*, 2018).

Predictive capacity can be enhanced by looking at temporal patterns. Long-term ecological monitoring programmes allow us to determine how ecosystems are changing over time, whether they are responding to management, and how functions might change in the future (Lindenmayer *et al.*, 2012). Monitoring changes in functional traits can provide an indication of the effects of disturbances on communities and the functions and services they provide (Coleman *et al.*, 2015). However, very few studies have looked at shifts in coral reef ecosystem processes, functional diversity, and functional traits over time.

3. Marine Protected Areas

The Convention on Biological Diversity (CBD) set out a strategy for 2011-2020 with the aim of achieving 20 "Aichi Biodiversity Targets". Aichi Target 11 of the CBD promotes the expansion of the global protected area network to cover 17 percent of all terrestrial land and 10 percent of coastal and marine areas by 2020 (Secretariat of the Convention on Biological Diversity, 2014). Currently, 7.9% of coastal and marine areas are classified as Marine Protected Areas (MPAs) in the World Database on Protected Areas (www.protectedplanet.net). MPAs can broadly be defined as coastal or marine areas that are managed for the conservation of biodiversity or to ensure the provision of ecosystem services (Horta e Costa *et al.*, 2016). A range of different MPA classification systems exist. For instance, The International Union for the Conservation of Nature (IUCN) classifies MPAs according to their management objectives (e.g., National Park, Natural Monument or Feature, Wilderness Area, etc.) (Keleher, 2000), while the MPA Guide categorises MPAs by stage of establishment and level of protection (Grorud-Colvert *et al.*, 2021), and others argue for a regulation-based classification system (Horta e Costa *et al.*, 2016). Management regulation classifications of MPAs include no-take marine reserves (McClanahan *et al.*, 2007b), fishing gear restrictions (Campbell *et al.*, 2018), periodically-harvested closures (Cohen *et al.*, 2013), community protected areas (Chirico *et al.*, 2017), and Other Effective Area Based Conservation Measures (OECMs) (Beazley *et al.*, 2021).

MPAs are one of the most widely applied and studied conservation tools at our disposal. It has been argued that MPAs are most effective for biodiversity conservation if they are: 1) no-take, 2) well-enforced, 3) old (>10 years), 4) large (>100 KM^2), and 5) isolated by deep water or sand (Edgar *et al.*, 2014). However, protected areas, especially no-take MPAs, can come at a cost to humans. They have been associated with exacerbating unjust power dynamics by excluding certain people from decision making and having access to essential resources (Richmond and Kotowicz, 2015; Zafra-Calvo and Geldmann, 2020). The use of justly-created and context-appropriate MPAs can increase compliance with governance (Dudley *et al.*, 2017) and can help achieve multiple socio-ecological goals that align with the functionalist paradigm of nature conservation.

Fish biomass responds to well-enforced fishing protections (Lester *et al.*, 2009b). Globally, MPAs average biomass 27% higher than fished reefs (MacNeil *et al.*, 2015). Moreover, biomass provides an important and simple measure of the health of fish stocks and the impact of MPAs. For example, McClanahan et al. (2015) propose a conservation target of 1150 kg/ha for MPAs in the Indian Ocean to ensure a functioning reef ecosystem. A number of changes in fish community structure tend to occur along an increasing biomass gradient. These changes can include shifts in the shape of community trophic distributions (Graham *et al.*, 2017; Campbell *et al.*, 2020), size structures (Robinson *et al.*, 2017), and life history strategies (McClanahan, 2019b).

If MPAs are performing well, biomass tends to increase over time with protection, theoretically approaching site carrying capacity (McClanahan *et al.*, 2007c; Russ and Alcala, 2004; Chapman and Byron, 2018). In this scenario, biomass is correlated with the age of the MPA, and we might expect similar changes to those that occur over a biomass gradient to occur over time. However, time introduces another plane of multiple variables that can affect ecosystems. For example, an MPA with low structural complexity might be effectively conserving large, old individuals at a site, but failing to effectively recruit new fish over time, thereby decoupling standing biomass from productivity (Darling *et al.*, 2017; Morais *et al.*, 2020b). Such examples illustrate the need to look at shifts in traits over time that could point towards early signs of functional changes occurring in MPAs that might be undetected by looking at traditional biomass or species richness measures (Coleman *et al.*, 2015).

The effect an MPA has on ecosystem functioning depends on its context, environment, and the time being investigated (Robinson *et al.*, 2020). Crucially, fishing can interact with other stressors such as climate change. Stressors on a reef can act synergistically, antagonistically, or additively (Côté *et al.*, 2016; Darling *et al.*, 2010). For example, fishing and climate change can both affect coral cover on a reef; fishing can change the size and trophic structure of fish communities, resulting in changes to functions important to maintaining coral dominance (Robinson *et al.*, 2020; Hempson *et al.*, 2018), while increasing temperatures associated with climate change can lead to coral bleaching, resulting in the loss of live coral cover and shifts to algal-dominated benthic communities (Bellwood *et al.*, 2004). In Kenya, these two stressors were found to have a combined antagonistic or weakly additive effect, with temperature extremes resulting in bleaching being the more dominant driver of change (Darling *et al.*, 2010). While fishing and pollution can sometimes be addressed through local management actions, climate change necessitates urgent global action (Mumby *et al.*, 2013). MPAs can enhance ecosystem functioning (Allgeier *et al.*, 2016; Topor *et al.*, 2019), but climate change may be altering the ways in which we expect MPAs to affect ecosystem functioning. Some functional groups, and therefore ecosystem processes, could end up benefiting more than others (Graham *et al.*, 2020).

Maintaining ecosystem processes that replenish fish stocks is essential for ensuring that fisheries are sustainable (Russ, 2002). MPAs can produce fisheries benefits through adult spillover effects, the protection of spawning grounds, and larval subsidies (Chirico *et al.*, 2017; Marshall *et al.*, 2019). These benefits act as win-wins for biodiversity and human needs. However, some studies have suggested that there can be a negative effect of MPAs on fisheries through reduced space for fishing and higher degradation of fishing grounds (Ban *et al.*, 2017, 2015). In places where poorly managed fisheries persist and are difficult to change, MPAs, when near to fished areas, can increase fish catch without necessitating reform in fished areas (Cabral *et al.*, 2020). However, Sala et al. (2021) demonstrate that if fisheries management were to improve across fisheries and restricted areas, there would be less of a need for no-take MPAs to ensure the same levels of food provisioning.

While significant progress has been made towards the CBD targets, none have them have been fully achieved (Obura *et al.*, 2021). The current global MPA system is thought to only secure 1.7% of the tree of life for corals and 17.6% for tropical fishes (Mouillot *et al.*, 2016). The post-2020 CBD targets are currently being negotiated at the time of writing this thesis (Grorud-Colvert *et al.*, 2021; Convention on Biological Diversity, 2021), with the second part of the Conference of Parties set to take place in May 2022. This makes reassessments of the value of MPAs in light of new functional conservation priorities critical and timely.

4. Monitoring

One of the ways in which we assess the state of ecosystems, understand how they are changing over time, and what is causing them to change, is through monitoring efforts (Lindenmayer and Likens, 2010). Monitoring is also a critical component for assessing the impact of a conservation measure, such as the implementation of an MPA (Mascia *et al.*, 2017). How things are monitored, what is monitored, and who does the monitoring, however, can be complex questions driven by a range of different conservation values (Jepson *et al.*, 2011).

Ecological monitoring of coral reefs typically includes surveys of reef fish communities and benthic communities. Coral cover is often used as an indicator of reef health (Strain *et al.*, 2019a). However, the functional composition of corals and the structural complexity of the reef as a habitat for other organisms can provide more detailed insight into ecosystem functions that integrate across a network of ecological actors (Fontoura *et al.*, 2020; Darling *et al.*, 2012, 2017; McWilliam *et al.*, 2020). For example, a number of studies have reported the effects of coral bleaching on the composition and functioning of some reef fish communities (Pratchett *et al.*, 2018; Garpe *et al.*, 2006).

Underwater Visual Census (UVC) surveys are commonly used on coral reefs for long-term and spatially widespread ecological monitoring of fish communities (Samoilys and Carlos, 2000). UVC methods encompass belt transects, video transects, and stationary point counts, amongst other methods (Caldwell *et al.*, 2016). They typically involve recording some form of taxonomic identity, abundance, and size. UVC surveys can require training and equipment, making them prohibitive in some cases. In addition to UVCs, data collected on fish catch - such as taxonomy, abundance, length, and mass - can also be used in long-term, large-scale ecological monitoring (Obura *et al.*, 2002). Other forms of reef fish surveys can involve experiments such as predation and herbivory assays (Boada *et al.*, 2015; Hoey and Bellwood, 2009). Ecological monitoring can be paired with the collection of sociological monitoring data such as social surveys, economic surveys, wellbeing surveys, and surveys on compliance with MPA regulations (Maire *et al.*, 2020; Mahajan and Daw, 2016; Bergseth *et al.*, 2015).

Within a functionalist conservation paradigm, measuring ecosystem functioning is important, be it directly or indirectly. Ecosystem processes that have been directly measured or modelled include herbivory rates (Streit *et al.*, 2015), predation rates (Burkepile and Hay, 2008), bioerosion rates (Yarlett *et al.*, 2018), and nutrient cycling (Schiettekatte *et al.*, 2020). One critical measure of ecosystem functioning on a reef is reef fish biomass (Brandl *et al.*, 2019). Standing biomass, when recorded as a static measure, is a proxy for ecosystem functioning (e.g., secondary production), not an ecosystem process in itself. Rather, biomass production is the ecosystem process (Morais and Bellwood, 2020). In order to obtain estimates of fish biomass at a given site, surveys that record the length, abundance, and taxonomic identity of a representative sample of fish in that area need to be conducted. Established length-mass relationships for species or families can then be used to convert an individual fish from length to mass. Where biomass production or other ecosystem processes are modelled to extrapolate beyond species or areas that haven’t been directly measured, functional traits, such as fecundity, length at maturity, and other life history parameters can provide predictive power (White and Marshall, 2019). There is scope to gain new functional insights into coral reef ecosystem health by applying functional traits to conventional ecosystem monitoring data. For example, by integrating standing biomass with demographic models that account for traits such as reproduction, growth, and mortality, biomass production has been calculated as an ecosystem process (Morais and Bellwood, 2020). Similarly, models predicting rates of nutrient cycling have been constructed using traits such as fish body mass, growth rate, and trophic level (Schiettekatte *et al.*, 2020). This points to the value and need to build a general understanding and a robust dataset on functional traits and how they relate to ecosystem processes.

Monitoring changes in functional traits can provide an indication of the effects of disturbances on communities and the functions and services they provide (Coleman *et al.*, 2015). For example, size is known to respond to disturbances such as fishing and is also known to affect ecosystem processes such as predation rates (Jacob *et al.*, 2011). The individual lengths of fish are typically recorded in UVC surveys, so it is an example of an intraspecific trait that can be studied. At present, the majority of functional trait-based studies work at the species level, but there is a move towards incorporating intraspecific trait variation across functional ecology (Siefert *et al.*, 2015). The benefit of using an interspecific approach, however, is that it makes assessing functional dynamics accessible retrospectively; where monitoring traits and functions was not an explicit goal of a project, but recording the taxonomic identity of fish was, species can be assigned traits after data collection (e.g. Mclean et al., 2021).

Westernised modes of conservation have historically perpetuated social inequalities (Lele *et al.*, 2010). A classic example of this can be found in the colonial legacy of protected areas which were established across occupied lands and excluded local people (Hingston, 1931). Valuing social equity requires us to ask the question of who is included in all stages of the conservation process (Bennett *et al.*, 2021). Danielsen et al. (2009) identify five levels of local involvement in monitoring: "1) externally driven, professionally executed, 2) externally driven with local data collectors, 3) collaborative monitoring with external data interpretation, 4) collaborative monitoring with local data interpretation, and 5) autonomous local monitoring". Participatory monitoring (PM) is the process by which local people monitor their own resources. There are numerous potential benefits of PM. Becker et al. (2005) outline a case-study in Ecuador where local community resource monitoring efforts enhanced learning, social capital, and "institutional nesting" to allow for effective conservation. PM can also "encourage cooperation" with scientific objectives and be used to fill a gap in information provision (Uychiaoco *et al.*, 2005). Conservationists also benefit from the potential longevity of the monitoring project by establishing a means of information gathering that is not dependent on prolonged funding, and therefore is not susceptible in many cases to being cut short at any point (Andrianandrasana *et al.*, 2005). The monitoring of the state of a system, in cases where the process is driven by scientists or NGOs, can end abruptly if the researchers have to leave the research site or if the donor money runs out (Bene and Neiland, 2006). The focus of such research is often driven by the demands of the donor and the aims of the scientists, rather than by the needs of the people living at the site of conservation. Moreover, results from such studies may never be disseminated to the local people and findings can often not have any positive local impact (McDUFF, 2001). This points to the need to develop methods for monitoring that are locally relevant, can be done with mixed levels of training, potential high staff turnover, and short funding cycles. Moreover, we need to examine how these potential new methods measure up to old methods in their ability to detect the effect of management or capture the effects of environmental change.

5. Thesis aims and outline

In this thesis, I use traits and functional theory to assess the impacts of MPAs on coral reef fishes across scales of time and space. I aim to build the evidence base for using traits in this ecological context to monitor and understand ecosystem functioning and community responses to protection (Fig. 1). Specifically, I ask:

1. What are the response and effect traits of coral reef fish and what evidence is there that they respond to disturbances or management and affect ecosystem processes?
2. How are these traits changing over time with protection and what is the likely impact of this on ecosystem functioning?
3. How can we make monitoring of ecosystem functioning indicators a learning tool that is accessible to marine managers and local resource users?
4. How is a critical functional trait responding to protection and other socio-ecological drivers of change at a global scale?

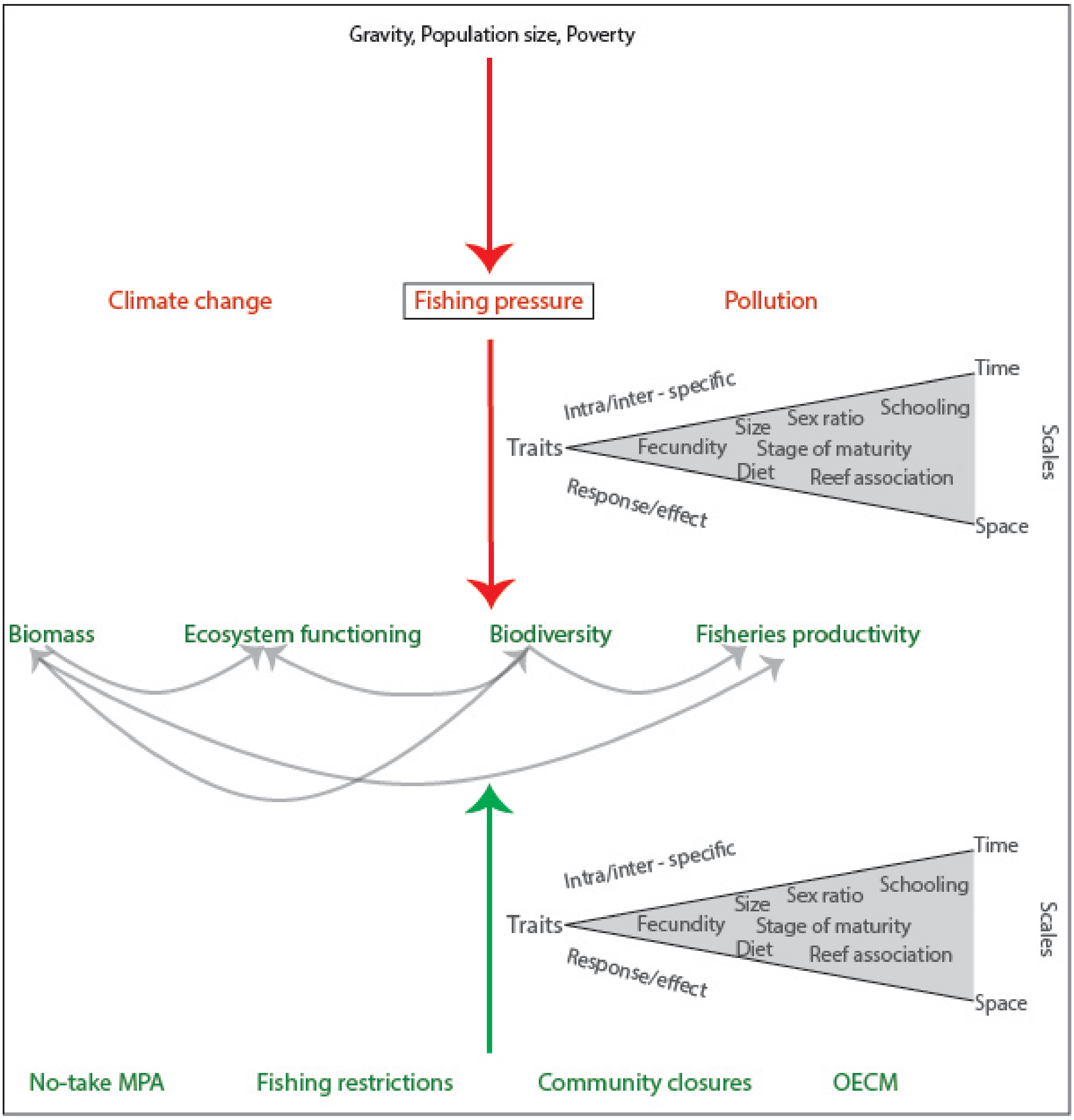

Figure 1. Schematic diagram of the relationship between the core topics and themes covered in this thesis.

I address the first question in **Chapter 1** of this thesis, where I conduct a systematic review of the literature on coral reef fish traits structured through the response-and-effect framework. In **Chapter 2**, I apply the findings from the systematic review to inform my choice of traits used to assess the functional implications of changes over time within Kenyan MPAs, using a long time-series dataset collected by one individual. In contrast to this time-series dataset, in **Chapter 3**, I work with the Wildlife Conservation Society in Kenya and Tanzania to establish more accessible and decentralised learning tools to monitor fish communities and biomass in a proposed Transboundary

Conservation Area and compare differences in the traits captured by using different monitoring methods. Finally, in **Chapter 4**, I hone in on one of the traits necessary to sustain biomass production, fecundity, to look at the impact of MPAs and other socio-ecological drivers of its global distribution.

6. Positionality statement

In line with recommendations to build an anti-oppressive and decolonial ecology and academic practice (Cronin *et al.*, 2021; Trisos *et al.*, 2021), I would like to acknowledge my positionality and the basic premise that science is not objective or apolitical. My positionality has influenced my access to this PhD, the research questions I have pursued, my approach to research, and my overall writing of this thesis. I identify as a woman. I am from, and grew up in, the Middle East, with privileged access to an international school education and attended elite British universities for graduate and post-graduate study. My study sites for this thesis are located in East Africa (Kenya and Tanzania). I am not East African, but I spent four months in Kenya working on a PhD project not included in this thesis and three months completing an internship with local and international partners at the Wildlife Conservation Society.

Chapter 1. Response and effect traits of coral reef fish

Abstract

The response-and-effect framework is a trait-based approach that seeks to break down the mechanistic links between ecosystem disturbances, species' traits, and ecosystem processes. We apply this framework to a review of the literature on coral reef fish traits, in order to illustrate the research landscape and structure a path forward for the field. Traits were categorised into five broad groupings: behavioural, life history, morphological, diet, and physiological. Overall, there are fewer studies linking effect traits to ecosystem processes (number of papers on herbivory, n=14; predation, n=12; bioerosion, n=2; nutrient cycling, n=0) than there are linking response traits to disturbances (climate change, n=26; fishing, n=20; pollution, n=4). Through a network analysis, we show that the size and diet of fish are two of the most common response and effect traits currently used in the literature, central to studies on both ecosystem disturbances and processes. Behavioural and life history traits are more commonly shown to respond to disturbances, while morphological traits tend to be used in capturing ecosystem processes. Pearson correlation coefficients quantifying the strength of the relationships between the most commonly studied process, herbivory, and key effect traits (size, gregariousness, and diel activity) are provided. We find that the most popular cluster of traits used in functional diversity metrics (e.g. functional richness, functional dispersion) is comprised of size, diet, space use/position in the water column, diel activity, gregariousness, and mobility, which encompass three of the broad trait categories. Our assessment of the literature highlights that more research is needed to support an evidence-based selection of traits to understand and predict ecosystem functioning. In synthesising the literature, we identify research gaps and provide an avenue towards a more robust trait-selection process.

Keywords

ecosystem processes, environmental disturbances, functional diversity, coral reef ecology, ecosystem function, trait-based ecology, systematic review

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1. Introduction

Trait-based approaches in ecology and conservation are increasingly applied as the fields shift towards prioritising an understanding of ecosystem functioning and maintaining ecosystem services (Kissling *et al.*, 2018; Madin *et al.*, 2016a; Barnett *et al.*, 2019). Such an approach allows for mechanistic insight into how species interact with, react to, and shape their habitats (Violle and Jiang, 2009; McLean *et al.*, 2018). The application of trait-based functional ecology to coral reef ecosystems is still in its nascent stages (Bellwood *et al.*, 2019b). The launch of the Coral Trait Database in 2016 (Madin *et al.*, 2016b) was a milestone to consolidate the use of coral traits, much like the publication of the first terrestrial plant functional trait handbook (Pérez-Harguindeguy *et al.*, 2013), or the terrestrial invertebrate functional trait handbook (Moretti *et al.*, 2017). Similarly, for coral reef fish, several crucial review papers and projects have begun to provide direction and clarity around which traits could be measured consistently, what is meant by the term ecosystem functioning, and what a novel functional approach might look like (Kublicki, 2010; Villéger *et al.*, 2017; Bellwood *et al.*, 2019; Brandl *et al.*, 2019; Woodhead *et al.*, 2019; Quimbayo *et al.,* in press).

The “response-and-effect framework” posits that it is useful to determine which traits respond to environmental gradients (“response traits”) and which traits affect ecosystem processes (“effect traits”) (Suding *et al.*, 2008; Díaz and Cabido, 2001; Grime, 2006; Loreau *et al.*, 2001; Lavorel and Garnier, 2002). This concept runs parallel to that of the distinction between Eltonian and Grinnellian dimensions of a niche, where the Grinnellian dimension refers to the resource needs of a species, and the Eltonian dimension refers to the impact of a species on the environment (Devictor *et al.*, 2010). The use of such a framework provides a practical way of addressing how disturbances are likely to affect population dynamics and ecosystem functioning as a whole (Díaz *et al.*, 2013; Salguero-Gómez *et al.*, 2018). The trait structure of a community not only affects its sensitivity to disturbance (McLean *et al.*, 2019b), but also its capacity to support long-term functioning (Debouk *et al.*, 2015; Duffy *et al.*, 2016). Response traits have also been proposed as a basis for building Essential Biodiversity Variables, allowing for the effective monitoring of biodiversity change over time (Kissling *et al.*, 2018). By identifying traits that overlap as both response and effect traits, or correlated response and effect traits, predictions about how disturbances could affect ecosystem processes can be made (Gross *et al.*, 2008; Suding *et al.*, 2008).

Several studies have found that functional diversity metrics respond to disturbances but also determine potential ecosystem functioning (Díaz and Cabido, 2001; Mouillot *et al.*, 2013; Sitters *et al.*, 2016). The use of trait-based approaches to estimate the functional diversity of coral reef fishes has become common (e.g. Richardson et al. 2017; Floeter et al. 2018; Mbaru et al. 2019). Yet, the number and selection of traits used in functional indices may greatly influence the outcomes and conclusions that can be drawn from analyses. The creation of functional groups and the use of trait-based approaches to understanding ecological dynamics is only useful if the prior selection of traits and functional groups are ecologically relevant to the questions at hand. Therefore, when applying the response-and-effect framework, it is necessary to determine which traits should be used as response traits and which traits should be used as effect traits, and where there is sufficient evidence mechanistically linking these traits to disturbances and processes.

In this paper we review the literature on coral reef fish response and effect traits. We do this by asking which fish traits have been investigated in relation to responding to disturbances (response traits) or affecting ecosystem processes (effect traits) and how many papers have studied each of these links. We also ask which traits are being used together and why. We then explore the consistency of the direction of influence for comparable traits and extract quantitative data linking predominant traits with a commonly assessed ecosystem process. In synthesising the literature, we provide guidance for an evidence-based selection of traits for functional research in coral reef ecology and conservation, and establish where future research and experimentation is needed to strengthen the field.

2. Materials and methods

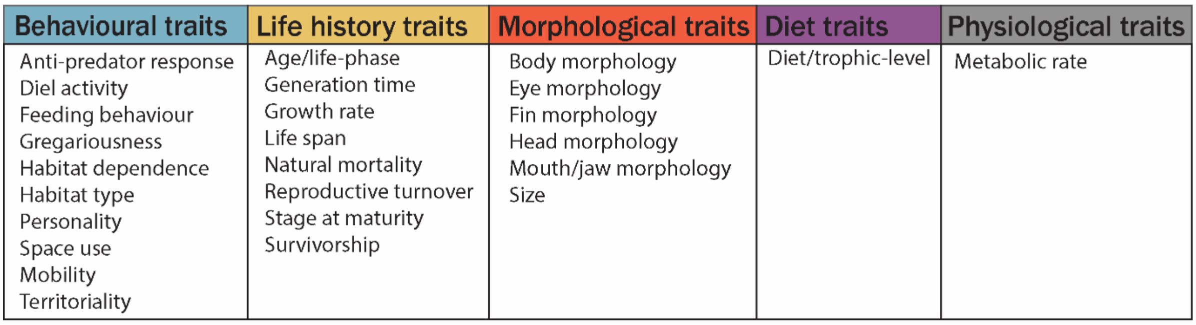
We examined response traits in relation to three disturbances and effect traits in relation to four processes common on coral reefs. The disturbances were pollution, fishing, and climate change (Hughes *et al.*, 2017b, 2010). The processes were herbivory, bioerosion, predation, and nutrient recycling (Brandl *et al.*, 2019; Villéger *et al.*, 2017). These limits to inclusion of disturbances and processes were applied to structure the review through the response-and-effect framework.

A comprehensive search of the literature was conducted using the Web of Science database (1974-2018). An initial search on September 26, 2018 used the terms: Topic Sentence (TS) = (fish* AND coral AND reef*) AND trait* AND ("functional diversity" OR "functional evenness" OR "functional richness" OR "functional dispersion" OR "functional divergence" OR "functional redundancy" OR "functional group*" OR "functional complimentary")) OR TS= (("coral reef" OR "coral reefs") AND (fish OR fishes) AND (trait OR "life history") AND (function OR functions OR functional OR process OR processes OR disturbance OR disturbances)). This search yielded 380 titles. Further search terms were used to find papers specifically related to relevant ecosystem processes and/or disturbances. For example: TS = ((fish* AND coral AND reef*) AND trait* AND “climate change”). A total of 227 papers were found with these follow up search terms. Furthermore, the reference lists of four review papers that appeared in the searches were “snowballed”. A total of 17 new references were added to the database using this method.

Paper inclusion criteria were that 1) one or more of the processes or disturbances were being investigated in relation to 2) one or more traits of coral reef fish. Papers were excluded if 1) they were looking specifically at larval fish traits (e.g. pelagic larval duration), 2) the process or disturbance was not one that is being reviewed for this paper, 3) the paper was not accessible or not in English, and/or 4) the paper was a review article (although references were checked and snowballed). Papers were first filtered by titles, then abstracts, and finally full body texts. From a total of 624 papers accumulated with the three search strategies, 80 papers met the above criteria and were included in the systematic review (see PRISMA flow diagram, Figure S1).

The traits, processes, and disturbances being studied in each paper were identified. Where possible, the direction of the relationship between the trait and process or disturbance was assessed. After a full list of traits had been accumulated, similar traits were grouped together to generate a succinct selection of relevant traits. For example, “size” was used as a way to group together traits such as “total length”, “maximum length”, and “body mass”. Traits were classified as either “behavioural”, “life history”, “morphological”, “diet and trophic level”, or “physiological” (Table 1).

Table 1. Broad groupings of traits, where blue corresponds to behavioural traits, yellow to life-history traits, red to morphological traits, purple to diet traits, and grey to physiological traits. This colour scheme is used throughout the paper.



Behavioural traits	Life history traits	Morphological traits	Diet traits	Physiological traits
Anti-predator response	Age/life-phase	Body morphology	Diet/trophic-level	Metabolic rate
Diel activity	Generation time	Eye morphology		
Feeding behaviour	Growth rate	Fin morphology		
Gregariousness	Life span	Head morphology		
Habitat dependence	Natural mortality	Mouth/jaw morphology		
Habitat type	Reproductive turnover	Size		
Personality	Stage at maturity			
Space use	Survivorship			
Mobility				
Territoriality				

In order to address the first question, “which traits have been investigated in relation to responding to disturbances (response traits) or affecting ecosystem processes (effect traits), and how many papers have studied each of these links?”, a weighted and directed tripartite network diagram was produced using the R package “igraph” (Csárdi, 2019). The diagram illustrates the number of papers, displayed as thickness of the lines (edges), linking traits to disturbances or processes (nodes).

To address the second research question, “which traits are being used together?”, the R packages “igraph” (Csárdi, 2019) and “CINNA” (Ashtiani, Minoo; Mirzaie, Mehdi; Jafari, 2019) were used to produce an undirected, weighted network diagram. This diagram shows the links between traits used together in papers, where the size of the nodes shows the number of papers using the trait, and the size of the edges illustrates the frequency of trait combinations being included together in papers. The centrality of the nodes shows how commonly traits were used in combination with other traits. These centrality measures were quantified for the five most central traits. Centrality metrics used include degree centrality, subgraph centrality, and the topological coefficient. These metrics were selected as the top three most informative centrality measures, based on the output of a Principal Component Analysis (Ashtiani *et al.*, 2018). Degree centrality can be defined as the number of nodes linked to a given node (Zhang *et al.*, 2007), while subgraph centrality accounts for the participation of a node in the network’s sub graphs and deals with more complex networks (Estrada and Rodríguez-Velázquez, 2005), and the topological coefficient quantifies the extent to which neighbours share pairs of nodes

(Doncheva *et al.*, 2012). The median rank for the centrality metrics and the individual metric values were plotted using the R package "ggplot2" (Wickam, 2016).

To illustrate the traits being used together to generate functional diversity and related metrics, a Principal Coordinate Analysis (PCoA) (Kenkel, 2006) was carried out using the R package "ape" (Paradis *et al.*, 2019). The analysis was conducted on a Jaccard's dissimilarity matrix based on a presence/absence matrix (Cheetham and Hazel, 1969) of traits within papers looking at functional diversity metrics. Two principal component axes, explaining 49% of the variation in the distance matrix, are illustrated. The number of clusters of traits within the plot was selected using the R package "NbClust". This package determines the optimum number of clusters based on 30 indices (Charrad *et al.*, 2015). Clusters were illustrated as convex hulls grouping traits together.

The type of evidence used in each paper to test/support disturbance-trait or trait-process links was then categorised as one of the following: ex situ, experiment; ex situ, measurement; ex situ, specimen measurement; in situ + ex situ, measurement; in situ, experiment; in situ, observation; modelling/theoretical approach; other. For example, if a paper assessed the effect of climate change-associated rises in temperature on reef fish boldness behaviour in a controlled experimental lab environment, it would be counted in the "ex situ, experiment" category.

Next, we assessed the direction of the relationship between continuous or ordinal traits and processes/disturbances. Trait-process/disturbance linkages were assessed as either being positive, negative, or insignificant based on trends reported in the papers. For Bayesian analyses, where statistical significance is not relevant, only the direction of influence was recorded. For example, if a response trait, such as "generation time", was shown to decrease in response to a disturbance such as "fishing", it would be classified as a "negative" relationship. Similarly, if a process, such as "herbivory", measured as the amount of algae removed in a given time/space, was shown to increase with the "size" (effect trait) of fish, the relationship would be classified as "positive". Categorical trait relationships were excluded from this analysis, but paper result summaries are provided as a supplementary table (Supplementary Table S1).

To test the quantitative applicability of the framework to coral reef fish, we investigated the effect size of effect traits on the process of herbivory. Herbivory was selected as the ecosystem process for which to extract quantitative effect sizes, because

1) it was the most commonly studied process found in our search, and 2) herbivory was the process with the most consistent measurement in the literature (bite rate or impact). Three of the most common traits related to herbivory in the literature – size, gregariousness and diel activity – were selected as effect traits to assess. Diet was excluded from the quantitative assessment because its relevance is in relation to diet categories which is implicit for herbivory. Because the initial search term limited papers to those using the term "trait", whereas some papers use traits without explicitly naming them as such, an additional search was conducted to identify papers which may not have used the terms "trait" or "function" but had quantified herbivory. An additional four papers were found looking at the impact of traits on herbivory and directly measuring the process.

Where effect sizes were extracted from the literature, they were converted into Pearson r correlation coefficients according to Wolf (1986) and Friedman (1982). Pearson's r was selected because it allows for contrasts between two or more groups without computational corrections and is easily interpreted as it sits on a limited scale from -1 to 1 (Rosenthal and DiMatteo, 2001). Relevant statistical information needed to compute the effect size was extracted where available. WebPlotDigitizer (Rohatgi, 2019) was used to extract raw data from figures. Where data was provided but not analysed in relation to traits of interest (eg. Humphries et al. 2014), a simple correlation was conducted using raw data. For size bins/categories, the average size was used. In papers presenting data on trait-bite-rate relationships for more than one species or more than one site, average effect sizes and 95% confidence intervals are calculated. Additionally, for each trait, an average Pearson's r based on all the papers is presented with 95% confidence intervals. All statistical analysis were performed using R software version 3.5.2. (R Core Team, 2018).

3. Results

Based on our search results (See PRISMA flow diagram, Supplementary Figure S1), the most studied disturbance affecting coral reef fish traits is climate change (number of papers, n =26), followed by fishing (n=20), and then pollution (n=4). Climate change encompassed papers assessing the impacts of increasing temperatures, rising levels of CO_2, extreme weather events and coral bleaching. Fewer papers investigated ecosystem processes using an explicit trait-based approach. The process most studied was herbivory (n=14), then predation (n=12), bioerosion (n=2), and finally no papers were identified through our search terms that quantified nutrient transfer through a trait-based approach (n=0). Predation captured papers assessing prey traits, predator traits, or the interaction between both. The most studied disturbance-response trait links were between size and fishing (n=16), size and climate change (n=15), diet and fishing (n=11), and diet and climate change (n=8). The most studied effect trait-process links were diet and herbivory (n=9), size and predation (n=8), and size and herbivory (n=6). Size and diet had the greatest number of papers that link the traits both to disturbances and processes, making them both well studied response and effect traits (Figure 1; Figure S2).

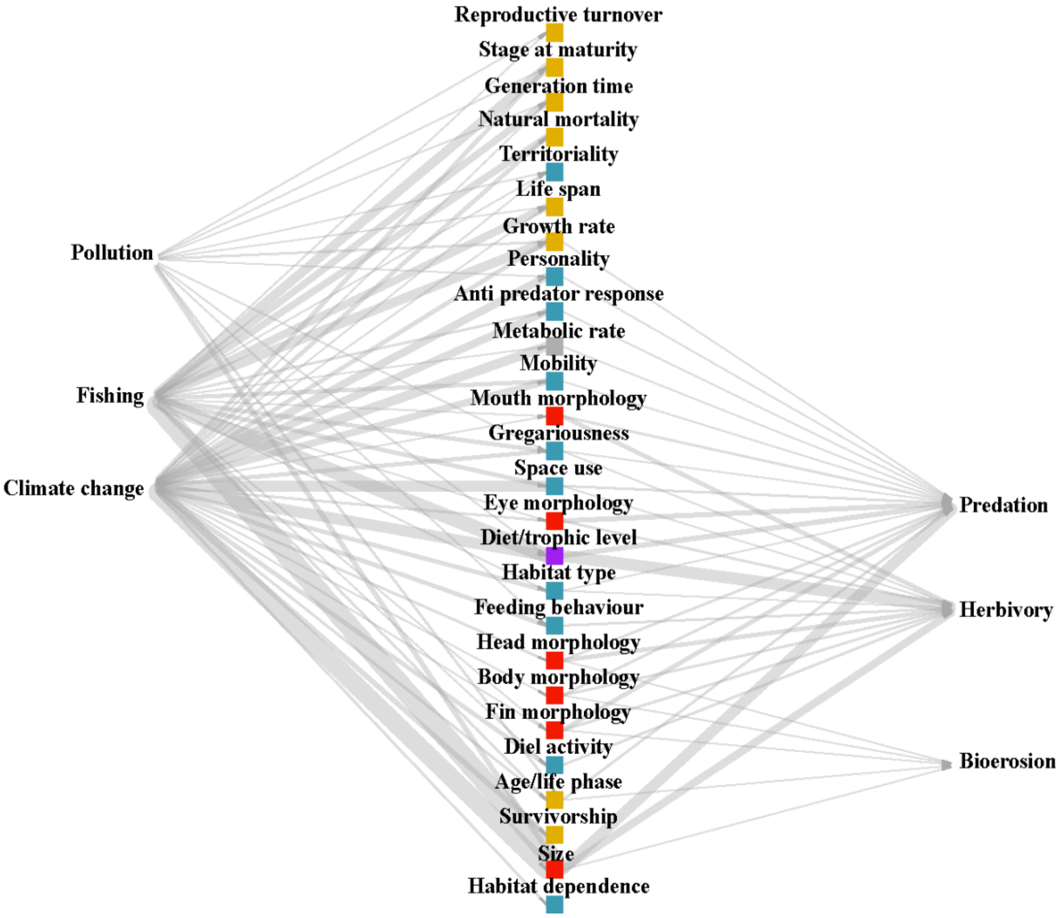


Figure 1. Tripartite network diagram showing the number of papers linking each disturbance and process to response and effect traits. The colour of trait points corresponds to broad trait groupings (blue: behavioural, yellow: life-history, red: morphological, grey: physiological, purple: diet).

The network analysis plot, based on the traits of all papers included in the database, illustrates three key findings. Firstly, size and diet, followed by space use, gregariousness, and growth rate, are the most commonly used traits in the literature (Figure 2). Secondly, trait categories, for example, behavioural or morphological (depicted by colour), tend to group together in network space. Size, a morphological trait, and gregariousness, a behavioural trait, are the exceptions to this, being situated in the middle of the plot (Figure 2; Figure S3). Thirdly, size is almost consistently ranked as the most central trait, followed by diet, gregariousness, habitat type and feeding behaviour (Figure S4). High centrality scores indicate that these traits as the ones most commonly used with combinations of other traits.

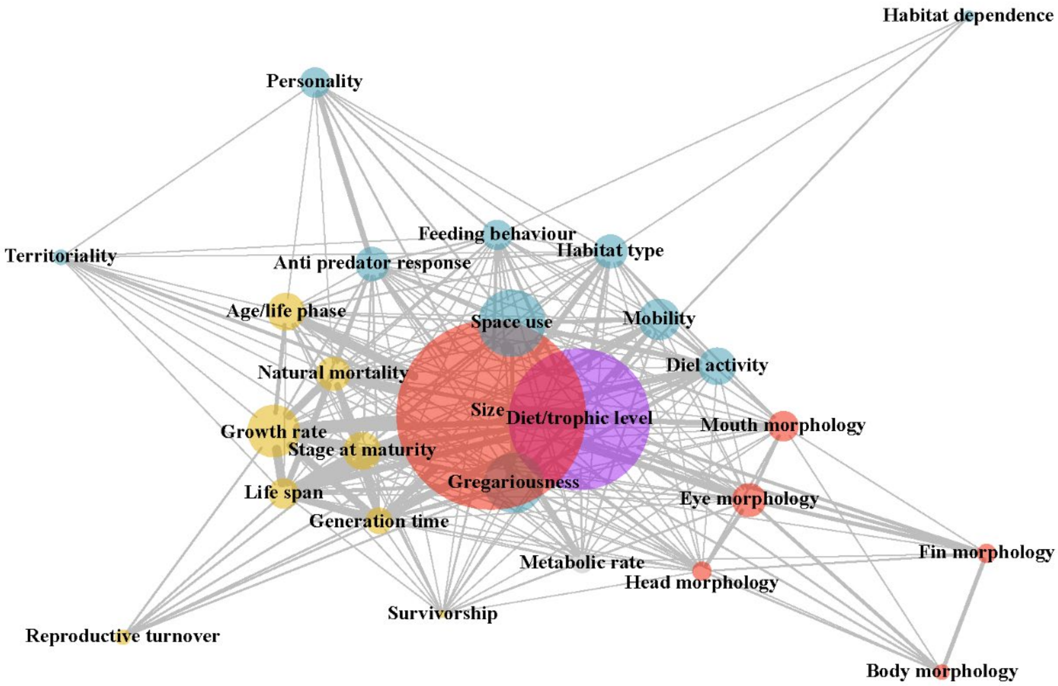


Figure 2. Network diagram showing the use of traits together within papers. Each node corresponds to a trait, with its size representing the number of papers using that trait. The colour of trait nodes corresponds to broad trait groupings (blue: behavioural, yellow: life-history, red: morphological, grey: physiological, purple: diet). The thickness of the edges (ie. lines) illustrates the number of papers in which two traits being connected were used together. The spatial position of the node indicates which traits it is most often used in conjunction with, where the more central nodes represent traits used frequently with all other traits. Rankings of centrality scores (median of degree centrality, subgraph centrality, and topological coefficient) showed size to be the most central trait, diet and gregariousness as the second most central traits, and habitat type and feeding behaviour as the third most central traits (see Figure S4).

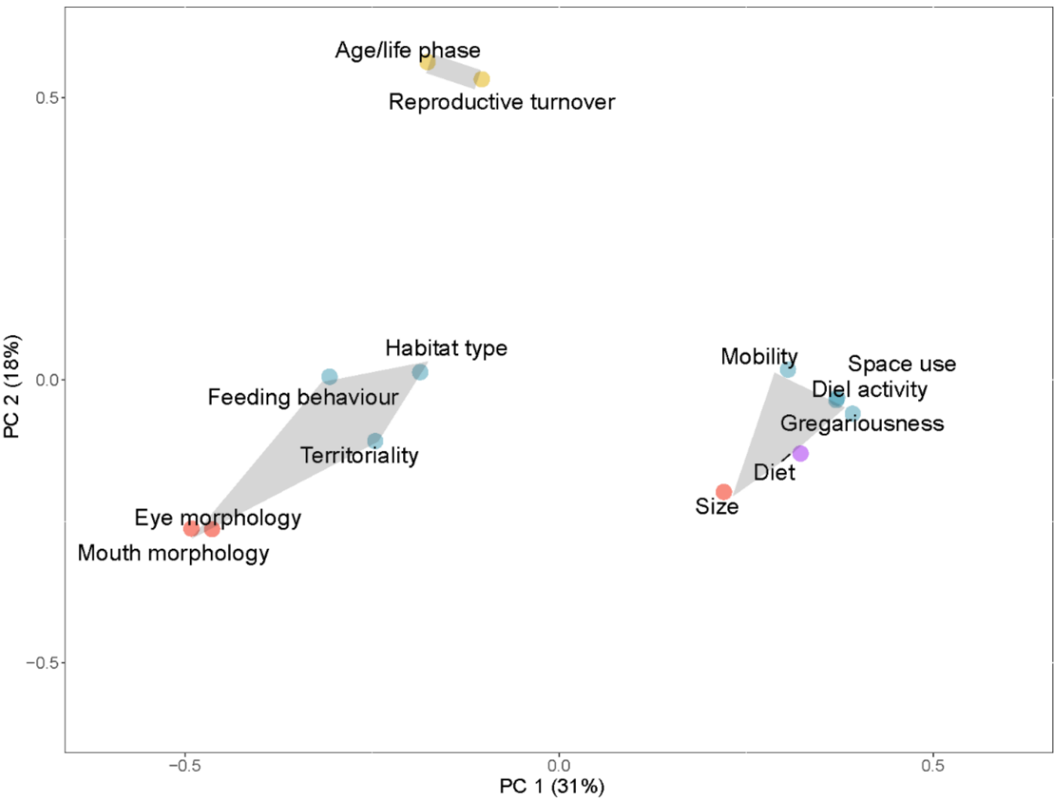


Figure 3. PCoA plot of traits used to estimate functional diversity or to determine functional entities. Three clusters show traits commonly used together in functional diversity metrics. Colour of trait points corresponds to broad trait groupings (blue: behavioural, yellow: life-history, red: morphological, grey: physiological, purple: diet).

A total of 17 papers used traits to calculate functional diversity metrics for coral reef fish, or to derive functional entities. Functional diversity indices were most commonly calculated using size (n=15), diet (n=14), and space use (n=9). The traits most commonly used together are size, diet, gregariousness, mobility, diel activity, and space use (eg. position in the water column) (n=5) (Figure 3). Two other groupings of traits were also apparent: age/life phase with reproductive turnover; and eye morphology with mouth morphology, feeding behaviour, habitat type and territoriality. These groupings were based on Euclidean space in the PCoA axes and the traits encompassed were not necessarily used consistently all together in the literature. For example, habitat type was used in five papers; some of these papers also used traits located in the cluster of the most frequently applied six traits. In Brandl *et al.* (2016), habitat type is used along with diet, size, and territoriality to examine how coral reef fish functional diversity responds to a disturbance in the form of a tropical cyclone. Age/life phase and reproductive turnover represent a lesser studied cluster of traits, produced by papers that include broader life history strategies in functional analyses (eg. Tuya *et al.*, 2018).

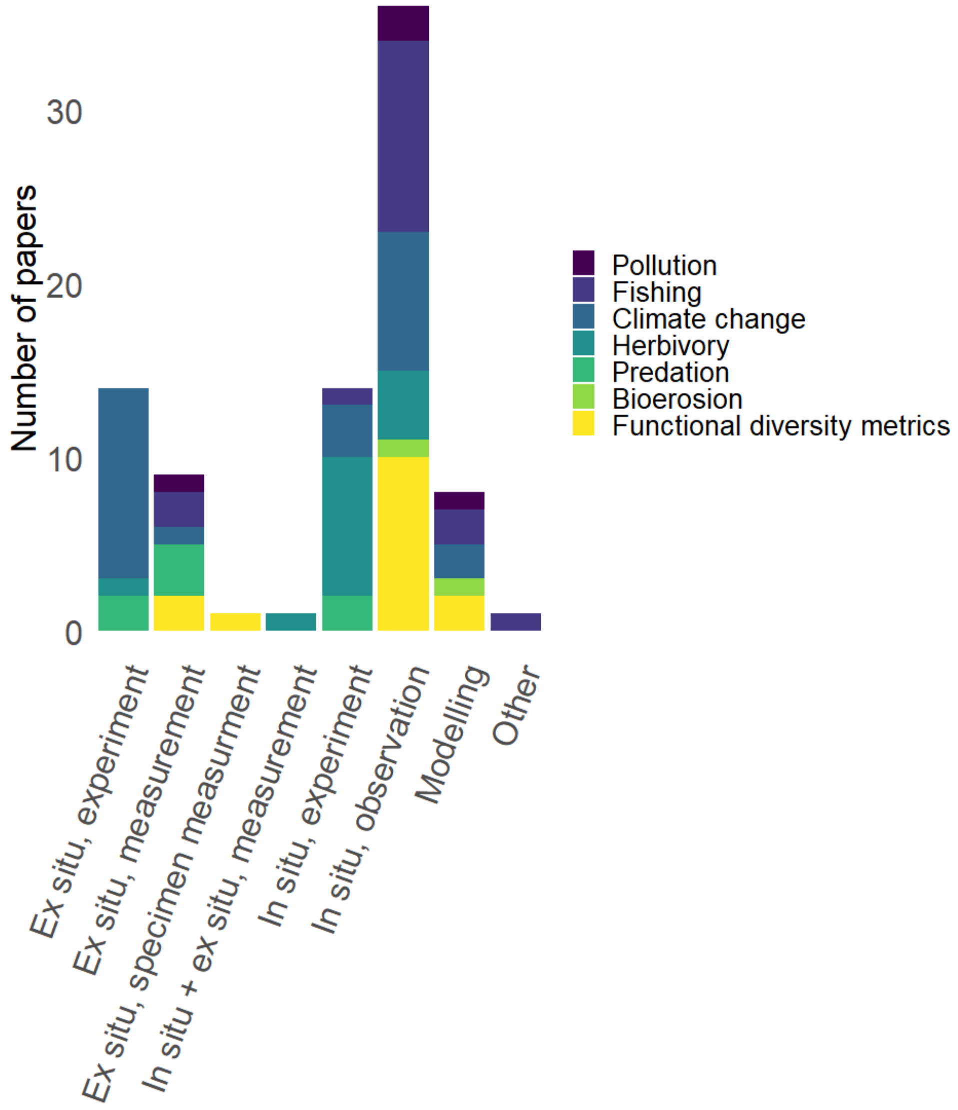


Figure 4. Number of papers (coloured according to disturbance, process, or functional diversity) in each evidence category.

Overall, the evidence for the majority of functional diversity papers is based on in situ observational evidence (n=10; total in situ observational n=36). The number of papers based on this type of evidence is more than double the number of papers based on ex situ experimental (n=14) and in situ experimental (n=14) evidence. Trait-relationships based on ex situ measurements (n=9) and purely theoretical or modelling-based papers (n=8) were less common. Ex situ specimen trait measurements (n=1) and a combination of in situ and ex situ measurements (n=1) were each only represented by one paper (Figure 4).

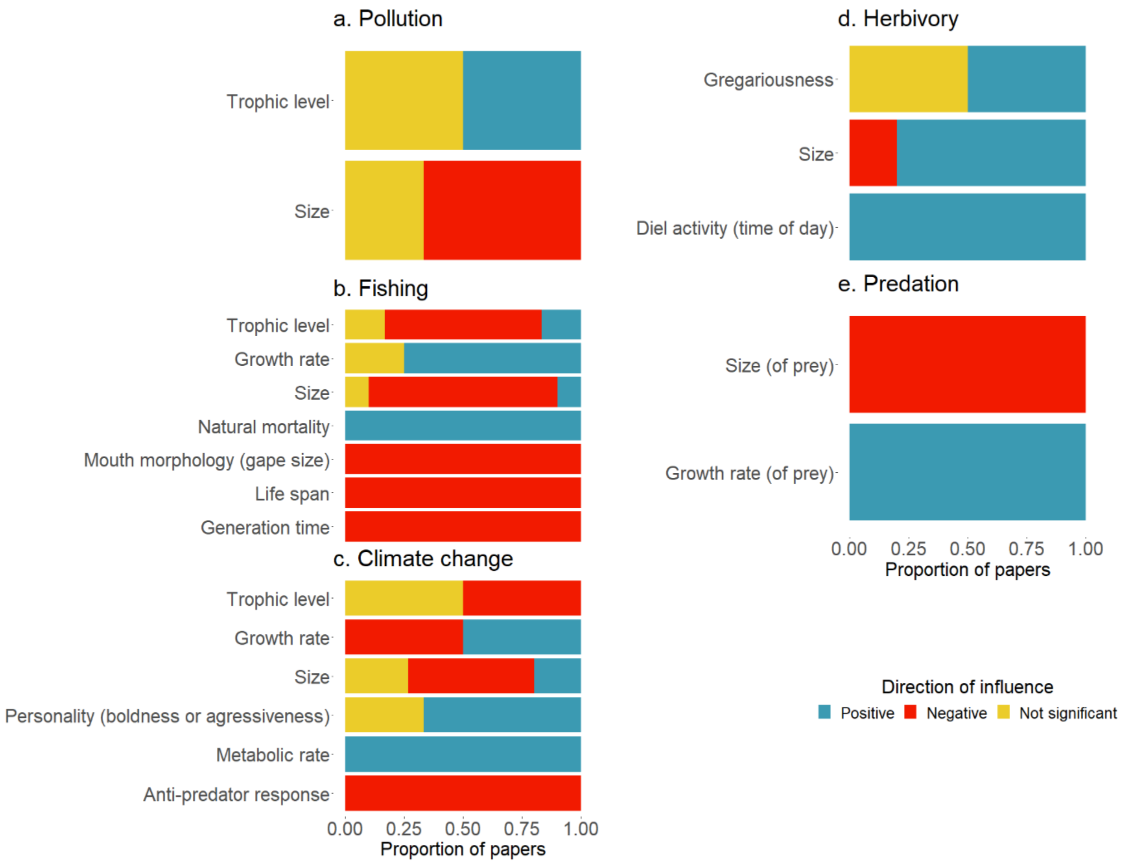


Figure 5. Proportion of papers linking traits positively (blue), negatively (red) or without significance (yellow) to (A) pollution, (B) fishing, (C) climate change, (D) herbivory, and (E) predation.

The direction of influence of disturbances on response traits and effect traits on ecosystem processes shows the consistency of findings across the limited set of papers identified in the review (Figure 5). Most papers found a negative influence of pollution on the size of fish (n=3). There was an even split between the number of papers finding an insignificant and positive effect of pollution on the trophic level of coral reef fish (n=2). There was 100% agreement on the negative relationship between fishing and the life history traits of life span (n=3) and generation time (n=3), showing that all papers framed as trait-based and/or functional in the literature identified, found that high fishing pressure results in short life spans and generation times. Fishing had a negative impact on gape size (n=1), a mostly negative impact on the size (n=10) and trophic level (n=5) of fish, but a positive influence on natural mortality (n=3), and a mostly positive impact on growth rate (n=4). All papers assessing the impact of climate change on anti-predator responses (n=4) found a negative relationship. On the other hand, climate change was found to have a positive relationship with metabolic rate (n=4). There was a mixed effect of climate change on fish size and the growth rate of fish. Climate change was either found to insignificantly affect fish trophic level or have a negative impact on trophic level (n=2).

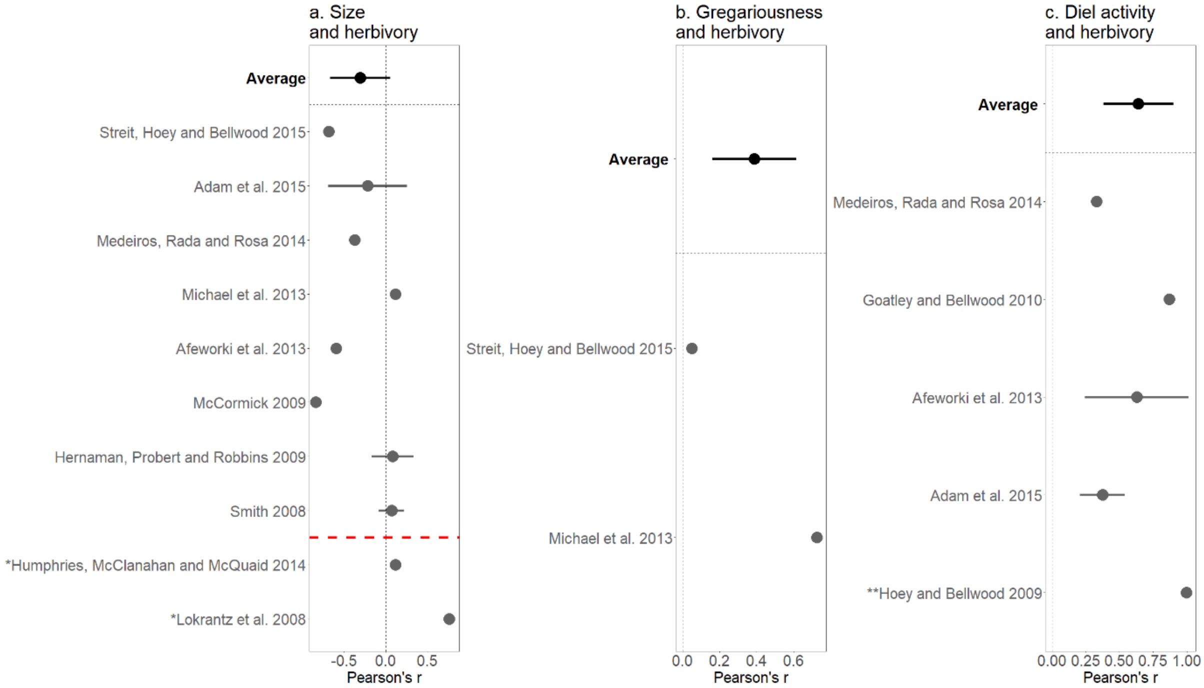


*Figure 6. Pearson's r correlation coefficients with 95% confidence intervals for papers linking (A) size and herbivory, (B) gregariousness and herbivory, (C) diel activity and herbivory. Averages of Pearson scores for all the papers are highlighted in bold for each graph. The red dotted line in (A) separates out two papers excluded from average as they measured herbivory in a form other than bite rate. * Bite impact rather than rate (eg. amount of algae removed). ** Bite rate standardised by size.*

The small sample size of papers looking at continuous traits linking to measured ecosystem processes showed that there was a positive impact of time of day on herbivory (n=1), and a mostly positive impact of size on herbivory (n=5). Gregariousness was found to either have an insignificant or positive impact on herbivory (n=2). Few papers quantified the process of predation in trait-based terms. However, of those that did, there was a negative effect of the size of prey on the rate of predation (n=2) and a positive effect of the growth rate of prey on the extent of predation (n=2) (Figure 6).

The initial search results highlighted that herbivory was the most consistently quantified ecosystem process and was typically measured as bite rate (eg. bites/minute) or bite impact (eg. kg x bites/minute). A Pearson correlation coefficient was calculated for each paper quantifying the relationship between effect traits and this measure of herbivory. There was a negative correlation between fish size and bite rate, as shown by the average of papers above the red dotted line in Fig 6.a. However, papers looking at fish size and measures of bite impact (below the red line in Fig 6.a.) tended to find a positive correlation. A strong average positive correlation between gregariousness and herbivory was identified but note, this is based on only two studies. A positive relationship between diel activity and herbivory was also found. Diel activity was sometimes measured as a categorical trait (eg. nocturnal and diurnal in Hoey and Bellwood 2009) or on different time-scales (eg. minutes after sunrise in Goatley and Bellwood 2010), and the correlation coefficient reflects the strong magnitude of influence rather than the direction of influence (Figure 6).

4. Discussion

Our review highlights four main findings: 1) size and diet are used as both response and effect traits with a relatively large number of studies investigating their importance to the range of different disturbances and processes explored in this paper; 2) nutrient cycling and bioerosion are understudied processes in the trait-based coral reef fish literature; 3) there is a distinct clustering of trait types (e.g. morphological traits, life history traits, *etc*.) in functional diversity studies, in addition to a cluster of six mixed trait types frequently used together (size, diet, position in the water column, gregariousness, mobility, diel activity); 4) because traits are not consistently coded across the literature, amassing an informative sample size to quantify the effect size of disturbance-trait or trait-process relationships is a challenge. Nevertheless, using a small sample size of papers measuring the relationship between key traits and the process of herbivory, we highlight variation in even the most seemingly well-known interactions. We reflect on these findings and propose a way forward for trait-based approaches in coral reef fish ecology and conservation.

4.1. Trends in the literature

Size and diet were identified as both response and effect traits (Figure 1). As illustrated in the network diagram, both traits are centrally located, with size having a median centrality ranking as the top trait, and diet ranking alongside gregariousness as the second most central trait, indicating their use in conjunction with a range of other traits within papers (Figure 2; Figure S4). Size is also demonstrated to have a consistent relationship with herbivory, whereby bite rate is negatively correlated with size and bite impact is positively correlated with size (Figure 6). These findings support the view that size acts as a super-trait, as it scales with, and therefore shapes, a range of other functional traits (Jacob *et al.*, 2011). However, the relationship between size and diet or trophic level is not linear, but rather, it is mediated by traits such as body depth, tooth shape, and mouth width (Keppeler *et al.*, 2020).

In comparison to ecosystem processes, trait-based approaches to studying the effects of disturbances on coral reef fish (response) traits were more numerous. Specifically, fishing and climate change were both studied in 20 or more papers, whereas only four papers focused on pollution (Figure 1). Disturbances can interact additively or synergistically to affect the coral reef environment at a number of different levels ranging from microbial to large fish (Zaneveld *et al.*, 2016; Darling *et al.*, 2010; Ban *et al.*, 2014). While fishing pressure and pollution could involve, in some cases, local solutions, climate change is likely to necessitate urgent global cooperation and decision making (Mumby *et al.*, 2013; Hughes *et al.*, 2017a). The level of uncertainty associated with global decision making has led scientists to consider the consequences of different possible climate change scenarios (Pandolfi, 2015; Hoegh-Guldberg *et al.*, 2007). A trait-based approach could be particularly useful to understand what novel ecosystem configurations might arise under these different scenarios (Graham *et al.*, 2014; McClure *et al.*, 2019).

The most commonly studied ecosystem processes were herbivory and predation. This focus in the literature is likely due to the emphasis of herbivory as a key process that prevents phase shifts to non-coral benthic communities (Hughes, 1994; Bozec *et al.*, 2016; Cramer *et al.*, 2017). Unlike herbivory, where only consumer traits were being studied, predation was often researched in terms of both consumer (predator) and prey traits. Studying the interactions of predators and prey contributes to an understanding of community dynamics that support ecosystem functioning (Schmitz, 2017). Although this review was limited to investigating fish traits, the interaction of fish traits with coral traits or algal traits represents a similar avenue to exploring the relationship between community producer-consumer dynamics (Rasher *et al.*, 2013).

4.2. Gaps in the literature

Few papers explored relationships between effect traits and bioerosion and nutrient cycling. While bioerosion is a widely recognised process on coral reefs (Lokrantz *et al.*, 2008; Bellwood *et al.*, 2012), only two papers were identified that measured it using an *explicit* trait-based approach. Such gaps in the literature highlight the need for further research quantifying such ecosystem processes, so that they can be more confidently linked to coral reef fish traits. However, since conducting the review (September 2018), there have already been strides taken to fill in research gaps and drive forward the application of trait-based approaches to estimate important functions and processes on coral reefs. For example, when this review was conducted, no papers were found linking traits to nutrient cycling, even though the process of nutrient cycling is important to the productivity of the ecosystem (Allgeier *et al.*, 2016). A notable addition to the literature addressing this gap is a paper and companion R package proposing a trait-based approach to model nutrient cycling (Schiettekatte *et al.*, 2020). The authors use traits such as body size, life stage, and diet to model fish ingestion and excretion rates, and accurately predict these rates for three species. Similarly, another notable publication in the field proposes a trait-based methodology and R package to facilitate the estimation of reef fish productivity (Morais and Bellwood, 2020). While productivity was not considered as a process in this review, it is an essential indicator of ecosystem functioning. The productivity of consumers on the reef (process) is demonstrated to respond to habitat degradation (disturbance) through a trait-mediated pathway (Morais *et al.*, 2020b). Thus, while the approach is not explicitly framed in the response-and-effect framework, it applies the logic of overlapping response and effect traits to demonstrate the value of traits in detailing the mechanisms through which disturbances affect ecosystem functioning.

4.3. Trait centrality and clustering

The results of the network and centrality analyses highlight which traits are most commonly being used together. Amongst the evidence base, there is a distinct clustering by trait type (Figure 2). Results from the ordination plot also show that the six traits popularised in Mouillot et al. (2014) (size, diet, space use/position in the water column, diel activity, gregariousness, and mobility) are frequently grouped together to compute functional diversity metrics (Figure 3). These traits cover all broad trait categories except for life history traits and physiological traits. Physiological traits, such as metabolic rate, are often difficult to obtain and vary regionally (Killen *et al.*, 2017). Conversely, life history traits are easily obtainable (Thorson *et al.*, 2017). However, we found that they are not commonly used in functional diversity studies and form their own cluster in the

PCoA analysis (Figure 3). This is also partly attributable to the conservative definition we used for the term "life history" traits; in this paper, "life history" traits are restricted to those directly associated with survival and reproduction, as outlined in the seminal work by Stearns (1976). Such traits might compliment the selected six traits to better reflect the response diversity of coral reef fish, as such traits are frequently used to measure the response of coral reef fish to disturbances (Figure 1; Figure S3). Nevertheless, the six traits capture a broad range of response and effect traits that have been linked to both ecosystem processes and disturbances. Three of the six traits were assessed quantitatively with respect to their impact on the process of herbivory; several studies show the importance of size, gregariousness, and diel activity in influencing the bite rates and algal removal rates of fish (Figure 6). Furthermore, the six traits have been used to effectively elucidate both global and small-scale ecosystem changes (Brandl *et al.*, 2016; Stuart-Smith *et al.*, 2013) and the ease at which they are obtainable likely means they have great potential for further use in functional studies (Bellwood *et al.*, 2019b).

Conversely, morphological traits, which form a cluster driven by ecosystem processes (Figure S3), and are sometimes used as stand-alone traits in studies looking at functional morphospace (e.g. Goatley *et al.*, 2010; Quimbayo *et al.,* in press) (Figure 3), are not as easily available, and as such have typically been used in studies conducted on historical records, at a small geographical scale, or for few species (eg. Munday et al. 2011; Fox and Bellwood 2013; Streit et al. 2015). Thus, there is scope to build upon morphological trait databases, so that ecosystem functioning can be better understood at a larger scale (Kiørboe *et al.*, 2018). If such traits become more readily available, they might start being used in conjunction with behavioural and life history traits to bridge together research being conducted on the impact of disturbances and ecosystem functioning.

Although this review provides a broad overview of coral reef fish traits through a response-and-effect framework, it should be noted that it does not extensively cover all of the literature dealing with traits. This is partly because the term "trait" is extremely broad and partly because systematic reviews are always somewhat biased through search terms and database algorithms (Pullin & Stewart, 2006; Drucker et al., 2016). Nevertheless, one of the purposes in this paper was to bring some structure to the coral reef fish trait literature through the response-and-effect framework.

4.4. Towards a trait-based approach for coral reef fish ecology

4.4.1. Identify overlapping or correlated response and effect traits

A dichotomy does not exist between response and effect traits. On the contrary, many traits, especially those related to resource use, both respond to disturbances and affect ecosystem processes (Díaz & Cabido, 2001). In our review of the literature, both size and diet were found to be extensively used as response and effect traits (Figure 1). Identifying traits that are both response and effect, as well as response/effect traits that are strongly correlated, allows for a parsimonious prediction of the impacts of disturbances on ecosystem functioning (Suding *et al.*, 2008). Correlated traits can be identified through multivariate ordination techniques. For example, Beukhof *et al.* (2019) demonstrate how traits positioned in close proximity in a PCA of trait-space (e.g. length and fecundity) follow similar temporal trends when exposed to environmental disturbances.

In cases where two traits are known to correlate, and one of those traits is known to respond to an ecosystem disturbance, while the other is known to affect an ecosystem process, they can be used together to harness predictive capacity. Working with microbial communities, Amend et al. (2016) found that response traits affected by drought that were strongly correlated with traits responsible for ecosystem processes allowed for the effective prediction of shifts in the functioning of microbial communities with disturbances characteristic of global change. Similarly, this review determined that the traits metabolic rate (positive relationship) and anti-predator responses (negative relationship) are linked to climate change (Figure 5). However, both traits have also been linked to the process of predation (White *et al.*, 2013; Ferrari *et al.*, 2015) (Figure 1). Therefore, such traits provide an opportunity for determining the pathways through which disturbances can affect ecosystem processes.

4.4.2. Establish causation and build the predictive abilities of trait-based approaches

One concern with the response-and-effect framework could be the implied causation in the relationships between disturbances and response traits and effect traits and ecosystem processes. While the framework does attempt to structure the direction of correlations by explaining mechanisms, causation is a notoriously hard concept to prove within science (Anjum and Mumford, 2018). However, it is generally accepted that if hypothesised causal relationships have supporting data that can be theoretically justified, used, and applied, directionality in such relationships can be recognised. Such justifications underlie the processes of mechanistic and causal modelling (Connolly *et al.*, 2017). In this review, the effect traits demonstrated to impact the process of herbivory (Figure 6) were able to be identified as effect traits, because there was a plausible causal pathway. Considering another example: size-selective fishing is proposed as the mechanism underlying a shift in the size structure of fish communities. The clear causal pathway and breadth of observational evidence supporting this disturbance-response trait link, in addition to the predictive power that comes with assuming this causal relationship, illustrates the value and purpose of structuring traits according to the response-and-effect framework. Like many of the tools applied decades ago to understand ecosystem functioning, the response-and-effect framework originates in the terrestrial plant ecology field. One of the central goals of the approach is to enable the prediction of changes in community composition and ecosystem functioning (Lavorel and Garnier, 2002).

Body size is somewhat of an anomalous trait, as it is easily recorded and has great functional importance. For other traits with less well-known causal pathways, building up an evidence base of observations under a range of conditions is important. Moreover, experimentation could be used as a controlled method of assessing causality. While this approach may not always be feasible or appropriate, small-scale controlled experiments can further test or corroborate relationships observed on a large scale (Figure 4). For example, disturbances associated with climate change provide natural experiments on a global scale (e.g. Keith *et al.*, 2018; Richardson *et al.*, 2018). Observations following such events offer useful information about response traits to form hypotheses that can be further tested through experimentation (e.g. Biro *et al.*, 2010).

4.4.3. Favour continuous traits or standardised trait categories, and consider intraspecific variation

This review demonstrates the centrality of size in the literature (Figure 2) and its versality as a response and effect trait (Figure 1). Moreover, size can be measured on a continuous scale. In order to model the overall direction of a response or effect trait across a number of studies, consistency in measurement is essential. With categorical data, a range of potential errors get introduced in the effort to standardise (Nakagawa and

Cuthill, 2007). Categorical traits have also been shown to decrease the quality of functional space (Maire *et al.*, 2015). Maintaining consistency of categories and/or using continuous traits allows for useful meta-analyses to be compiled for a range of disturbance-trait-process relationships.

In addition to being a super-trait, size provides an avenue for investigating the importance of intraspecific variation. Intraspecific variation is a burgeoning field of research within functional ecology (Albert *et al.*, 2011; Allgeier *et al.*, 2017; Des Roches *et al.*, 2018). Where substantial variability exists within species, it may no longer be sufficient to use species-level trait data (Bolnick *et al.*, 2011a). One example of the importance of intraspecific variability is illustrated in a paper by Barneche et al. (2018). The authors show that there is hyperallometric scaling in reproductive output; larger coral reef fish mothers, within the same species, have a far greater reproductive output than smaller mothers. The functional trait of an individual fish might also depend on its sex, age, or size at which it was sampled. For example, many species undergo ontogenetic shifts in their diet; it has been found that some piscivores are able to expand their diet breadth as they grow older and bigger, and their gape size can accommodate larger prey (Dunic and Baum, 2017). This diversity of size amongst individuals of a species, can be easily recorded. The size and species identity of fish is often collected using routine visual surveying techniques (Caldwell *et al.*, 2016). Indeed, total length is a relatively simple trait to measure observationally and non-invasively in situ (Villéger *et al.*, 2017).

Diet, on the other hand, is not typically measured for each fish during a survey, unless it is one of the explicit aims of the research. Rather, species are assigned a diet category post data collection using expert knowledge, published literature, or databases such as Fishbase (e.g. MacNeil et al., 2015). More recently, Parravicini *et al.*, (2020) highlight the disagreement in the literature about broad reef fish trophic guilds, and provide a standardised set of diet classifications using phylogeny and maximum body size to predict trophic guild with high accuracy. However, improvements can still be made by accounting for intraspecific variation. Intraspecific variation linked to ontogenetic shifts in diet could be accounted for by assigning diet to an individual fish count based both on species information and size, where that species-level data exists. Further, technological developments such as video surveys coupled with deep learning may allow the automated estimation of diet and other individual fish characteristics beyond size (Villon *et al.*, 2018; Li *et al.*, 2020). Progress has also been made using gut content DNA metabarcoding to rapidly and confidently estimate diet across diverse food webs. With DNA barcode libraries expanding, there is the potential to estimate high resolution diet across large scales (Casey *et al.*, 2019). The incorporation of between-individual variation to a trait-based approach, with traits such as size and diet, would allow for a more dynamic view of environment~trait~function relationships – a dynamism which is essential to scaling up to population dynamics, whereby such dynamics ultimately shape multiple interacting ecosystem processes (Salguero-Gómez *et al.*, 2018).

4.5. Conclusions

This review demonstrates the ability of the response-and-effect framework to guide future research directions based on the understanding that environmental changes will undoubtedly produce functional changes. Evidence suggests that some traits provide a crucial link between fish responses to disturbances and effects on ecosystem processes. However, the evidence base is thin for linking effect traits to many processes. Thus, if an emphasis on the conservation of ecosystem functioning on coral reefs is to be made, there is much scope to develop a more concrete understanding of how traits link to individual processes and eventually the multifunctionality of the reef. Identifying overlapping traits, causation, and improving our ability to capture intra-species trait information will greatly advance this endeavour.

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Author contributions

J.H.H. collected data, did the data analysis, and wrote the first draft of the manuscript. N.A.J.G. and D.M. helped to conceive the project, provided supervision, data analysis suggestions, and editorial comments.

Chapter 2. Decadal shifts in traits of reef fish communities in marine reserves

Abstract

Marine reserves are known to impact the biomass, biodiversity, and functions of coral reef fish communities, but the effect of protective management on fish traits is less explored. We used a time- series modelling approach to simultaneously evaluate the abundance, biomass, and traits of eight fish families over a chronosequence spanning 44 years of protection. We constructed a multivariate functional space based on six traits known to respond to management or disturbance and affect ecosystem processes: size, diet, position in the water column, gregariousness, reef association, and length at maturity. We show that biomass increased with a log-linear trend over the time-series, but abundance only increased after 20 years of closure, and with more variation among reserves. This difference is attributed to recovery rates being dependent on body sizes. Abundance-weighted traits and the associated multivariate space of the community change is driven by increased proportions over time of the trait categories: 7–15 cm body size; planktivorous; species low in the water column; medium-large schools; and species with high levels of reef association. These findings suggest that the trait compositions emerging after the cessation of fishing are novel and dynamic.

Keywords

Novel ecosystem, Marine Protected Area, Fishing, Time-series, Coral reef ecology, Kenya

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1. Introduction

No-take marine reserves are a widely used management and conservation tool, the implementation of which has been linked to a range of outcomes including increases in fish abundance, biomass, diversity, and the presence of functionally important species (O'Leary *et al.*, 2016; Edgar *et al.*, 2014; Lester *et al.*, 2009a). Quantifying the trajectories of key groups of organisms in reserves can help identify the mechanisms driving community-level responses (Brandl *et al.*, 2016; Ramírez-Ortiz *et al.*, 2020). However, variability in the temporal trends of traits and how they relate to community biomass and abundance in marine reserves remains largely unexplored. Looking at such temporal trends can often point to useful information about the response of ecosystem functional potential to conservation measures (Miatta *et al.*, 2021), with traits sometimes responding earlier than taxonomic measures (Coleman *et al.*, 2015).

Functional approaches to conservation prioritise the maintenance of ecosystem functions and services of highly diverse ecosystems in the dynamic and changing world of the Anthropocene (Bellwood *et al.*, 2019b). Ecosystem functioning can be measured directly as the rates of an ecosystem process (e.g., herbivory, predation, bioerosion, nutrient cycling) or indirectly as the functional potential of the ecosystem by looking at the functional groups or traits present within a community (Brandl *et al.*, 2019). While only indirectly capturing ecological processes, traits are more available in literature compilations and therefore can be applied to datasets retrospectively (McLean *et al.*, 2019a).

"Functional traits" are suggestive of the mechanistic links between species' responses to disturbances and management practices and their potential effects on ecosystem processes (Hadj-Hammou *et al.*, 2021). The first step in applying a trait-based approach is therefore to carefully select the traits most applicable to the ecological processes and research questions of interest. Trait selection is important to understanding the pathways of community responses and associated conclusions (Griffin-Nolan *et al.*, 2018). When assessing the functional structure of a community, traits can be weighted by abundance or biomass, allowing for proportional representation (Lefcheck *et al.*, 2019; McLean *et al.*, 2018), with abundance-weighting common practice in broad trait-based approaches (Mouillot *et al.*, 2013).

Changes in species and traits with time since protection can produce novel functional configurations. Such novel configurations can sometimes produce the same ecosystem processes as previous communities, result in the loss of some functioning, or a new balance of functions and services can establish (Harborne and Mumby, 2011; Graham *et al.*, 2014; Woodhead *et al.*, 2019). Key traits such as fish body size, trophic level, and life history strategies mediate the relationship between disturbance/recovery and abundance, biomass, and biomass production – all essential components for sustainable ecosystem functioning (Munday and Jones, 1998; Babcock *et al.*, 2010; Robinson *et al.*, 2017; Villéger *et al.*, 2017; Cinner *et al.*, 2020).

An assessment of changes over time in the traits of coral reef fish following establishment of marine reserves would enable a better understanding of the indicative impacts of protection on ecosystem functioning. In this paper, we apply a trait-based approach to a unique long-term dataset on high-compliance no-take marine reserves in Kenya, enabling a range of theory-based predictions to be evaluated (Supplementary Table S1). Specifically, we ask:

1. Do biomass and abundance trends vary over time in marine reserves?
2. Does the abundance-based trait-space of the fish community change over time in marine reserves?
3. Do the relative abundances of individual trait categories progressively shift over time in marine reserves?

2. Materials and methods

2.1. Study sites

Kenya has four high compliance no-take marine reserves. Each of the reserves are regularly patrolled government national parks and differ in when they were legally established. Malindi Marine Park is the oldest reserve and was created in 1968, followed by Watamu Marine Park in 1972, Kisite Marine Park in 1973, and Mombasa Marine Park in 1991 (see map in (McClanahan, 1994)). The sizes of the reserves' closures vary. Mombasa is 6km^2, Malindi is 6.3km^2, Watamu is 10km^2, and Kisite is 28km^2; however, the amount of coral reef area within Kisite Marine park is ~10km^2. Thus, the range in effective coral reef protected area is 6km^2 – 10km^2 (McClanahan and Graham, 2005). Malindi and Watamu are situated in close proximity. Malindi was excluded from the analyses of this study, because it was severely impacted by the 1998 bleaching event, with the fish community following lagged trends in benthic condition (Supplementary Fig. S2). Inclusion would bias the results towards benthic influence (Graham *et al.*, 2020). For the purposes of this paper, we were more interested in the effect of protection from fishing on the fish community, and as explained below, treated the reserves as a chronosequence (see section 2.4.1). The remaining three marine reserves provide a powerful dataset, spanning 44 years of protection from fishing and 732 ecological surveys.

2.2. Fish and benthic surveying

Visual censuses of fish were conducted by the same observer (TRM) during neap tides along two to five 5 x 100m belt transects in each site. All surveyed sites in the parks were located in the shallow back-reef lagoon or leeward areas. Eight fish families were sampled at species level with abundance counted consistently across the full duration of monitoring from 1991 to 2018: Acanthuridae, Balistidae, Chaetodontidae, Diodontidae, Labridae (including Scarinae), Monacanthidae, Pomacanthidae, and Pomacentridae. These families include all of the trait categories explored in this analysis. However, some trait categories were less well represented than others, namely piscivores, pelagic species, and species with low levels of reef association. Species were counted using a discrete group sampling (DGS) method, whereby families or species with similar body shapes or behaviours were identified and counted during separate passes along a transect (McClanahan, 1994; Greene, 1990). Total fish abundances (as well as trait-level abundances) were calculated as the mean number of fish/transect and standardised to the mean number of fish/ha. DGS survey dates and sites are presented in Supplementary Table S7. Benthic surveys were conducted on 9-27 10m line transects at each site using the line-intercept method. Distances of benthic cover categories under the line were assigned to nine groups: hard coral, soft coral, algal turf, coralline algae, calcareous algae, fleshy algae, seagrass, sand, and sponge.

Biomass was estimated using a different method whereby fish were surveyed at the family level within two to six 5 x 100m belt transects in each site(see (McClanahan *et al.*, 2007c) for further explanation of the two methods). Total lengths of individual fish were estimated and grouped into 10-cm size-class intervals. Total wet mass was estimated for each size-class using established length-mass relationships based on the centre point of the size-classes (McClanahan and Humphries, 2012). The families sampled in the species level abundance counts and used in the biomass analyses represented 74.2% of total biomass (in 2018). For the biomass over time model, individual site-year biomass values were used.

2.3. Fish traits

Six species-level fish traits were evaluated in this paper: body length (size), diet, schooling behaviour (gregariousness), position in the water column, reef association, and length at maturity. These traits were carefully selected according to whether they were likely to respond to protection from fishing and affect ecosystem functioning (Hadj-Hammou *et al.*, 2021) (see trait inclusion justification; Supplementary Table S1). The trait-based analysis was based on abundance data, as species level biomass estimates were not possible from the survey methodology, and the literature on trait-based ecology favours abundance-weighting (Mouillot *et al.*, 2013). Trait values were obtained from the Gaspar database (Kublicki, 2010), Fishbase (Froese, R.; Pauly, 2019), and FishLife (Thorson *et al.*, 2017). Data were available for 216 out of 219 species surveyed in the nine families; therefore, three species were excluded from the analyses.

2.4. Data analysis

2.4.1. Marine protection chronosequence

To assess how the abundance, biomass, and functional space of the fish community changed over time with protection, the temporal parameter "time since closure" was derived for each of the marine reserves. This was done for each sample point within each reserve by calculating the number of years since the establishment of the marine reserve (the year of data collection minus the year at which the marine reserve was established) to assemble a chronosequence of the data. This method has been applied to the same data to create a time-series spanning several decades of marine protection (McClanahan *et al.*, 2007b).

2.4.2. Functional space

A functional space based on fish traits within the marine reserves was constructed by carrying out a Principal Coordinates Analysis (PCoA). The PCoA was based on a Gower's distance matrix of species-level fish traits (size, diet, gregariousness, position in the water column, reef association, and length at maturity) for all years and sites using the R packages, "cluster" (Rousseeuw *et al.*, 2018) and "ape" (Paradis *et al.*, 2019). An abundance-weighted mean PCoA value for axes one and two was calculated for each site/year combination. A Pearson's correlation analysis between PCoA axes 1 and 2 values and community weighted mean (CWM) trait values shows the extent to which each of the traits were associated with the axes.

CWM trait values were calculated for each trait using the "FD" package(Laliberté *et al.*, 2015) as:

$$CWM = \sum_{z=1}^{n} p_z x_z$$

where the site-level abundance of a species z in a given year is denoted as p_z , and x_z is the trait value of species z (Lavorel *et al.*, 2007). For each categorical or ordinal trait, the proportion of trait categories within a trait was calculated as:

$$proportional\_abundance\ i = \frac{\sum Abundance\ of\ species\ with\ attribute\ class\ i}{\sum Abundance\ of\ all\ species}$$

The proportional abundance of individual traits over time were weighted by total abundance in each sampling unit. For the continuous trait, length at maturity, the abundance-weighted mean value of that trait was modelled.

2.4.3. Covariates

Several covariates explaining variation in the trait space (Supplementary Fig. S6) were included in the global models. The first covariate controlled for in the models represented the benthic community of the sites. A Principal Component Analysis (PCA) was conducted on percentage cover of 1) hard coral, 2) macroalgae, 3) coralline algae, and 4) other calcareous algae across all sites. This produced a succinct multivariate value (PCA axis 1 explaining 50% of the variation) for each site/year that captured multiple aspects of the benthos and at the same time reduced the number of parameters needed to be included in the models. Rugosity, a measure of the structural complexity of the reef (Fontoura *et al.*, 2020), was included as covariate in the models separate to the PCA of the benthic community. The mean biomass (of the eight fish families) for each marine reserve per year was also calculated and used as a covariate. For years and sites where fish survey data were collected, but other covariate data (e.g. benthic, rugosity, biomass) were missing at random points across the time-series, a Generalized Additive Mixed Models (GAMM) of the covariate over time (calendar year), with reserve as a random effect, was conducted to impute missing data from fitted values. The models were fit with a Gaussian error distribution and followed model validation protocol described below.

The next covariate incorporated into the models was a time-series of Thermal Stress Anomalies (TSAs). TSAs were included in the models as they were associated with coral bleaching events. Moreover, McClanahan(McClanahan, 2019a) showed that variation in TSA is associated with the biomass of certain fish families. Fish communities were expected to exhibit a lagged response to disturbances such as thermal stress(McLean *et al.*, 2018). TSA data from 1991-2018 for each marine park were extracted from The Coral Reef Temperature Anomaly Database (CoRTAD) hosted by NOAA Coral Reef Watch. TSAs were calculated for 4 km grid cells as the weekly sea surface temperature minus the maximum weekly climatological (long-term average) sea surface temperature(Selig *et al.*, 2010). The maximum TSA (magnitude) for each reserve in each year was selected for modelling. Therefore, the optimal time-lag for the effect of TSAs on fish functional space was assessed by lagging TSA values from 0 to 9 years and incorporating this lag into a GAMM model of the first PCoA axis. Lagged models were compared (for the same dataset years), and an optimal-fit lag of 4 years was selected to be included in the models, using the AIC selection procedure described below. The Granger Test, convergent cross-mapping and cross-correlation methods of detecting causality and time-lagged effects of covariates were trialled (McLean *et al.*, 2018; Ye *et al.*, 2015). However, due to uneven time-steps in the time-series, a modelling approach for selecting the optimal thermal stress time-lag was favoured (e.g.(Wilson *et al.*, 2016)). The four-year lag fits with previous findings showing that coral cover took approximately four years to return close to pre-1998 bleaching levels(McClanahan, 2020).

Oceanic productivity was estimated using chlorophyll a for the years 1997-2018, which were available from the Ocean Colour Climate Change Initiative dataset esa-cci-chla-monthly-v4-1 by the European Space Agency (http://www.esa-oceancolour-cci.org/). Daily data were averaged to get annual values at a 4-km resolution. For years prior to 1997, the average value of chlorophyll a for each park over the time-series was taken. Net Primary Productivity (NPP), another measure of oceanic productivity, was obtained as a static average value for the centre of each park from the Marine Socio-Environmental Covariates database (Yeager *et al.*, 2017).

An initial set of covariates including time since closure, calendar year, axis 1 of a benthic PCA, rugosity, chlorophyll a, NPP, TSA, and biomass were tested for collinearity using VIF values and checking the correlation matrices (Zuur *et al.*, 2009). Biomass, calendar year, and NPP had VIF values >3 and were therefore removed from models. All continuous covariates were scaled and centred to a mean of zero and standard deviation of one for model fitting.

Two modelling approaches were taken to explore community changes in biomass, abundance, and functional space (PCoA) over time. The first approach was to include the marine reserve (Mombasa, Kisite, Watamu) as a random effect. The second approach was to allow slopes and intercepts to vary by marine reserve. In applying these two approaches, we illustrate how the reserves form continuous patterns across the chronosequence and where they differ. For illustration purposes, all covariates aside from time since closure were held to their means and partial residuals that account for covariate effects in the models (rather than raw data points) were presented. A summary of covariates can be found in Supplementary Table S2.

2.4.4. Modelling

All research questions were addressed using GAMMs with the R package "mgcv" (Wood, 2017) to model changes of respective variables of interest over time since closure of the marine parks. GAMMs were favoured over other modelling tools, because they allow for the detection of non-linear patterns discovered in this dataset with exploratory analyses and typically present in time-series data (Simpson, 2018). A backwards selection process, whereby each variable was eliminated until all variables left in the model were significant ($p<0.05$), was used to select the optimal model, as determined by AIC scores (optimal model <2 AIC from other models). Where models did not differ more than 2 AIC, the simplest model with the fewest parameters was selected. Smoother functions for continuous covariates were fit with cubic regression splines (Wood, 2006). The number of knots (k) in a smoother determines the "wiggliness" of the smoother parameter's curve (Pedersen *et al.*, 2019). This number was estimated by comparing Estimated Degrees of Freedom (EDF) values to k and through a generalized cross validation technique. The number of knots was restricted to four for the time since closure parameter, in order to allow for polynomial relationships and to detect a range of non-linear trends, but also to restrain the flexibility of model fits for ease of interpretation and to limit computation time (Pecuchet *et al.*, 2017). An ARMA(1,0) residual autocorrelation structure was added to the models to account for dependent values on preceding years within the same site (F. Dormann *et al.*, 2007). The need for an autocorrelation structure was assessed visually using the auto-correlation function (ACF) (Zuur *et al.*, 2009). For the biomass model with the marine reserve as a random effect, a residual variation structure, VarPower, was also incorporated. Optimal model equations and outputs can be found in Supplementary Tables S3-S5.

All models were validated following protocols outlined in Zuur & Ieno (2016). Significant outliers, as determined by Cook's Distance, were removed to ensure they did not over-influence results (Zuur *et al.*, 2009) (but see Supplementary Fig. S5). Model assumptions were checked by plotting model residuals against fitted values as well as covariates included and excluded from the models. Biomass and abundance data were log-transformed and trait proportions were logit transformed in order to normalise the residuals (as in (Schulp *et al.*, 2014; Pecuchet *et al.*, 2017)), after trialling the use of different distribution families (Warton and Hui, 2011). Biomass, abundance, and proportional trait models had a Gaussian distributed error term, while PCoA and length at maturity (logged cm) had a Gamma distributed error term. All data analysis was conducted using R Version 3.6.3. (R Core Team, 2020).

3. Results

3.1. Biomass and abundance models

Biomass and abundance both increased over time since the cessation of fishing, while holding other covariates to their means (Fig.1). However, while the slope of biomass was close to log-linear (EDF = 1.330, R^2 = 0.255), with the rate of increase slowing just after 20 years of closure, the abundance curve was relatively flat to 17 years, and then steeply increases to a peak at 35 years (EDF = 2.68, R^2 = 0.83; Supplementary Table S3). When the slope of the biomass curve was allowed to vary by marine reserve, the marine reserve trends remained very similar to the global trend. However, when the slope of the abundance curve was allowed to vary by marine reserve, only Mombasa had a significant, positive trend (EDF = 2.28, R^2 = 0.74, $p<0.001$). Kisite's abundance slope was not significant when looked at independently ($p=0.20$), but in the hierarchical global model, it appears to drive the steep increase in the overall trend, whereas, Watamu flattens the curve (Supplementary Table S3). Importantly, the overlap between abundance values in Kisite and Mombasa around 20 years of closure, indicates that this increase was more likely due to time since closure, rather than Kisite having a higher abundance of fish than Mombasa. There was a mass bleaching event in 1998, which corresponded to 7 years of closure for Mombasa, 25 years of closure for Kisite, and 26 years of closure for Watamu, but this does not appear to have an overall effect on the recovery trajectory of fish abundances in each of the reserves included in this analysis (Fig. 1.b.; Supplementary Fig. S1).

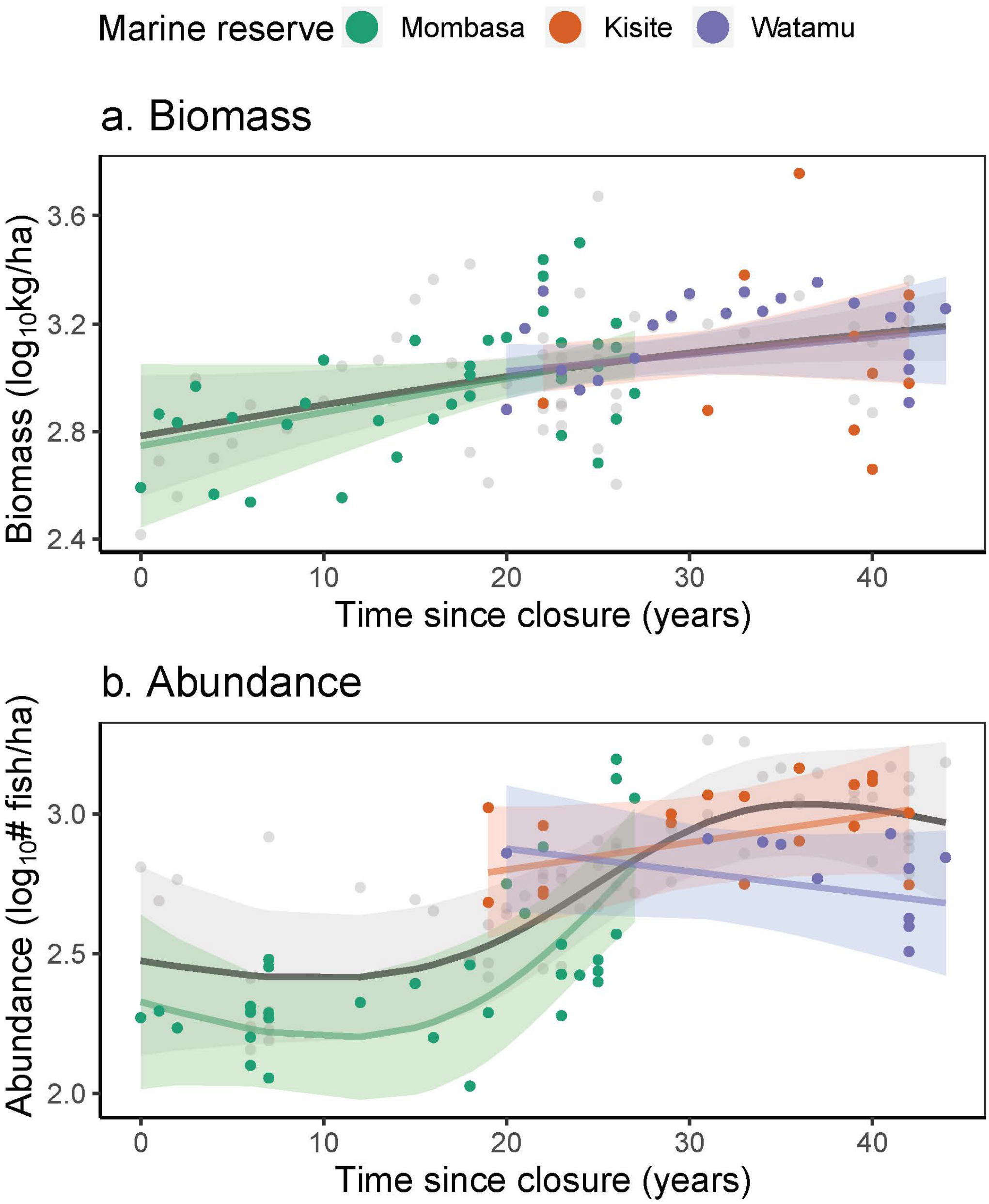

Figure 1. Modelled changes in a) mean biomass (logged) and b) mean abundance (logged) over time since closure of the marine parks, holding other covariates to their means, with 95% confidence intervals shaded. Points are partial residuals for the models with colours corresponding to the marine reserve, where Mombasa = green, Kisite = orange and Watamu = purple. The model with marine reserve as a random effect is illustrated in grey.

3.2. Functional space

The first two PCoA axes captured 75% of the variation in the trait space of the 216 species assessed in this analysis (Fig. 2.a.). The top five trait categories most positively associated with axis 1 of the fish community PCoA are bottom-dweller, large length at maturity, solitary, invertivorous (mobile invertebrate feeders), and medium reef association. The most negatively associated traits with PCoA axis 1 were planktivorous, low in the water column, medium group, high reef association, and 7.1-15cm sized fish (Fig. 2.b.). The top five traits most positively associated with PCoA axis 2 were 7.1-15cm sized fish, high reef association, small group forming, bottom dweller, and invertivorous (mobile invertebrate feeders). The most negatively associated traits with PCoA axis 2 were 15.1-30cm, medium reef association, 50.1-80cm, medium group forming, and pelagic (Fig. 2.c.).

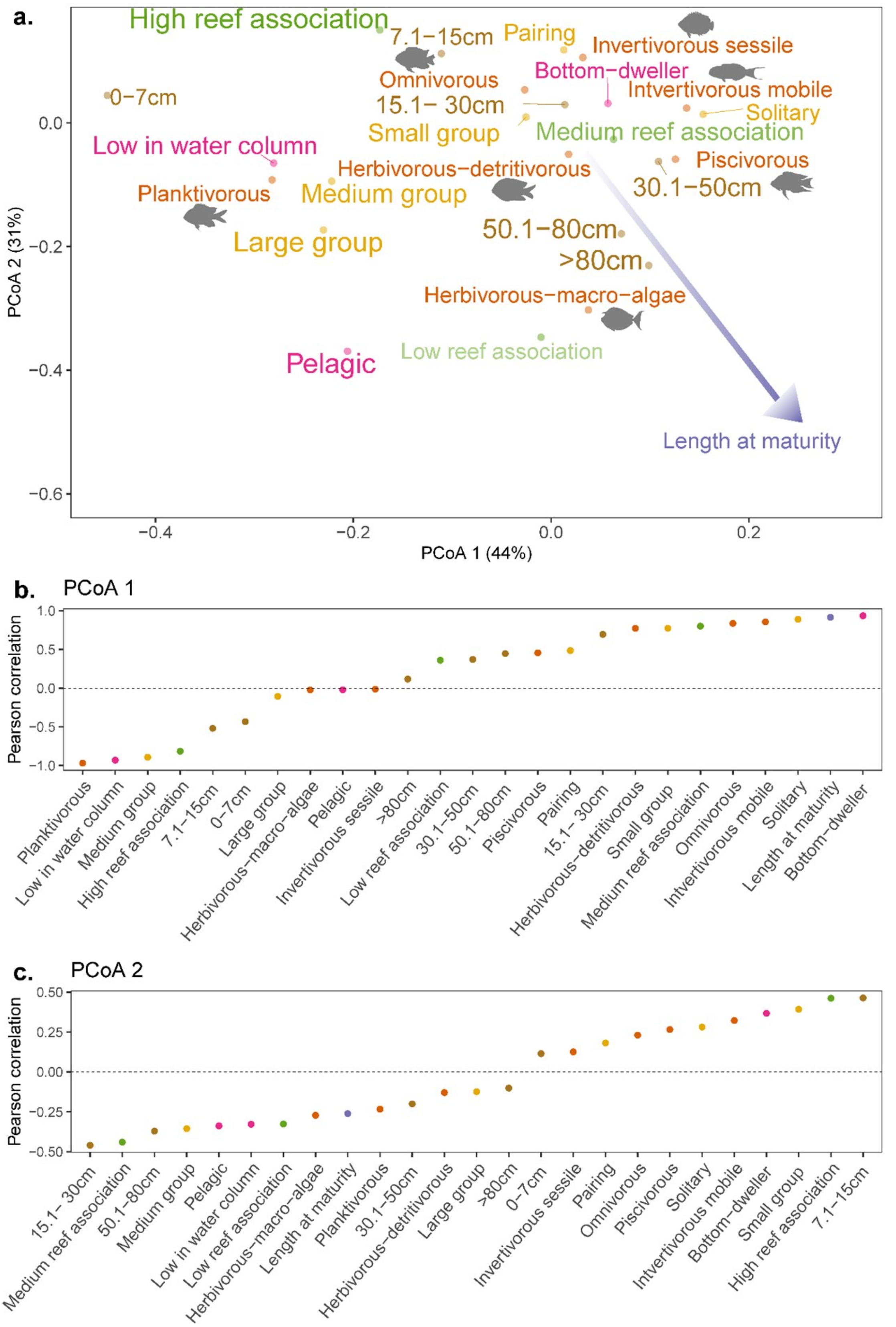

Figure 2. a) Functional space of Kenyan marine parks across all sites and years spanning the chronosequence. Traits included: size, diet, gregariousness, position in the water column, reef association, length at maturity. Traits grouped by colour: purple = length at maturity, green = reef association, yellow = gregariousness, pink = position in

the water column, brown = size, and orange = diet. A colour and size gradient are applied to each ordinal trait, increasing in size and opacity along the gradient. b) Pearson correlation between community weighted mean values of trait categories and PCoA axis 1 and c) PCoA axis 2.

Both PCoA axes' 1 and 2 mean community values had a negative relationship with time since closure of the marine parks, while holding other covariates to their means (Fig. 3), and the time smoother was significant for both axes (Axis 1, $p = 0.01$; Axis 2, $p = 0.03$). However, a greater proportion of the variance was described in the model by PCoA 1 ($R^2 = 0.75$) compared to PCoA 2 ($R^2 = 0.44$) (Supplementary Table S3). This indicated a shift from solitary bottom dwellers, with large lengths at maturity, and invertivorous diets, towards medium size group forming, high to medium level of reef association fish found low in the water column, sized 7-15cm, with planktivorous diets. These traits were mostly represented by species in Pomacentridae, with *Chromis dimidiata, Chromis viridis, Neopomacentrus azysron*, and *Pomacentrus caeruleus* largely driving the trends (Supplementary Fig. S3). While the overall axis trends decrease, when the slopes were allowed to vary by marine park, we see a difference in trends between Kisite and Watamu. The PCoA axis 1 values for Kisite decreased significantly over time ($p<0.001$), while the PCoA axis 1 values for Watamu do not change significantly over time ($p = 0.908$). For PCoA axis 2, Kisite increases over time ($p = 0.012$), while Watamu decreased over time ($p < 0.001$). However, the PCoA axis 1 model explained more variance ($R^2 = 0.645$; deviance explained = 67%) than the PCoA axis 2 model ($R^2 =0.48$; deviance explained = 50.2%).

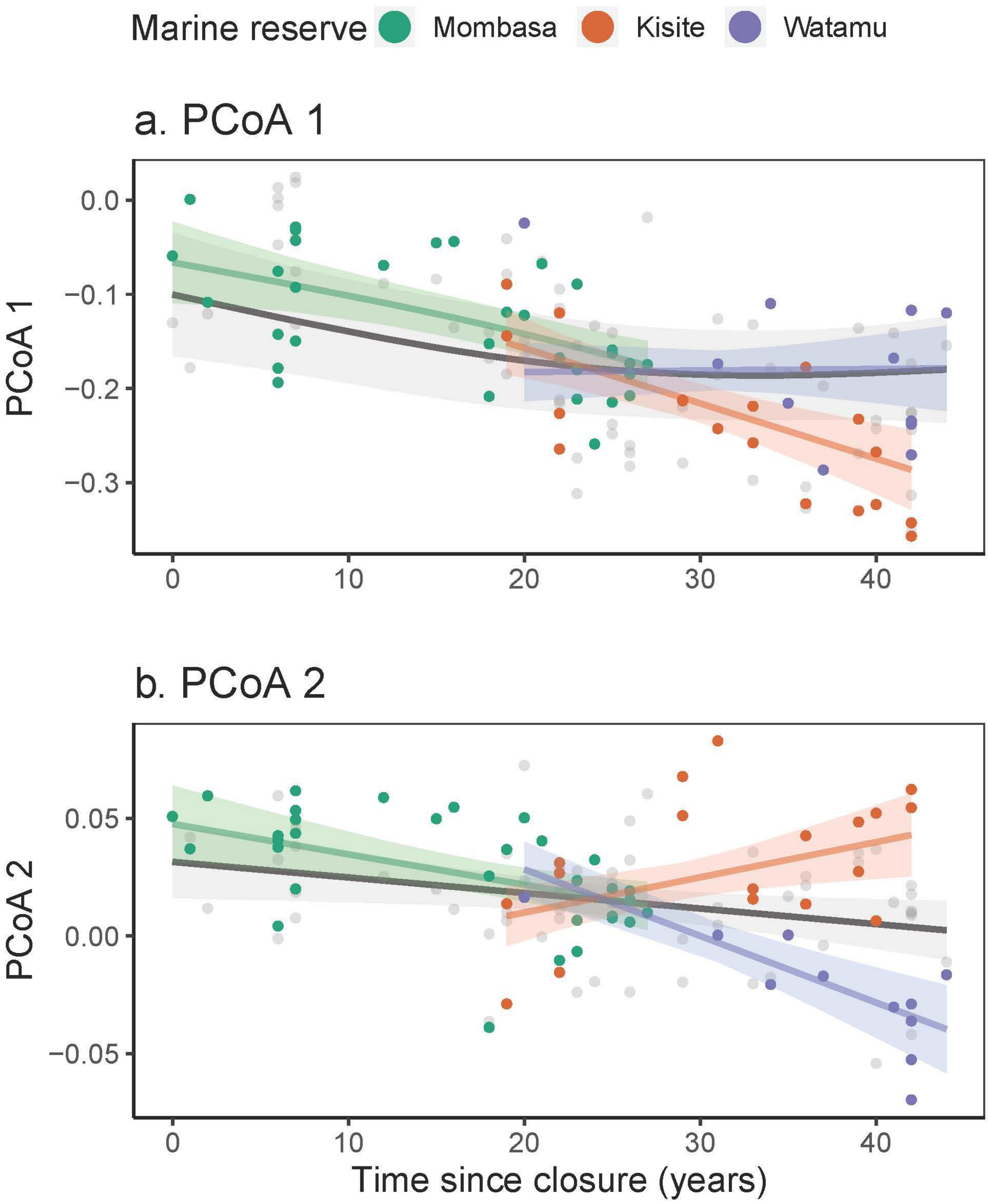

Figure 3. Modelled changes in a) PCoA 1 and b) PCoA 2 over time since closure of the marine parks, holding other covariates to their means, with 95% confidence intervals shaded. Points are partial residuals for the models with colours corresponding to the marine reserve, where Mombasa = green, Kisite = orange and Watamu = purple. The model with marine reserve as a random effect is illustrated in grey.

3.3. Shifts in trait proportions and means

Individual trait proportions enable a clearer understanding of the mechanisms behind shifts in the multivariate trait space. We found that the majority of trait categories exhibited some change over time with protection (Fig. 4). Within the first 20 years of protection, a significant shift towards the increasing dominance of fish in the size-class 7-15cm is observable, particularly increasing after 17 years, likely driving the overall abundance trend. The 15-30cm size-class declined over time, while there was a slight increase in the proportion of fish in the 30-50cm size-class between the beginning and end of the chronosequence, likely driving the overall biomass trend (Fig. 4.a.).

Planktivores, the most dominant diet category, become more proportionally abundant over time with protection (Fig 4b). When holding all other model covariates to their means, the rate of increase in proportional abundance steepens after 20 years of protection and declines again after 30 years of protection (EDF = 2.60). Sessile invertebrate feeders, piscivores, and macroalgal feeders also increased, while detritivores, omnivores, and mobile invertebrate feeders decreased (Fig. 4.b.).

The proportion of pelagic fish recorded in the survey sites within the marine parks was consistently lower than both bottom-dwellers and fish low in the water column, likely due to the location of the survey sites on lagoonal back reefs. However, an increase in the dominance of fish low in the water column over bottom dwellers is observable after 20 years of protection, which corresponds to the first recordings of Watamu and Kisite marine reserves in the chronosequence (Fig. 4.c.). The random effect term “marine reserve” however, was not significant in the model, suggesting the patterns were more likely attributable to time since closure across the chronosequence (Supplementary Table S4).

Medium group-forming species, initially equally as dominant as solitary and small group (3-20 individuals) forming species become more dominant over time. All trends for schooling categories were linear or close to linear (EDF between 1.000031-1.000505). While large (>50 individuals) groups increase over time, solitary, pairing, and small group (3-20 individuals) forming fish species decrease (Fig. 4.d.).

Patterns of change observed in levels of reef association were similar to those found for position in the water column. Fish with low levels of reef association were proportionally less abundant in the surveys than those with medium and high association across the time series, due to similar issues with sampling design that resulted in few pelagic fish being detected; Figure 2.a. highlights the proximity of these two traits within the functional space. A switch from the dominance of medium to high levels of reef association can be observed after 20 years of protection (Fig. 4.e.).

The last trait assessed was an abundance-weighted means of the continuous measure, length at maturity. Mean length at maturity did not significantly change over time (Fig. 4.f.), but this was likely due to the retrospective allocation of lengths at maturity at the species level, as intraspecific data on this were not available over time (see model outputs in Supplementary Table S5).

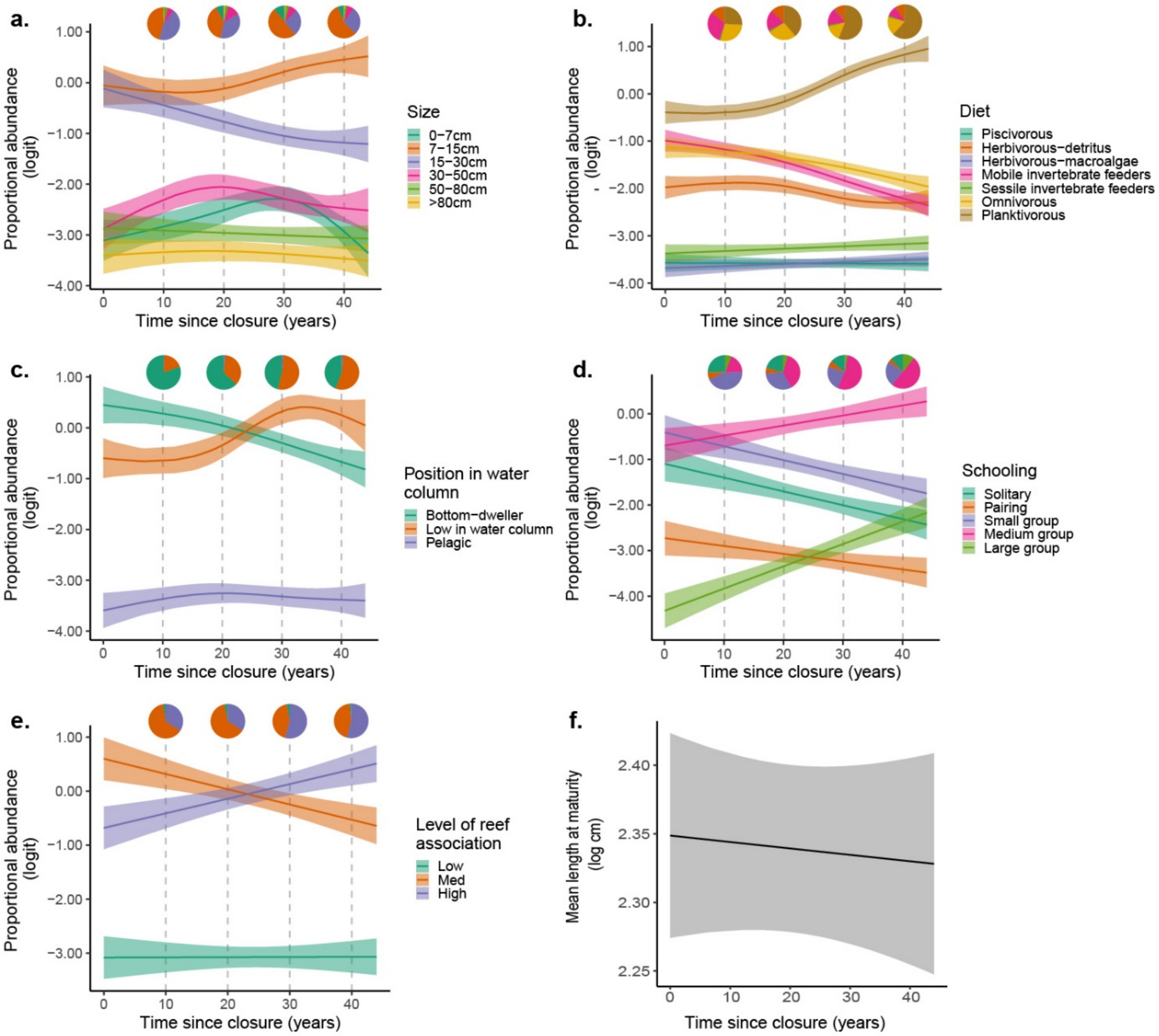

Figure 4. Modelled changes in proportional abundance of trait categories (a-e; a. Size, b. Diet, c. Position in the water column, d. Schooling, e. Level of reef association) and mean values (f. Mean length at maturity) of coral reef fish traits over a chronosequence of time since closure of marine parks, holding other covariates to their means, with 95% confidence intervals. Colours of the curves indicate the trait categories. Vertical dashed lines indicate ten year marks in the chronosequence for which average trait category proportional abundances.

4. Discussion

Developing our understanding of the mechanisms by which marine reserves affect ecosystem functioning is critical to identifying how, when, and if marine ecosystems recover from fishing(MacNeil *et al.*, 2015). We illustrate a shift in functional space over time with protection towards communities numerically dominated by fish in the size-class 7-15cm, with a planktivorous diet, found low in the water column, forming medium-large schools, and with a high level of reef association. These findings were based on species' trait abundances, and while both overall biomass and abundance increased over time, their patterns of increase differed.

The difference in shape between the biomass and abundance curves reflected community shifts occurring at the level of species' traits. While the slope of the biomass curve increased steeply immediately following protection, the abundance curve did not follow suit until nearly 20 years of closure, when the rate of increase in biomass began to decline. The number and size of larger fish (e.g., 30-50cm) increased early in the chronosequence, while the abundance of small, more proportionally abundant fish (e.g. 7-15cm) did not increase significantly until 20 years of closure. This shift appeared to be largely driven by Kisite, which did not have as much absolute change in hard coral cover following the 1998 bleaching event as Watamu and Mombasa(McClanahan *et al.*, 2007a). Kisite's benthic PCA had a positive relationship with axis 2 of the fish community functional space, for which the 7-15cm size class trait was strongly correlated (Supplementary Fig. S10). This was reflected in Kisite's deviation from the overall trend in PCoA 2. Kisite marine reserve is located further offshore than the other two reserves, had less coral cover than the other reserves prior to 1998, and has less market gravity than both Mombasa and Watamu(Chirico *et al.*, 2017). It is possible that these factors interacted to create a greater buffer against fish community change driven by disturbance to the benthos. After time since closure, thermal stress and benthic composition explained the most variance in the functional space models (Supplementary Fig. S7).

Because the fish trait size bins were somewhat arbitrary, as size is a continuous trait, and the 7-15cm and 15-30cm categories were sequential, the patterns observed were not easily distinguishable from those driven by shifts in species composition, a consequence of using an interspecific trait-based approach(McLean *et al.*, 2019a). However, a sensitivity analysis revealed that even when the most abundant species in the 7-15cm size-class, *Chromis dimidiata*, was removed, the same trends persisted (Supplementary Fig. S4). Larger bodied fish were likely to be driving overall biomass trends, while small fish were likely to be driving the overall abundance trends and appear to be responding in sequence and contrary to the ecological succession expectation that small fish will respond more rapidly than large fish(McClanahan *et al.*, 2020). Perhaps the deviation from expectation occurs because fish in the 30-50cm size-class were disproportionately targeted in Kenyan fisheries(Mbaru *et al.*, 2019), and therefore, they increase rapidly when released from predation. Smaller fish, in contrast, responding to slower contextual changes in the food web.

We hypothesised that there would be a decrease in smaller size-classes and an increase in larger size-classes, as fishing exploitation has been shown to increase the steepness of the slopes of coral reef fish size spectra, due partly to the effects of predation release(Dulvy *et al.*, 2004). Increased predation in reserves may therefore be expected to drive a reduction in smaller size-classes and an increase in larger size-classes. However, previous research has demonstrated that piscivores are not disproportionately caught in Kenyan fisheries, and therefore they do not experience the rapid recovery following protection that might lead to a decrease in smaller fish (Fig. 4) (Mbaru *et al.*, 2019). In geographies where piscivores are a more prominent component of the fish community, these patterns may differ. Similar work evaluating shifts in the biomass of trophic groups indicated that the overall trophic level of fish within Kenyan marine parks was decreasing over time as slow-growing herbivores come to dominate the biomass(McClanahan and Humphries, 2012). It may be that these small to modest-size urban parks are not large enough to support the space requirements of large piscivores(D'Agata *et al.*, 2016). Therefore, the responses observed here may only be applicable to these types of modest-size closures of <10 km^2.

The four most economically valuable fish families in Kenya, including Lutjanidae (Snappers), Lethrinidae (Emperors), Siganidae (Rabbitfishes), and Serranidae (Groupers), were not included in the list of eight families surveyed for the full duration of the chronosequence. The species list for this study comprised of mid-value and bycatch families that are more common in the fisheries (e.g. Scarinae)(Mbaru and McClanahan, 2013) and contribute most to fish biodiversity. They make up the bulk of the abundance and biomass. Thus, the functional importance of the trait shifts observed in this study should be interpreted through the lens of the mass-ratio hypothesis – whereby it is the more abundant traits or species that have the greatest functional impact(Grime, 1998). For example, for diet, the most abundant trait class (planktivores) became even more abundant with protection. Where the abundance of mainly small planktivores adds up to produce large proportions of the biomass, systems can be said to be “middle-driven”; these middle-driven trophic pyramids have been found to exist at high levels of biomass, regardless of protection regime(Campbell *et al.*, 2020; Heenan *et al.*, 2020). Planktivores provide important pelagic subsidies to a reef, increasing overall productivity and playing a key role in nutrient cycling(Morais and Bellwood, 2019). Many planktivores are also dependent on reef structure for recruitment and predator avoidance(González-Rivero *et al.*, 2017; Coker *et al.*, 2012). Their abundances have been shown to decline with coral bleaching and the loss of structural complexity and increase with protection from fishing(Benkwitt *et al.*, 2019; Russ *et al.*, 2017). Some planktivorous families, such as the Pomacentridae, are considered “bycatch” in Kenyan fisheries and are not specifically targeted. The increase in the proportional abundance of planktivores could therefore primarily be linked to the recovering habitat within protected areas(Darling *et al.*, 2013; Strain *et al.*, 2019b).

Evolutionarily, shifts to planktivory are linked to increasing schooling behaviour(Floeter *et al.*, 2018). Our analysis showed that these trait categories, which tend to cluster, were both increasing over time with protection. An increase in the abundance of fish exhibiting gregarious behaviour has implications for functional processes related to how much fish consume. For example, Michael et al.(Michael *et al.*, 2013) found that both herbivory rates and the amount of algae consumed by three studied species were higher when individuals fed in monospecific groups. Social aggregations should theoretically lead to more protection, and therefore the increased ability to forage(Paijmans *et al.*, 2020). However, resource competition among those in the group can also lead to less overall consumption. It has been demonstrated that for a planktivorous species, this trade-off between protection and competition is mediated by the availability of resources(White and Warner, 2007).

Competition within groups also affects life history characteristics dependent on environmental stochasticity, so that individuals in larger groups tend to have slower growth rates(van Kooten *et al.*, 2007). Interestingly, however, we did not see a significant positive response to protection in the length at maturity trait. This may be due to the interspecific approach taken in the analysis that doesn’t account for changes in the phenotypic plasticity of individuals and evolutionary adaptations inherited in specific populations over time(Kelley *et al.*, 2018; Rochet, 1998). Again, the patterns here may also be a function of the limited space of the closures that could exclude long-lived and late-reproducing species. These closures should not be viewed as undisturbed systems but rather islands within fished seascapes(McClanahan *et al.*, 2019). Nevertheless, given the interspecific approach, we would expect that considering the overall PCoA abundance trends towards smaller or moderate-sized species, these species would have smaller lengths at maturity. This is because length at maturity, like many traits, is highly correlated with size (Jacob *et al.*, 2011).

The trait-based analyses presented in this paper were abundance-weighted. This provides a species-level approach to compliment previous family-level studies weighted by biomass investigating the Kenyan marine park system (McClanahan and Graham, 2015; McClanahan and Humphries, 2012). If intraspecific or species-level body sizes were available to evaluate biomass-weighted trends, it is possible that different patterns could emerge, with implications for ecosystem functioning. For example, families such as Labridae (Scarinae) and Acanthuridae have been shown to dominate the biomass of marine reserves in Kenya over time with protection from fishing(McClanahan *et al.*, 2007b). These families consist of herbivorous and large-bodied fish, and their functional impact has been demonstrated in experiments(Humphries, 2020). Abundance-based metrics may not reflect the dominance of these groups as much as biomass-based metrics. Therefore, it is necessary to interpret these results as a component of a multi-faceted approach to understanding ecosystem processes as a function of both abundance and biomass. Furthermore, directly measuring ecosystem processes (e.g. herbivory, predation, etc.) would also provide a fuller picture(Brandl *et al.*, 2019).

Increases in fish biomass, abundance, and the proportion of functionally important traits over time with high compliance protection is expected to represent recovery from fishing pressure(Ward *et al.*, 2001; Bergseth *et al.*, 2017). However, this recovery is taking place in the context of a changing climate and a dynamic ocean(McClanahan, 2014; Graham *et al.*, 2020). While we see an increase in the biomass and abundance of fish in Kenya's marine reserves, species and traits have not necessarily recovered, in that they have not returned to historic compositional "baselines"(Mcclanahan and Omukoto, 2011). Incorporating the concept of a novel ecosystem into conservation moves away from the *de facto* goal of restoration to ecological baselines(Graham *et al.*, 2014). In this paper, we demonstrate how fish traits respond over time to the establishment of marine reserves. The resulting community after 44 years of protection appears to still be changing and not approaching a plateau. While some traits have become more dominant over time (e.g., 7-15cm, planktivores), other traits (e.g., high gregariousness, high reef association) have started to surpass those that were previously dominant. This highlights the importance of interpreting patterns within the socio-ecological context in which marine reserves are situated, the dynamic nature of recovery, and the potential for novel trait configurations to shape the provision of altered ecosystem functions and services(Williams and Graham, 2019).

Data availability

The data and code used for this study will be made available on https://github.com/Jeneen/trait_time_series

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Author Contributions

JHH did the data curation, data analysis, and wrote the first draft of the manuscript. TM collected the field data. NG and TM helped to conceive the project, provided supervision, data analysis suggestions, and editorial comments. All authors contributed to the article and approved the submitted version.

Chapter 3. Evaluation of coral reef fish biomass estimation methods for marine management in a proposed Transboundary Conservation Area

Abstract

Fish biomass is a critical indicator of ecosystem functioning and fisheries sustainability. It is also key to assessing the effectiveness of fisheries closures in Marine Protected Areas (MPAs). However, underwater surveys commonly used to assess fish biomass on coral reefs require fish identification and snorkelling/diving skills, meaning MPA managers and fishing communities are not always able to routinely collect relevant data and use it in decision-making. We compare the ability of three methods (Underwater Visual Census (UVC) surveys, single-camera video transect surveys, and baited fish traps) to distinguish between biomass differences in a proposed Trans-Boundary Conservation Area between southern Kenya and northern Tanzania across a range of management regimes. UVC surveys are the primary scientific method used in fish biomass assessments and provide globally comparable metrics, but they require substantial skills, including the ability to rapidly assess fish size, and cannot be done as a team, reducing the opportunity for collective learning. We therefore compared biomass assessments from UVC surveys to single-camera video transects and locally made baited basket traps. For the video transects, we estimated biomass using maximum fish lengths from FishBase and found that there were no statistical differences between biomass estimates obtained using UVC and video methods. Video transects provide a long-term record and can allow teams to learn fish identification through videos, but the method has extensive post-processing times that may make it prohibitive in management contexts. Biomass estimated from baited fish traps could not be compared to UVC and video data as, unlike transect data, traps cannot be used to calculate an area-based biomass density estimate, and thus the units were incomparable. However, we present the results from a pilot study assessing the potential for fish traps to be used as a management tool and demonstrate that fish traps produce large variation and a high percentage of zeros over all the sites, but they capture broad biomass trends across management regimes (e.g. fished versus protected). Furthermore, we used the preliminary results to inform an *a priori* power analysis to determine that 25 traps at each site would be needed to detect biomass differences between management regimes, and 41 sites across the region would be needed to build a linear model to predict fish biomass density (kg/ha). We also compared the functional space of fish species recorded using each of the methods. Both the UVC and video surveys captured the majority of the functional space (79% and 89%, respectively) based on 6 traits, but the trapping method detected a more limited suite of species and their traits (62%). The evaluation of methods opens up options for a wider variety of people to engage in fish biomass assessments and learn from them for management purposes, and we evaluate the advantages and disadvantages of each approach.

Keywords

Participatory monitoring; Fish traps; Video transects; Kenya; Tanzania

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1. Introduction

Approximately 90% of the world's fish workers and 50% of global fish catches can be attributed to small-scale fisheries (SSF; Kurien, 2015), with over a quarter of the world's small-scale fishers operating on coral reefs (Teh *et al.*, 2013). Fish biomass is an important indicator of ecosystem functioning and fishery sustainability. Monitoring the standing-stock biomass of fish on a reef can enable ecosystem-based fisheries management, as the functional composition of fish communities has been shown to vary across a biomass gradient, with important functional groups being present above biomass thresholds (McClanahan *et al.*, 2015). Fish biomass also responds to well-enforced fishing protections including gear restrictions and no-take Marine Protected Areas (MPAs) - averaging biomass 27% higher than fished reefs, globally (MacNeil *et al.*, 2015). While well-enforced no-take MPAs are good predictors of high fish biomass on a reef (Cinner et al., 2016), Other Effective Area-Based Measures (OECMs) have been shown to be successful in managing fish biomass and can enable "equitable and effective" conservation (Gurney *et al.*, 2021). When considering social equity in conservation management, a key factor is that local people are able to "participate or take an active role in management activities" (Bennett *et al.*, 2021). In some regions, the COVID-19 pandemic accelerated the move towards ensuring more local actors are involved in evaluation and management of the marine environment, especially through monitoring efforts. This is because travel restrictions resulted in survey sites becoming inaccessible to non-local data collectors, and data-collection field seasons were cancelled or postponed due to infection risks. Sugai (2020) asserts that the COVID-19 pandemic has exemplified the need for automated biodiversity monitoring where possible, as it would allow scientists to gather data without being physically present at study sites. In remote areas without local scientists, resource users, or data collectors present, this might be necessary. However, international travel restrictions have also resulted in the empowerment of local scientists through a decrease in "parachute science" (Mangubhai *et al.*, 2021; Stefanoudis *et al.*, 2021; Braun, 2021). In many areas, local capacity for conducting monitoring efforts might already be present, but this capacity will vary geographically. Therefore, developing inclusive monitoring approaches that allow collective learning is increasingly important.

Data on coral reef fish biomass has successfully been collected by trained volunteers, citizen scientists, community members, marine managers, and professional scientists. But, as with many observational sciences, the variance and quality of the data can vary greatly depending on the data collector (Uychiaoco *et al.*, 2005). Crucially, monitoring fish biomass is not always feasible for fishing communities and MPA managers and is contingent on local capacity. In order to obtain estimates of fish biomass at a given site, surveys that record the length, abundance, and taxonomic identity of a representative sample of fish in that area need to be conducted. Established length-mass relationships for species or families can then be used to convert an individual fish from length to mass. Total fish biomass is then typically presented per unit area, and can be compared across management regimes, over space and time, or in any way that best suits resource user, management, or research needs. Conducting surveys and processing data in this way to derive fish biomass estimates requires some training or expertise. Alternatively, automated methods are being developed, but are still in nascent stages and are prohibitively costly in many cases (Maslin *et al.*, 2021). The challenges in conducting UVC surveys highlight the need to explore other methods to collect biomass information and evaluate how comparable estimates are among approaches.

In this paper, we explore three methods for collecting fish biomass data at sites in the proposed Marine Transboundary Conservation Area (TBCA) between Kenya and Tanzania (MPRU and KWS, 2017). The TBCA, spanning from Diani-Chale in Kenya to the northern border of the Tanga Coelacanth Marine Park in Tanzania, has two broad objectives: 1) “Conserve and sustainably manage the biodiversity and productivity of the coastal and marine ecosystems in the transboundary conservation area between Kenya and Tanzania”, and 2) “Enhance the contribution of the transboundary conservation area to the socio-economic development and the wellbeing of human communities in both countries” (Secretariat of the Nairobi Convention, 2018). Differences in fish biomass exist across the region due to differences in management regimes, fishing pressures, national governance approaches between Kenya and Tanzania, and environmental drivers. In particular, fish biomass tends to be notably higher in the East Africa region in well-enforced (high compliance) fisheries closures (McClanahan *et al.*, 2009). Within the proposed TBCA, there are several types of MPA (high compliance no fishing, gear restricted access, general use), community closures, and fished zones.

The three methods we assess to evaluate fish biomass trends between management regimes across the TBCA are:

1) UVC belt-transect biomass surveys conducted by an experienced international scientist (McClanahan et al., 2007).
2) Video belt-transect surveys conducted by local researchers using a single, hand-held camera, requiring post-processing analysis of videos.
3) Artisanal fish traps deployed collaboratively with community members (done only in the Kenya portion of the TBCA).

We then explore the advantages and disadvantages of each of the approaches and compare the functional space of species based on 6 common fish traits surveyed using each of the methods. Finally, using the fish video transects that were done consistently across the TBCA in the same time period, we evaluate fisheries and MPA management effectiveness in this ecologically important region.

2. Methods

2.1.Study sites

A total of 28 coral reef sites were included in this study. Sites ranged from 4.31°S (Tradewinds, Kenya) to 5.28°S (Tanga Coaelacanth-Mwamba Makome, Tanzania). All sites were on forereef or backreef lagoon habitats with substantial coral cover (Table 1; Figure 1). Fish biomass was estimated at each of the sites using one or a combination of several of the three methods explored in this paper: UVC biomass surveys, video surveys, and fish traps (Table 1; Figure 1). Prior to 2020, UVC surveys were the method used to collect fish community data. However, the capacity to conduct UVC surveys was not available during the COVID-19 pandemic. Video surveys emerged as a potential solution to this limitation. At the same time, we had begun trialling the use of fish traps as community learning tools. This was an opportunistic study. Therefore, UVC, video and fish trap sites were pooled across management categories and countries for comparison. The sites are not necessarily the same across methodologies. Moreover, because fish traps were still being trialled, they were only deployed in Kenya (Table 1).

In Kenya, sites represent one of four management regimes. Government-run MPAs in Kenya are managed by the Kenya Wildlife Service (KWS) and include two zones: parks, which are closed to all extractive use, and reserves which allow only legal fishing gears. Kenyan parks are well-enforced and thus considered “high compliance” MPAs. Kenyan reserves currently do not have any legal restrictions on fishing beyond use of legal gears but may be higher compliance than non-MPA fished sites due the enforcement by the KWS. In the TBCA, there are two MPAs in Kenya: the Kisite Mpunguti Marine Park and Reserve and the Diani-Chale Marine Reserve. However, due to historic community resistance, the Diani-Chale Marine Reserve remains a paper park and has no active management. The Kisite Mpunguti Marine Park and Reserve is comprised of the 28 km^2 park (closed to extractive use) and the 11 km^2 reserve (legal fishing gears only). In Kenya, there are also community-run fisheries closures (locally known as *tengefu*), though these tend to be low-compliance due to poor community enforcement ability. Areas outside MPAs are referred to here as “fished”, and though there are national laws regulating the use of harmful fishing gears (e.g., beach seines), compliance is quite low in fished areas.

In Tanzania, sites represent one of six management regimes. Government-run MPAs in Tanzania are managed by the Marine Parks and Reserves Unit of Tanzania (MPRU) and are either part of multi-zone marine parks or are single-zone marine reserves. Marine Parks in Tanzania are comprised of three zones: a core zone closed to all extractive use, a specified use zone that allows only resident fishers to fish the area and only non-harmful fishing gears, and a general use zone that is managed by the MPRU but allows all legal fishing gears. Marine Reserves in Tanzania are single-zone MPAs that are closed to all extractive use. However, due to staff and budget limitations, MPAs in Tanzania (regardless of zone or designation) are generally not well enforced and are therefore considered “low compliance”. In the current TBCA boundaries, there are four marine reserves: Kwale Island (12 km^2), Mwewe Island (0.4 km^2), Kirui (36 km^2) and Ulenge Island (3 km^2). Just south of the current TBCA boundary (and under consideration for inclusion in the TBCA by the governments) is the Tanga Coelacanth Marine Park. In the Tanzanian TBCA, at the time of the study, there were no community closures. As in Kenya, areas outside MPAs are referred to here as “fished”, and though there are national laws regulating the use of harmful fishing gears (e.g., beach seines), compliance is quite low in fished areas.

Table 1. Site classifications by management type fish survey method (UVC transect, video transect, trapping), and mean coral cover.

Country	**Site**	**Management type**	**Survey method**	**Date of fish survey**	**Date of coral cover survey**	**Mean coral cover (+/- 1 SD)**
Kenya	Diani	Fished	UVC-a, UVC-b	January, 2020	January, 2020	8.60+/-1.23
	Kasa Msambweni	Fished	UVC-a, UVC-b	January, 2020	January, 2020	15.88+/-2.69
	Vanga-Midjira	Fished	Trapping	January, 2019	April, 2013	31.62 +/-6.27
	Jimbo-Mwipwa	Fished	Video, Trapping	January, 2019	November, 2020	37.92+/-7.74
	Tradewinds	Community closure	Video, Trapping	January, 2019	December, 2020	25+/-5.77
	Kibuyuni (2 sites)	Community closure	UVC-a, UVC-b	January, 2019	January, 2019	42.28 +/-6.46
	Wasini	Community closure	UVC-a, UVC-b	January, 2019	January, 2019	48.67 +/-3.50
	Vanga	Community closure	Video, Trapping	October, 2020	October, 2020	26.25+/-8.43
	Jimbo	Community closure	Video, Trapping	November, 2020	November, 2020	17.92+/-7.74
	Mkwiro	Marine Reserve (gear restricted)	Video, Trapping	November, 2020	November, 2020	29.17+/-9.28
	Kisite (2 sites)	Marine Park (no fishing)	Video, Trapping, UVC-a, UVC-b	January, 2019	January, 2019	60.64 +/-5.82
Tanzania	Jasini-Mwambwa Mbayai	Fished	Video	November, 2020	November, 2020	8.33+/-10.14
	Jasini-Mwambwa Mijira Kaskazini	Fished	Video	November, 2020	November, 2020	7.2+/-5.53
	Moa-Mwambwa Mwezi Kusini	Fished	Video	November, 2020	November, 2020	42.08+/-17.1
	Ndumbani-Mwamba Bunju Kusini	Fished	Video	November, 2020	November, 2020	30.42+/-14.3
	Mgandi	Fished	UVC-a, UVC-b	October, 2018	October, 2018	39.38 +/-4.18
	Kasa Boma	Fished	UVC-a, UVC-b	October, 2018	October, 2018	45.00 +/-4.25

	Kirui-Mwambwa Shangani	Marine Reserve (no fishing)	Video	November, 2020	November, 2020	27.08+/-8.54
	Kwale-Mwambwa Mvinjeni	Marine Reserve (no fishing)	Video	December, 2020	December, 2020	44.58+/-12.28
	Ulenge-Mwambwa Mnarani (2 sites)	Marine Reserve (no fishing)	Video; UVC-a, UVC-b	December, 2020 (video); 2017 (UVC)	December, 2020	44.58+/-5.99
	Tanga-Coelacanth-Mwambwa Shengue	Marine Park (general use)	Video	December, 2020	December, 2020	52.5+/-34.18
	Tanga-Coelacanth-Mwambwa Makome (3 sites)	Marine Park (gear restricted)	Video; UVC-a, UVC-b	December, 2020 (video); October, 2019 (UVC)	December, 2020	34.17+/-27.11

*UVC-a = UVC abundance surveys, UVC-b = UVC biomass surveys.

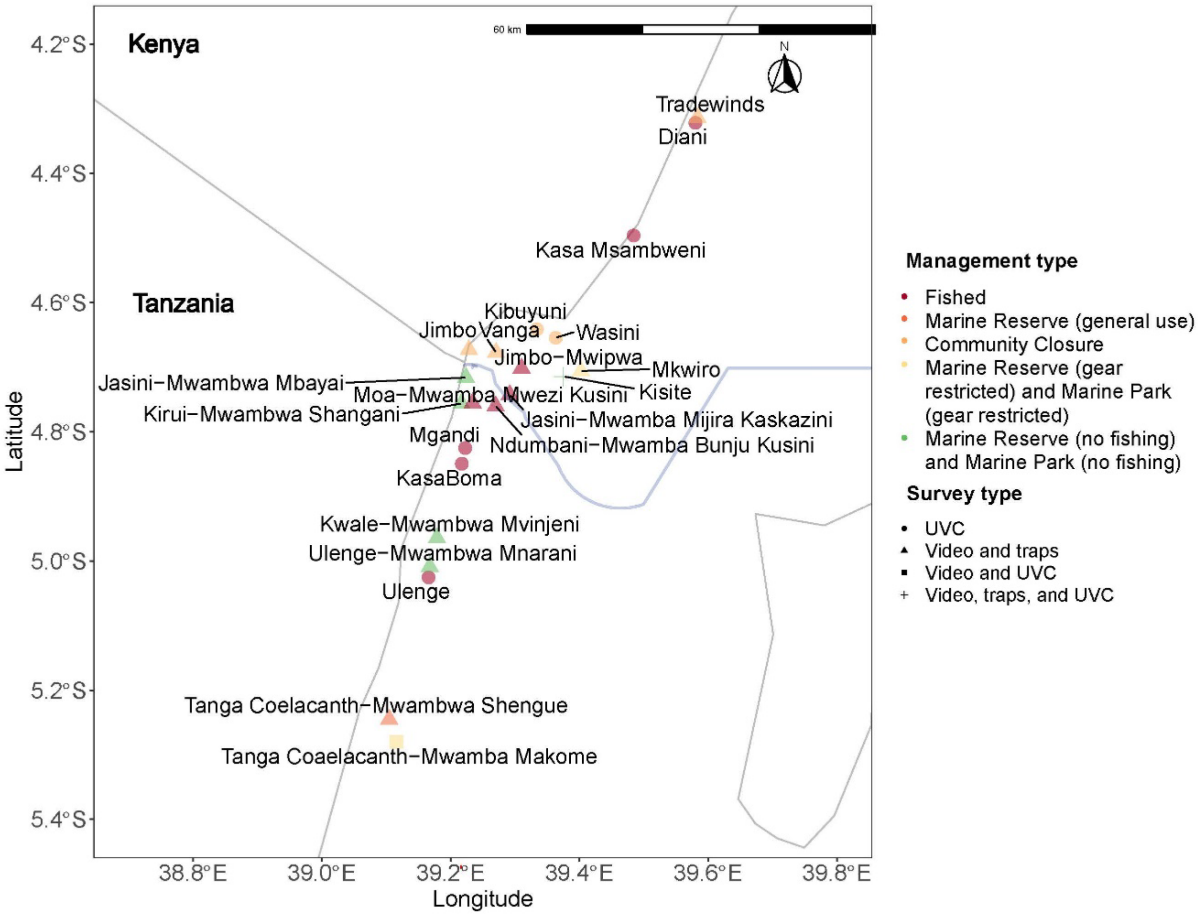

Figure 1. Map of surveyed sites. Colors correspond to management type (from red = fished, to green = no fishing). Shapes correspond to survey method (circle = UVC, triangle = video and traps, square = video, traps, and UVC). Exclusive Economic Zone border is marked in blue. See Supplementary Figure 2 for a more detailed map indicating site substrate.

2.2.Survey methods

We explore three methods for surveying fish biomass in this paper (UVC, video, fish traps). The UVC surveys are subdivided into two categories: biomass surveys (2.2.1.) and abundance surveys (2.2.2.). UVC biomass surveys are used in the biomass analyses, and the abundance surveys are only used in the abundance-weighted trait analyses (see 2.3.2. Functional space).

2.2.1. Underwater Visual Census – biomass surveys

Underwater visual census (UVC) biomass surveys from 13 reef sites in Kenya (n=7) and Tanzania (n=8) were included in this study (Table 1). All UVC surveys were conducted between 2017-2020, as this enabled us to include data from a range of management regimes. Two to four 100x5 m belt transects were surveyed at each site during neap tides by the same individual observer (TRM) at a depth of 1-6m. Fish were identified to family level and the total length of each fish was estimated and assigned to 10cm size bins (McClanahan and Humphries, 2012).

2.2.2. Underwater Visual Census – abundance surveys

UVC abundance surveys were conducted in 12 reef sites in Kenya (n=7) and Tanzania (n=5) from 2017-2020. The UVC abundance surveys involved a Discrete Group Sampling method, whereby families or species with similar body shapes or behaviours were identified and counted during separate passes along a transect. This method, in addition to separating abundance and biomass surveys, has been used in the region over a long timeseries and facilitates the ease and speed at which the data can be collected (McClanahan and Graham, 2005; McClanahan *et al.*, 1999). Two 100x5m belt transects were surveyed at each site during neap tides by the same individual observer (TRM) at a depth of 1-6m. Fish were identified to species level for this survey, but no length estimates were made.

2.2.3. Video surveys

Video surveys were conducted at 15 reef sites in Kenya (n=6) and Tanzania (n=9) between October and December 2020 (Table 1) using equipment available to the field teams. Video survey methods involved scuba-diving along a 50m transect at a pace of 2.5m/min while angling a single camera (Olympus TG-5 with settings at 1,280×720p, 29 fps) slightly towards the benthos at an angle of approximately 100◦ with the water surface. Divers were positioned 1m above the benthos as consistently as possible (methods adapted from "I transect" outlined in Pelletier et al., 2011). We used single camera surveys, rather than the more common stereo video methods that also allow fish length estimation (Goetze *et al.*, 2019), because single cameras are more easily available to marine managers in the region, are simpler to set up, and were the equipment available to the survey teams in this study. Video surveys were conducted during spring low tides at a depth of 1-3m. Two to four transects were surveyed at each site. Once field data had been collected, videos were processed by the same individual (JHH). The protocol involved watching each video on VLC Media Player twice. During the first playback, all small and highly abundant species of the Pomacentridae family (e.g., *Chromis dimidiata*) within the scope of the video transect were identified and counted. During the second playback, all other species were identified and counted. Playback speed was adjusted depending on species' abundances, but never exceeded 1x speed. The area of the transect (250m^2) was calculated by multiplying transect length by the width of the camera view at a 5m marker distance from the camera (marked on the transect with brightly coloured pegs), as calibrated underwater, to maintain consistency of recordings across visibility conditions (adapted from Wartenberg and Booth, 2015).

2.2.4. Fish trapping

Basket traps (Supplementary Figure 1) are used across Africa, as well as globally (Mbaru and McClanahan, 2013). In Kenya and Tanzania, they are considered one of the more sustainable fishing gears, as they do not cause harm to reef and seagrass substrates when compared to drag nets such as beach seines, though extensive use can still cause overfishing and harvest of juveniles (Mbaru and McClanahan, 2013). Though intended to target high-value fish (e.g. groupers and snappers) non-gated basket traps are weakly selective and retain most fish that enter, and thus there have been recent efforts to increase the use of traps with an escape slot that allows juvenile fish to exit (Mbaru and McClanahan, 2013). There are differences in trap design across countries. While all traps have the same general shape and size, Kenyan traps have a frame built of rebar and use nylon mesh in the weave on sides. In contrast, Tanzanian traps, due to national laws, are built with a frame of biodegradable bamboo with basket materials forming the weave on the sides and are weighted with stones.

A total of 110 fish traps were deployed at 5 sites in Kenya between November 2020 and January 2021 (Table 1). As this was an experimental pilot study for the trapping methodology, no traps were deployed in Tanzania, and we used the Kenyan trap design (metal frame and nylon weave). Traps were baited with sea urchins (Tripneustes gratilla) or algae (mixed species that is typically used by fishers) (n=24 traps/site). It should be noted that bait may not influence trap effectiveness (Munro, 1974; Mbaru and McClanahan, 2013). Traps were deployed at spring low for 24 hours by local basket trap fishers. As per procedures used by Kenyan trap fishers, traps were deployed on seagrass that is adjacent to coral reef areas. Using local fishers ensured that traps were placed in a way that would maximize fish catch (according to the fisher experience). After 24 hours had passed, traps were removed from the water, and fish were taken out of the trap, identified to species level, and measured to the nearest millimetre at total length. After species-level identification and measurement, fish were returned to the water.

2.3.Data processing and analysis

2.3.1. Biomass estimation

Fish biomass was calculated from data obtained using each of the methods. UVC (A) and video surveys (B) can be used to produce an area-based biomass estimates, while the trapping method (C) (without extrapolation – see section 2.3.2. Fish trap analyses) is used to estimate fish biomass per trap.

A) **UVC biomass surveys:** the total length of fish was estimated underwater, and each fish was assigned to a 10cm size-class bin. Total wet mass was estimated for each size-class using established length-mass relationships based on the centre point of the size-bin recorded (McClanahan and Humphries, 2012; https://collect.datamermaid.org). Biomass values for all the transects at each site were then averaged and scaled up into units of kg/ha.

B) **Video transect surveys:** individual fish sizes were not available, because stereo-video is required to obtain reliable length estimates of fish during video surveys (Wilson et al., 2018). The mass of an individual fish was thus calculated as $W = a \times L^b$, where L is the maximum length of each species, and a and b are species-specific length-weight coefficients. Coefficients (L, a, b) for each species were extracted from FishBase (Froese, R.; Pauly, 2019). Biomass values for all the transects at each site were then averaged and scaled up into units of kg/ha.

C) **Fish traps**: the total length and abundance of all fish caught in the traps was recorded at each site. The mass of each fish was calculated using species' length-weight conversion values taken from FishBase (as with video surveys). Biomass was then calculated as the sum of the mass (kg) of fish caught in each trap.

2.3.2. Statistical analysis

UVC and video

For UVC and video surveys, we were able to calculate area-based biomass density estimates (kg/ha), but for the fish trapping methodology, biomass was measured as the mean of mass caught in fish traps. Therefore, we were able to conduct a three-way ANOVA to determine if there was a difference in the mean biomass estimates obtained using UVC and video methods across management categories and countries (sites were pooled by management type and country). Fish traps were excluded from this analysis. For the ANOVA, biomass values (kg/ha) were logged to normalise the data. Logged biomass was then modelled as a function of survey method, accounting for the interacting effects of management and survey method, as well as country and survey method. Model assumptions were checked according to protocol outlined in Zuur et al., (2010).

Fish trap analyses

We conducted a power analysis to determine how many traps per site would be needed to detect a significant difference ($p<0.05$) in fish biomass between sites with different management regimes. We calculated the power of a t-test given four effect sizes (0.2, 0.4, 0.6, 0.8) and sample sizes ranging from 0-50 using the *pwr.2p.test* function in R. We then used the established large effect size for the difference in biomass between fished sites and protected areas in Kenya (~0.8), the sample size of 25 suggested by the power analysis, and the known means, standard deviations, and percentage of zeros in the preliminary sampling study (60%), to simulate 1,000 distributions of trap-recorded biomasses of fish in fished and unfished sites. We conducted a one-tailed t-test on the 1000 distributions and calculated the number of significant results ($p<0.05$) obtained in the simulated data models.

We conducted a second power analysis to assess how many sites would need to be surveyed using the trapping method (with biomass data obtained from UVC surveys in paired sites) in order to be confident in predictions made using fish biomass caught in traps to predict biomass density (kg/ha) at a site. We did this by using a small sample size ($n=5$) to learn about the distribution of the data (mean and variance) and likely relationship between total biomass in traps and biomass density recorded by video transects (effect size of a log-linear model = 0.2). Using this informed distribution of parameters, we simulated 1,000 linear models, wherein biomass densities obtained from UVC transects are a function of trap biomasses for the same sites, to determine how big the sample size would need to be to ensure that the relationship was significant at a $p<0.05$ level in at least 80% of the models (power=0.8). We illustrated this power curve for sample sizes of 0, 10, 15, 20, 30, 40, 45, 50. The R package "lme4" (Bates et al., 2020) was used to estimate the effect size in the log-linear relationship between video-based biomass estimates and trap-based biomass estimates.

Functional space

In addition to comparing the ability of each of the three survey methodologies to detect biomass trends, we looked at the differences in the species' trait compositions captured using the different methods. Six species-level traits sourced from the GASPAR database (Kublicki, 2010) were selected to represent the functional space of the fish community within the TBCA: body length (size), diet, schooling behaviour (gregariousness), position in the water column, diel activity, and mobility (Mouillot *et al.*, 2014). A multidimensional trait space was constructed by applying a Principal Coordinates Analysis (PCoA) to a Gower's distance matrix of species' traits using the R packages "cluster" (Rousseeuw *et al.*, 2018) and "ape" (Paradis *et al.*, 2019). The first PCoA axis explained 47% of the variation in the trait space, and the second axis explained 25% of the variation. To ensure the trait space was comparable across the methodologies, we removed fish families that were not surveyed in the original UVC abundance surveys from all analysis in the in the main figures of this manuscript. However, the full functional space of all families recorded in the surveys can be seen in Supplementary Figure 5.

Data analyses were carried out using R Version 3.6.3. (R Core Team, 2020). The R package "ggplot2" (Wickam, 2016) was used to create all figures.

3. Results

When stratifying by management type and country, we found no significant difference between the mean biomass of fish estimated through UVC survey methods and underwater video transect methods (ANOVA, $p = 0.138$; $F_{(1, 77)} = 2.247$; generalized eta squared (effect size, GES) = 0.028; Figure 2). All of the surveying methods detect the large difference in fish biomass between fished and unfished sites in Kenya (based on ANOVA for UVC and video, and graphical data visualisation for traps). The UVC and video methods found no difference between fished and unfished sites in Tanzania (Figure 2; Figure 3).

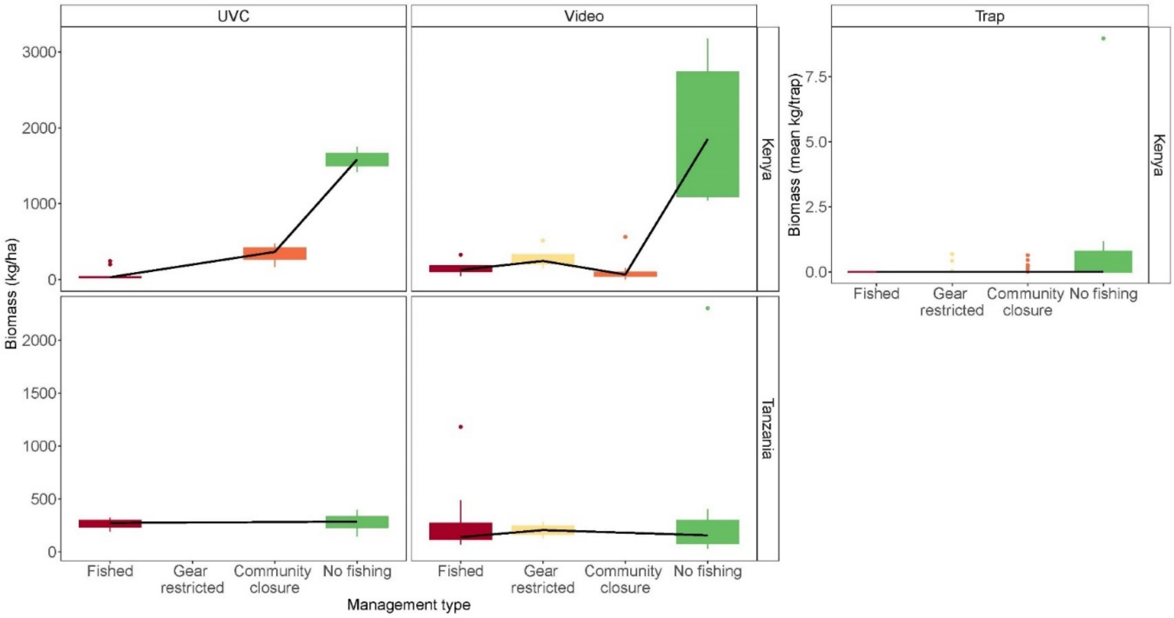

Figure 2. Comparison of fish biomass between fished (red) and unfished (green) sites using different survey methods (boxplot of UVC and video transect methods for Kenya and Tanzania (biomass in kg/ha) and bar chart of fish biomass (total kg in traps) recorded using traps in Kenya).

Reef fish biomass estimates derived from video transect data ranged from 36.83kg/ha in the Tradewinds community closure (*Tengefu*) site in Kenya, to 1979.77kg/ha in Kisite Marine Park in Kenya (Figure 3). Biomass decreased with less management in Kenya. In contrast, there were no clear patters associated with management regime in Tanzania; for example, Kirui-Mwambwa Sahngani, a marine reserve with no fishing, had an average biomass of 628.54kg/ha, while Ndumbani-Mwabwa Bunju Kusini, a fished site, had an average biomass of 622.99kg/ha (Figure 3).

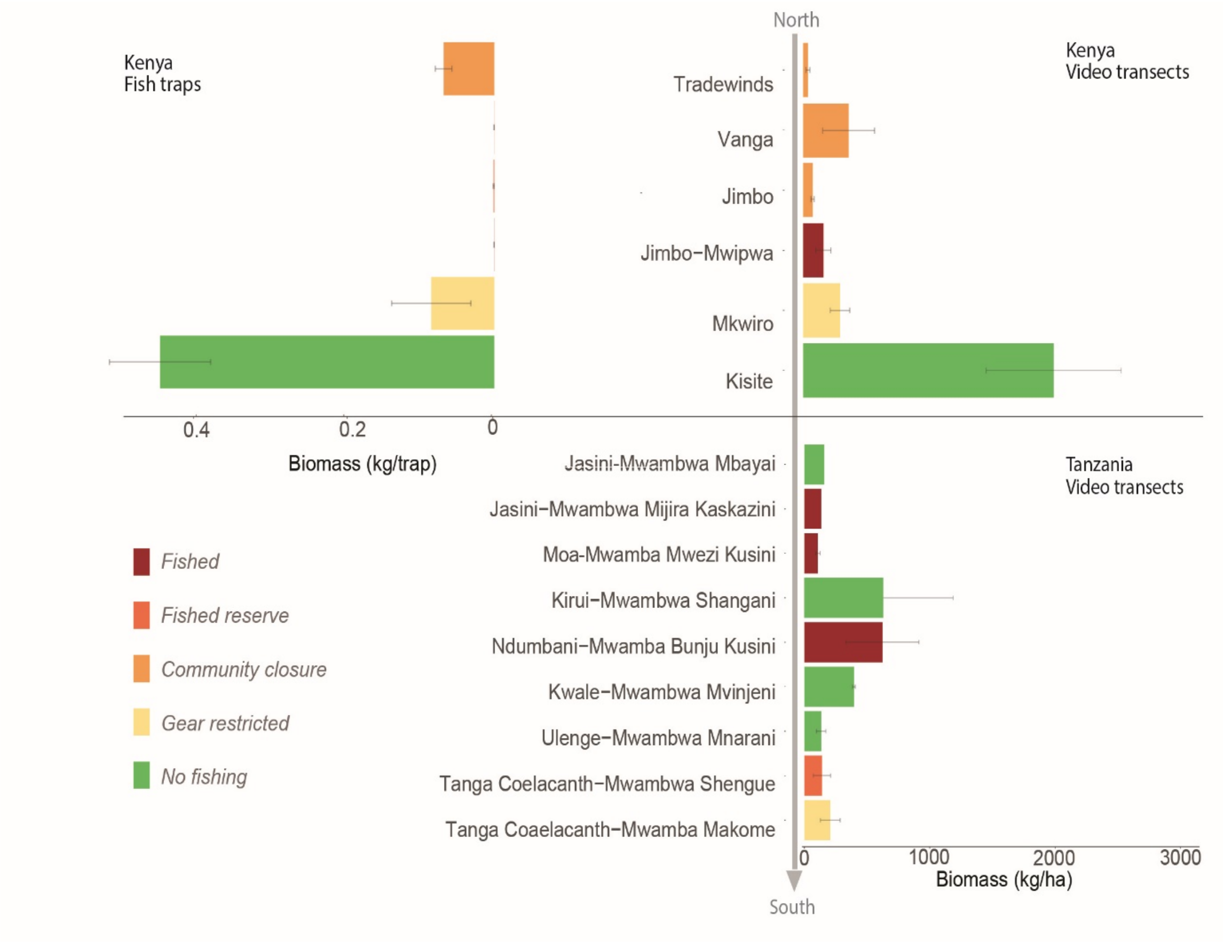

Figure 3. Mean fish biomass (kg/ha +/- 1 SE) recorded from video transect (right side) and total fish biomass (kg) recorded in traps (left side), at each survey site. Sites are arranged from North to South. The colours of the bars correspond to protection level of the sites, ranging from red (fished) to green (no fishing allowed).

We asked how many traps per site would be needed to detect a significant difference ($p<0.05$) in fish biomass between sites with sufficient power (80%). We determined that 25 traps per site would need to be deployed at fished and unfished sites in order to detect a difference in fish biomass between sites, if the effect size was as high (0.8) as UVC survey data would suggest (Welch Two Sample t-test, $p<0.01$, $t_{(1,6)} = -7.636$, GES = 0.76). In a simulation of 1000 t-tests, there were 948 significant results, indicating a difference between the biomass recorded in traps in fished and unfished sites when assuming a sample size of 25 traps/site and a likely high effect size of 0.8 using zero-inflated distributions and informed means and standard deviations of biomass/traps (Figure 4.A.).

A second power analysis based on 1000 simulated linear models revealed that in order to use the trapping method to reliably predict biomass as an area-based density metric (kg/ha) with an effect size of at least 0.2 (slope of linear model with only four points), a significance level of p<0.05, and 80% power, at least 41 sites must be sampled (Figure 4.B.).

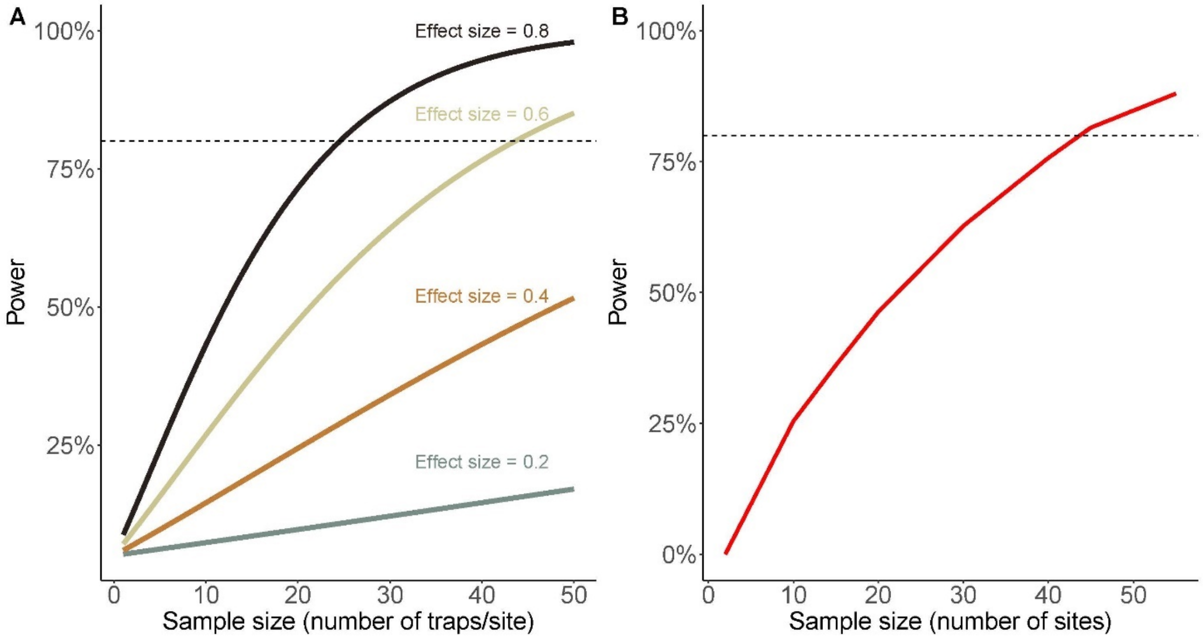

Figure 4. A) Power analysis illustrating the number of traps/site necessary to detect a significant difference in biomass of fish between fished and unfished sites, depending on the effect size of that difference (t-test), ranging from 0.2 to 0.8. Sufficient power, indicated with a dotted line, is suggested to be 80%. B) Power analysis based on 1000 model simulations, illustrating the number of sites necessary to model the log-linear relationship between total biomass obtained through fish trapping and logged mean biomass density (kg/ha) obtained through video transects.

The functional space of the reef fish community highlights that the UVC and video methodologies captured similar species' traits, with the abundances small, planktivorous fish being equally represented as the most dominant traits through the two survey methods (Fig.5.A). However, the abundances of pelagic and highly mobile species were more represented in video surveys, and the abundances of larger (>50cm) fish were more represented in UVC surveys. Overall, species recorded using the UVC method covered 79% of the total trait space (Fig.5.B.), while the video method recorded species across 89% of the total trait space (Fig.5.C.). Although the trap survey method could not be used to estimate area-based abundance densities, the trait composition of the fish species surveyed is displayed. Species recorded in the trapping method cover 62% of the trait space.

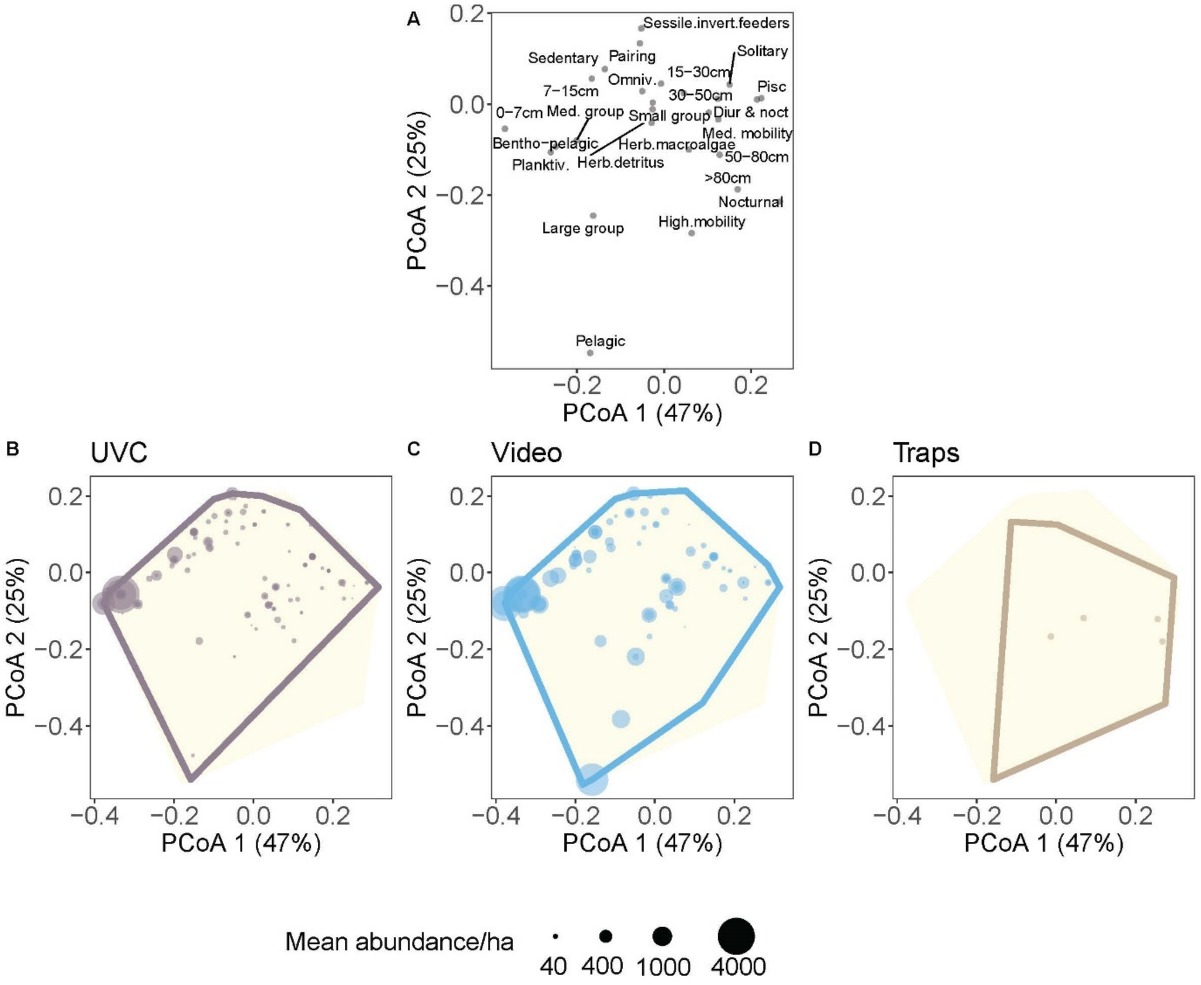

Figure 5. PCoA based on six functional traits of fish species (size, diet, gregariousness, mobility, diel activity, and position in the water column). A) Functional space across all surveys, B) functional space of species surveyed through UVC transects, C) functional space of species surveyed through video transects, D) functional space of species sampled in traps. Point size in B and C corresponds to the mean abundance/ha of species.

4. Discussion

The newly proposed marine TBCA between Kenya and Tanzania is comprised of a matrix of management types, with differences in enforcement capacity of MPAs between nations. While biomass estimates of fish were higher in unfished, protected sites on the Kenyan side of the TBCA, there were no significant differences between fish biomass estimates in protected areas and fished sites in Tanzania. Both UVC surveys and single-camera video surveys were able to detect these trends. Similarly, fish traps, while only deployed in Kenya, also captured broad biomass differences between management regimes, but the data was a lot more variable. Moreover, there was no significant difference between biomass estimates obtained from UVC and video transects when pooling sites by country and management type. While there was only enough data to statistically compare UVC and video surveys in this way, we were able to use the small sample-size of the trapping surveys to simulate data and conduct a power analysis to determine the sample-size necessary for traps to be able to detect a difference in biomass between fished and unfished sites. Despite very large biomass differences, a minimum of 25 traps would likely need to be deployed at each site to capture statistical differences between high compliance fisheries closures and low-compliance or fished sites. Furthermore, a second power-analysis indicated that if traps were deployed across 41 sites or more, we could apply results from the trapping method to model biomass densities across sites in kg/ha, a standardised unit that would allow for more widespread comparisons across the region and over time. When looking at the efficacy of the methods to detect differences in community composition, we demonstrate that the UVC and video methods allow us to capture a greater proportion of the fish functional space than the trapping method. Moreover, traps have the potential to be destructive, harmful to fish, and potentially encourage poaching within protected areas, and should therefore only be considered as a learning tool in appropriate management settings, rather than a verified method to deploy for estimating biomass and diversity in fish populations.

Each of the survey methods have advantages and disadvantages (summarised in Table 2), and these vary depending on the context in which they are deployed. One element of this context is the purpose of the monitoring effort. In the management setting of the TBCA, one of the primary needs is to determine whether fisheries closures and gear restricted sites are functioning to increase fish biomass. MPA managers and community members need this information as part of adaptive management approaches to evaluate whether their current suite of management actions (including control and surveillance, as well as community outreach) are working. When managers and community members see data showing that fish biomass is not increasing in low-compliance areas, it can motivate change and enhance willingness to engage in control and surveillance, as well as increase fishers' compliance (Ban *et al.*, 2012). However, this assumes that managers and communities understand the data being presented and believe in the results.

UVC surveys are advantageous because they are a scientifically accepted, widely used method for estimating biomass on coral reefs and tend to produce data with reasonable accuracy (Murphy and Jenkins, 2010). Having the surveyor estimate the size of individual fish underwater also allows for intraspecific variation of size within fish communities to be recorded. This is crucial, because fish size can vary substantially within a species, having an impact on ecosystem functioning and fishable biomass (Nash *et al.*, 2016). The main disadvantage of the UVC survey method is that it requires resources (e.g., SCUBA) as well as expertise or resources for training in order to complete at a high standard. For example, Uychiaoco et al. (2005) show that community-conducted snorkelling UVC surveys had higher variance and higher abundances than biologist-collected data. Further, UVC methods require few people in the water at any one time to avoid scattering of fish. Thus, this method does not easily allow for collective learning. However, Kawaka et al. 2016 describe a co-management method for monitoring the status of coral reef fish communities in East Africa using a UVC belt transect survey method. In this method, participants record the length and abundance of a few key species. One of the drawbacks of this method is that it does not record all species, thereby making comprehensive site biomass estimates difficult, and data may have inaccuracies. Nevertheless, it does allow for the collection of indicator data on reef health and engages local communities with research partners.

Table 2. Advantages and disadvantages of each of the biomass survey methods

Method	**Advantages**	**Disadvantages**
UVC transect	Widely used and accepted methodology Produces comparable area-based biomass estimates No substantial post-processing time Captures a broad range of species and their traits	Requires in situ fish identification and size estimation skills Requires SCUBA or snorkelling access/skills Does not allow collective learning
Video transect (single camera)	Long term records available to check and learn from No in situ fish identification skills needed Only 1 camera needed Captures a broad range of species and their traits Can allow collective learning during post-processing if done as a group	Substantial post-processing time (~2-4 x video time, e.g., 30min-1hr processing time/15min video) Need good video quality (e.g., 1080p at 60 fps) and underwater cameras not always available to MPA staff or communities Requires SCUBA access/skills No in situ size measurements possible with single camera
Traps	Hands-on Uses available and relatively inexpensive materials (locally made traps) Instant results (fish identified and measured in situ) Allows visual learning during surveys (e.g., seeing differences in fish abundance, sizes, and types caught) Uses methods that fishing communities intuitively understand	Experimental conversion to biomass per unit area Costs of building, transporting, storage, and repair. Often high loss rates over time. Few species captured with targeting of specific traits due to trap design, bait, and placement Many empty traps, so requires high sampling effort at each site (25 traps) Potential mortality that is not well known in terms of size and species May promote inappropriate usage in protected areas

In our study, we show that across management regimes and country boundaries, there is no significant difference between UVC biomass estimates and video survey biomass estimates. However, when breaking down the results by management category, we can see higher variation in unfished sites for video surveys than UVC surveys and higher biomass estimates for video surveys in fished sites than UVC surveys in fished sites. One possible explanation for this is that UVC surveys are less likely than video surveys to result in counting the same fish twice, especially for more mobile species

(Rassweiler *et al.*, 2020; Ward-Paige *et al.*, 2010). We attempted to control for this in our study by ensuring each of the video transects were traversed at a similar speed to UVC transects. However, we had to modify this speed to be slightly slower, in order to achieve high video quality. We suggest increasing the speed of the transect swim in further studies using video surveys, and instead using a buoyancy aid to stabilise the camera, if resources are available to do this.

Another reason for higher variation in the video surveys is that we were not able to record fish size and, instead, had to use maximum length estimates from FishBase to calculate the overall biomass of a site. This was done at a species level; therefore, the taxonomic composition of fish surveyed in a transect greatly influences the biomass estimates. Moreover, maximum size is likely to be more realistic for some species than others (Fisher *et al.*, 2010), and its use resulted in inflated biomass estimates for some sites (e.g., Kisite Marine Park). This reflects more noise in the data due to less precise methodology, rather than more variability in biomass between sites. Stereo-video surveys are a possible solution to this problem, as they allow for individual fish size estimates to be made (Wilson *et al.*, 2018), though stereo-video technology is often cost-prohibitive for MPA managers and communities. Stereo-video was not used in this project, because it is more expensive and harder to use and process than single-camera video surveys (see Goetze et al. 2019). All video surveys need to be analysed after field data collection. This can be a time-consuming process (Table 2), but machine learning automation is constantly improving and facilitating the ease and speed of this step (Goetze et al. 2019). There is scope to make the post-processing of video surveys a more participatory process. For example, video footage may be used as a learning tool, whereby species identification skills (for scientific purposes) can be developed. Furthermore, cameras have been used in a variety of Participatory Action Research projects around the world to influence decision making behaviours and inspire important conversations around community concerns (Bennett and Lantz, 2014; Wang and Burris, 1997; Suprapto *et al.*, 2020). Thus, although our methodology focussed on assessing the value of using video footage to assess fish biomass, camera-based methods more generally have the potential to integrate scientific data collection with community change.

The most participatory method, as deployed in our study, was fish trapping, whereby artisanal fish traps (Supplementary Figure 1) already available to coastal communities were repurposed for biomass data collection and community learning.

Trapping is a hands-on method and allows for a monitoring approach which blends participatory monitoring and traditional scientific monitoring to allow collective learning and facilitate co-management with communities. Danielsen et al. (2009) identify five levels of local involvement in monitoring: "1) externally driven, professionally executed, 2) externally driven with local data collectors, 3) collaborative monitoring with external data interpretation, 4) collaborative monitoring with local data interpretation, and 5) autonomous local monitoring". The trapping methodology would fall under category 4 for MPAs, where MPA staff can collect their own data and get local assistance to interpret data. Coupled with the visual learning inherent in the exercise, whereby participants see differences in fish species composition, abundance, and size, fish trapping offers a hands-on approach that may be more likely to motivate management change than the provision of externally collected data (e.g., level 1). With time, MPAs will likely be able to do this exercise and produce graphic data representation autonomously (moving them to level 5). For fishing communities seeking to manage their resources and implement locally managed fisheries closures, the trapping exercise would fall under a level 3 or 4, depending on who is helping them with data management. The power analyses conducted in this study indicate that the trapping method can be used to detect differences in fish biomass between fished and protected sites if 25+ traps are deployed at each site. Providing a tool that allows managers and communities to visually learn about differences in management regimes may prove to be a powerful way to create new management initiatives and to influence fisher behaviour. If this method were to be applied to collect data in at least 41 sites, a linear model could be built to predict the biomass of a site. It could be feasible to scale up to more than 41 sites at a regional level (Western Indian Ocean), with for example, eight sites per country across five nations.

Crucially, however, there are some potential negative outcomes that could result from using fish traps, especially in a conservation setting. Firstly, the use of traps within protected areas, even for monitoring or learning purposes, could lead to poaching within the reserves. Researchers and conservation organisations using fish traps in reserves can set a precedent for others to use them. For example, some have argued that the practice of granting licenses for "trophy hunting" in order to finance conservation, promotes anti-conservation values through encouraging hunting of prized animals for those that can afford it (Dellinger, 2019). In signaling fish trap use is acceptable for some (e.g., those using the traps in training exercises), but not for others, NGOs and conservation organisations can invertedly reinforce power inequalities and promote values antithetical to conservation (Edwards and Sen, 2000). Moreover, traps require resources to produce and can be lost and damaged, or they can accumulate as waste in important ecosystems. For example, derelict fish traps that are lost or discarded in the sea can lead to fish mortality through ghost fishing (Vadziutsina *et al.*, 2019). Finally, the potential harm caused to fish caught in the traps is unknown. Even though the fish are released after identification and measurement, the process is likely to be stressful to species and could potentially result in some mortality (Stewart and Ferrell, 2003).

All three methods assessed here capture a the majority (>50%) of the fish community functional space. While we find that the fish trap methodology surveys the least amount of functional space, Mbaru et al. (2019) show that, relative to other artisanal fishing gears used in Kenya, basket traps capture a large number of functional entities (FE; unique combinations of traits), but the number of species in a large proportion of these FEs is low. Additionally, 25% of the FEs caught in basket traps were Rarely Targeted Functional Entities, or FEs contained in 1% of total number of individuals captured. This suggests that because basket traps are somewhat selective, the majority of species captured are functionally similar, but as the number of fish caught increases, new FEs are likely to be surveyed. This was not incorporated into our power analysis, meaning that it is likely that if traps were to be used to understand community composition, in addition to biomass trends, “accumulation curves” would be need to be considered (Ugland *et al.*, 2003; Bady *et al.*, 2005). It is important to acknowledge that environmental change and fishing pressure can affect some functional groups of fish more than others, resulting in changes in community composition, without large shifts in the overall community biomass or fisheries catch rates (Robinson *et al.*, 2019; Maureaud *et al.*, 2019a). Moreover, biomass can be decoupled from ecosystem productivity and the provision of ecosystem services (Morais *et al.*, 2020a). So, while biomass is a critical indicator of ecosystem health, it is necessary to consider finer-scale shifts in biodiversity patterns as drivers of long-term ecosystem functioning (Maureaud *et al.*, 2019a). Therefore, less sophisticated methods like fish traps are best accompanied with periodic UVC or video surveys (likely conducted by scientific teams) to ensure that more subtle changes in fish community composition are assessed and communicated.

The TBCA has been identified as a coral climate refugia (McClanahan 2020), making it an ecologically important area. The coral reefs in the region support high biodiversity and when protected, have the potential for recovery of fish biomass. In most sites in this study, coral cover is high enough to support additional fish biomass (Table 1). Past work in the region has defined conservation targets and thresholds for fish biomass: biomass above 1150 kg/ha is a "conservation target" for fisheries closures, while biomass below 500 kg/ha indicates overfishing with risk of fisheries collapse (McClanahan *et al.*, 2015, 2007b). Based on the UVC and video surveys, the Kisite Marine Park (no fishing zone) in Kenya, has a biomass of over 1150 kg/ha, the proposed conservation target (McClanahan *et al.*, 2015). While no sites in Tanzania reach the conservation target, two sites, Kirui-Mwambwa Shangani Marine Reserve (no fishing) and Ndumbani-Mwamba Bunju Kusini (fished) had biomasses greater than 600 kg/ha, the upper bound of the multi-species maximum sustainable yield (B_{MMSY}) window associated with ecological sustainability in the region (500-600 kg/ha) (McClanahan *et al.*, 2007b). The similarity in biomass between Kirui and Ndumbani demonstrates that in Tanzania, where enforcement and compliance are low, factors other than management regime likely drive differences in fish biomass. With the exception of the Ndumbani-Mwamba Bunju Kusini fished reef in Tanzania, however, all fished sites assessed in this study had fish biomass below the 500 kg/ha threshold. Further, in Kenya, where communities have established small locally managed fisheries closures, fish biomass was equally low (37-359 kg/ha), indicating that these areas are not functioning as intended in replenishing stocks.

Currently, due to extensive artisanal fishing, the proposed TBCA is largely overfished. Given the ecological importance of this area as a climate refuge, working with communities to improve fisheries management and with governments to enhance effectiveness of MPAs is critical. The well-enforced Kisite Marine Park demonstrates that achieving conservation targets for fish biomass is possible and can help communities visualise what is regionally feasible when fisheries closures are enforced or complied with. There is a major opportunity in this region to support effective management of the MPAs in Tanzania, especially with the larger MPAs (Tanga Coelacanth, Kirui Island, and Kwale Island), where fish biomass could likely recover and provide spill-over benefits to adjacent fished reefs (McClanahan et al., 2016). In addition, there are ongoing initiatives in both countries led by county or district fisheries management agencies and

NGOs to improve small-scale fisheries' management and either establish or improve effectiveness of community closures. In the TBCA, both in Kenya and Tanzania, there is an initiative to bring together groups of fishing communities with overlapping fishing areas in joint management approaches (McClanahan et al., 2016; Wells et al., 2007).

In this study, we illustrate the potential for using a range of monitoring methods to meet multiple conservation goals through an applied case study of the proposed marine TBCA between Kenya and Tanzania. All methods (UVC surveys, single-camera video transect surveys, fish traps) were able to detect important biomass trends across management regimes and sample the majority of the functional space occupied by the reef fish community. Through a series of power analyses based on the preliminary data collected using the trapping methodology, we highlight the potential for this easy, hands-on learning tool to provide crucial data on reef fish biomass. This comparison of methods widens the opportunity for a greater range of actors to engage in fish biomass assessments and marine resource management.

Author contributions

JHH planned data collection protocol, watched and recorded the data for the video surveys, did the data analysis, and wrote the first version of the manuscript. TM collected data and provided supervision and editorial guidance. NM contributed to project management and helped to conceive the project idea. JM contributed to project management, design, and data collection. JK, RO, SM contributed to project design and data collection. NG provided editorial comments and supervision. JL conceived the idea for the project, oversaw and supervised the project funding, data collection and analysis, and provided editorial guidance.

Chapter 4: Global drivers of coral reef fish fecundity

Abstract

The reproductive contribution of fish inside protected areas has historically been underestimated owing to an assumption that fecundity scales isometrically with female fish mass. However, it has recently been demonstrated that fish mass scales hyperallometrically (exponent >1) with fecundity, rather than isometrically, meaning that larger fish produce disproportionately more eggs than smaller fish. We test how this finding scales up beyond the species-level and apply it to estimate the reproductive potential of coral reef fish assemblages at 1650 sites distributed globally. We find that, at the site-level, fish community biomass also scales hyperallometrically with fecundity, but with an average exponent of 1.05, rather than the species-level exponent of 1.18. We illustrate a global hotspot of potential fecundity in the Western Indio-Pacific and highlight fishing restrictions and no-take Marine Protected Areas as some of the most important socio-ecological drivers of fecundity. Important fisheries targets, such as the family Serranidae, are shown to have 7.5 times higher potential fecundity in protected sites than in fished sites. Using our global-drivers model of fecundity, we show that if fished sites were to be protected, there could be up to an 11% gain in fecundity for some regions. In estimating the distribution and drivers of global fecundity potential of coral reef fish, we facilitate a move towards understanding the management imperatives and options that ensure the sustainability of population replenishment.

Keywords

MPA, Traits, Conservation, Reproduction, Fishing

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1. Introduction

Marine Protected Areas (MPAs) are some of the most common conservation and management tools used across marine ecosystems (Kriegl *et al.*, 2021; Duarte *et al.*, 2020). They are deployed as a method to increase fish biomass, diversity, and ecosystem functioning, to help replenish fish stocks, and to conserve important species or habitats (Worm *et al.*, 2009; Graham *et al.*, 2020; Mellin *et al.*, 2016a; Humphreys and Clark, 2019). It has been demonstrated that within coral reef ecosystems, the likelihood of reaching a combination of these fisheries and ecological goals increases with the implementation of MPAs (Cinner *et al.*, 2020). Moreover, the presence of MPAs enhances fish larval supply, and connectivity between reserves helps to ensure long-term population sustainability through consistent recruitment and population replenishment (Harrison *et al.*, 2020; Saenz-Agudelo *et al.*, 2015). The reproductive contribution of fish inside MPAs has historically been underestimated (Marshall *et al.*, 2019), owing to an assumption that fecundity scaled isometrically with female fish mass. However, Barneche et al. (2018) illustrated that, on average, fecundity scales hyperallometrically (with an average exponent of 1.18) with fish size, meaning that larger fish produce disproportionately more eggs than smaller fish. As fish are typically larger in reserves than in fished areas (Edgar *et al.*, 2014), this suggests that the reproductive potential of protected areas far outweighs that of fished systems.

We use fecundity-mass scaling theory to estimate the fecundity potential of fish across 1650 coral reef sites distributed globally, including 88 sites in unfished, no-take MPAs and 1079 sites in fished areas. We calculate fish community fecundity potential as the total egg density of all mature female fish. First, we estimate the biomass of mature females at each site by extrapolating phylogenetic Bayesian regression models on each species length at maturity and published sex ratios. We then estimate site-level community fecundity as a snapshot of the batch fecundity of all mature female fish on a reef by extrapolating the fecundity model developed in Barneche et al., (2018) to 831 reef fish species, based on high resolution phylogenetic trees from Siqueira et al., (2020). In doing so, we elaborate on the use of "spawning stock biomass" as a fisheries' proxy for reproductive capacity (Kell *et al.*, 2016) to incorporate more complexity through community-level fecundity outputs accounting for variation in sex-ratios and length at maturity. Specifically, we ask:

1) How does the relationship between female biomass and fecundity scale beyond the species-level to the community-level?
2) How does community-level fecundity vary across socio-ecological gradients?
3) How does marine protection influence community-level fecundity?

Outlining these trends can contribute to conceptualising the process of biomass production (Morais and Bellwood, 2020) and further our understanding of the conditions that facilitate another important fisheries and conservation goal, sustained reproduction.

2. Results

2.1. Global fecundity potential estimates

Our results show the fecundity potential of 1650 reef sites distributed aross 35 countries, states, or territories, and 5 geographic basins as it scales with mature female biomass (Fig. 1A; Fig. 1B). We find that estimated log fecundity scales with log mature female biomass with a slope of 1.05 (95% UI: 1.04-1.07) at the site level (Fig. 1C). The Western Indo-Pacific is a hotspot of fecundity potential (Fig. 1A). Unfished (no-take MPA) sites in Tanzania have the largest positive random intercept value (1.27) in the the log-log linear relationship between population fecundity and mature female biomass. Unfished sites in Tanzania also have the highest raw estimated fecundity values, but not the highest raw estimated mature female biomass values (Fig.1B; Fig.1C; Sup. Fig.2A). Fished and restricted sites in Venezuela have the lowest random intercept value (-0.941 and -0.938, respectively), followed by restricted sites in Hawaii (-0.74), and fished sites in Tonga (-0.72).

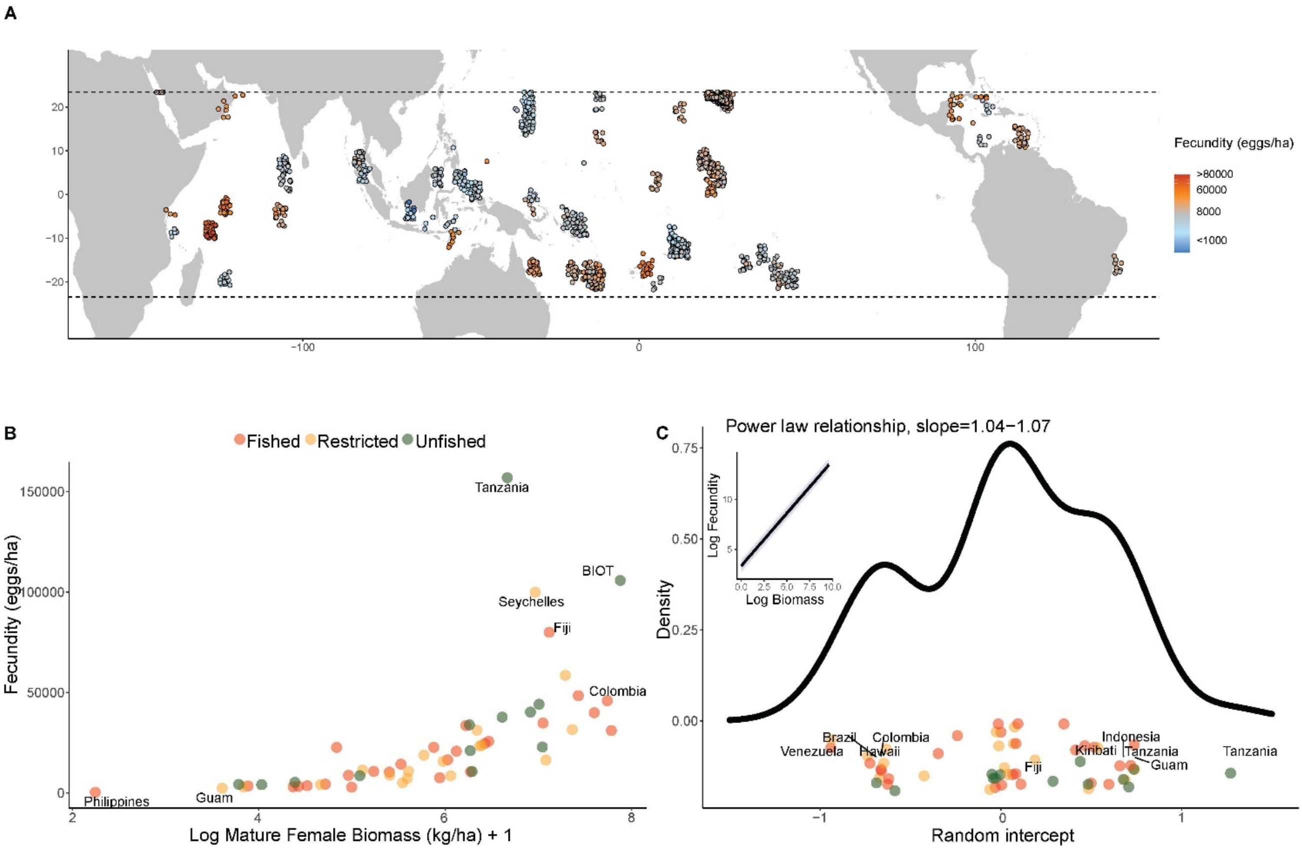

Figure 1. A) Map of global coral reef fish fecundity (eggs/ha) across 1,650 reefs, ranging from <1000 eggs/ha (blue) to >80,000 egg/ha (orange). B) Relationship between raw values of mature female biomass (log kg/ha + 1) and fecundity (eggs/ha), where points correspond to country average values grouped by protection level. Red points are fished sites, yellow points are restricted sites, and green points are high compliance reserves (unfished sites). C) Distribution of country + reef cluster random intercepts (points coloured as in B), illustrating a power law relationship between community-level fecundity ~ biomass. This relationship has exponent 1.04-1.07 (inset figure), but accounting for species composition and biomass distribution on reefs caused community reproduction to scale more (larger exponent) or less (smaller exponent) than predicted by theory.

2.2. Socio-ecological drivers of fecundity potential

Fishing restrictions, defined here as areas where there were active restrictions on gears or fishing effort, had a strong effect on the reproductive potential of reef fish assemblages. High compliance reserves had the greatest positive effect size on the fecundity of all fish families (0.86, 95%UI:0.43-1.28), followed by fishing restrictions (0.45, 95%UI:0.20-0.69) (Fig.2). For three important reef fish families for fisheries, reserves had a positive effect on Lutjanidae (0.77, 95%UI:0.16-1.38), Labridae (Scarinae) (0.72, 95%UI:0.31-1.11), and Serranidae (2.02, 95%UI:1.32-2.71) fecundity, but fishing restrictions only positively affected Labridae (Scarinae) (0.31, 95%UI:0.08-0.54) and

Serranidae (0.68, 95%UI:0.26-1.1), not Lutjanidae (0.08, 95%UI:-0.34-0.51). Oceanic productivity also had a positive effect size on Labridae (Scarinae) (0.57, 95% UI:-0.93--0.21), but no other family. Total gravity had the strongest negative effect on fecundity of all reef fish (-0.92, 95%UI:-1.15--0.68), whereas reef fish landings had the strongest negative effect on Serranidae fecundity (-2.76, 95%UI:-4.39--1.10), and population size had the strongest negative effect on Labridae (Scarinae) (-0.77, 95% UI:-1.44--0.13). Across community and family-level fecundity, total gravity had a consistently negative influence on fecundity potential.

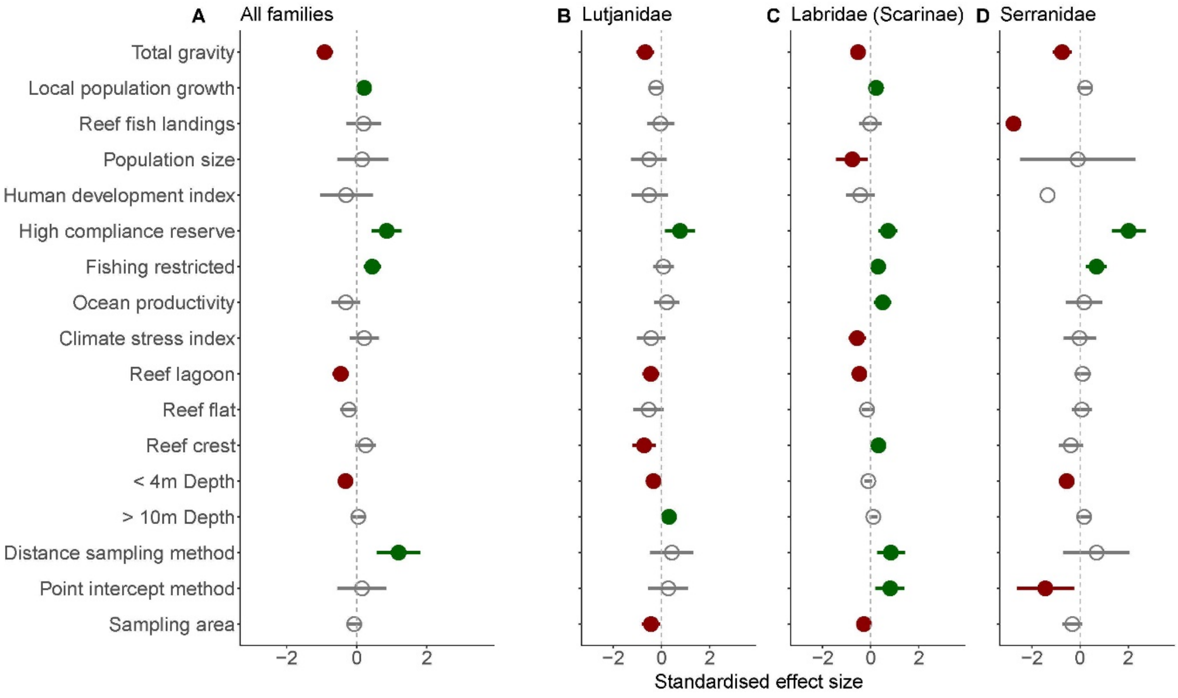

Figure 2. Standardised effect size and 95% UI of predictors on A) fecundity of all families, as well as the fecundity of economically important families including B) Lutjanidae, C) Labridae (Scarinae), and D) Serranidae.

To examine management effects, we assessed the ratios of unfished/fished and restricted/fished posterior draws from global drivers of fish with a biomass > 20cm, mature female fish biomass, fecundity of all fish families, fecundity of Lutjanidae, fecundity of Labridae (Scarinae), and fecundity of Serranidae. These ratios are depicted in Figure 3. There is approximately a 10% higher fecundity in unfished areas relative to fished areas (ratio of 1.1 unfished/fished; Fig.3.C.). However, greater differences can be observed at the level of economically important families. The biggest difference between the fecundity of unfished/fished and restricted/fished sites is for the Serranidae family; fecundity is 7.5 times higher than fished sites in unfished sites and 2.5 times higher in restricted sites than unrestricted sites (Fig.3.F.).

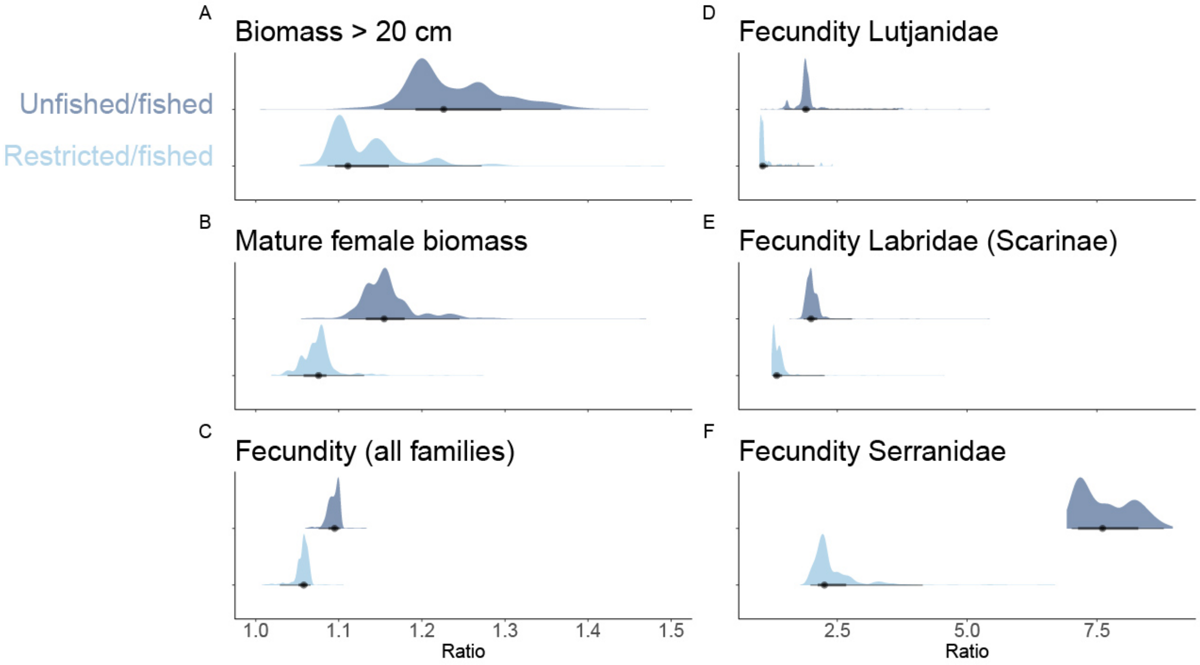

Figure 3. Ratios of draws from the posterior distributions of unfished sites/fished sites (dark blue) and restricted sites/fished sites (light blue) for models of A) fish with a biomass > 20cm, B) mature female fish biomass, C) fecundity of all fish families, D) fecundity of Lutjanidae, E) fecundity of Labridae (Scarinae), and F) fecundity of Serranidae.

2.3. Fecundity potential gains with protection

We used posterior distributions of management effects to evaluate the capacity for fisheries management to raise fecundity potential on fished reefs globally. On a national/territorial level, the Philippines had the greatest potential fecundity gains from establishing no-take MPAs in currently fished sites (10.74%), whereas locations that are already fully protected, such as the British Indian Ocean Territory had no potential fecundity gains (Fig.4.A.). At the level of geographic basins, fecundity gains ranged from a potential 8.62% increase in the Eastern Indo-Pacific, to a potential 4.98% increase in the Western Indo-Pacific (Fig.4.B.).

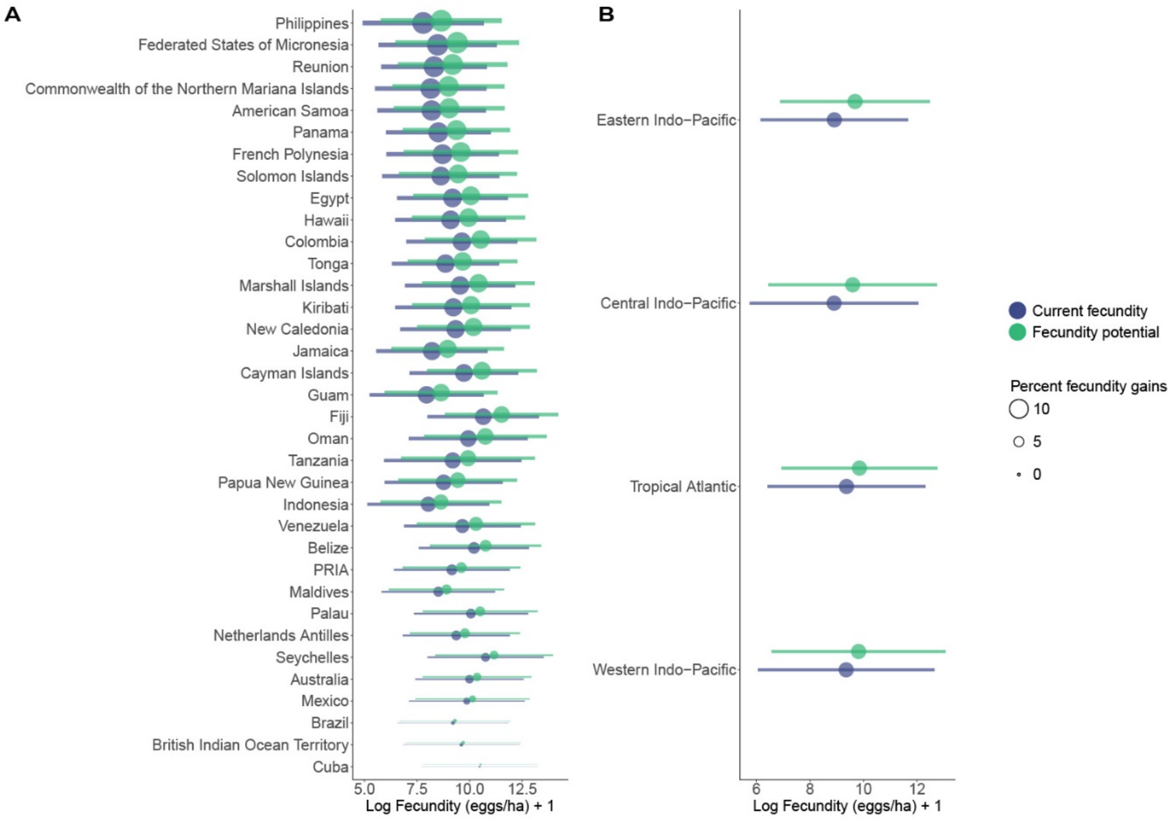

Figure 4. Current fecundity (blue) of all sites, ranging from fished to high compliance unfished reserves, and potential fecundity (green), if fished sites were to be protected across A) countries, and B) geographical regions. Countries and geographical regions are ordered from greatest potential percent fecundity gains (larger points) to smallest potential percent fecundity gains (smaller points).

3. Discussion

Protected areas and fishing restrictions have a large, positive effect on the fecundity potential of coral reef fish. In particular, high compliance no-take MPAs (unfished sites) protect and enhance the fecundity of economically important fisheries species, such as those in the Serranidae family, where fecundity potential in reserves was over 7.5 times higher than fecundity potential in fished areas. Reef fisheries landings also had a strong negative effect on Serranidae fecundity, highlighting its value as a target fisheries family and fishing selectivity for large, mature Serranidae on coral reefs, including in restricted fishing areas such as in the Great Barrier Reef, where the common coral trout is heavily targeted (Gillett and Moy, 2006). With the magnitude of difference between fecundity of Serranidae inside and outside reserves, larval export benefits from protected areas to fisheries could be substantial (Pelc *et al.*, 2010; Harrison *et al.*, 2012).

Contrary to patterns observed at the level of individual species (Marshall *et al.*, 2019), the ratio of fecundity between unfished and fished sites was lower than the ratio of biomass between unfished and fished sites (>20cm and mature female biomass). This was an unexpected because, at the species level, biomass was found to scale hyperallometrically with fecundity, with exponent 1.19. As biomass varies strongly between fished and unfished sites (Cinner *et al.*, 2016), we therefore expected unfished fecundity to be exponentially larger than fished fecundity. In our model of site-level fecundity ~ mature female biomass, we expected restricted or unfished sites to have a large positive random intercept and fished sites to have a small random intercept, where intercepts indicate site-level differences in biomass-fecundity scaling exponents. Yet, no such pattern was apparent. We did, however, find outliers, such as unfished sites in Tanzania, which had a much higher random intercept than other sites, indicating the greater abundance of highly fecund fish. At the global level across all species, there was a log-log linear relationship between community-level fecundity and biomass with a slope of 1.05. The strong hyperallometric relationship between biomass and fecundity observed at the species level, gets somewhat dampened when comparing sites at a large scale. This could be attributable to the community composition of these sites. Specifically, 1) the greater abundance of highly fecund or poorly fecund fish at some sites, 2) the presence of many small individuals below their species' length at maturity, making up a high proportion of the biomass, or 3) at a community scale, relatively few large species demonstrate disproportionate large size effects with protection, and many species of reef fish have similar body size inside versus outside protected areas.

The legacy of fishing can impact individual and species-level traits, including fecundity, that feed into the cycle of biomass production through phenotypic plasticity and evolutionary mechanisms, respectively (Barnett *et al.*, 2019). We demonstrated the potential fecundity gains each country and geographic region could make if no-take MPAs were established in place of fished areas, based off a snapshot of current estimated batch fecundity at each surveyed site. However, the effectiveness of our modelled management benefits to fecundity will depend on trajectories of population recovery in reef fishes, which can be affected by exploitation-induced evolutionary changes in fish fecundity (Walsh *et al.*, 2006). The underlying resilience of the community to fishing pressure can determine the number of generations it might take for such impacts to be observable, and in turn, the time it takes for the impacts to be reversed (Wootton *et al.*, 2021). Similarly, population sex ratios and lengths at sex change have been shown to be affected by fishing on individual and evolutionary timescales (O'Farrell *et al.*, 2016; Taylor, 2014). Some species and families might be more susceptible to these impacts, or respond equally as well to full protection as they do restrictions, such as minimum mesh size limits on fishing gears (Mcclanahan and Hicks, 2011). For example, our results show that the fecundity of both Scarids and Serranids responds well to fishing restrictions, but Lutjanids do not. It could be that this is because some restricted areas have restrictions specific to Scarids and Serranids. For example, some sites in the Caribbean have parrotfish-specific fishing bans (O'Farrell *et al.*, 2016), and some sites in the Pacific have restrictions on spearfishing at night which can heavily target both Scarids and Serranids (Gillett and Moy, 2006).

Across families, an average of 5% increase fecundity can be gained with the implementation of fishing restrictions. Fully protected areas can be challenging to implement and can lead to creating local inequities through restricting access to important resources needed for local livelihoods (Gurney *et al.*, 2021). Fishing restrictions, however, can be easier and more equitable to establish, and have been shown to produce positive fisheries and conservation outcomes (Campbell *et al.*, 2020; McClanahan and Abunge, 2020; Mumby and Steneck, 2008). Nevertheless, it can take decades of full protection for biomass and targeted long-lived, large species to recover in fished sites (MacNeil *et al.*, 2015).

Understanding how fecundity-biomass relationships scale beyond the species level informs our understanding of large-scale patterns of a critical ecosystem process, biomass production. Fecundity is a key part of the biomass production cycle, influencing reproductive success and thus recruitment, growth, and mortality in fish populations (Morais and Bellwood, 2020). Nevertheless, even the first successional step in the cycle, reproductive success, or the production of offspring that survive to a reproductive life stage, is a complicated process that can be impacted across ecological scales, from individual fish traits that could be unaccounted for by including a phylogenetic covariance matrix in our fecundity models, to population dynamics, such as density-dependence (Lowerre-Barbieri *et al.*, 2017). Barneche et al. (2018) calculate reproductive-energy output, which incorporates measures of fecundity, egg volume, and egg energy. This output bridges the gap between fecundity and reproductive success, and while unaccounted for in this analysis, it forms part of the next steps of this research.

Our findings have three critical implications for coral reef ecosystem functioning management and conservation. Firstly, by demonstrating that the scaling exponent of the fecundity and female biomass relationship is not as large at the community-level as at the species-level, we show that on a global scale, while MPAs result in higher fecundity potential for reef fish communities, the benefits are not exponentially larger than that for biomass. However, many no-take MPAs in the Western Indian Ocean are old (e.g., Tanzania, Kenya, Seychelles). Older and larger MPAs support more old, large, fecund fish (Kaplan, 2009). In such MPAs, the community-level scaling exponent is greater than the mean. This highlights the value of old MPAs in securing population replenishment. Secondly, we show how fishing restrictions have a large positive effect on the fecundity of important fisheries targets. Therefore, establishing fishing restrictions in areas where no-take MPAs cannot be created would make a valuable contribution to enhancing fecundity. However, trade-offs between the gains and losses of management actions can only be considered with a full understanding of what is feasible and desirable in a local context. Finally, the models and methods developed in this paper can be applied to extrapolate the fecundity potential of any species-pool and size-pool of coral reef fish. Future work will need to bridge the gaps between the subsequent stages of biomass production to move beyond the static snapshot statistic of potential batch fecundity, to a dynamic understanding of reproduction and recruitment.

4. Methods

4.1. Reef fish survey methods

A total of 4,137 surveys conducted between 2004 and 2013 from 1,650 tropical reef sites across 35 nations, states, or territories were included in this study. Surveys used either standard belt-transect, distance sampling, or point-count methods to identify fishes to species level, estimate total length, and estimate abundance. To standardise the data, we 1) retained >10cm, non-cryptic fishes from families that are resident on the reef, 2) directly accounted for depth, survey method, survey area, and habitat as covariates in the model, and 3) excluded cryptic reef fish, sharks, and semi-pelagic species.

4.2. Scales of data

We separated the data into four nested scales (listed from smallest scale to largest scale):

1. **Surveys** = as specified above.
2. **Reef site** = aggregations of replicate surveys within a few hundred meters (mean of 2.4 surveys/site).

3. **Reef cluster** = reef sites within 4km of each other were clustered together as specified in the methodology of Cinner et al. (2020). Social and environmental covariates of the global drivers models were estimated at this scale.
4. **Nation/state/territory**

4.3.Statistical analyses

Fecundity is defined as the number of eggs produced per mature female (Barneche *et al.*, 2018). In this paper, we scale fecundity up to the level of the community, and define community fecundity as the total number of eggs produced by all mature female fish per hectare (Lambert, 2008). UVC survey-data records the number, taxonomic identity, and total length of fish. We applied a five-step process to convert site-level fish observations to estimates of population fecundity: estimate 1) biomass, 2) fecundity, 3) sex ratios, and 4) length at maturity of each fish, and then 5) calculate the mature female biomass and population fecundity at each site, as outlined below. Steps 2-4 all involved fitting a phylogenetic Bayesian regression in the R package BRMS (Bürkner, 2017). The phylogenetic tree was obtained from Siqueira et al., (2020). All models were run with 4 chains, each with 5,000 iterations and a warm-up of 1,500 iterations. All analyses and figures were produced in R 4.1.1 (R Core Team, 2020).

4.3.1. Phylogenetic extrapolation

We used the R package "ape" (Paradis *et al.*, 2019) to calculate a variance-covariance matrix of phylogeny to account for species non-independence in the models. We used the R package "picante" (Cowan *et al.*, 2020) to predict the phylogenetic effects for species without data and estimated response variables by combining the predicted phylogenetic effects with the intercepts and slopes of each model, as described in Parravicini et al., (2020).

4.3.2. Step 1. Biomass estimation

The biomass of each fish was calculated using length-weight conversions from FishBase according to the equation: W = a × Lb, where L is the median value of the 5cm size bin for the total length of each fish recorded in the field, and a and b are species-specific length-weight coefficients (Froese, R.; Pauly, 2019).

4.3.3. Step 2. Species fecundity

We used the "picante" method described above to predict the phylogenetic effects for missing species in our dataset and combined them with the intercepts and slopes of the fecundity model in Barneche et al., (2018) :

Equation 1

$$\ln\text{Fecundity} = (\ln\alpha_0 + \ln\gamma_{0spp} + \ln\gamma_{0phy}) + (\beta_1 + \gamma_{1spp}) * \ln\text{Biomass} + \ln\varepsilon$$

Where ln(fecundity) is the natural log-transformed vector of fecundity values, $\ln\alpha_0$ is a fixed-effect intercept, $\ln\gamma_{0spp}$ and $\ln\gamma_{0phy}$ are respectively vectors of random-effect coefficients that account for residual intercept deviations attributable to species uniqueness and patterns of relatedness as described by the phylogeny, β_1 is a fixed-effect slope for the natural log-transformed predictor vector, mature female mass, γ_{1spp} is a vector of random-effect coefficients that account for residual slope deviations attributable to species uniqueness, and $\ln\varepsilon$ is the model unexplained residual variation. Fixed effects were assigned informative priors following a Gaussian distribution (β_1: mean = 1, standard deviation = 2; $\ln\alpha_0$: mean = 3, standard deviation = 3). We found that logged fecundity scaled positively with logged biomass with a slope of 1.19 (95% UI: 1.11-1.26). The phylogenetic heritability, estimated as the proportion of the variance (conditioned on the fixed effects) explained by the random effects (phylogeny) was 78.9%.

4.3.4. Step 3. Sex ratios

The sexual pattern of each family was characterised extracted from De Mitcheson and Liu, (2008) and Demartini and Sikkel (2006). Protogynous and protandrous species typically have sex ratios that deviate from 1:1 (Coscia *et al.*, 2016), whereas gonochoristic species typically have close to 1:1 female to male sex ratios (Ospina-Álvarez and Piferrer, 2008). We therefore applied a 1:1 sex-ratio for gonochoristic species (497 species) and collected data to model the sex ratios of non-gonochoristic species (1123 species) at the family level.

For each protogynous or protandrous family, we conducted a literature search using Google Scholar to obtain sex ratio data on five species with the highest proportional biomass. Where this data was not available, we expanded the search to ten species with the highest biomass, or where this information was not available, any other species from our species-list within that family, so that at least five sex ratio data points for each family were obtained.

Sex ratio was then modelled as:

Equation 2

$$\text{Sex ratio} \sim \text{Beta}(\text{N}, \bar{\text{p}}, \text{phi})$$

$$\text{logit}(\bar{\text{p}}) = \alpha + \gamma_{\text{spp}} + \gamma_{\text{phy}} + \varepsilon$$

Where α is a fixed-effect intercept, γ_{spp} and γ_{phy} are vectors of random-effect coefficients that account for residual intercept deviations attributable to species uniqueness (spp) and patterns of relatedness as described by the phylogeny (phy), and ε is unexplained residual variation. Fixed effects were assigned weakly informative priors following a Gaussian distribution, and random effects were assigned weakly informative priors following a Gamma distribution, and the phi precision parameter was assigned a weakly informative prior following the Gamma distribution. We calculated the Intraclass Correlation Coefficient of the model to assess phylogenetic heritability using variance decomposition methods (Nakagawa *et al.*, 2017). The proportion of the variance explained by the grouping structure (species and phylogeny) was 33%.

We then sampled the dataset based on the sex ratio of each species by transect to select females. For example, if Species A was recorded 10 times in Transect 1, and the sex ratio of Species A was 6 females to 1 male, 86% of those records would be sampled randomly as females. We repeated this process 100 times. The mean biomass of mature female fish and population fecundity at each site across the 100 samples was calculated (see Step 5).

4.3.5. Step 4. Length at maturity

Temperature affects the life-history traits of fish (Wang *et al.*, 2020). Bergmann's Rule and the Temperature-Size Rule suggest that there is a negative relationship between size at maturity and temperature in ectotherms (Angilletta and Dunham, 2003; Kingsolver and Huey, 2008; Forster and Hirst, 2012; Bergmann, 1847). As our dataset spans a large geographical scope, we wanted to account for the potential differences in the size at which species reach maturity across a temperature gradient. We therefore collected data on the relationship between length at maturity (LMat) and sea surface temperature (SST) from Morais and Bellwood (2020), Morat et al. (2020), Thorson et al. (2017), and Wang et al., (2020). We then modelled LMat as:

Equation 3

$$\mathrm{lnLMat} \sim \mathrm{normal}(\mu, \sigma)$$

$$\mu = (\alpha + \gamma_{0spp} + \gamma_{0phy}) + (\beta + \gamma_{1spp})*\mathrm{SST} + \varepsilon$$

where α_0 is a fixed-effect intercept, γ_{0spp} and $\gamma 0phy$ are respectively vectors of random-effect coefficients that account for residual intercept deviations attributable to species uniqueness and patterns of relatedness as described by the phylogeny, β is a fixed-effect slope for the predictor vector, SST, γ_{1spp} is a vector of random-effect coefficients that account for residual slope deviations attributable to species uniqueness, and ε is the model unexplained residual variation. Fixed intercepts and slopes were assigned weakly informative priors following a Gaussian distribution, and random effects were assigned weakly informative priors following a Gamma distribution. The phylogenetic heritability, estimated as the proportion of the variance (conditioned on the fixed effects) explained by the random effects (phylogeny) was 97%.

We then used the NOAA Optimum Interpolation (OI) Sea Surface Temperature (SST) V2 product (https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.html) to calculate SST for all sites included in our dataset. The latitude and longitude coordinates corresponding to the centroid of each social site were assigned to the nearest coordinates available with SST data. The median date for fish survey data was 2008. We therefore used the mean annual SST values from 2003-2013 (2008 +/- 5 years). We extrapolated species' lengths at maturity using the "picante" method described above (see "Phylogenetic Extrapolation" section) for the range of SSTs in which those species were recorded. We found a negative relationship between LMat and SST (slope = -0.05, 95% UI: -0.08 - -0.03), which is consistent with previous studies and theory (Bergmann, 1847; Heibo *et al.*, 2005).

4.3.6. Step 5. Biomass of mature females and population fecundity

The biomass of mature females and population fecundity at each site was estimated by selecting all fish the same length or larger than the estimated length at maturity for that site. This was done across the 100 samples of female fish (see "Sex ratios" section). The mean biomass of mature female fish and population fecundity at each site across the 100 samples was calculated and converted into units of kg/ha and eggs/ha respectively to standardise across sampling area. We then took the median biomass and fecundity values of those 100 samples.

4.3.7. Relationship between mature female biomass and population fecundity

We used a Bayesian hierarchical mixed effects model to identify the parameters of the relationship between mature female biomass and population fecundity at the site level. We set reef cluster and nation/state/territory as random effects where reef sites are nested in reef clusters, and reef clusters are nested in nations/states/territories.

Equation 4

$$\text{Fecundity}_{0jk} \sim \text{Normal}(\mu_{0jk}, \sigma)$$

$$\ln(\mu_{0jk}) = \alpha + \beta * \ln(\text{mature female biomass}_{0jk}) + \gamma_{0jk} + \varepsilon$$

Where α is a fixed intercept, β is the slope, γ_{0jk} is the matrix of random effect coefficients (reef cluster, nation/state/territory) that account for intercept variation, and ε is the model unexplained residual variation.

4.3.8. Global drivers models

We elaborated on previous work looking at the global drivers of biomass (Cinner *et al.*, 2016, 2020) to assess if patterns were similar for mature female biomass, the fecundity of all families, and the fecundity of three economically important families:

Lutjanidae, Labridae (Scarinae), and Serranidae. We also replicated the model of fish biomass >20 cm from Cinner et al. (2020) for comparison to fecundity. The social and environmental potential drivers established in previous work and incorporated into our models are:

1. **Management** = each *reef site* was assessed as being i) unfished – a high compliance fully protected reserves, ii) restricted – active restrictions on gears or fishing efforts, or iii) openly fished – fished sites without any restrictions.
2. **Local population growth** = the population growth of each *reef cluster* was calculated as the proportional difference between the population in 2000 and 2010, based on data from the Socioeconomic Data and Application Centre (SEDAC and CIESIN, 2015).
3. **Gravity** = an estimate of human pressure based on population size and travel time to the *reef site* from a population grid cell (see (Cinner *et al.*, 2018)).
4. **Human Development Index** = for each *nation/state/territory*, a measure obtained from the United Nations Development Program for 2010 was used where available.
5. **Population size** = for each *nation/state/territory*, a population estimate for 2010 was derived from the national census reports CIA fact book (https://www.cia.gov/library/publications/the-world-factbook/rankorder/2119rank.html) and Wikipedia (https://en.wikipedia.org/wiki/Main_Page).
6. **National Reef Fish Landings** = data was obtained at the *nation/state/territory* level from the Sea Around Us Project (SAUP) catch database (http://www.seaaroundus.org). Estimates corresponding to 2010 and only included reef associated species were retained. Catch per unit area (catch/km2/y) was calculated by dividing a nation/state/territory's catch by its estimated reef area.
7. **Oceanic productivity** = average of monthly chlorophyll-a concentrations were calculated at the *reef cluster* scale using data provided at a 4km-resolution by Aqua MODIS (Moderate Resolution Imaging Spectro-radiometer) for years 2005 to 2010 as per Cinner et al., (2020).
8. **Climate stress** = a measure of climate stress for corals developed by Maina et al., (2011) was incorporated at the *reef site* scale.

We checked for collinearity between covariates using bivariate correlations and Variance Inflation Factors (VIF). All covariates had VIF scores less than 2, indicating no collinearity issues. We then modelled biomass of fish >20cm, mature female biomass, fecundity of all families, and the fecundity of specified families with the same hierarchical structure specified in **Equation 4**, with reef cluster and nation/state/territory as random effects. All global drivers were scaled to a mean of zero (where continuous) and included in the model along with covariates accounting for methodological effects, sampling area, census method, sampled habitat, and depth. In the models for biomass >20cm, mature female biomass, and fecundity of all families, response variables were logged and the models were fit with a gaussian-distributed error. For the family-specific models on fecundity, a hurdle-lognormal distribution was used to account for the large percentage of zeros. The two-part hurdle model was composed of 1) a binomial distribution to predict the probability of observing species in the specified family, and 2) a log-normal distribution of non-zero fecundity data. We conducted graphical posterior predictive checks to assess all model fits to the data and ensured model convergence by checking traceplots and R-hat values (Gelman *et al.*, 2020; Bürkner, 2017).

Simulating the influence of establishing new protected areas

Covariate effect sizes were visualised by sampling 1000 values from the posterior distributions of each model and estimating 50% and 95% credible intervals. After identifying the importance of management type in all models, we estimated the ratio of biomass or fecundity between unfished/fished and restricted/fished sites. We did this by holding all the covariates to their means or reference levels, while accounting for the random effect structure, and allowing management to vary. We then sampled 1000 values from the posterior distributions of the model from each management type and took the ratios of the posteriors. In order to predict the fecundity potential of a nation/state/territory and geographic basin, we simulated a dataset where all fished sites were changed to fully protected sites and held all other covariates to their means or reference levels. We drew samples from the model posterior based on a new dataset where all fished sites were assigned protected status, and samples from the model posterior using the original fitted dataset (i.e., current protection levels). We then quantified how enforcing fisheries restrictions would change total fish fecundity by calculating the percent difference between fished sites and predicted protected sites, pooled by country.

Author contributions

JHH gathered literature-based data, did the data analysis, and wrote the manuscript. JR provided supervision, data analysis support, and editorial comments. DB wrote the species fecundity model and provided guidance on analysis. AS provided phylogenetic trees. NS developed the code to extrapolate phylogenetic effects. IC curated the data. DM conceived the idea and provided supervisory support. NG provided supervision and editorial comments. Authors from the SERF working group provided data.

General discussion

Change is an integral part of the socio-ecological systems of the Anthropocene (Barlow *et al.*, 2018; García *et al.*, 2020). Conservation in the Anthropocene needs frameworks that accommodate this dynamism. Bellwood et al. (2019) pose the questions, “what do we want to conserve on Anthropocene reefs, why, and how?” In this thesis, I explore the option of using a trait-based approach to conserve ecosystem functions on Anthropocene reefs using MPAs. I look at how this approach can accommodate change on reefs while also conserving the traits and functions that are necessary for coral reef ecosystems to persist in the future (Norström *et al.*, 2016). In this overarching discussion section, I first summarise the findings of each chapter (Fig. 1), then I explore crosscutting themes, and finally, I look at the implications my work has for future research and conservation management.

1. Synthesis

Without an empirical evaluation of the evidence-base for the links between ecosystem disturbances, species’ traits, and ecosystem processes, we cannot confidently use traits to understand the functional dynamics of coral reef fishes (Bellwood *et al.*, 2019b). Therefore, in **Chapter 1**, I used the response-and-effect framework to structure a systematic review of the literature on coral reef fish traits. I used this review to identify research gaps and determine where there was evidence linking traits to disturbances, management actions, and ecosystem processes. Firstly, I categorised traits into broad groups: behavioural, life history, morphological, diet and trophic level, or physiological. I found that behavioural and life history traits were more commonly shown to respond to disturbances, while morphological traits tended to be used in capturing ecosystem processes. Moreover, I identified size and diet as both response and effect traits central to the literature. My review supports the view that size acts as a super-trait, as it scales with, and therefore shapes, a range of other functional traits (Jacob et al., 2011). When looking at a specific process, herbivory, I demonstrated that on average, bite impact was positively correlated with size, while bite rate was negatively correlated with size. I also found that the most popular cluster of traits used in functional diversity metrics (e.g., functional richness, functional dispersion) is comprised of size, diet, space use/position in the water column, diel activity, gregariousness, and mobility, which encompass three of the broad trait categories.

In **Chapter 2**, I used the response-and-effect framework and the findings from **Chapter 1** to select traits that, based on the evidence in the literature, were likely to respond to protection from fishing and have an impact on ecosystem functioning: size, diet, position in the water column, gregariousness, reef association, and length at maturity. Looking at high-compliance no-take MPAs in Kenya, I showed that species that become more proportionally abundant over time with protection were characterised by the traits: 7-15cm body size, planktivorous diet, low in the water column, forming medium-large schools, and with high levels of reef association. I interpreted these results through a functional lens to show that MPAs could increase ecosystem productivity through the import of pelagic subsidies by planktivores as well as ecosystem processes like herbivory that increase with species' gregariousness. Moreover, I showed that while both biomass and abundance increased over time with protection from fishing, the patterns and rates of increase differed due to shifts in community size structures. In Kenyan no-take MPAs, larger bodied fish were likely to be driving overall biomass trends, while small fish were likely to be driving the overall abundance trends. The time-series used in this analysis was unique because the data-collection was performed by the same person and spanned a 44-year chronosequence. However, there has been little success in expanding the capacity for ecological monitoring in the region, which, during the COVID-19 pandemic, manifested as an immediate problem, as travel restrictions meant that international scientists were not able to conduct fieldwork.

The process of monitoring can be just as important to conservation as the implementation of regulations, because it can be used as a learning tool that increases participation in management and fosters pro-conservation values (Alexander *et al.*, 2018; Armitage *et al.*, 2020). In **Chapter 3**, I worked with the Wildlife Conservation Society (WCS) to explore ways to design ecological data-collection methods that are more accessible and capable of being used for learning purposes. Specifically, I explored how video transects and fish traps compared to UVC methods in their ability capture data on fish community composition and biomass. I found that there were no statistical differences between biomass estimates obtained using UVC and video methods. Fish traps were able to capture broad trends across levels of protection and act as a hands-on learning tool, but there was a lot of variation in the data, and only preliminary results were collected. I applied these methods to explore the ecological status of a newly proposed Transboundary Conservation Area (TBCA) between Kenya and Tanzania and showed that protection has more of an effect on biomass in Kenya, where the MPAs are well enforced, compared to Tanzania.

Biomass can scale with a range of ecosystem functions (Humphries, 2020; Robinson *et al.*, 2020), and under certain pressures or gradients, it can also decouple from ecosystem functions (Morais *et al.*, 2020a). In **Chapter 4**, I look at how biomass scales with fecundity on a global level and ask what potential effect MPAs could have on a fecundity as an important functional trait. I find that at the site-level, fish community biomass scales hyperallometrically with fecundity, but with an average exponent of 1.05, rather than the species-level exponent of 1.19. I also looked at Western Indo-Pacific, and especially Tanzania, as a potential fecundity hotspot. Overall, I find that MPAs could increase the fecundity potential of sites by up to 11%. Through these findings, I showed that MPAs potentially secure biomass production through enabling the sustainability of population replenishment through increased fish fecundity.

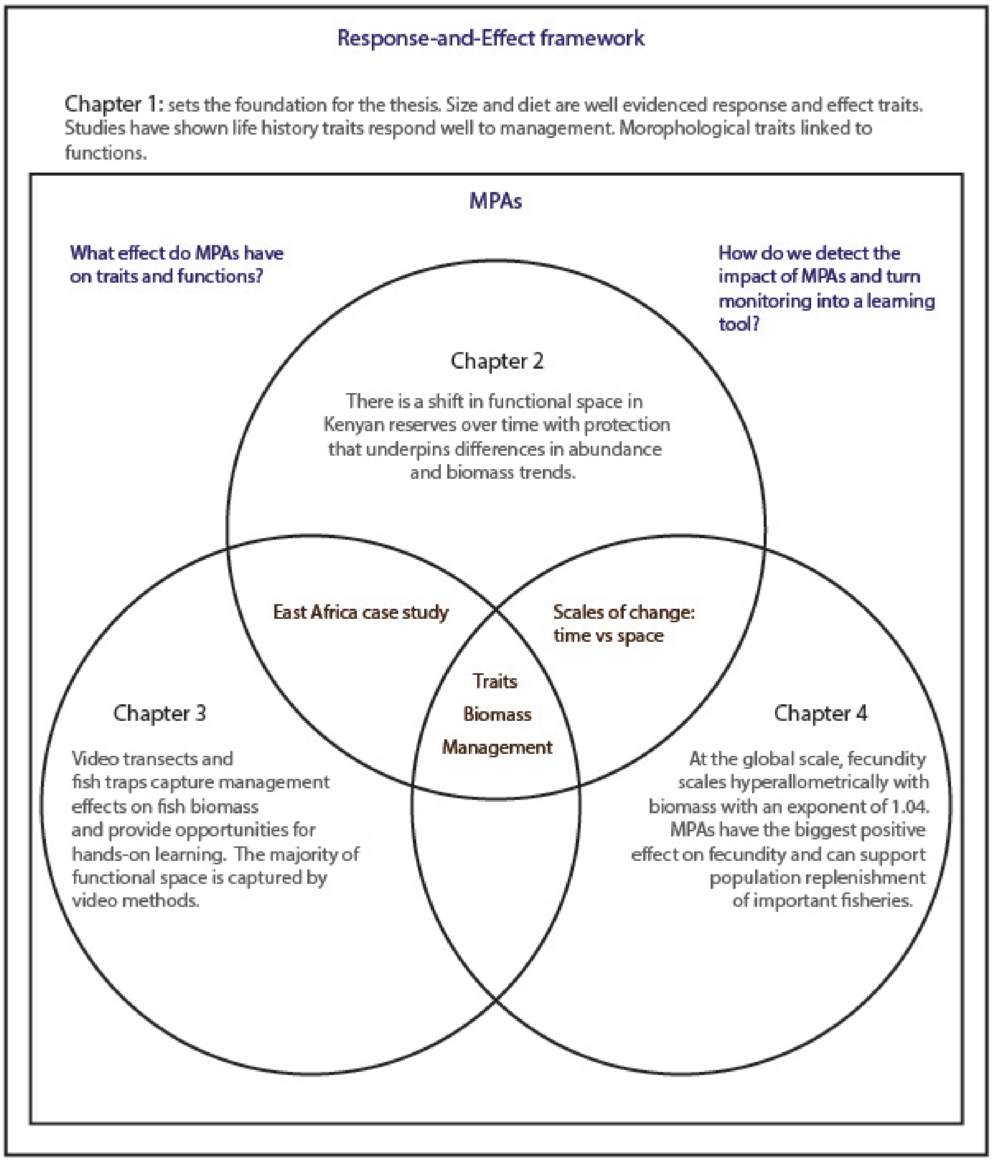

Figure 1. Schematic diagram integrating the key findings of this thesis.

2. Building capacity for trait-based approaches to coral reef fish functional ecology

Trait-based approaches ask the question, “how”: How do communities respond to their environments? How do they affect their environments? Before using trait-based approaches, however, we need to answer the question, “what”: What traits? What mechanisms? What scales? In Chapter 1, I outline the traits used in the literature and categorise the mechanisms and scales at which they operate. I find that there is a need to build on our understanding of the “what” to better be able to address the “how”.

There is not enough data on coral reef fish traits to be able to pick and choose the most appropriate traits at the right scales. This highlights the need for efforts such as The

Open Traits Network (OTN), an initiative that seeks to collate and standardise trait data across the Tree of Life (Gallagher *et al.*, 2020). There could be an open database specifically for coral reef fish traits, similar to the Coral Traits database (Madin et al., 2016; https://coraltraits.org/). Creating ways of sharing data and methods is critical to developing the predictive capacity of trait-based coral reef ecology. Currently, databases such as FishBase and GASPAR provide useful species-level data on fish (Kublicki, 2010; Froese, R.; Pauly, 2019), but the variety of traits with data available is limited.

Species-level traits are advantageous because they can be retrospectively assigned to survey data that record species biomass and abundance. In Chapter 2, I demonstrated this advantage by investigating functional patterns over time in Kenyan marine reserves. I retrospectively assigned traits to species-level UVC abundance data, thereby allowing me to interpret change through a functional lens, even though assessing function was not a research aim at the time of data collection. Trait-interactions can occur at many biological scales. Fontana et al. (2021) propose in their "trait-integration continuum" framework that higher order traits are useful in predicting processes while lower order traits are more useful in understanding mechanisms. They expand on the definition of functional traits established in Violle et al. (2007) to include characteristics beyond and below the level of the individual. In this framework, traits can interact across scales, whereby "genes integrate into metabolic pathways, whose interactions make phenotypes, which determine trait syndromes, and dictate population dynamics through interaction with the environment, and community composition" which "ultimately result[s] in the formulation of functional groups that define emerging ecosystem properties". One interesting finding from Chapter 3 was that even though measuring intraspecific traits might be one of the gold standards of functional ecological monitoring (Bolnick *et al.*, 2011b), they might not be necessary to obtaining an answer to the management question of whether an MPA is working to increase fish biomass. Even though I used maximum fish length sizes from FishBase to calculate the biomass of sites across the Kenya-Tanzania TBCA, I was able to get reasonable biomass estimates. It can be argued that the power of a model lies in its capacity to predict processes or generate useful testable hypotheses (White and Marshall, 2019). Similarly, it can be argued that the power of traits is that they can be used to understand niche-based mechanisms to predict community patterns and generate testable hypotheses (Cadotte *et al.*, 2015). Species-level traits could be powerful enough to answer higher-level research or management questions, while requiring minimal resource investment.

Where data is available for some species, but not others, phylogenetic imputation can be used as a powerful tool to fill in the gaps. In Chapter 4, I apply a phylogenetic imputation method to predict the sex ratio, length at maturity, and fecundity values of coral reef fishes. This method works best when there is a strong phylogenetic signal and a short branch length of the tip of the phylogenetic tree to be imputed (Debastiani *et al.*, 2021; Molina-Venegas *et al.*, 2018). This is a useful tool that can be used to infer trait distributions and diversity in novel settings (Swenson *et al.*, 2017; Swenson, 2014). Moreover, it can be combined with other predictors to estimate traits at an intraspecific level. For example, in Chapter 4, I used individual size measurements and allometric scaling theory to predict fecundity, and I used temperature across a geographical gradient to predict length at maturity. Phylogenetic imputation can therefore be an important tool in building a coral reef fish functional trait database.

3. Approaches to monitoring and conserving reefs for functions in the Anthropocene

Protected areas have a long international history in conservation (Phillips, 2004). However, priorities for conservation have shifted over time as the discipline has developed and ecologies have changed. Nevertheless, protected areas seem to have kept pace with these changes and are still the most cited solution to conservation challenges (Godet and Devictor, 2018). In my thesis, I found that MPAs are fit for purpose, even in the functionalist conservation paradigm. MPAs have a positive effect on indicators of high functional potential such as biomass (Chapter 2 and Chapter 3) and important functional traits such as fecundity (Chapter 4) and gregariousness (Chapter 2). These results fit with findings that measure rates of ecosystem processes. For example, Cinner et al. (2020) demonstrate the positive effect of MPAs on trait diversity and parrotfish scraping, and Cheng et al. (2019) demonstrate the positive effect of MPAs on predation.

Building the predictive capacity of effect traits by collecting quantitative data on how they relate to rates of ecosystem processes is a necessary progression for coral reef functional ecology (Chapter 1). However, it can be challenging to collect this kind of data on fish. Trait-based approaches originate from terrestrial plant ecology (Grime, 1977), where the same plants remain in the same place. Fish, on the other hand, can be very mobile, and it is harder to attribute the rates of a process occurring in a certain place to specific individuals without observing the process directly or conducting an experiment with controls. In Chapter 1, I outlined a typology of evidence for response and effect traits. For example, papers that manipulated traits in a controlled setting such as a lab and measured resulting ecosystem processes were characterised as "ex situ experiments". "In situ experiments" included trait inclusion and exclusion experimental designs that occurred on the reef, such as those conducted by Burkepile and Hay, 2008 and Hughes et al., 2007. "In situ observation" papers included studies such as by Streit et al. (2015), where video methods were used to record the species feeding on *Sargassum*. Such experiments and observational studies of ecosystem processes provide critical data, but they can be costly and time consuming. Having a diversity of methods to choose from is therefore necessary. Where resources are more limited, modelling or hybrid methods such as pairing surveys of fish communities with data from assays measuring rates of ecosystem processes could be used. For example, McClanahan (1994) established a simple urchin predation assay which can be coupled with UVC surveys conducted in the same sites as the assays to model the trait mechanisms driving the ecosystem process. Looking at old data through a functional lens can be a simple way of building the evidence-base for trait-based approaches.

Simple data collection methods can be an important tool in building a more equitable conservation practice. Data collection and the distribution of capacity (through expertise, status, or resources) for monitoring can affect social power dynamics (Bene and Neiland, 2006). For example, an international NGO might have more capital than local communities to affect management plans on a coral reef because they have institutional legitimacy and hold the data that suggests the validity of one management approach over another (Jepson, 2005). Participatory monitoring recognises the idea that data=power, and as such, it can be used as a method to challenge who sets the conservation agenda (Denney *et al.*, 2018). However, Bene and Neiland (2006) also highlight the potential for "pseudo-participation", where there is a co-option of local community labour to achieve the goals of the elite – be they scientists, NGOs or governments. One disadvantage of the trait-based approach is that it is not necessarily as intuitive as a compositionalist approach, and thus might not be as suited towards participatory monitoring.

There can be a disconnect between academic discourse in conservation science and conservation practice on-the-ground (Gossa *et al.*, 2015). Many of the world's biodiversity hotspots, including a number of tropical coral reefs, occur in poor regions (Fisher and Christopher, 2007). Moreover, while biodiversity hotspots are often located in the Global South, the majority of research on these ecosystems is produced by English speaking researchers from the Global North (Barlow *et al.*, 2018). There may not be the desire or the capacity for people living local to tropical coral reefs to commit to measuring traits and ecosystem processes. However, as I discuss in Chapter 3, in the case of the Kenya-Tanzania TBCA, there *was* value seen in developing participatory monitoring for fish biomass. Conservation can benefit from developing a wide range of tools that can be deployed in the right contexts, and monitoring biomass and species composition rather than traits does not mean that results can't be interpreted through a functional lens, where or if that approach is valuable. The temporal and spatial scale of conservation questions is what matters. In Chapter 4, I look at reproductive potential on a global scale, and provide a potential functional benefit of MPAs for marine managers to explore. However, in casting this large scope, I had to set aside a number of assumptions about local governance and suitability of MPAs. The goal then is to not only integrate ideas generated in the academic sphere into local and global conservation practice, but also to create space for local conservation practices to influence academic ideas.

4. Future directions

Throughout my thesis and general discussion, I have identified the ways in which we can build our capacity to use trait-based approaches in coral reef fish functional conservation: we need to build trait databases, measure ecosystem processes, develop useful predictive modelling methods, and find ways to adapt our research to conservation capabilities and needs on the ground. Beyond these next steps, however, there are two horizons that are becoming increasingly important to tackle:

The first is addressing ecosystem "multifunctionality", or the co-occurrence of multiple ecosystem functions (Zavaleta *et al.*, 2010), across geographic scales. For coral reef ecosystems, this means looking at the networks and connections between functions on a reef and between reefs (Tebbett *et al.*, 2020). For example, it could be that biodiversity is even more important in predicting ecosystem multifunctionality than just one ecosystem process (Manning *et al.*, 2018), or different aspects of biodiversity (e.g. richness vs. evenness) have different effects on the relationship between processes (Maureaud *et al.*, 2019b). We could ask whether there is a trade-off between ecosystem processes and their associated ecosystem services (Lee and Lautenbach, 2016; Cheng *et al.*, 2019), or whether conserving them in one site affects another (Di Lorenzo *et al.*, 2020).

The second is addressing how to adapt place-based conservation tools like MPAs to accommodate changes where species and functions are occurring. For example, climate change is likely to create novel conditions in 97% of the world's large MPAs by 2100 (Johnson and Watson, 2021). It is also likely that climate change will result in entire coral reef island nations becoming uninhabitable due to sea level rise (Hauer *et al.*, 2020). There is scope to adapt tools like strategic conservation planning and marine spatial planning to make sure that MPAs don't remain static and in places where they no longer serve a purpose (Sala *et al.*, 2021; Mills *et al.*, 2010).

5. Conclusion

Bellwood et al. (2019) asked, "what do we want to conserve on Anthropocene reefs, why, and how?" In my thesis, I explored the option of using a trait-based approach to conserve ecosystem functions on Anthropocene reefs using MPAs. Ultimately, however, the conclusion of this thesis is probably the most academic response possible: there is no single right answer, and a diversity of options is necessary in a global context. In Chapter 1, I set out to find the gold standards for trait-based approaches to coral reef fish functional ecology. By Chapter 2, I was immediately confronted with all the limitations to achieving this gold standard. But I found that even if I could not get the trait data I wanted (there was a failed attempt to look at gape size as an important functional morphological trait), I could develop a new functional understanding of the changes over time that occurred in MPAs. When I finally came around to Chapter 3, I dug into the practicalities of collecting meaningful data, and found that, in some cases, there is value in coming up with the simplest participatory approach, because MPAs are only useful if they work for the people most dependent on them. In cases like the Kenya-Tanzania TBCA, collecting trait-based data was never going to be an immediate priority for marine managers, but developing monitoring methods that also capture a range of functional traits means that managers will be able to detect the functional benefits of MPAs as well as establish basic biomass estimates for sites. MPAs are an old tool being applied to achieve a new goal in potentially novel ecosystems. This paradoxical relationship, for me, is epitomised in Chapter 4. The SERF dataset has been used in several papers to look at global distributions and drivers of coral reef fish biomass (e.g. Cinner et al., 2020, 2016). By using a trait-based approach, I was able to take the same data and combine it with new models and phylogenetic trees, to calculate site-level fecundity distributions and look at biomass production as a more dynamic process.

One of the reasons I love coral reef conservation research is because it is inherently value-driven and incredibly complex. It brings together several “wicked problems”: How do we ensure food security and prevent ecosystem collapse? What do we want to conserve and how? How do we want to value ecosystems? How do we prevent and accept ecosystem change? Who and what are we protecting ecosystems for? A wicked problem is by definition “messy, intractable, subject to multiple interpretations, and for which solutions at present are not evident or inscrutable” (Redford *et al.*, 2013). In my thesis I aim to contribute to the pool of solutions to the wicked problem of conserving coral reefs in the Anthropocene. Trait-based approaches to understanding coral reef fish functional dynamics and the use of MPAs to conserve functions are essential contributions to what needs to be the largest ocean of possible solutions to an underwater world of wicked problems.

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Appendix A: supplementary material

1. Supplementary material for Chapter 1

Supplementary Table 1. *Results from papers looking at categorical response and effect traits or categorical disturbances and processes.*

Citation	Trait	Process/ Disturbance	Results
Adam et al. 2015, Oecologia	Habitat type	Herbivory	Found distinct clusters of preferential substrate in feeding parrotfish - species with similar diets (herbivory) had different habitat preferences and feeding substrate.

Bejarano et al. 2017, Functional Ecology	Head morphology	Herbivory	Looked at the effect of the interaction of wave exposure and traits on herbivory - found grazers–detritivores were associated with laterally compressed body plans, whereas scrapers–small excavators occupied the full extent of fusiform body plans. See below (diet) for secondary link to herbivory rates.
Bejarano et al. 2017, Functional Ecology	Body morphology	Herbivory	Looked at the effect of the interaction of wave exposure and traits on herbivory - found grazers–detritivores were associated with laterally compressed body plans, whereas scrapers–small excavators occupied the full extent of fusiform body plans. See below (diet) for secondary link to herbivory rates.
Bejarano et al. 2017, Functional Ecology	Fin morphology	Herbivory	Looked at the effect of the interaction of wave exposure and traits on herbivory - found grazers–detritivores were associated with laterally compressed body plans, whereas scrapers–small excavators occupied the full extent of fusiform body plans. See below (diet) for secondary link to herbivory rates.
Bejarano et al. 2017, Functional Ecology	Diet/trophic level	Bioerosion	Feeding functional groups (here classified within diet trait) are assessed in relation to functioning at different wave exposures. Bioeroding species fed only at low wave exposures.
Bejarano et al. 2017, Functional Ecology	Diet/trophic level	Herbivory	Feeding functional groups (here classified within diet trait) are assessed in relation to functioning at different wave exposures. Grazer-detritivores and scrapers-small excavators greater herbivory at higher wave intensities.
Bellwood, Hoey and Choat 2003, Ecology Letters	Diet/trophic level	Herbivory	Naso unicornis = key consumer of erect brown macroalgae.
Bellwood, Hoey and Choat 2003, Ecology Letters	Diel activity	Herbivory	Diurnal higher than nocturnal.
Bellwood, Hughes and Hoey 2006, Current Biology	Diet/trophic level	Herbivory	Mixed: single species *Platax pinnatus* (key functional group) responsible for Sargassum removal, but normal herbivorous spp had little impact on macroalgal removal.
Brandl et al. 2016, Ecosphere	Diet/trophic level	Climate change: extreme weather	Omnivores and planktivores decline. Turf-feeders/detritivores, macro-invertivores, and micro- invertivores increase.

Brandl et al. 2016, Ecosphere	Habitat type	Climate change: extreme weather	Fish dependent on live coral and loose coral rubble decrease, but weakly. Species associated with the underlying rocky reef matrix were likely to increase following cyclone.
Brandl et al. 2016, Ecosphere	Territoriality	Climate change: extreme weather	Non-territorial species were likely to benefit from the cyclone, while territoriality had no discernable effect.
Fox and Bellwood 2013, Coral Reefs	Head morphology	Herbivory	Rabbitfish slower than parrotfish and surgeonfish. Rabbitfish have elongate snout for crevices (slower).
Humphries, McClanahan and McQuaid 2014, Marine Ecology Progress Series	Diet/trophic level	Herbivory	Herbivory rates lowest in fenced/caged areas.
Humphries, McClanahan and McQuaid 2014, Marine Ecology Progress Series	Diet/trophic level	Fishing	Herbivory rates of grazers and scapers decreased with fishing pressure but not browsers.
Karkarey et al. 2017, Animal Behaviour	Feeding behaviour	Climate change: bleaching	Foraging mode greater than ambush mode in low structure sites.
Marshell and Mumby 2012, Coral Reefs	Diet/trophic level	Herbivory	Detritivore removed more turf than other grazers.
McClanahan and Hicks 2011, Fisheries Management and Ecology	Stage at maturity	Fishing	Gear type specific: positive (older at first maturity with fishing).
McClanahan and Hicks 2011, Fisheries Management and Ecology	Life span	Fishing	Gear type specific: positive.
McClanahan and Hicks 2011, Fisheries	Generation time	Fishing	Gear type specific: positive.

Management and Ecology			
McClanahan and Hicks 2011, Fisheries Management and Ecology	Size	Fishing	Gear type specific: negative.
McClanahan and Hicks 2011, Fisheries Management and Ecology	Natural mortality	Fishing	Gear type specific: negative.
McClanahan and Hicks 2011, Fisheries Management and Ecology	Growth rate	Fishing	Gear type specific: negative.
McClanahan and Hicks 2011, Fisheries Management and Ecology	Diet/trophic level	Fishing	South-coast sites increased in trophic level with fishing management.
Mellin et al. 2008, Ecological Modelling	Size	Fishing	Modelling approach. Large fish abundances and fish in size class 8-15cm lower with fishing.
Mellin et al. 2008, Ecological Modelling	Diet/trophic level	Fishing	Modelling approach. Macrocarnivore and piscivore abundances lower with fishing.
Mellin et al. 2008, Ecological Modelling	Stage at maturity	Fishing	Modelling approach. Late reproducing and early reproducing (life history categories 6 and 2) species abundances lower with fishing.
Mellin et al. 2008, Ecological Modelling	Growth rate	Fishing	Modelling approach. Slow-growing and fast-growing (life history categories 6 and 2) species abundances lower with fishing.
Mellin et al. 2008, Ecological Modelling	Natural mortality	Fishing	Modelling approach. Long-lived and short-lived (life history categories 6 and 2) species lower with fishing.
Mumby et al. 2006, Science	Diet/trophic level	Fishing	Double the number of parrotfish predators inside the reserve.

Mumby et al. 2006, Science	Size	Fishing	Individuals of the smaller bodied scarid species (max 23 cm) (Scarus iserti and Sparisoma aurofrenatum) were smaller inside the reserve. Scarids that reached consistently large adult sizes, such as the terminal-phase males of Sc. vetula and Sp. viride, exhibited no difference in their size across the reserve boundary. Parrotfishes that occupied a wide range of size categories (6 to 32 cm) were either larger in the reserve (Sp. viride intermediate phase) or larger outside the reserve (Sc. vetula IP).
Olivier et al. 2014, Frontiers in Zoology	Mouth morphology	Herbivory	Negative impact with c-ligament ablated.
Pereira et al. 2014, Reviews in Fish Biology and Fisheries	Size	Predation: predator	Small (\5.0 cm) and medium size classes (5.0–10.0 cm) fed more on small invertebrates such as copepoda, tanaidacea, amphipoda, and ostracoda. Larger individuals had a higher proportion of polychaete, brachyura, and fish fragments in their stomachs.
Pereira et al. 2014, Reviews in Fish Biology and Fisheries	Diet/trophic level	Predation: predator	Haemulon species were classified as mobile invertebrate feeders, capturing prey on the bottom or in the water column depending on their size, and having a variety of crustaceans and polychaetes in their stomachs.
Rasher, Hoey and Hay 2013, Ecology	Diet/trophic level	Herbivory	Bite rate higher for browsers than grazers.
Rocha et al. 2015, Coral Reefs	Space use	Predation: prey	Just above ground in water column = more predated on.
Streit, Hoey and Bellwood 2015, Coral Reefs	Mouth morphology	Herbivory	Larger gape, more bite power, ate whole macroalgal thallus.
Streit, Hoey and Bellwood 2015, Coral Reefs	Size	Herbivory	Longer fish ate macroalgal thallus and occasionally leaves only.

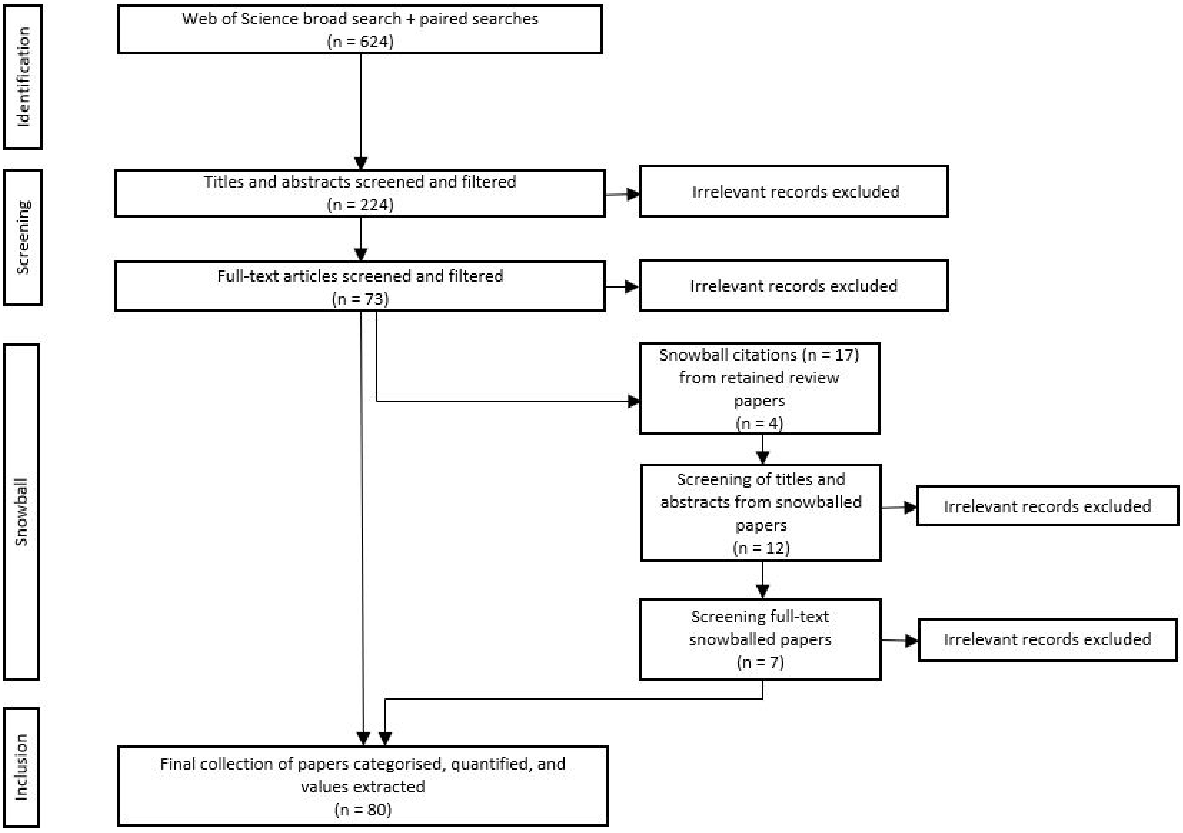


Figure S1 *PRISMA flow diagram for systematic review paper inclusion*

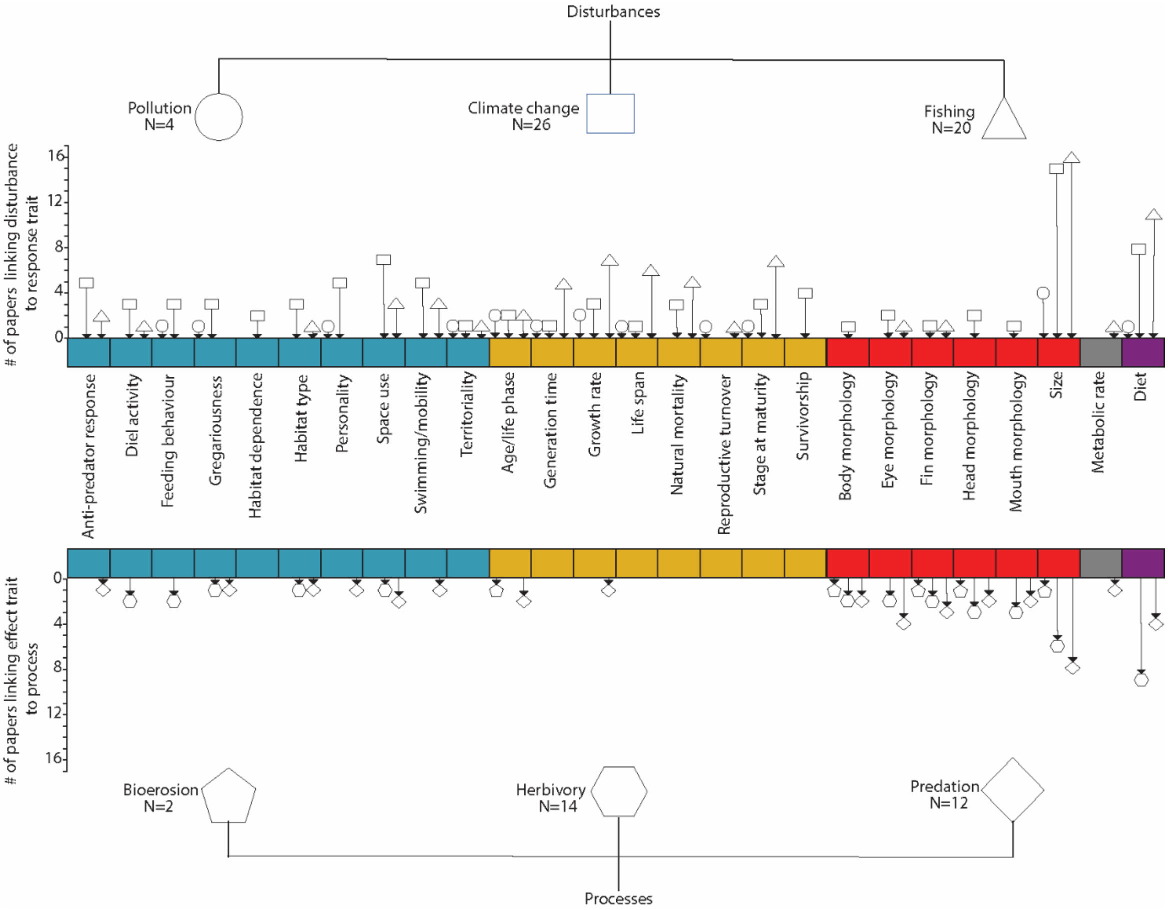


Figure S2 *Three-stage network diagram showing the number of papers linking each disturbance and process to response and effect traits. Each disturbance and process correspond to a shape, where pollution = circle, climate change = rectangle, fishing = triangle, bioerosion = pentagon, herbivory = hexagon, and predation = diamond. The colour of trait points corresponds to broad trait groupings (blue: behavioural, yellow: life-history, red: morphological, grey: physiological, purple: diet)*

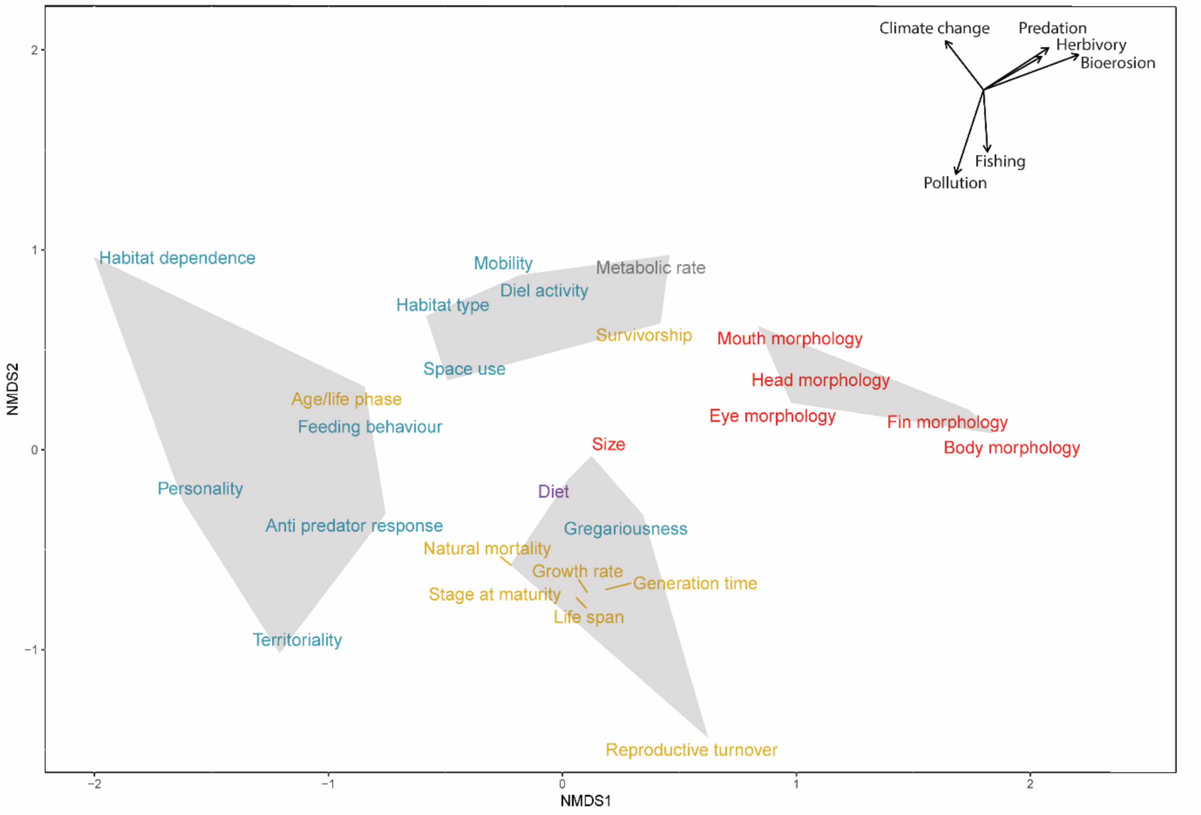


Figure S3 *Non-metric multidimensional (nMDS) ordination plot for traits of all papers. Four clusters show individual traits commonly used together in studies. Vectors show which disturbances and processes are driving these clusters. Colour of trait points corresponds to broad trait groupings (blue: behavioural, yellow: life-history, red: morphological, grey: physiological, purple: diet). The nMDS stress is 0.16*

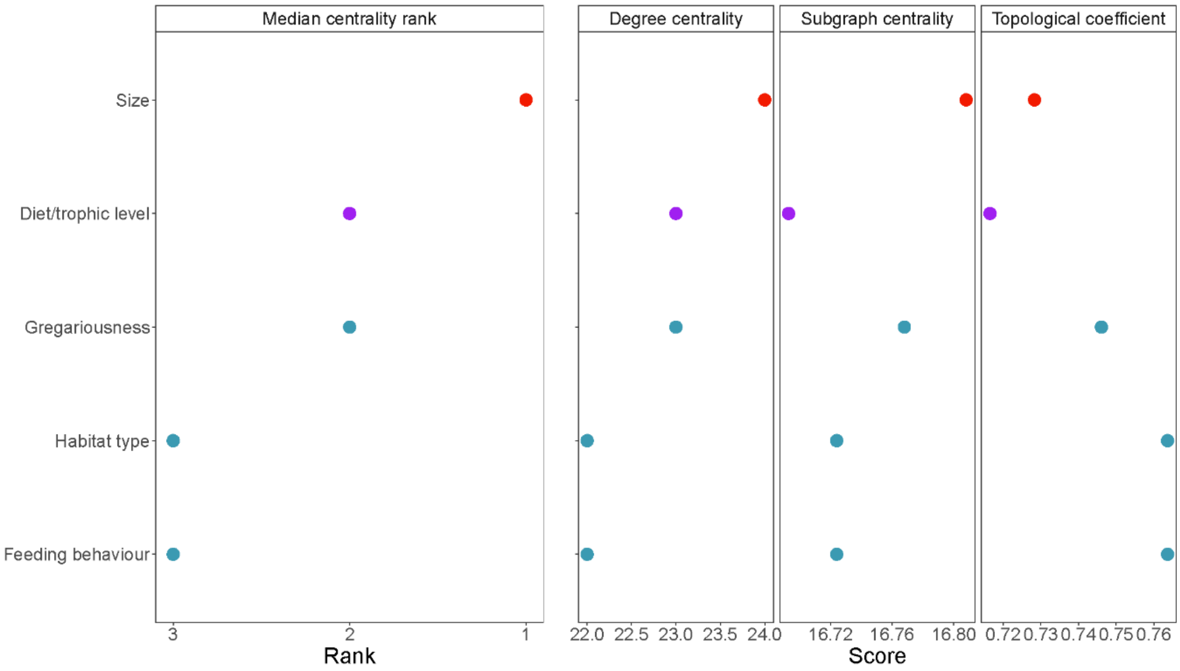


Figure S4 *Mean ranking of five most central traits in network diagram, based on degree centrality, subgraph centrality (logged) and topological coefficient scores. The colour of trait node corresponds to broad trait groupings (blue: behavioural, yellow: life-history, red: morphological, grey: physiological, purple: diet)*

2. Supplementary material for Chapter 2

Supplementary Table S1. Coral reef fish traits and justification for selection

Trait	*Trait grouping*	*Trait type*	*Source*	*Justification*
Total body length	Morphological	Ordinal: 0–7 cm < 7.1–15 cm < 15.1–30 cm < 30.1–50 cm < 50.1–80 cm < >80 cm	GASPAR	Size is known to respond to fishing pressure (McClanahan and Graham, 2015), and size-selective fishing tends to select for larger-bodied species (Robinson *et al.*, 2017). Size can determine the functional impact of a fish on processes such as nutrient cycling (Allgeier *et al.*, 2016), bioerosion (Bonaldo and Bellwood, 2008), herbivory (Lokrantz *et al.*, 2008)·(Nash *et al.*, 2013), and predation (Scharf *et al.*, 2000). It corelates with a number of other traits that are not as easily measured but are known to have functional significance (Jacob *et al.*, 2011).
Diet	Diet/trophic	Categorical: herbivorous-detritivorous (i.e., fish feeding on turf or filamentous algae and/or undefined organic material), macroalgal herbivorous (i.e., fish eating large fleshy algae and/or seagrass), invertivorous targeting sessile invertebrates (i.e., corals, sponges, ascidians), invertivorous targeting mobile invertebrate (i.e., benthic species such as crustaceans), planktivorous (i.e., fish eating small organisms in the water column), piscivorous (including fish and cephalopods), and omnivorous (i.e., fish for which both vegetal and animal material are important in their diet)	GASPAR	Higher trophic levels of fish tend to be more targeted by fishing and benefit more from protection (Coleman *et al.*, 2015). The diet of a fish influences which ecosystem processes species have an effect on by defining an essential axis of their ecological niche; for example, species can be predators that mediate the process of predation (Boaden and Kingsford, 2015), herbivores that feed on algae and mediate competition with other benthic organisms (Suchley and Alvarez-Filip, 2017), or bioeroders enabling sediment production and coral recovery (Bellwood *et al.*, 2012; Ruttenberg *et al.*, 2019).
Schooling	Behaviour	Ordinal: solitary < pairing, or living in small (3–20 individuals) < medium (20–50 individuals) < large (>50 individuals) groups	GASPAR	The number of fish in a school has been shown to affect feeding and influence the total number of bites taken by fish (Michael *et al.*, 2013). Schooling behaviour also influences predator-prey functional dynamics in a number of ways (Spitz *et al.*, 2014). Gregariousness is also known to interact with fishing. For example, schooling influences catachability of a species as well as how targeted a fish might be by certain fishing technologies (Fréon and Misund, 1999; Paramo *et al.*, 2010).

Position in the water column	Behaviour	Ordinal: bottom-dweller < bentho-pelagic (low in water column) < pelagic	GASPAR	Water column position influences potential prey items for predators, likelihood of predation for prey, and general resource use (Magoulick, 2004; Rocha *et al.*, 2015). Evolutionary shifts in water column position are linked to changes in body morphology (Mason *et al.*, 2008; Floeter *et al.*, 2018).
Reef association	Behaviour	Ordinal: low reef association < medium reef association < high reef association	Fishbase and expert opinion	Fishing pressure and protection from fishing can impact the benthic environment of coral reef ecosystems (McClanahan, 2008; Mellin *et al.*, 2016b). Species that are dependent on the coral reef habitat are therefore vulnerable to the effects of fishing (Cinner *et al.*, 2009). While small fish, associated with high levels of reef association (Hixon and Beets, 1993), are typically not targeted by fisheries in Kenya (Kaunda-Arara *et al.*, 2004), fishing can impact the level of reef association of fish communities through indirect effects by damaging the benthos. The level of reef association of a fish will also determine where in space it is able to live and therefore have a functional impact (Wilson *et al.*, 2008).
Length at maturity	Life history	Continuous	FishLife (Thorson *et al.*, 2017)	Life history traits, often grouped together into life history strategies, tend to be highly correlated (King and McFarlane, 2003). Length at maturity was selected as a representative life history trait because length-based life history measurements have been shown to be particularly sensitive to fishing pressure (Taylor *et al.*, 2014; McClanahan, 2018). Fishing can often have a greater negative impact on the abundances of long-lived, slow growing, late maturing, larger species, leading to changes in community compositions (Jennings *et al.*, 1999; Rochet *et al.*, 2000).

Supplementary Table S2. Final set of covariates included in the models and their justifications for use

Covariates	***Justification***	***Calculation/source***
Benthic PCA	The interplay between the coral reef habitat and the fish (abundance, biomass, and traits) that live in the habitat is complex(Darling *et al.*, 2017). We attempted to partially account for this by including a multivariate measure of the benthic habitat in the models. After some preliminary analyses, we decided to use this multivariate measure to address our questions, instead of looking at coral reef genus traits, because this measure sufficiently accounted for the benthic change over time at the scale we required.	A Principal Component Analysis (PCA) was conducted on percentage cover of 1) hard coral, 2) macroalgae, 3) coralline algae, and 4) other calcareous algae across all sites. This produced a succinct multivariate value (PCA axis 1 explaining 50% of the variation) for each site/year that captures multiple aspects of the benthos and at the same time reduced the number of parameters needed to be included in the models.
Rugosity	Rugosity, a measure of the structural complexity of the reef, was included as covariate in the global models separate to the PCA of the benthic community because it has been found to be an important predictor of reef fish abundance, biomass, and trophic structure (Darling *et al.*, 2017).	Rugosity was measured in the field.
Thermal stress anomaly - lagged	Thermal Stress Anomalies (TSAs) were included in the models as they can potentially affect reef fish traits via two pathways. Firstly, they are associated with coral bleaching events, and therefore can alter the reefs that the fish depend on through a lagged effect. Secondly, McClanahan(McClanahan, 2019a) showed that variation in TSA is associated with the biomass of certain fish families; this could be through a benthic pathway or another unknown/unmeasured pathway. Fish communities are expected to exhibit a lagged response to disturbances such as thermal stress (McLean *et al.*, 2018).	TSA data from 1991-2018 for each marine park were extracted from The Coral Reef Temperature Anomaly Database (CoRTAD) hosted by NOAA Coral Reef Watch. TSAs are calculated for 4 km grid cells as the weekly sea surface temperature minus the maximum weekly climatological (long-term average) sea surface temperature 34. The maximum TSA (magnitude) for each reserve in each year was selected for modelling. Therefore, the optimal time-lag for the effect of TSAs on fish functional space was assessed by lagging TSA values from 0 to 9 years and incorporating this lag into a GAMM model of the first PCoA axis. Lagged models were compared (for the same dataset years), and an optimal-fit lag of 4 years was selected to be included in the models, using the AIC selection procedure
Chlorophyll a	Chlorophyll a, a measure of phytoplankton density and therefore oceanic productivity, was included in the models because it is likely to influence reef fish trophic structure(Heenan *et al.*, 2020) and the state of the coral reef habitat (Riegl *et al.*, 2015).	Oceanic productivity was estimated using chlorophyll a for the years 1997-2018, which were available from the Ocean Colour Climate Change Initiative dataset esa-cci-chla-monthly-v4-1 by the European Space Agency (http://www.esa-oceancolour-cci.org/). Daily data were averaged to get annual values at a 4-km resolution. For years prior to 1997, the average value of chlorophyll a for each park over the time-series was taken.

The following 5 pages of tables are presented in landscape view.

Supplementary Table S3. Model output summaries (biomass, abundance, PCoA)

	Biomass (log 10 kg/ha)				**Abundance (log 10 fish/ha)**				**PCoA axis 1**				**PCoA axis 2**			
Optimal model	*biomass ~ s(time) + re(MPA) + VarPower (~time) + corAR1(~year | site)*				*abundance ~ s(time) + s(chlorophyll a) + s(tsa_lagged) + re(MPA) + VarPower (~time) + corAR1(~year | site)*				*PCoA axis 1 ~ s(time) + s(tsa_lagged) + s(rugosity) + re(MPA) + corAR1(~year | site)*				*PCoA axis 2 ~ s(time) + s(tsa_lagged) + s(rugosity) + s(benthic PCA 1) + re(MPA) + corAR1(~year | site)*			
Predictors	***Estimates***	***CI***	***p***	***EDF***	***Estimates***	***CI***	***p***	***EDF***	***Estimates***	***CI***	***p***	***EDF***	***Estimates***	***CI***	***p***	***EDF***
(Intercept)	3.04	2.98 – 3.10	**<0.001**		2.79	2.74 – 2.83	**<0.001**		-0.16	-0.18 – -0.15	**<0.001**		0.02	0.01 – 0.03	**<0.001**	
Smooth term (Time since closure)	1.33		**0.012**	1.330449	2.74		**<0.001**	2.738685	1.92		**0.01**	1.919623	1		**0.026**	1.000453
Smooth term, random effect (MPA)	0		0.965	5.41E-09	0		0.704	1.49E-06	0.5		0.178	0.495737	0		0.6	1.59E-05
Smooth term (Chlorophyll a)					4.76		**<0.001**	4.757037	3.95		**<0.001**	3.945773				
Smooth term (TSA max lagged 4 years)					1		**0.001**	1.000016	2.44		**<0.001**	2.436247				
Smooth term (Rugosity)									1		**0.016**	1.000088	1		**0.004**	1.000032
Smooth term (benthic PCA 1)					5.05		0.058	5.054051					1		**<0.001**	1.000058
Observations	69				60				61				61			
R^2	0.255				0.819				0.751				0.439			
Deviance explained					86.10%				79.10%				46.70%			

Supplementary Table S4. Model output summaries (individual traits - categorical)

	Size (logit)				**Diet (logit)**				**Position in water column (logit)**				**Schooling (logit)**				**Reef association (logit)**			
Optimal model	*proportional abundance of trait category ~ s(time by size category) + size + re(MPA) + corAR1(~year | site)*				*proportional abundance of trait category ~ s(time by diet category) + diet + s(tsa_lagged) + re(MPA) + corAR1(~year | site)*				*proportional abundance of trait category ~ s(time by position category) + position + s(rugosity) + re(MPA) + corAR1(~year | site)*				*proportional abundance of trait category ~ s(time by schooling category) + schooling + s(benthic PCA 1) + re(MPA) + corAR1(~year | site)*				*proportional abundance of trait category ~ s(time by association category) + association + re(MPA) + corAR1(~year | site)*			
Predictors	***Estimates***	***CI***	***P***	***EDF***	***Estimates***	***CI***	***p***	***EDF***	***Estimates***	***CI***	***p***	***EDF***	***Estimates***	***CI***	***p***	***EDF***	***Estimates***	***CI***	***p***	***EDF***
(Intercept)	-2.7	-2.86 – -2.55	**<0.001**		-3.57	-3.66 – -3.48	**<0.001**		-0.16	-0.31 – -0.01	**0.032**		-1.83	-2.01 – -1.65	**<0.001**		-3.07	-3.26 – -2.89	**<0.001**	
Smooth term (Time since closure)																				
Smooth term, random effect (MPA)	0.6		0.206	0.597316	0.48		0.232	0.480526	0		0.862	1.31 E-05	0		0.849	1.39 E-05	0		1	0.000143
Smooth term (Chlorophyll a)																				
Smooth term (TSA max lagged 4 years)					1		0.063													
Smooth term (Rugosity)									1		0.054	1.000068								
Smooth term (benthic PCA 1)													1		**0.043**	1.000779				
Size2 (7.1-15cm)	2.77	2.56 – 2.97	**<0.001**																	
Size3 (15.1-30cm)	1.84	1.63 – 2.04	**<0.001**																	

Size4 (30.1-50cm)	0.36	0.15 – 0.56	**0.001**				
Size5 (50.1-80cm)	-0.31	-0.51 – -0.10	**0.003**				
Size6 (>80cm)	-0.71	-0.91 – -0.50	**<0.001**				
Smooth term (Time since closure)							
x Size1 (0-7cm)	2.71		**0.001**	2.712033			
x Size2 (7.1-15cm)	2.22		**0.008**	2.217212			
x Size3 (15.1- 30cm)	1.79		**<0.001**	1.790748			
x Size4 (30.1-50cm)	2.48		**0.009**	2.476543			
x Size5 (50.1-80cm)	1		0.404	1.000569			
x Size6 (>80cm)	1.53		0.595	1.525904			
DietHD					1.49	1.37 – 1.62	**<0.001**
DietHM					0	-0.12 – 0.13	0.946
DietIM					1.93	1.81 – 2.05	**<0.001**
DietIS					0.33	0.21 – 0.45	**<0.001**
DietOM					2.1	1.97 – 2.22	**<0.001**
DietPK					3.74	3.62 – 3.87	**<0.001**

Smooth term (Time since closure)																				
x DietFC					1		0.901	1.00003												
x DietHD					2.47		**0.002**	2.471613												
x DietHM					1		0.215	1.00003												
x DietIM					2		**<0.001**	2.002488												
x DietIS					1		0.145	1.000046												
x DietOM					1.83		**<0.001**	1.831862												
x DietPK					2.6		**<0.001**	2.602779												
Position2									0.06	-0.15 – 0.27	0.547									
Position3									-3.2	-3.41 – -3.00	**<0.001**									
Smooth term (Time since closure)																				
x Position1 (benthic)									1.65		**<0.001**	1.646404								
x Position2 (low in water colum)									2.74		**<0.001**	2.735291								
x Position3 (pelagic)									1		0.227	1.000027								
Schooling2 (Pairing)													-1.31	-1.57 – -1.06	**<0.001**					
Schooling3 (Small group)													0.69	0.43 – 0.94	**<0.001**					
Schooling4 (Medium group)													1.67	1.41 – 1.92	**<0.001**					

Schooling5 (Large group)														-1.3	-1.56 – -1.05	**<0.001**				
Smooth term (Time since closure)																				
x Schooling1 (Solitary)														1		**<0.001**	1.000128			
x Schooling2 (Pairing)														1		**0.015**	1.000139			
x Schooling3 (Small group)														1		**<0.001**	1.000031			
x Schooling4 (Medium group)														1		**0.002**	1.000159			
x Schooling5 (Large group)														1		**<0.001**	1.000505			
Reef.AssociationMed																		2.99	2.72 – 3.26	**<0.001**	
Reef.AssociationHigh																		3.05	2.78 – 3.32	**<0.001**	
Smooth term (Time since closure)																				
x Reef.AssociationLow																		1		0.964	1.000109
x Reef.AssociationMed																		1		**<0.001**	1.000221
x Reef.AssociationHigh																		1		**<0.001**	1.004593
Observations	366				427				173				305				183			
R^2	0.834				0.935				0.89				0.747				0.79			
Deviance explained	84.20%				93.80%				89.50%				75.50%				79.60%			

End of landscape view

Supplementary Table S5. Model output summaries (individual traits - continuous)

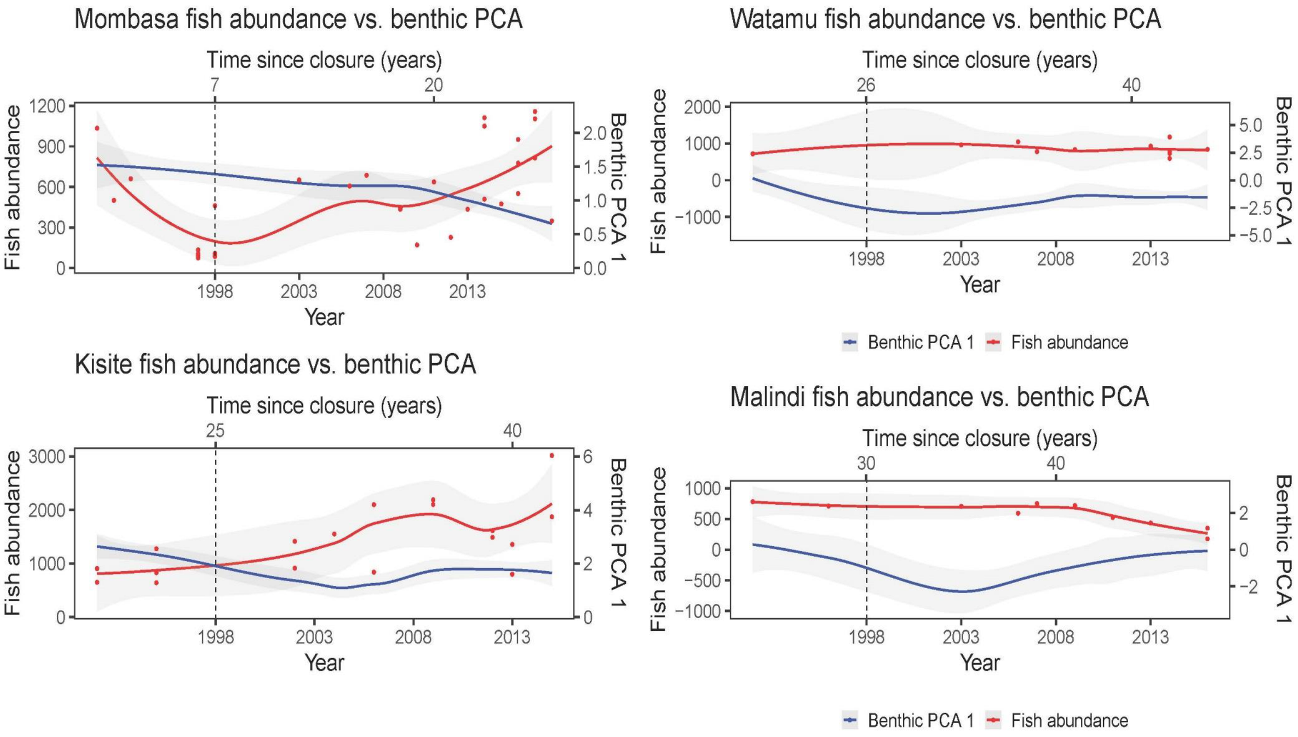
	Mean length at maturity (log cm)			
Optimal model	*mean length ~ s(time) + s(tsa_lagged) + s(rugosity) s(benthic PCA 1) +s(chlorophyll a) + re(MPA) + corAR1(~year | site)*			
Predictors	***Estimates***	***CI***	***p***	***EDF***
(Intercept)	23.6	23.44 – 23.77	**<0.001**	
Smooth term (Time since closure)	2.72		0.677	1.000017
Smooth term, random effect (MPA)	1		1	7.69E-06
Smooth term (Chlorophyll a)	39.08		**0.001**	3.665715
Smooth term (TSA max lagged 4 years)	2.72		**<0.001**	1.000525
Smooth term (Rugosity)	2.72		**0.007**	1.000015
Smooth term (benthic PCA 1)	63.51		**0.018**	4.151209
Observations	61			
R^2	0.708			
Deviance explained	75.80%			

Supplementary Table S6. Species list

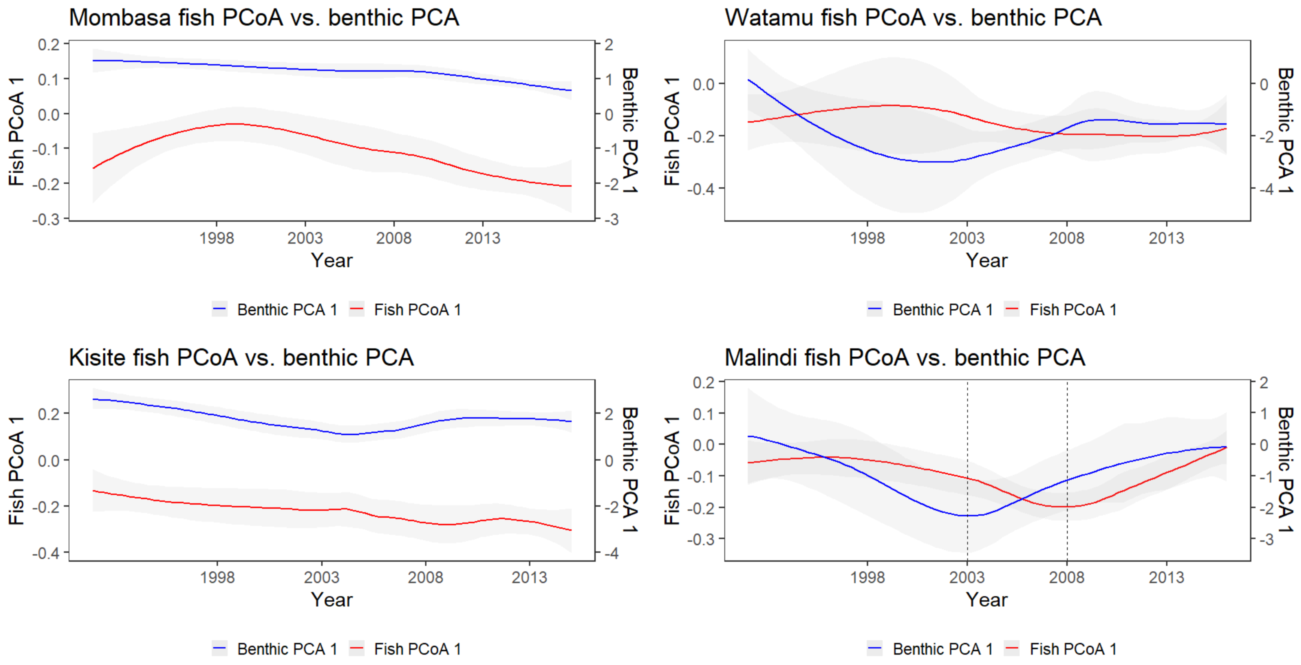
Abudefduf septemfasciatus
Abudefduf sexfasciatus
Abudefduf sparoides
Abudefduf vaigiensis
Acanthurus auranticavus
Acanthurus blochii
Acanthurus dussumieri
Acanthurus leucosternon
Acanthurus lineatus
Acanthurus mata
Acanthurus nigricauda
Acanthurus nigrofuscus
Chaetodon flavirostris
Chaetodon guttatissimus
Chaetodon kleinii
Chaetodon leucopleura
Chaetodon lineolatus
Chaetodon lunula
Chaetodon madagaskariensis
Chaetodon melannotus
Chaetodon meyeri
Chaetodon trifascialis
Chaetodon trifasciatus
Chaetodon unimaculatus
Diodon eydouxii
Diodon holocanthus
Diodon hystrix
Diodon liturosus
Epibulus insidiator
Forcipiger flavissimus
Forcipiger longirostris
Gomphosus caeruleus
Halichoeres cosmetus
Halichoeres hortulanus
Halichoeres iridis
Halichoeres lapillus
Oxymonacanthus longirostris
Paracanthurus hepatus
Paraluteres prionurus
Pervagor janthinosoma
Pervagor melanocephalus
Plectroglyphidodon dickii
Plectroglyphidodon johnstonianus
Plectroglyphidodon lacrymatus
Pomacanthus chrysurus
Pomacanthus imperator
Pomacanthus maculosus
Pomacanthus rhomboides
Stegastes limbatus
Stegastes lividus
Stegastes nigricans
Stegastes pelicieri
Stethojulis albovittata
Stethojulis interrupta
Stethojulis strigiventer
Sufflamen bursa
Sufflamen chrysopterum
Sufflamen fraenatum
Thalassoma amblycephalum
Thalassoma genivittatum

Acanthurus nubilus
Acanthurus tennentii
Acanthurus thompsoni
Acanthurus triostegus
Acanthurus xanthopterus
Acreichthys radiatus
Acreichthys tomentosus
Aluterus monoceros
Aluterus scriptus
Amanses scopas
Amblyglyphidodon leucogaster
Amphiprion akallopisos
Amphiprion allardi
Amphiprion latifasciatus
Anampses caeruleopunctatus
Anampses lineatus
Anampses meleagrides
Anampses twistii
Apolemichthys trimaculatus
Balistapus undulatus
Balistoides conspicillum
Balistoides viridescens
Bodianus anthioides
Bodianus axillaris
Bodianus bilunulatus
Bodianus diana
Calotomus carolinus
Cantherhines dumerilii
Cantherhines fronticinctus
Cantherhines pardalis
Centropyge acanthops
Centropyge bispinosa
Centropyge multispinis
Cetoscarus bicolor
Chaetodon vagabundus
Chaetodon xanthocephalus
Chaetodon zanzibarensis
Cheilinus fasciatus
Cheilinus oxycephalus
Cheilinus trilobatus
Cheilinus undulatus
Cheilio inermis
Chlorurus atrilunula
Chlorurus gibbus
Chlorurus sordidus
Chlorurus strongylocephalus
Chromis agilis
Chromis dimidiata
Chromis nigrura
Chromis opercularis
Chromis pembae
Chromis ternatensis
Chromis vanderbilti
Chromis viridis
Chromis weberi
Chromis xutha
Chrysiptera annulata
Chrysiptera biocellata
Chrysiptera brownriggii
Chrysiptera glauca
Chrysiptera unimaculata
Cirrhilabrus exquisitus
Coris aygula
Coris caudimacula
Coris cuvieri
Coris formosa
Ctenochaetus binotatus
Ctenochaetus striatus
Halichoeres marginatus
Halichoeres nebulosus
Halichoeres nigrescens
Halichoeres scapularis
Hemigymnus fasciatus
Hemigymnus melapterus
Hemitaurichthys zoster
Heniochus acuminatus
Hipposcarus harid
Hologymnosus annulatus
Hologymnosus doliatus
Labrichthys unilineatus
Labroides bicolor
Labroides dimidiatus
Labropsis xanthonota
Leptoscarus vaigiensis
Macropharyngodon bipartitus
Macropharyngodon cyanoguttatus
Melichthys indicus
Melichthys niger
Naso annulatus
Naso brachycentron
Naso brevirostris
Naso elegans
Naso fageni
Naso francolina
Naso hexacanthus
Naso tuberosus
Naso unicornis
Naso vlamingii
Neoglyphidodon melas
Neopomacentrus azysron
Neopomacentrus cyanomos
Novaculichthys taeniourus
Pomacanthus semicirculatus
Pomacentrus agassizii
Pomacentrus baenschi
Pomacentrus caeruleus
Pomacentrus pavo
Pomacentrus pikei
Pomacentrus sulfureus
Pomacentrus trichrourus
Pomacentrus trilineatus
Pomacentrus tripunctatus
Pomachromis richardsoni
Pseudalutarius nasicornis
Pseudobalistes flavimarginatus
Pseudobalistes fuscus
Pseudocheilinus evanidus
Pseudocheilinus hexataenia
Pseudodax moluccanus
Pseudojuloides cerasinus
Pteragogus flagellifer
Pteragogus pelycus
Pygoplites diacanthus
Rhinecanthus aculeatus
Rhinecanthus rectangulus
Scarus caudofasciatus
Scarus falcipinnis
Scarus ferrugineus
Scarus festivus
Scarus frenatus
Scarus ghobban
Scarus globiceps
Scarus niger
Scarus psittacus
Scarus rubroviolaceus
Scarus russelii
Thalassoma hardwicke
Thalassoma hebraicum
Thalassoma lunare
Thalassoma lutescens
Thalassoma purpureum
Zebrasoma scopas
Zebrasoma velifer

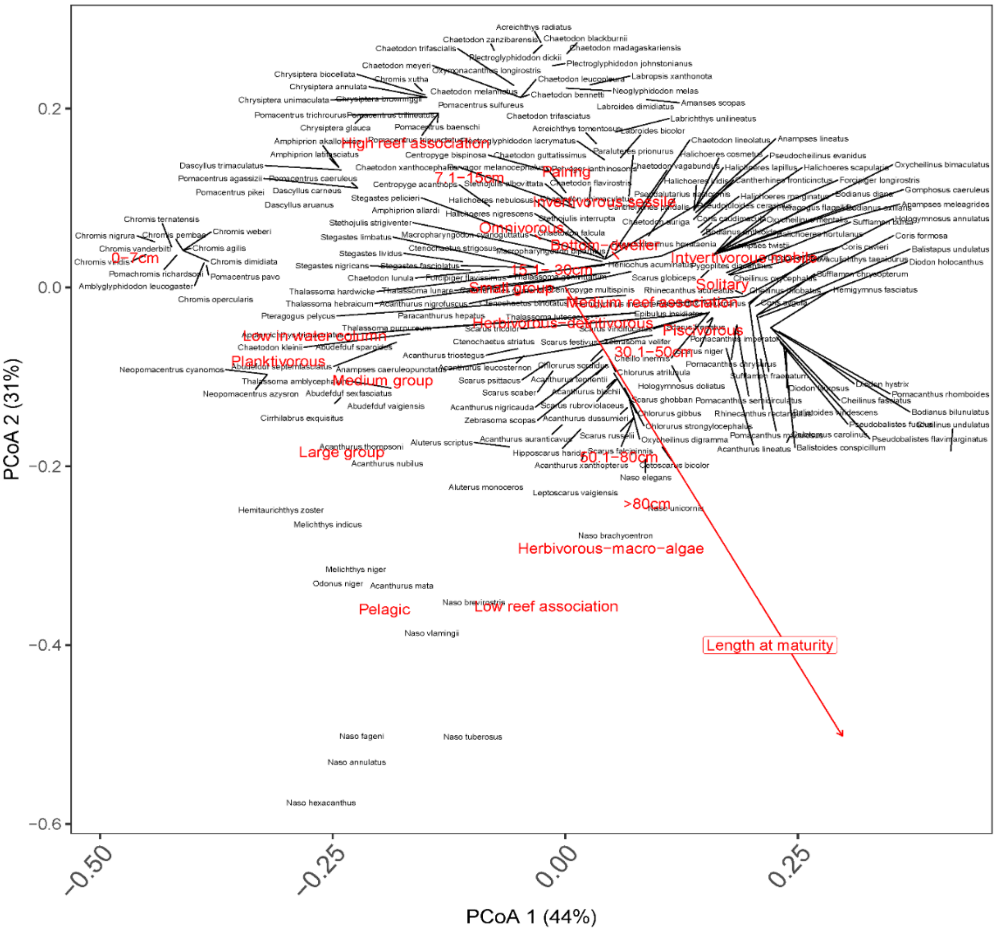
Chaetodon auriga	*Ctenochaetus strigosus*	*Odonus niger*	*Scarus scaber*
Chaetodon bennetti	*Dascyllus aruanus*	*Oxycheilinus bimaculatus*	*Scarus tricolor*
Chaetodon blackburnii	*Dascyllus carneus*	*Oxycheilinus digramma*	*Scarus viridifucatus*
Chaetodon falcula	*Dascyllus trimaculatus*	*Oxycheilinus mentalis*	*Stegastes fasciolatus*



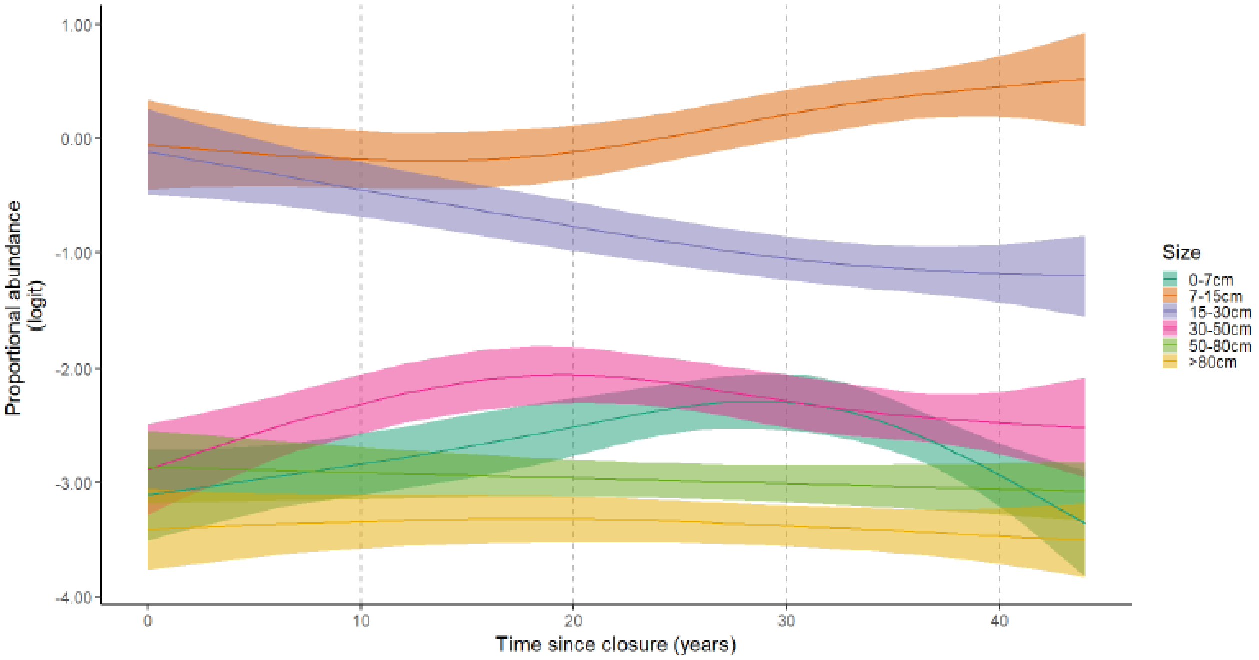
Supplementary Figure S1. *Smoothed conditional means of benthic PCA (blue) and fish abundance (red) for each marine park. Dotted vertical line indicates 1998 bleaching event.*



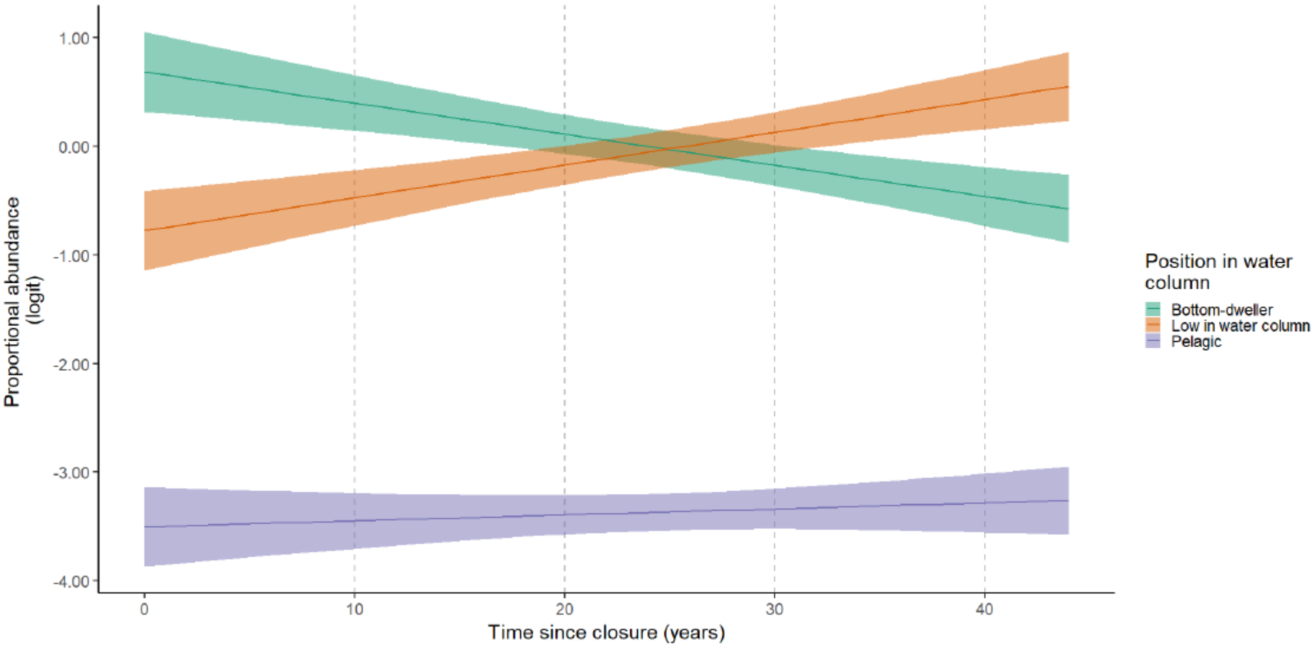
Supplementary Figure S2. *Smoothed conditional means of benthic PCA (blue) and fish PCoA (red) for each marine park. Justification for removal of Malindi from the time-series. Figure shows Malindi fish PCoA follows the same pattern as benthic PCA and lags behind benthic PCA by 5 years.*



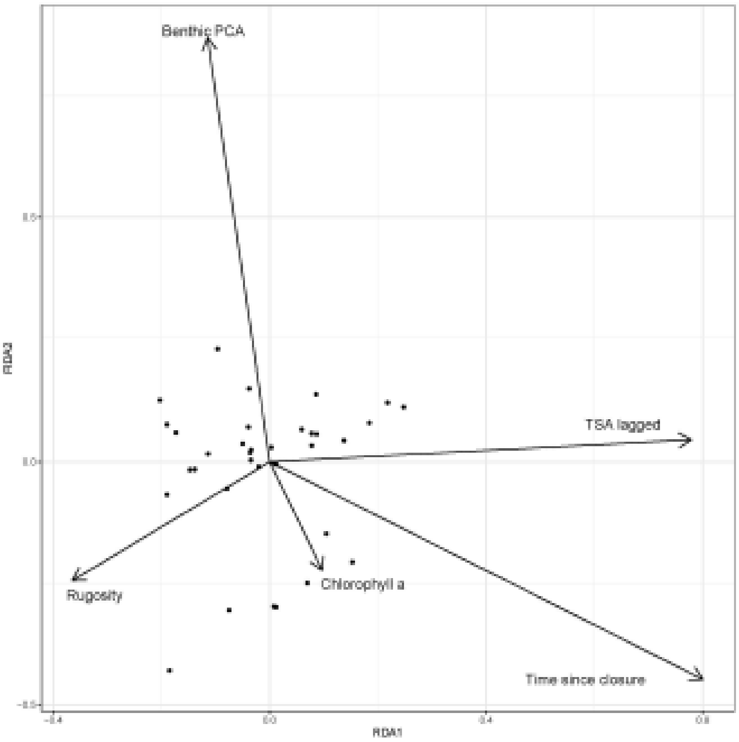
Supplementary Figure S3. *PCoA of fish traits with species included in the ordination plot.*



Supplementary Figure S4. *Size class trait models over time since closure – sensitivity analysis removing Chromis dimidiata.*

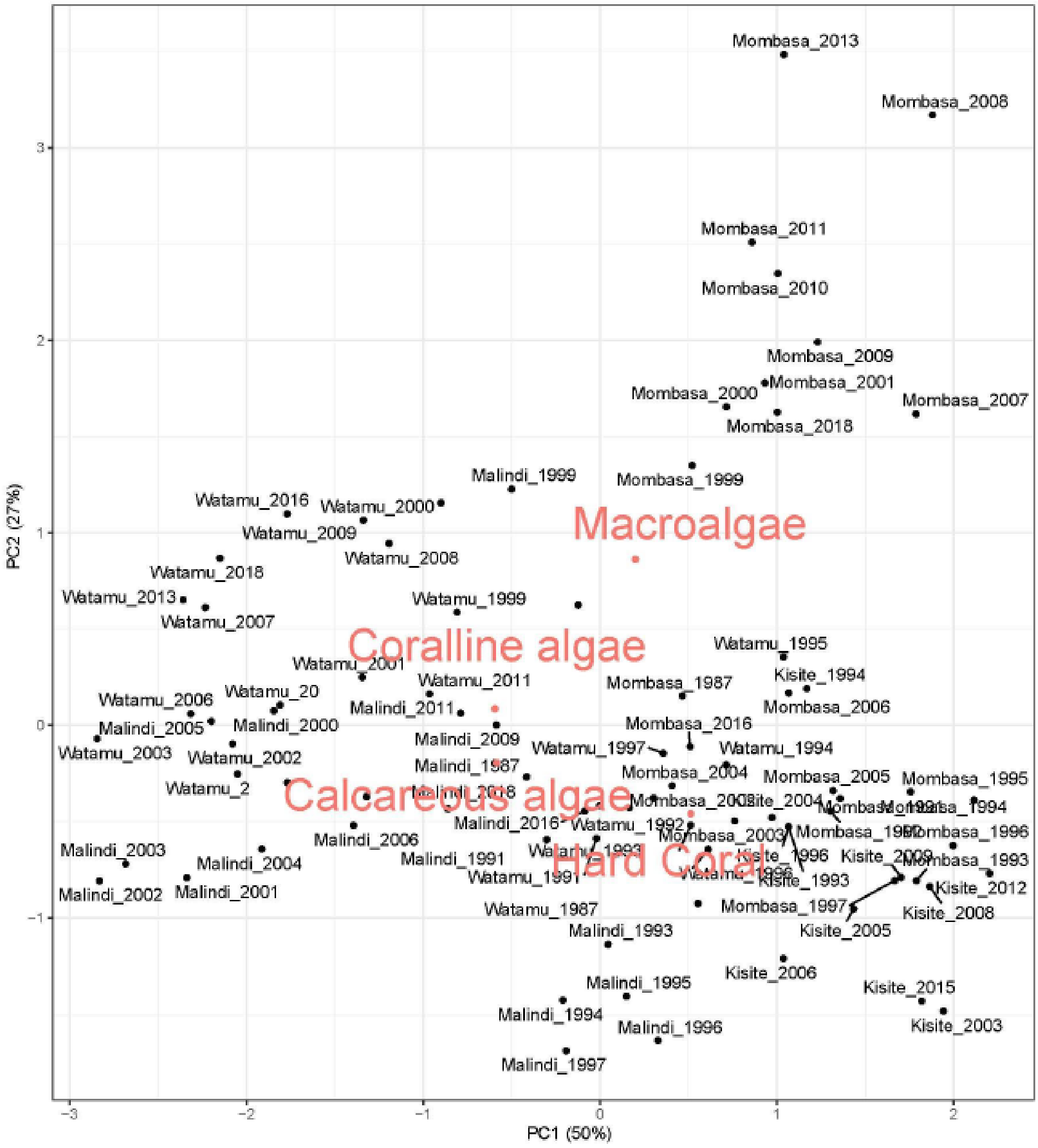


Supplementary Figure S5. *Position in the water column trait models over time since closure. In this model we include points that are removed from the main manuscript figure 4.e as outliers. The points that are removed are from Mombasa Marine Park after 6-7 years of closure, where the relative abundance of species low in the water column is recorded as 100% or close to 100%. Because all of these points are in the same site/year, we removed them from the main manuscript to ensure that the overall trends did not reflect sampling biases in those specific surveys.*



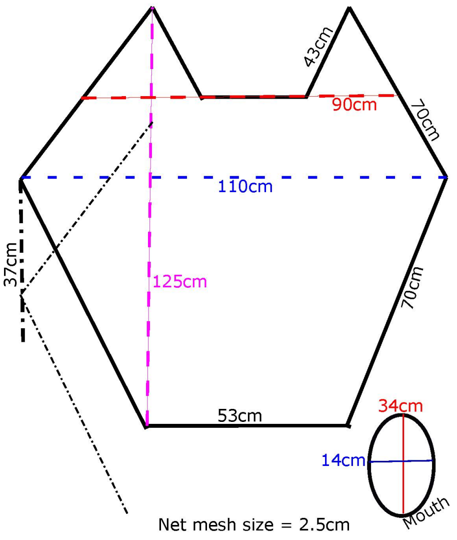
Supplementary Figure S6. *Partial redundancy analysis (RDA) of environmental and management drivers (explanatory covariates) influencing fish community functional space.*

Supplementary Figure S7. *Variance partitioning of environmental and management drivers (explanatory covariates) used in functional space models. Two plots are presented as only four covariates can be included in variance partitioning visualisations at a given time, and five covariates were used in the models.*

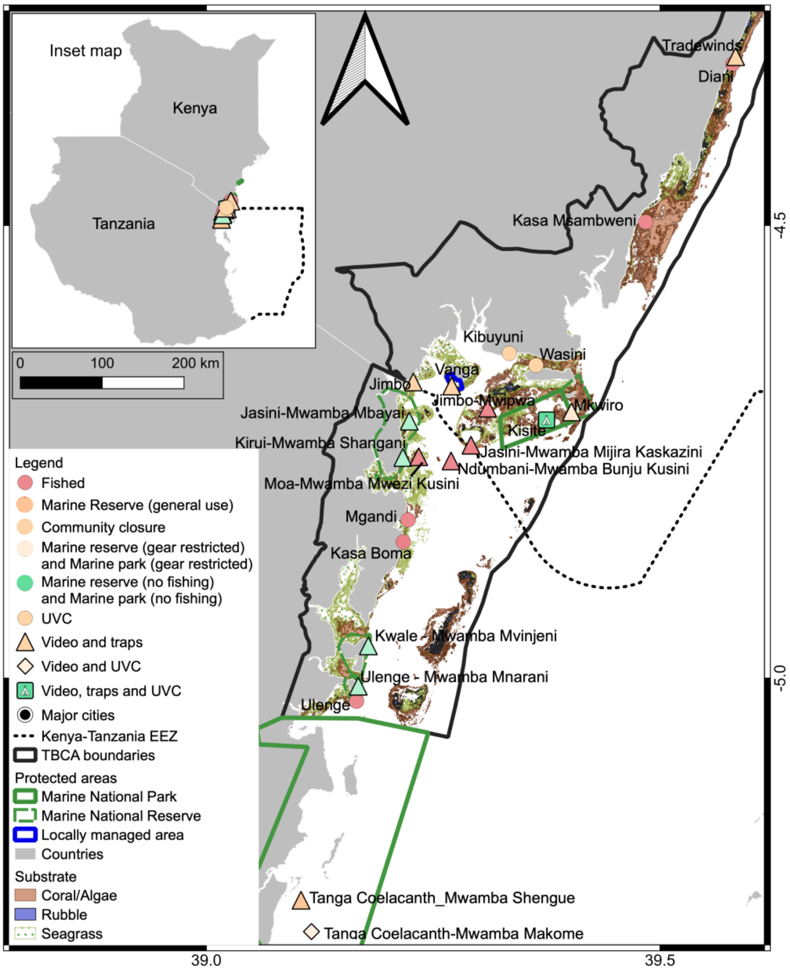


Supplementary Figure S8. *Benthic PCA for all marine reserves.*

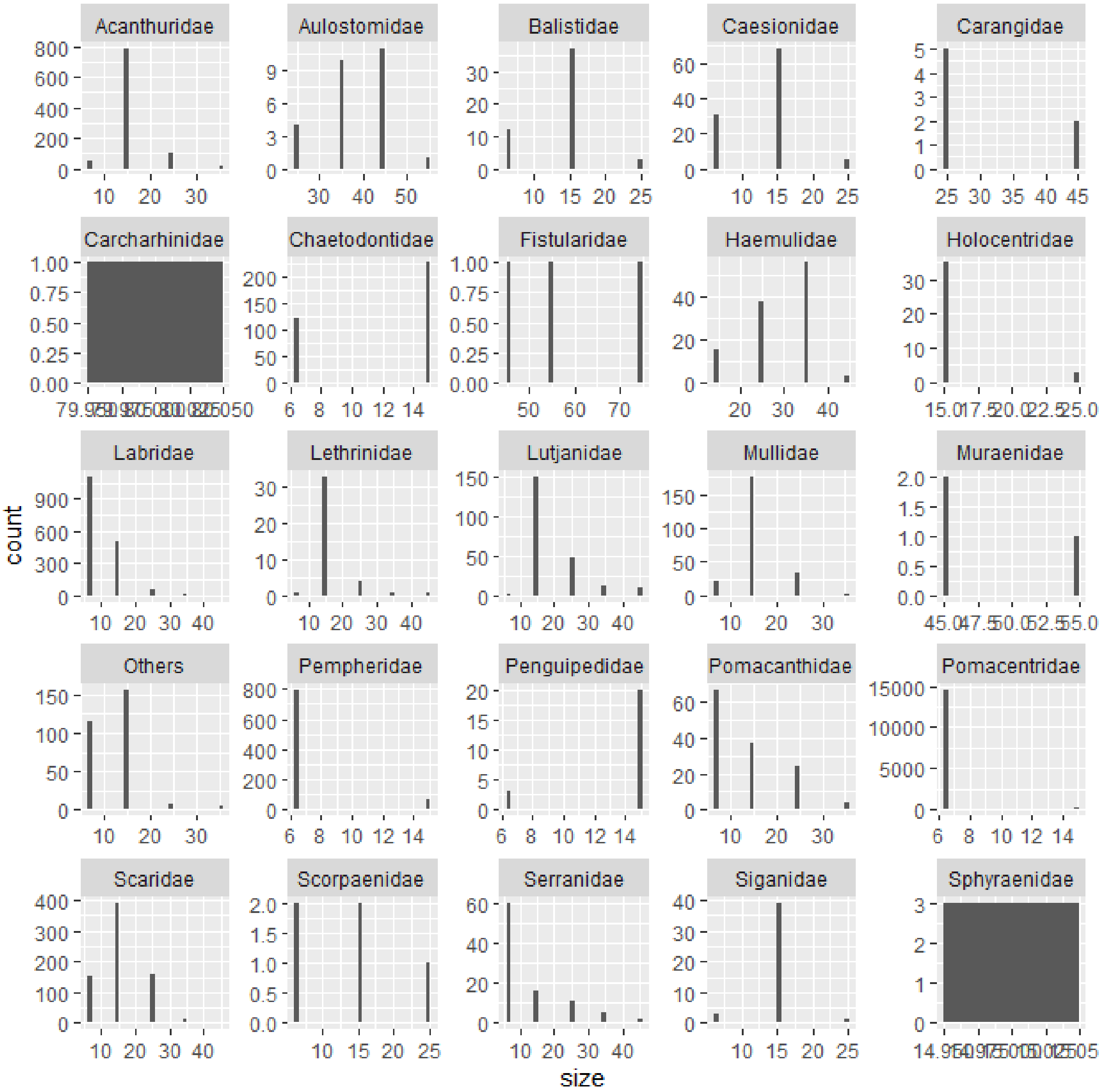
3. Supplementary material for Chapter 3



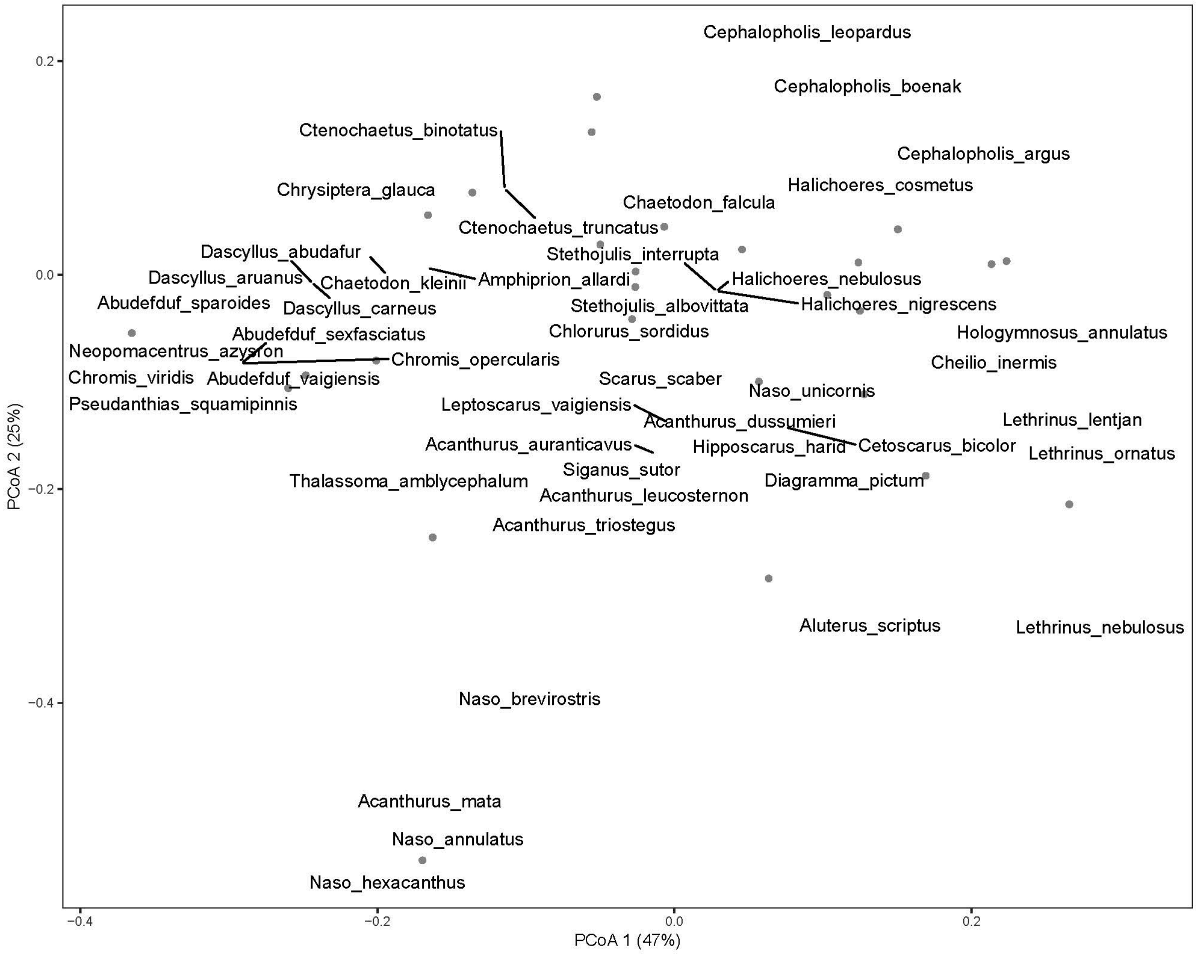
Supplementary Figure 1. *Illustration of fish trap dimensions.*



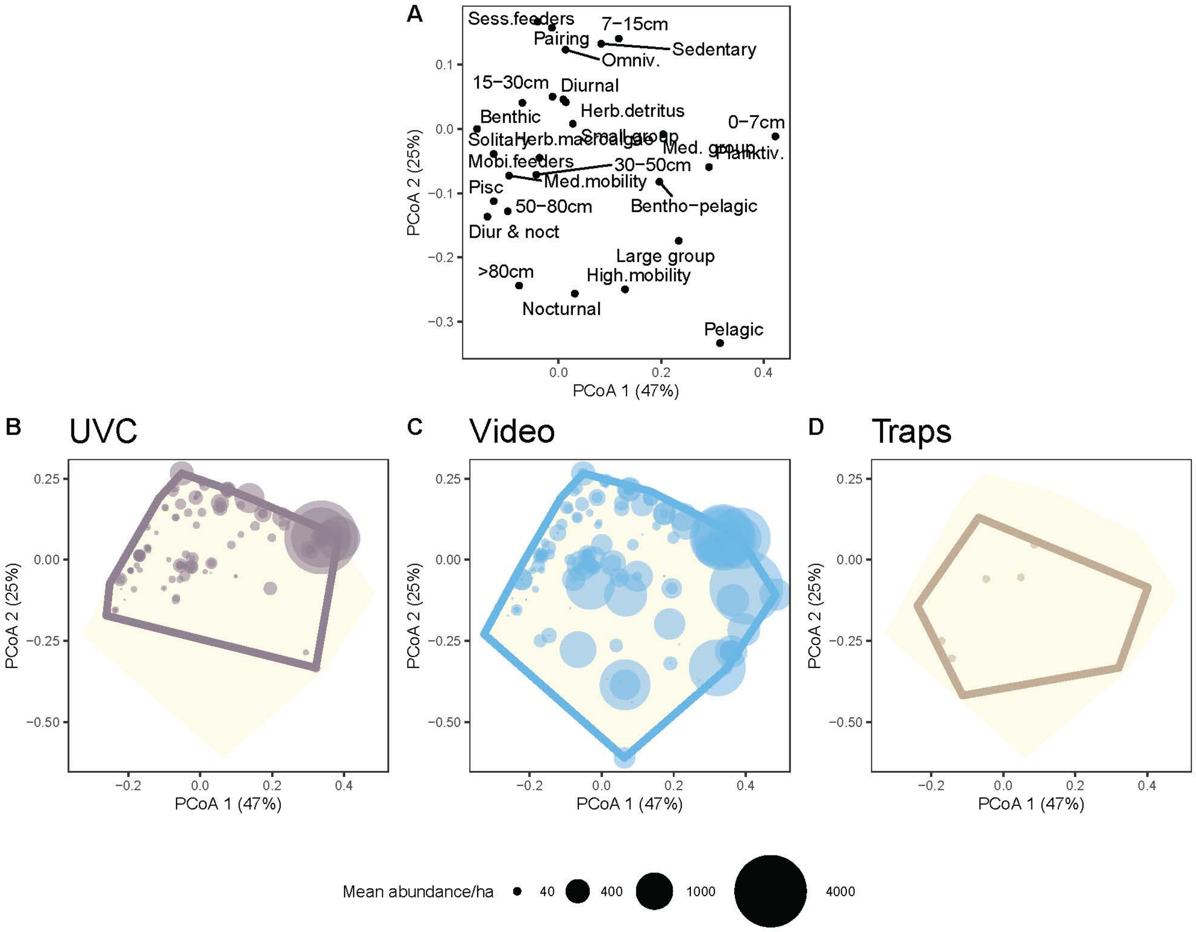
Supplementary Figure 2. *More detailed illustration of study sites indicating MPA zones and substrate.*



Supplementary Figure 3. *Size (cm) histogram of families in regional UVC biomass surveys.*

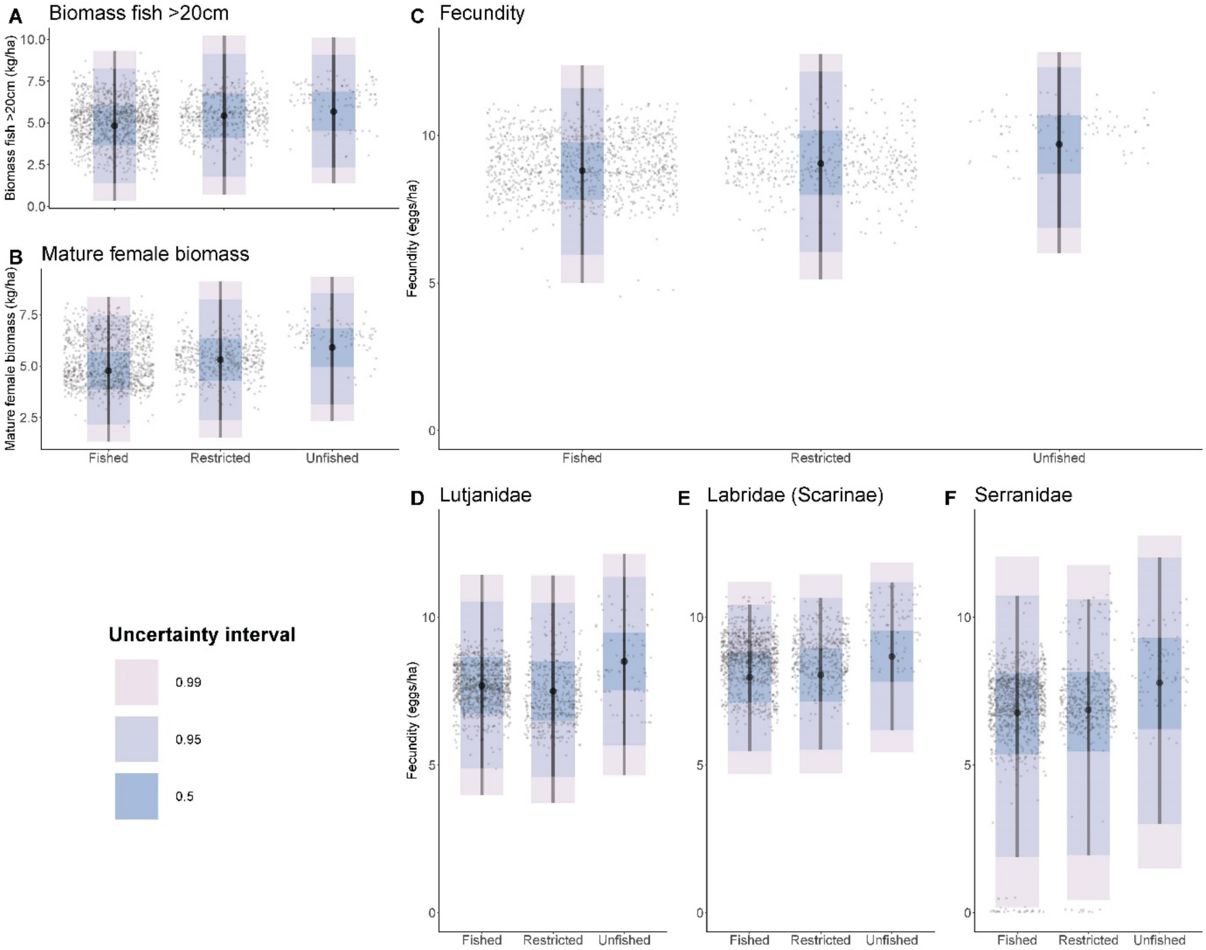


Supplementary Figure 4. *PCoA illustrating species' distributions in functional space.*

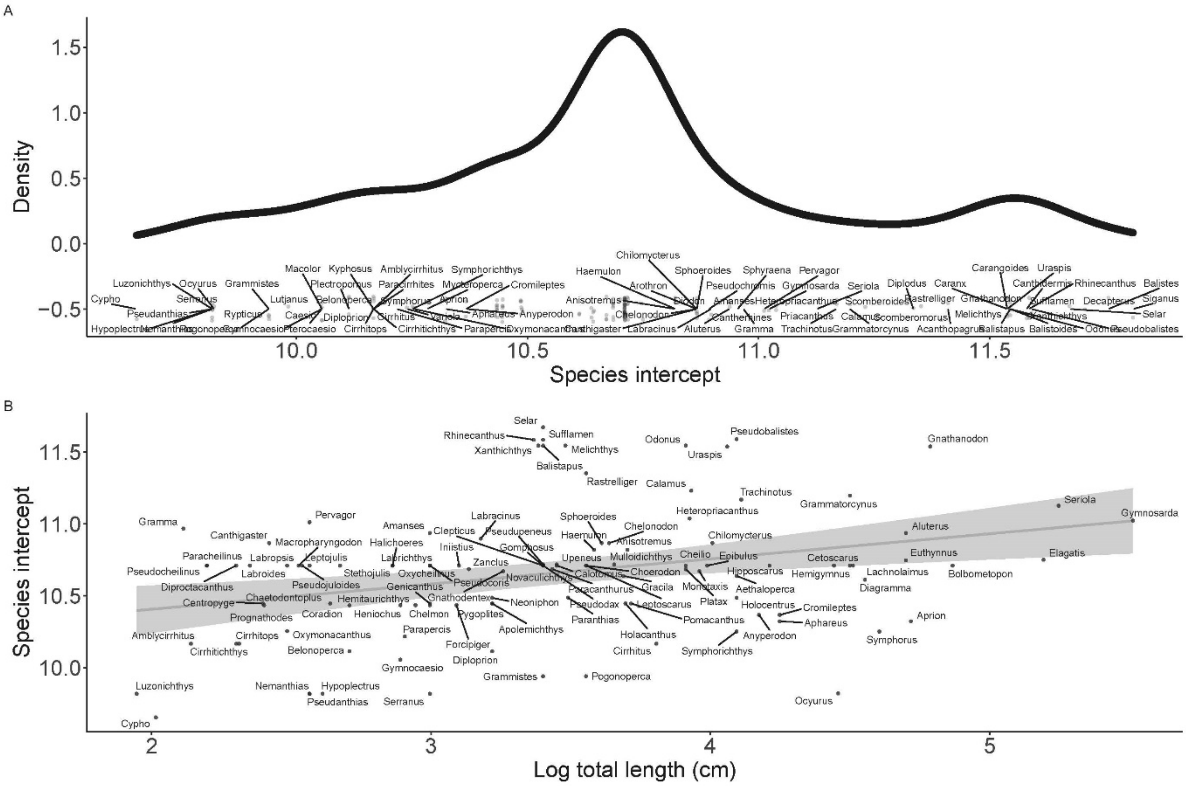


Supplementary Figure 5. *PCoA based on six functional traits of fish species (size, diet, gregariousness, mobility, diel activity, and position in the water column) with all species recorded in surveys included. A) Functional space across all surveys, B) functional space of species surveyed through UVC transects, C) functional space of species surveyed through video transects, D) functional space of species sampled in traps. Point size in B and C corresponds to the mean abundance/ha of species.*

4. Supplementary material for Chapter 4



Supplementary Figure 1. *A) Biomass (kg/ha) of fish >20cm, and B) biomass of mature female fish across fished, restricted, and unfished sites, and C) fecundity (eggs/ha) of all fish families, as well as D) just Lutjanidae, E) Labridae (Scarinae), F) and Serranidae across fished, restricted, and unfished sites. Colours of the bars correspond to uncertainty intervals, ranging from 0.5 (dark blue) to 0.99 (light pink).*



Supplementary Figure 2. *Species' intercepts from a phylogenetic regression of fecundity (equation 1), where A) is the density distribution of species' intercepts and B) is the spread of the intercepts as a function of (log) fish total lengths.*

Appendix B: publications arising from this thesis

Hadj-Hammou, J. et al. (2021) Response and Effect Traits of Coral Reef Fish. Frontiers in Marine Science, 8, 640619. Frontiers.

Hadj-Hammou, J. et al. (2021) Decadal shifts in traits of reef fish communities in marine reserves. Scientific Reports, 1–12. Nature Publishing Group UK.

frontiers
in Marine Science

SYSTEMATIC REVIEW
published: 25 March 2021
doi: 10.3389/fmars.2021.640619

Response and Effect Traits of Coral Reef Fish

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Front. Mar. Sci. 8:640619.
doi: 10.3389/fmars.2021.640619

The response-and-effect framework is a trait-based approach that seeks to break down the mechanistic links between ecosystem disturbances, species' traits, and ecosystem processes. We apply this framework to a review of the literature on coral reef fish traits, in order to illustrate the research landscape and structure a path forward for the field. Traits were categorized into five broad groupings: behavioral, life history, morphological, diet, and physiological. Overall, there are fewer studies linking effect traits to ecosystem processes (number of papers on herbivory, $n = 14$; predation, $n = 12$; bioerosion, $n = 2$; nutrient cycling, $n = 0$) than there are linking response traits to disturbances (climate change, $n = 26$; fishing, $n = 20$; pollution, $n = 4$). Through a network analysis, we show that the size and diet of fish are two of the most common response and effect traits currently used in the literature, central to studies on both ecosystem disturbances and processes. Behavioral and life history traits are more commonly shown to respond to disturbances, while morphological traits tend to be used in capturing ecosystem processes. Pearson correlation coefficients quantifying the strength of the relationships between the most commonly studied process, herbivory, and key effect traits (size, gregariousness, and diel activity) are provided. We find that the most popular cluster of traits used in functional diversity metrics (e.g., functional richness, functional dispersion) is comprised of size, diet, space use/position in the water column, diel activity, gregariousness, and mobility, which encompass three of the broad trait categories. Our assessment of the literature highlights that more research is needed to support an evidence-based selection of traits to understand and predict ecosystem functioning. In synthesizing the literature, we identify research gaps and provide an avenue toward a more robust trait-selection process.

Keywords: ecosystem processes, environmental disturbances, functional diversity, coral reef ecology, ecosystem function, trait-based ecology, systematic review

INTRODUCTION

Trait-based approaches in ecology and conservation are increasingly applied as the fields shift toward prioritizing an understanding of ecosystem functioning and maintaining ecosystem services (Madin et al., 2016a; Kissling et al., 2018; Barnett et al., 2019). Such an approach allows for mechanistic insight into how species interact with, react to, and shape their habitats (Violle and Jiang, 2009; McLean et al., 2018). The application of trait-based functional ecology to coral reef ecosystems is still in its nascent stages (Bellwood et al., 2019). The launch of the Coral Trait Database in 2016 (Madin et al., 2016b) was a milestone to consolidate the use of coral traits, much like the publication of the first terrestrial plant functional trait handbook (Pérez-Harguindeguy et al., 2013), or the terrestrial invertebrate functional trait handbook (Moretti et al., 2017). Similarly, for coral reef fish, several crucial review papers and projects have begun to provide direction and clarity around which traits could be measured consistently, what is meant by the term ecosystem functioning, and what a novel functional approach might look like (Kublicki, 2010; Villéger et al., 2017; Bellwood et al., 2019; Brandl et al., 2019; Woodhead et al., 2019; Quimbayo et al., 2021).

The "response-and-effect framework" posits that it is useful to determine which traits respond to environmental gradients ("response traits") and which traits affect ecosystem processes ("effect traits") (Diaz and Cabido, 2001; Loreau et al., 2001; Lavorel and Garnier, 2002; Grime, 2006; Suding et al., 2008). This concept runs parallel to that of the distinction between Eltonian and Grinnellian dimensions of a niche, where the Grinnellian dimension refers to the resource needs of a species, and the Eltonian dimension refers to the impact of a species on the environment (Devictor et al., 2010). The use of such a framework provides a practical way of addressing how disturbances are likely to affect population dynamics and ecosystem functioning as a whole (Díaz et al., 2013; Salguero-Gómez et al., 2018). The trait structure of a community not only affects its sensitivity to disturbance (McLean et al., 2019), but also its capacity to support long-term functioning (Debouk et al., 2015; Duffy et al., 2016). Response traits have also been proposed as a basis for building Essential Biodiversity Variables, allowing for the effective monitoring of biodiversity change over time (Kissling et al., 2018). By identifying traits that overlap as both response and effect traits, or correlated response and effect traits, predictions about how disturbances could affect ecosystem processes can be made (Gross et al., 2008; Suding et al., 2008).

Several studies have found that functional diversity metrics respond to disturbances but also determine potential ecosystem functioning (Diaz and Cabido, 2001; Mouillot et al., 2013; Sitters et al., 2016). The use of trait-based approaches to estimate the functional diversity of coral reef fishes has become common (e.g., Richardson et al., 2017; Floeter et al., 2018; Mbaru et al., 2019). Yet, the number and selection of traits used in functional indices may greatly influence the outcomes and conclusions that can be drawn from analyses. The creation of functional groups and the use of trait-based approaches to understanding ecological dynamics is only useful if the prior selection of traits and functional groups are ecologically relevant to the questions at hand. Therefore, when applying the response-and-effect framework, it is necessary to determine which traits should be used as response traits and which traits should be used as effect traits, and where there is sufficient evidence mechanistically linking these traits to disturbances and processes.

In this paper, we review the literature on coral reef fish response and effect traits. We do this by asking which fish traits have been investigated in relation to responding to disturbances (response traits) or affecting ecosystem processes (effect traits) and how many papers have studied each of these links. We also ask which traits are being used together and why. We then explore the consistency of the direction of influence for comparable traits and extract quantitative data linking predominant traits with a commonly assessed ecosystem process. In synthesizing the literature, we provide guidance for an evidence-based selection of traits for functional research in coral reef ecology and conservation, and establish where future research and experimentation is needed to strengthen the field.

MATERIALS AND METHODS

We examined response traits in relation to three disturbances and effect traits in relation to four processes common on coral reefs. The disturbances were pollution, fishing, and climate change (Hughes et al., 2010, 2017). The processes were herbivory, bioerosion, predation, and nutrient recycling (Villéger et al., 2017; Brandl et al., 2019). These limits to inclusion of disturbances and processes were applied to structure the review through the response-and-effect framework.

A comprehensive search of the literature was conducted using the Web of Science database (1974–2018). An initial search on September 26, 2018 used the terms: Topic Sentence (TS) = ((fish* AND coral AND reef*) AND trait* AND ("functional diversity" OR "functional evenness" OR "functional richness" OR "functional dispersion" OR "functional divergence" OR "functional redundancy" OR "functional group*" OR "functional complimentary")) OR TS = (("coral reef" OR "coral reefs") AND (fish OR fishes) AND (trait OR "life history") AND (function OR functions OR functional OR process OR processes OR disturbance OR disturbances)). This search yielded 380 titles. Further search terms were used to find papers specifically related to relevant ecosystem processes and/or disturbances. For example: TS = ((fish* AND coral AND reef*) AND trait* AND "climate change"). A total of 227 papers were found with these follow up search terms. Furthermore, the reference lists of four review papers that appeared in the searches were "snowballed". A total of 17 new references were added to the database using this method.

Paper inclusion criteria were that (1) one or more of the processes or disturbances were being investigated in relation to (2) one or more traits of coral reef fish. Papers were excluded if (1) they were looking specifically at larval fish traits (e.g., pelagic larval duration), (2) the process or disturbance was not one that is being reviewed for this paper, (3) the paper was not accessible or not in English, and/or (4) the paper was a review article (although references were checked and snowballed). Papers were first filtered by titles, then abstracts, and finally full body texts. From a total of 624 papers accumulated with the three search strategies, 80 papers met the above criteria and were included in the systematic review (see PRISMA flow diagram, **Supplementary Figure 1**).

The traits, processes, and disturbances being studied in each paper were identified. Where possible, the direction of the relationship between the trait and process or disturbance was assessed. After a full list of traits had been accumulated, similar traits were grouped together to generate a succinct selection of relevant traits. For example, "size" was used as a way to group together traits such as "total length," "maximum length,"

TABLE 1 | Broad groupings of traits, where blue corresponds to behavioral traits, yellow to life-history traits, red to morphological traits, purple to diet traits, and gray to physiological traits.

Behavioral traits	List history traits	Morphological traits	Diet traits	Physiological traits
Anti-predator response	Age/life-phase	Body morphology	Diet/trophic-level	Metabolic rate
Diel activity	Generation time	Eye morphology		
Feeding behavior	Growth rate	Fin morphology		
Gregariousness	Life span	Head morphology		
Habitat dependence	Natural mortality	Mouth/jaw morphology		
Habitat type	Reproductive turnover	Size		
Personality	Stage at maturity			
Space use	Survivorship			
Mobility				
Territoriality				

This color scheme is used throughout the paper.

and "body mass." Traits were classified as either "behavioral," "life history," "morphological," "diet and trophic level," or "physiological" (**Table 1**).

In order to address the first question, "which traits have been investigated in relation to responding to disturbances (response traits) or affecting ecosystem processes (effect traits), and how many papers have studied each of these links?," a weighted and directed tripartite network diagram was produced using the R package "igraph" (Csárdi, 2019). The diagram illustrates the number of papers, displayed as thickness of the lines (edges), linking traits to disturbances or processes (nodes).

To address the second research question, "which traits are being used together?," the R packages "igraph" (Csárdi, 2019) and "CINNA" (Ashtiani et al., 2019) were used to produce an undirected, weighted network diagram. This diagram shows the links between traits used together in papers, where the size of the nodes shows the number of papers using the trait, and the size of the edges illustrates the frequency of trait combinations being included together in papers. The centrality of the nodes shows how commonly traits were used in combination with other traits. These centrality measures were quantified for the five most central traits. Centrality metrics used include degree centrality, subgraph centrality, and the topological coefficient. These metrics were selected as the top three most informative centrality measures, based on the output of a Principal Component Analysis (Ashtiani et al., 2018). Degree centrality can be defined as the number of nodes linked to a given node (Zhang et al., 2007), while subgraph centrality accounts for the participation of a node in the network's sub graphs and deals with more complex networks (Estrada and Rodríguez-Velázquez, 2005), and the topological coefficient quantifies the extent to which neighbors share pairs of nodes (Doncheva et al., 2012). The median rank for the centrality metrics and the individual metric values were plotted using the R package "ggplot2" (Wickam, 2016).

To illustrate the traits being used together to generate functional diversity and related metrics, a Principal Coordinate Analysis (PCoA) (Kenkel, 2006) was carried out using the R package "ape" (Paradis et al., 2019). The analysis was conducted on a Jaccard's dissimilarity matrix based on a presence/absence matrix (Cheetham and Hazel, 1969) of traits within papers looking at functional diversity metrics. Two principal component axes, explaining 49% of the variation in the distance matrix, are illustrated. The number of clusters of traits within the plot was selected using the R package "NbClust." This package determines the optimum number of clusters based on 30 indices (Charrad et al., 2014). Clusters were illustrated as convex hulls grouping traits together.

The type of evidence used in each paper to test/support disturbance-trait or trait-process links was then categorized as one of the following: *ex situ*, experiment; *ex situ*, measurement; *ex situ*, specimen measurement; *in situ* + *ex situ*, measurement; *in situ*, experiment; *in situ*, observation; modeling/theoretical approach; other. For example, if a paper assessed the effect of climate change-associated rises in temperature on reef fish boldness behavior in a controlled experimental lab environment, it would be counted in the "*ex situ*, experiment" category.

Next, we assessed the direction of the relationship between continuous or ordinal traits and processes/disturbances. Trait-process/disturbance linkages were assessed as either being positive, negative, or insignificant based on trends reported in the papers. For Bayesian analyses, where statistical significance is not relevant, only the direction of influence was recorded. For example, if a response trait, such as "generation time," was shown to decrease in response to a disturbance such as "fishing," it would be classified as a "negative" relationship. Similarly, if a process, such as "herbivory," measured as the amount of algae removed in a given time/space, was shown to increase with the "size" (effect trait) of fish, the relationship would be classified as "positive." Categorical trait relationships were excluded from this analysis, but paper result summaries are provided as a **Supplementary Table 1**.

To test the quantitative applicability of the framework to coral reef fish, we investigated the effect size of effect traits on the process of herbivory. Herbivory was selected as the ecosystem process for which to extract quantitative effect sizes, because (1) it was the most commonly studied process found in our search, and (2) herbivory was the process with the most consistent measurement in the literature (bite rate or impact). Three of the most common traits related to herbivory in the literature—size, gregariousness and diel activity—were selected as effect traits to assess. Diet was excluded from the quantitative assessment because its relevance is in relation to diet categories which is implicit for herbivory. Because the initial search term limited papers to those using the term "trait," whereas some papers use traits without explicitly naming them as such, an additional search was conducted to identify papers which may not have used the terms "trait" or "function" but had quantified herbivory. An additional four papers were found looking at the impact of traits on herbivory and directly measuring the process.

Where effect sizes were extracted from the literature, they were converted into Pearson r correlation coefficients according to Beltramini and Wolf (1987) and Friedman (1982). Pearson's r was selected because it allows for contrasts between two or more groups without computational corrections and is easily interpreted as it sits on a limited scale from−1 to 1 (Rosenthal and DiMatteo, 2001). Relevant statistical information needed to compute the effect size was extracted where available. WebPlotDigitizer (Rohatgi, 2019) was used to extract raw data from figures. Where data was provided but not analyzed in relation to traits of interest (e.g., Humphries et al., 2014), a simple correlation was conducted using raw data. For size bins/categories, the average size was used. In papers presenting data on trait-bite-rate relationships for more than one species or more than one site, average effect sizes and 95% confidence intervals are calculated. Additionally, for each trait, an average Pearson's r based on all the papers is presented with 95% confidence intervals. All statistical analyses were performed using R software version 3.5.2. (R Core Team, 2018).

RESULTS

Based on our search results (See PRISMA flow diagram, **Supplementary Figure 1**), the most studied disturbance affecting coral reef fish traits is climate change (number of papers, $n = 26$), followed by fishing ($n = 20$), and then pollution ($n = 4$). Climate change encompassed papers assessing the impacts of increasing temperatures, rising levels of CO_2, extreme weather events and coral bleaching. Fewer papers investigated ecosystem processes using an explicit trait-based approach. The process most studied

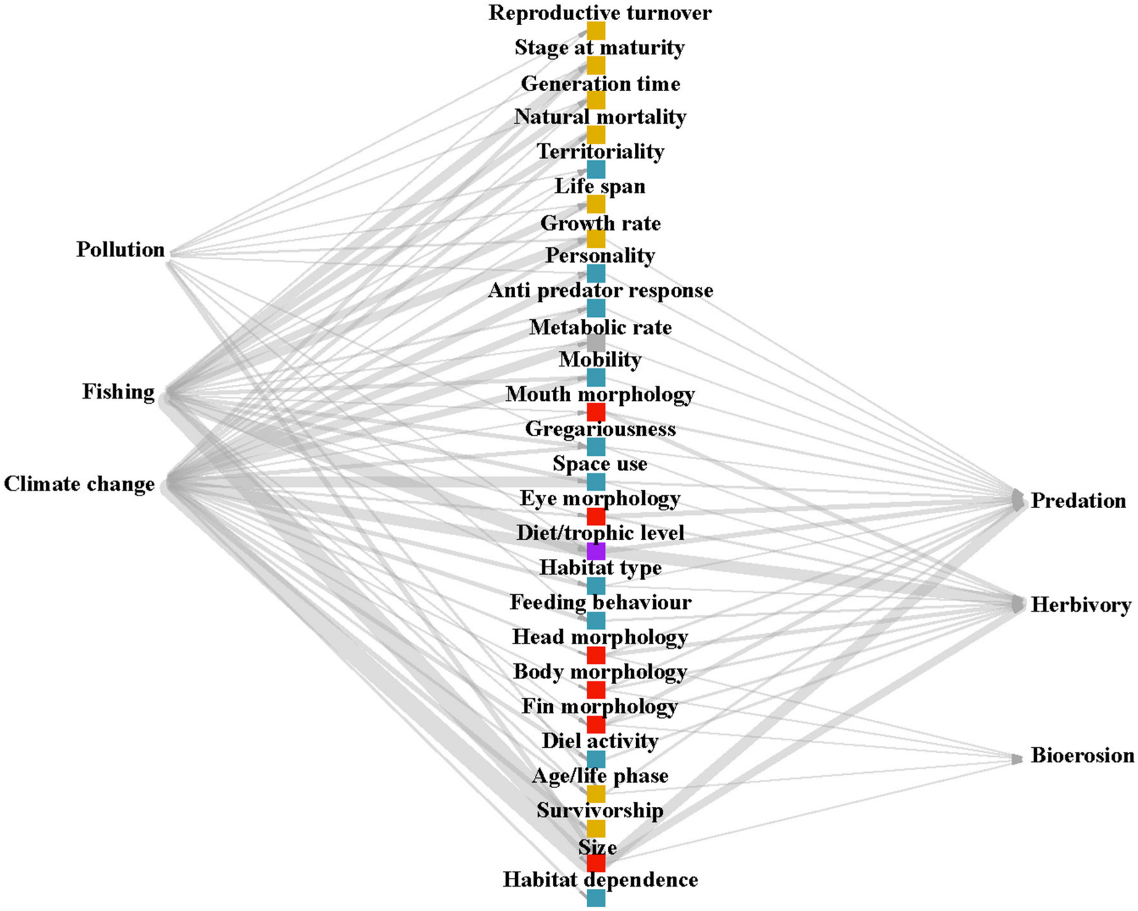

FIGURE 1 | Tripartite network diagram showing the number of papers linking each disturbance and process to response and effect traits. The color of trait points corresponds to broad trait groupings (blue: behavioral, yellow: life-history, red: morphological, gray: physiological, purple: diet).

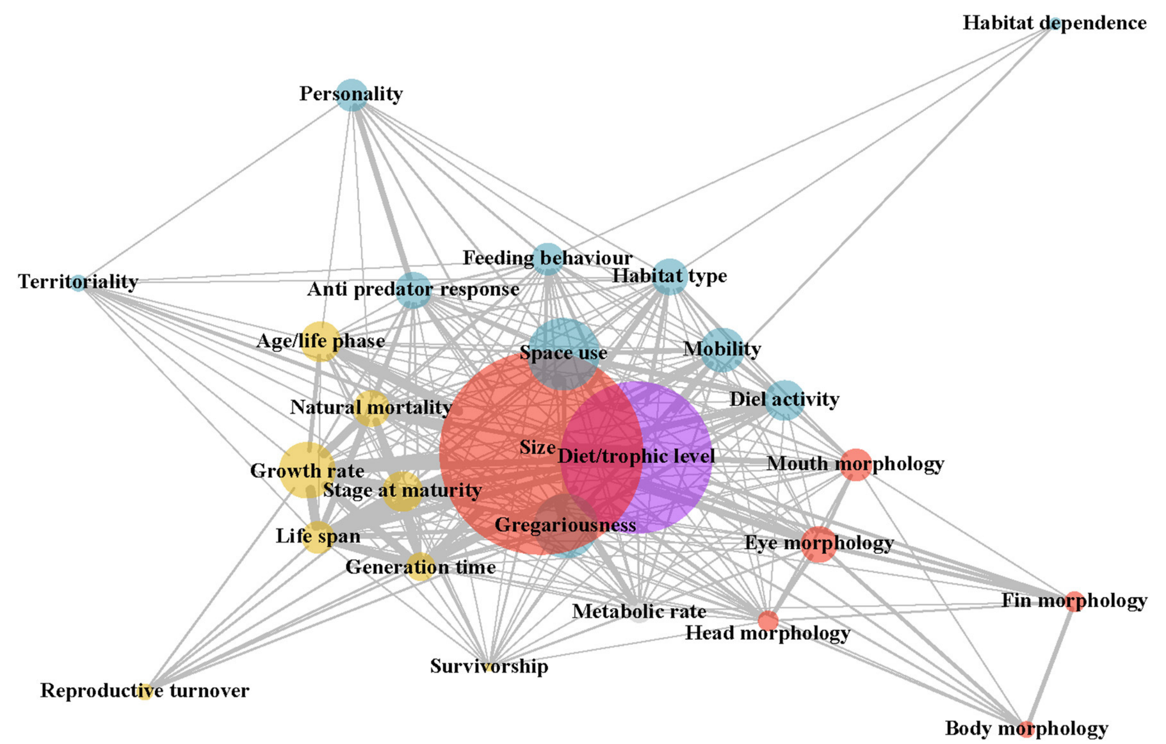

FIGURE 2 | Network diagram showing the use of traits together within papers. Each node corresponds to a trait, with its size representing the number of papers using that trait. The color of trait nodes corresponds to broad trait groupings (blue: behavioral, yellow: life-history, red: morphological, gray: physiological, purple: diet). The thickness of the edges (i.e., lines) illustrates the number of papers in which two traits being connected were used together. The spatial position of the node indicates which traits it is most often used in conjunction with, where the more central nodes represent traits used frequently with all other traits. Rankings of centrality scores (median of degree centrality, subgraph centrality, and topological coefficient) showed size to be the most central trait, diet and gregariousness as the second most central traits, and habitat type and feeding behavior as the third most central traits (see **Supplementary Figure 4**).

was herbivory ($n = 14$), then predation ($n = 12$), bioerosion ($n = 2$), and finally no papers were identified through our search terms that quantified nutrient transfer through a trait-based approach ($n = 0$). "Predation" captured papers assessing prey traits, predator traits, or the interaction between both. The most studied disturbance-response trait links were between size and fishing ($n = 16$), size and climate change ($n = 15$), diet and fishing ($n = 11$), and diet and climate change ($n = 8$). The most studied effect trait-process links were diet and herbivory ($n = 9$), size and predation ($n = 8$), and size and herbivory ($n = 6$). Size and diet had the greatest number of papers that link the traits both to disturbances and processes, making them both well-studied response and effect traits (**Figure 1**; **Supplementary Figure 2**).

The network analysis plot, based on the traits of all papers included in the database, illustrates three key findings. Firstly, size and diet, followed by space use, gregariousness, and growth rate, are the most commonly used traits in the literature (**Figure 2**). Secondly, trait categories, for example, behavioral or morphological (depicted by color), tend to group together in network space. Size, a morphological trait, and gregariousness, a behavioral trait, are the exceptions to this, being situated in the middle of the plot (**Figure 2**; **Supplementary Figure 3**). Thirdly, size is almost consistently ranked as the most central trait, followed by diet, gregariousness, habitat type and feeding behavior (**Supplementary Figure 4**). High centrality scores indicate that these traits as the ones most commonly used with combinations of other traits.

A total of 17 papers used traits to calculate functional diversity metrics for coral reef fish, or to derive functional entities. Functional diversity indices were most commonly calculated using size ($n = 15$), diet ($n = 14$), and space use ($n = 9$). The traits most commonly used together are size, diet, gregariousness, mobility, diel activity, and space use (e.g., position in the water column) ($n = 5$) (**Figure 3**). Two other groupings of traits were also apparent: age/life phase with reproductive turnover; and eye morphology with mouth morphology, feeding behavior, habitat type and territoriality. These groupings were based on Euclidean space in the PCoA axes and the traits encompassed were not necessarily used consistently all together in the literature. For example, habitat type was used in five papers; some of these papers also used traits located in the cluster of the most frequently applied six traits. In Brandl et al. (2016), habitat type is used along with diet, size, and territoriality to examine how coral reef fish functional diversity responds to a disturbance in the form of a tropical cyclone. Age/life phase and reproductive turnover represent a lesser studied cluster of traits, produced by papers that include broader life history strategies in functional analyses (e.g., Tuya et al., 2018).

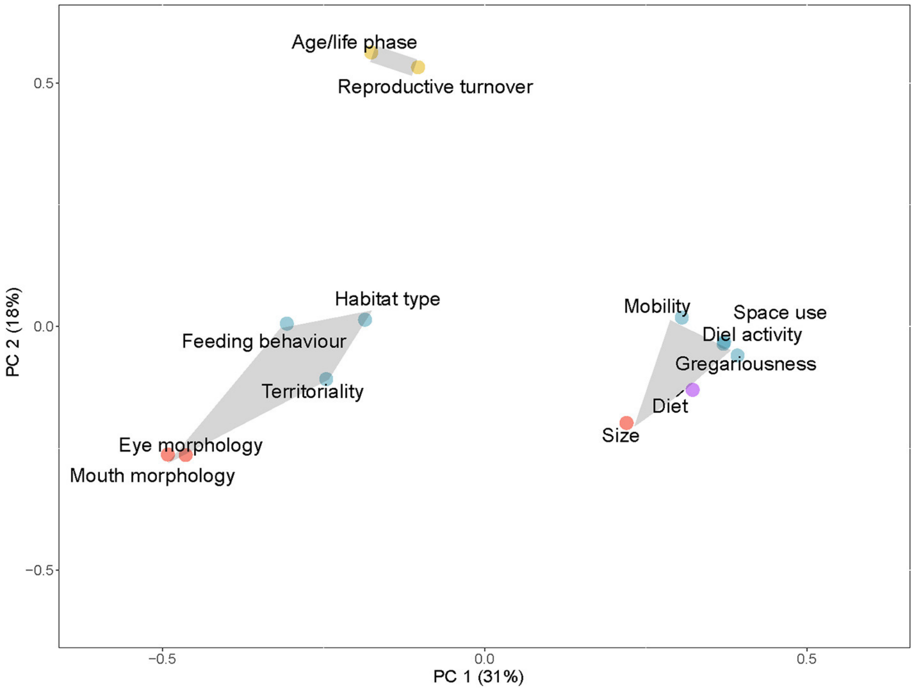

FIGURE 3 | PCoA plot of traits used to estimate functional diversity or to determine functional entities. Three clusters show traits commonly used together in functional diversity metrics. Color of trait points corresponds to broad trait groupings (blue: behavioral, yellow: life-history, red: morphological, gray: physiological, purple: diet).

Overall, the evidence for the majority of functional diversity papers is based on *in situ* observational evidence ($n = 10$; total *in situ* observational $n = 36$). The number of papers based on this type of evidence is more than double the number of papers based on *ex situ* experimental ($n = 14$) and *in situ* experimental ($n = 14$) evidence. Trait-relationships based on *ex situ* measurements ($n = 9$) and purely theoretical or modeling-based papers ($n = 8$) were less common. *Ex situ* specimen trait measurements ($n = 1$) and a combination of *in situ* and *ex situ* measurements ($n = 1$) were each only represented by one paper (**Figure 4**).

The direction of influence of disturbances on response traits and effect traits on ecosystem processes shows the consistency of findings across the limited set of papers identified in the review (**Figure 5**). Most papers found a negative influence of pollution on the size of fish ($n = 3$). There was an even split between the number of papers finding an insignificant and positive effect of pollution on the trophic level of coral reef fish ($n = 2$). There was 100% agreement on the negative relationship between fishing and the life history traits of life span ($n = 3$) and generation time ($n = 3$), showing that all papers framed as trait-based and/or functional in the literature identified, found that high fishing pressure results in short life spans and generation times. Fishing had a negative impact on gape size ($n = 1$), a mostly negative impact on the size ($n = 10$) and trophic level ($n = 5$) of fish, but a positive influence on natural mortality ($n = 3$), and a mostly positive impact on growth rate ($n = 4$). All papers assessing the impact of climate change on anti-predator responses ($n = 4$) found a negative relationship. On the other hand, climate change was found to have a positive relationship with metabolic rate ($n = 4$). There was a mixed effect of climate change on fish size and the growth rate of fish. Climate change was either found to insignificantly affect fish trophic level or have a negative impact on trophic level ($n = 2$) (**Figure 5**).

The small sample size of papers looking at continuous traits linking to measured ecosystem processes showed that there was a positive impact of time of day on herbivory ($n = 1$), and a mostly positive impact of size on herbivory ($n = 5$). Gregariousness was found to either have an insignificant or positive impact on herbivory ($n = 2$). Few papers quantified the process of predation in trait-based terms. However, of those that did, there was a negative effect of the size of prey on the rate of predation ($n = 2$) and a positive effect of the growth rate of prey on the extent of predation ($n = 2$) (**Figure 6**).

The initial search results highlighted that herbivory was the most consistently quantified ecosystem process and was typically measured as bite rate (e.g., bites/minute) or bite impact (e.g., kg × bites/minute). A Pearson correlation coefficient was calculated for each paper quantifying the relationship between effect traits and this measure of herbivory. There was a negative correlation between fish size and bite rate, as shown by the average of papers above the red dotted line in **Figure 6A**. However, papers looking at fish size and measures of bite impact (below the red line in **Figure 6A**) tended to find a positive correlation. A strong average positive, correlation between gregariousness and herbivory was identified, but note, this is based on only two studies. A positive relationship between diel activity and herbivory was also found. Diel activity was sometimes measured as a categorical trait [e.g., nocturnal and diurnal in Hoey and Bellwood (2009)] or

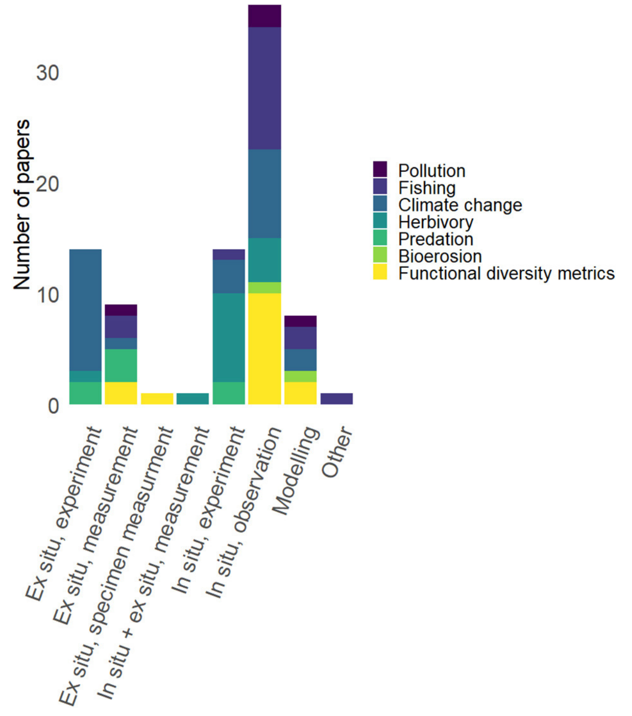

FIGURE 4 | Number of papers (colored according to disturbance, process, or functional diversity) in each evidence category.

on different time-scales [e.g., minutes after sunrise in Goatley and Bellwood (2010)], and the correlation coefficient reflects the strong magnitude of influence rather than the direction of influence (**Figure 6**).

DISCUSSION

Our review highlights four main findings: (1) size and diet are used as both response and effect traits with a relatively large number of studies investigating their importance to the range of different disturbances and processes explored in this paper; (2) nutrient cycling and bioerosion are understudied processes in the trait-based coral reef fish literature; (3) there is a distinct clustering of trait types (e.g., morphological traits, life history traits, etc.) in functional diversity studies, in addition to a cluster of six mixed trait types frequently used together (size, diet, position in the water column, gregariousness, mobility, diel activity); (4) because traits are not consistently coded across the literature, amassing an informative sample size to quantify the effect size of disturbance-trait or trait-process relationships is a challenge. Nevertheless, using a small sample size of papers measuring the relationship between key traits and the process of herbivory, we highlight variation in even the most seemingly well-known interactions. We reflect on these findings and propose a way forward for trait-based approaches in coral reef fish ecology and conservation.

Trends in the Literature

Size and diet were identified as both response and effect traits (**Figure 1**). As illustrated in the network diagram, both traits are centrally located, with size having a median centrality ranking as the top trait, and diet ranking alongside gregariousness as the second most central trait, indicating their use in conjunction with a range of other traits within papers (**Figure 2**; **Supplementary Figure 4**). Size is also demonstrated to have a consistent relationship with herbivory, whereby bite rate is negatively correlated with size and bite impact is positively correlated with size (**Figure 6**). These findings support the view that size acts as a super-trait, as it scales with, and therefore shapes, a range of other functional traits (Jacob et al., 2011). However, the relationship between size and diet or trophic level is not linear, but rather, it is mediated by traits such as body depth, tooth shape, and mouth width (Keppeler et al., 2020).

In comparison to ecosystem processes, trait-based approaches to studying the effects of disturbances on coral reef fish (response) traits were more numerous. Specifically, fishing and climate change were both studied in 20 or more papers, whereas only four papers focused on pollution (**Figure 1**). Disturbances can interact additively or synergistically to affect the coral reef environment at a number of different levels ranging from microbial to large fish (Darling et al., 2010; Ban et al., 2014; Zaneveld et al., 2016). While fishing pressure and pollution could involve, in some cases, local solutions, climate change is likely to necessitate urgent global cooperation and decision making (Mumby et al., 2013; Hughes et al., 2017). The level of uncertainty associated with global decision making has led scientists to consider the consequences of different possible climate change scenarios (Hoegh-Guldberg et al., 2007; Pandolfi, 2015). A trait-based approach could be particularly useful to understand what novel ecosystem configurations might arise under these different scenarios (Graham et al., 2014; McClure et al., 2019).

The most commonly studied ecosystem processes were herbivory and predation. This focus in the literature is likely due to the emphasis of herbivory as a key process that prevents phase shifts to non-coral benthic communities (Hughes, 1994; Bozec et al., 2016; Cramer et al., 2017). Unlike herbivory, where only consumer traits were being studied, predation was often researched in terms of both consumer (predator) and prey traits. Studying the interactions of predators and prey contributes to an understanding of community dynamics that support ecosystem functioning (Schmitz, 2017). Although this review was limited to investigating fish traits, the interaction of fish traits with coral traits or algal traits represents a similar avenue to exploring the relationship between community producer-consumer dynamics (Rasher et al., 2013).

Gaps in the Literature

Few papers explored relationships between effect traits and bioerosion and nutrient cycling. While bioerosion is a widely recognized process on coral reefs (Lokrantz et al., 2008; Bellwood et al., 2012), only two papers were identified that measured it using an *explicit* trait-based approach. Such gaps in the literature highlight the need for further research quantifying such ecosystem processes, so that they can be more confidently

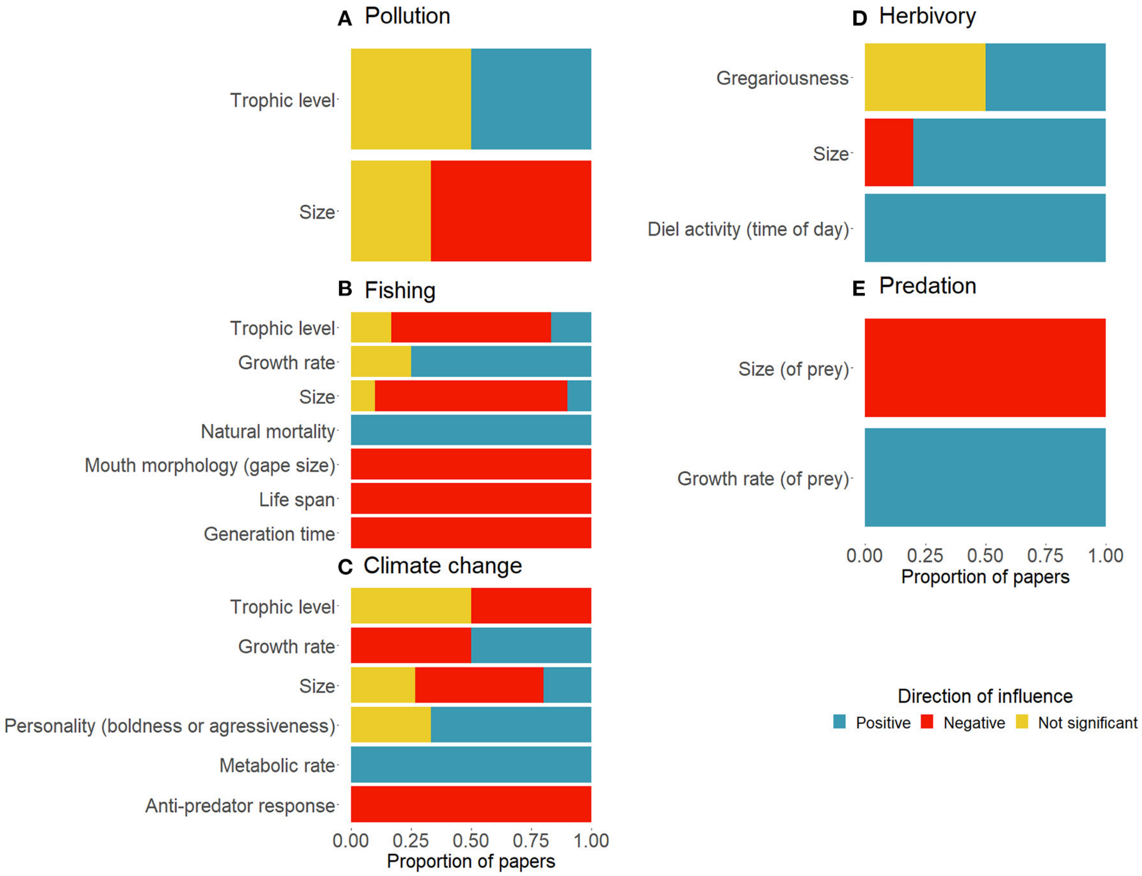

FIGURE 5 | Proportion of papers linking traits positively (blue), negatively (red) or without significance (yellow) to **(A)** pollution, **(B)** fishing, **(C)** climate change, **(D)** herbivory, and **(E)** predation.

linked to coral reef fish traits. However, since conducting the review (September 2018), there have already been strides taken to fill in research gaps and drive forward the application of trait-based approaches to estimate important functions and processes on coral reefs. For example, when this review was conducted, no papers were found linking traits to nutrient cycling, even though the process of nutrient cycling is important to the productivity of the ecosystem (Allgeier et al., 2016). A notable addition to the literature addressing this gap is a paper and companion R package proposing a trait-based approach to model nutrient cycling (Schiettekatte et al., 2020). The authors use traits such as body size, life stage, and diet to model fish ingestion and excretion rates, and accurately predict these rates for three species. Similarly, another notable publication in the field proposes a trait-based methodology and R package to facilitate the estimation of reef fish productivity (Morais and Bellwood, 2020). While productivity was not considered as a process in this review, it is an essential indicator of ecosystem functioning. The productivity of consumers on the reef (process) is demonstrated to respond to habitat degradation (disturbance) through a trait-mediated pathway (Morais et al., 2020). Thus, while the approach is not explicitly framed in the response-and-effect framework, it applies the logic of overlapping response and effect traits to demonstrate the value of traits in detailing the mechanisms through which disturbances affect ecosystem functioning.

Trait Centrality and Clustering

The results of the network and centrality analyses highlight which traits are most commonly being used together. Amongst the evidence base, there is a distinct clustering by trait type (**Figure 2**). Results from the ordination plot also show that the six traits popularized in Mouillot et al. (2014) (size, diet, space use/position in the water column, diel activity, gregariousness, and mobility) are frequently grouped together to compute functional diversity metrics (**Figure 3**). These traits cover all broad trait categories except for life history traits and physiological traits. Physiological traits, such as metabolic rate, are often difficult to obtain and vary regionally (Killen et al., 2017). Conversely, life history traits are easily obtainable (Thorson et al., 2017). However, we found that they are not commonly used in functional diversity studies and form their own cluster in the PCoA analysis (**Figure 3**). This is also partly attributable to the conservative definition we used for the term "life history" traits; in this paper, "life history" traits are restricted to those directly associated with survival and reproduction, as outlined in the seminal work by Stearns (1976). Such traits might

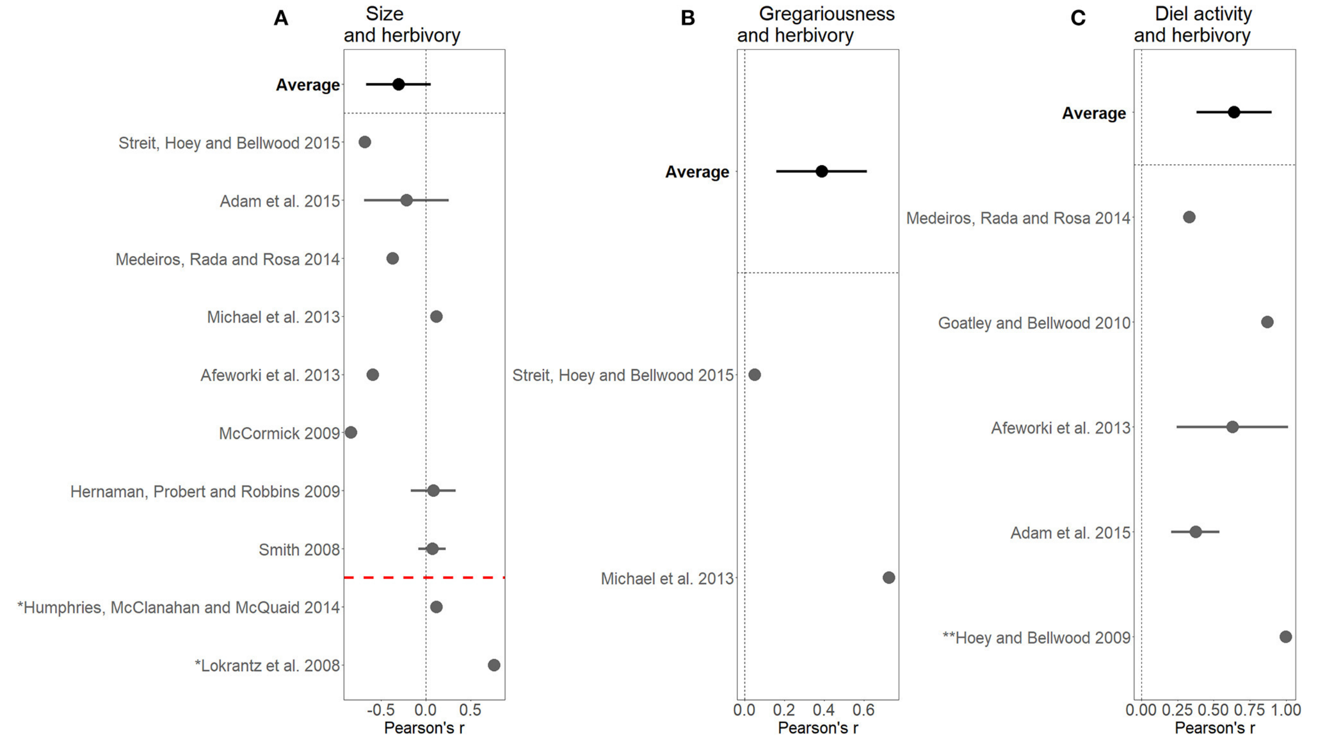

FIGURE 6 | Pearson's r correlation coefficients with 95% confidence intervals for papers linking **(A)** size and herbivory, **(B)** gregariousness and herbivory, **(C)** diel activity and herbivory. Averages of Pearson scores for all the papers are highlighted in bold for each graph. The red dotted line in **(A)** separates out two papers excluded from average as they measured herbivory in a form other than bite rate. * Bite impact rather than rate (e.g., amount of algae removed). ** Bite rate standardized by size.

compliment the selected six traits to better reflect the response diversity of coral reef fish, as such traits are frequently used to measure the response of coral reef fish to disturbances (**Figure 1**; **Supplementary Figure 3**). Nevertheless, the six traits capture a broad range of response and effect traits that have been linked to both ecosystem processes and disturbances. Three of the six traits were assessed quantitatively with respect to their impact on the process of herbivory; several studies show the importance of size, gregariousness, and diel activity in influencing the bite rates and algal removal rates of fish (**Figure 6**). Furthermore, the six traits have been used to effectively elucidate both global and small-scale ecosystem changes (Stuart-Smith et al., 2013; Brandl et al., 2016) and the ease at which they are obtainable likely means they have great potential for further use in functional studies (Bellwood et al., 2019).

Conversely, morphological traits, which form a cluster driven by ecosystem processes (**Supplementary Figure 3**), and are sometimes used as stand-alone traits in studies looking at functional morphospace (e.g., Goatley et al., 2010; Quimbayo et al., 2021) (**Figure 3**), are not as easily available, and as such have typically been used in studies conducted on historical records, at a small geographical scale, or for few species (e.g., Munday et al., 2011; Fox and Bellwood, 2013; Streit et al., 2015). Thus, there is scope to build upon morphological trait databases, so that ecosystem functioning can be better understood at a larger scale (Kiørboe et al., 2018). If such traits become more readily available, they might start being used in conjunction with behavioral and life history traits to bridge together research being conducted on the impact of disturbances and ecosystem functioning.

Although this review provides a broad overview of coral reef fish traits through a response-and-effect framework, it should be noted that it does not extensively cover all of the literature dealing with traits. This is partly because the term "trait" is extremely broad and partly because systematic reviews are always somewhat biased through search terms and database algorithms (Pullin and Stewart, 2006; Drucker et al., 2016). Nevertheless, one of the purposes in this paper was to bring some structure to the coral reef fish trait literature through the response-and-effect framework.

Toward a Trait-Based Approach for Coral Reef Fish Ecology

Identify Overlapping or Correlated Response and Effect Traits

A dichotomy does not exist between response and effect traits. On the contrary, many traits, especially those related to resource use, both respond to disturbances and affect ecosystem processes (Diaz and Cabido, 2001). In our review of the literature, both size and diet were found to be extensively used as response and effect traits (**Figure 1**). Identifying traits that are both response and effect, as well as response/effect traits that are strongly correlated, allows for a parsimonious prediction of the impacts of disturbances on ecosystem functioning (Suding et al., 2008). Correlated traits can be identified through multivariate ordination techniques. For example, Beukhof et al. (2019) demonstrate how traits positioned in close proximity in a PCA of trait-space (e.g., length and fecundity) follow similar temporal trends when exposed to environmental disturbances.

In cases where two traits are known to correlate, and one of those traits is known to respond to an ecosystem disturbance, while the other is known to affect an ecosystem process, they can be used together to harness predictive capacity. Working with microbial communities, Amend et al. (2016) found that response traits affected by drought that were strongly correlated with traits responsible for ecosystem processes allowed for the effective prediction of shifts in the functioning of microbial communities with disturbances characteristic of global change. Similarly, this review determined that the traits metabolic rate (positive relationship) and anti-predator responses (negative relationship) are linked to climate change (**Figure 5**). However, both traits have also been linked to the process of predation (White et al., 2013; Ferrari et al., 2015) (**Figure 1**). Therefore, such traits provide an opportunity for determining the pathways through which disturbances can affect ecosystem processes.

Establish Causation and Build the Predictive Abilities of Trait-Based Approaches

One concern with the response-and-effect framework could be the implied causation in the relationships between disturbances and response traits and effect traits and ecosystem processes. While the framework does attempt to structure the direction of correlations by explaining mechanisms, causation is a notoriously hard concept to prove within science (Anjum and Mumford, 2018). However, it is generally accepted that if hypothesized causal relationships have supporting data that can be theoretically justified, used, and applied, directionality in such relationships can be recognized. Such justifications underlie the processes of mechanistic and causal modeling (Connolly et al., 2017). In this review, the effect traits demonstrated to impact the process of herbivory (**Figure 6**) were able to be identified as effect traits, because there was a plausible causal pathway. Considering another example: size-selective fishing is proposed as the mechanism underlying a shift in the size structure of fish communities. The clear causal pathway and breadth of observational evidence supporting this disturbance-response trait link, in addition to the predictive power that comes with assuming this causal relationship, illustrates the value and purpose of structuring traits according to the response-and-effect framework. Like many of the tools applied decades ago to understand ecosystem functioning, the response-and-effect framework originates in the terrestrial plant ecology field. One of the central goals of the approach is to enable the prediction of changes in community composition and ecosystem functioning (Lavorel and Garnier, 2002).

Body size is somewhat of an anomalous trait, as it is easily recorded and has great functional importance. For other traits with less well-known causal pathways, building up an evidence base of observations under a range of conditions is important. Moreover, experimentation could be used as a controlled method of assessing causality. While this approach may not always be feasible or appropriate, small-scale controlled experiments can further test or corroborate relationships observed on a large scale (**Figure 4**). For example, disturbances associated with climate change provide natural experiments on a global scale (e.g., Keith et al., 2018; Richardson et al., 2018). Observations following such events offer useful information about response traits to form hypotheses that can be further tested through experimentation (e.g., Biro et al., 2010).

Favor Continuous Traits or Standardized Trait Categories, and Consider Intraspecific Variation

This review demonstrates the centrality of size in the literature (**Figure 2**) and its versality as a response and effect trait (**Figure 1**). Moreover, size can be measured on a continuous scale. In order to model the overall direction of a response or effect trait across a number of studies, consistency in measurement is essential. With categorical data, a range of potential errors get introduced in the effort to standardize (Nakagawa and Cuthill, 2007). Categorical traits have also been shown to decrease the quality of functional space (Maire et al., 2015). Maintaining consistency of categories and/or using continuous traits allows for useful meta-analyses to be compiled for a range of disturbance-trait-process relationships.

In addition to being a super-trait, size provides an avenue for investigating the importance of intraspecific variation. Intraspecific variation is a burgeoning field of research within functional ecology (Albert et al., 2011; Allgeier et al., 2017; Des Roches et al., 2018). Where substantial variability exists within species, it may no longer be sufficient to use species-level trait data (Bolnick et al., 2011). One example of the importance of intraspecific variability is illustrated in a paper by Barneche et al. (2018). The authors show that there is hyperallometric scaling in reproductive output; larger coral reef fish mothers, within the same species, have a far greater reproductive output than smaller mothers. The functional trait of an individual fish might also depend on its sex, age, or size at which it was sampled. For example, many species undergo ontogenetic shifts in their diet; it has been found that some piscivores are able to expand their diet breadth as they grow older and bigger, and their gape size can accommodate larger prey (Dunic and Baum, 2017). This diversity of size amongst individuals of a species, can be easily recorded. The size and species identity of fish is often collected using routine visual surveying techniques (Caldwell et al., 2016). Indeed, total length is a relatively simple trait to measure observationally and non-invasively *in situ* (Villéger et al., 2017).

Diet, on the other hand, is not typically measured for each fish during a survey, unless it is one of the explicit aims of the research. Rather, species are assigned a diet category post data collection using expert knowledge, published literature, or databases such as Fishbase (e.g., MacNeil et al., 2015). More recently, Parravicini et al. (2020) highlight the disagreement in the literature about broad reef fish trophic guilds, and provide a standardized set of diet classifications using phylogeny and maximum body size to predict trophic guild with high accuracy. However, improvements can still be made by accounting for intraspecific variation. Intraspecific variation linked to ontogenetic shifts in diet could be accounted for by assigning diet to an individual fish count based both on species information and size, where that species-level data exists. Further, technological developments such as video surveys coupled with deep learning may allow the automated estimation of diet and other individual fish characteristics beyond size (Villon et al., 2018; Li et al., 2020). Progress has also been made using gut content DNA metabarcoding to rapidly and confidently estimate diet across diverse food webs. With DNA barcode libraries expanding, there is the potential to estimate high resolution diet across large scales (Casey et al., 2019). The incorporation of between-individual variation to a trait-based approach, with traits such as size and diet, would allow for a more dynamic view of environment∼trait∼function relationships—a dynamism which is essential to scaling up to population dynamics, whereby such dynamics ultimately shape multiple interacting ecosystem processes (Salguero-Gómez et al., 2018).

CONCLUSIONS

This review demonstrates the ability of the response-and-effect framework to guide future research directions based on the understanding that environmental changes will undoubtedly produce functional changes. Evidence suggests that some traits provide a crucial link between fish responses to disturbances and effects on ecosystem processes. However, the evidence base is thin for linking effect traits to many processes. Thus, if an emphasis on the conservation of ecosystem functioning on coral reefs is to be made, there is much scope to develop a more concrete understanding of how traits link to individual processes and eventually the multifunctionality of the reef. Identifying overlapping traits, causation, and improving our ability to capture intra-species trait information will greatly advance this endeavor.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

JH-H collected data, did the data analysis, and wrote the first draft of the manuscript. NG and DM helped to conceive the project, provided supervision, data analysis suggestions, and editorial comments. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.640619/full#supplementary-material

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Decadal shifts in traits of reef fish communities in marine reserves

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Marine reserves are known to impact the biomass, biodiversity, and functions of coral reef fish communities, but the effect of protective management on fish traits is less explored. We used a time-series modelling approach to simultaneously evaluate the abundance, biomass, and traits of eight fish families over a chronosequence spanning 44 years of protection. We constructed a multivariate functional space based on six traits known to respond to management or disturbance and affect ecosystem processes: size, diet, position in the water column, gregariousness, reef association, and length at maturity. We show that biomass increased with a log-linear trend over the time-series, but abundance only increased after 20 years of closure, and with more variation among reserves. This difference is attributed to recovery rates being dependent on body sizes. Abundance-weighted traits and the associated multivariate space of the community change is driven by increased proportions over time of the trait categories: 7–15 cm body size; planktivorous; species low in the water column; medium-large schools; and species with high levels of reef association. These findings suggest that the trait compositions emerging after the cessation of fishing are novel and dynamic.

No-take marine reserves are a widely used management and conservation tool, the implementation of which has been linked to a range of outcomes including increases in fish abundance, biomass, diversity, and the presence of functionally important species[1–3]. Quantifying the trajectories of key groups of organisms in reserves can help identify the mechanisms driving community-level responses[4,5]. However, variability in the temporal trends of traits and how they relate to community biomass and abundance in marine reserves remains largely unexplored. Looking at such temporal trends can often point to useful information about the response of ecosystem functional potential to conservation measures[6], with traits sometimes responding earlier than taxonomic measures[7].

Functional approaches to conservation prioritise the maintenance of ecosystem functions and services of highly diverse ecosystems in the dynamic and changing world of the Anthropocene[8]. Ecosystem functioning can be measured directly as the rates of an ecosystem process (e.g., herbivory, predation, bioerosion, nutrient cycling) or indirectly as the functional potential of the ecosystem by looking at the functional groups or traits present within a community[9]. While only indirectly capturing ecological processes, traits are more available in literature compilations and therefore can be applied to datasets retrospectively[10].

"Functional traits" are suggestive of the mechanistic links between species' responses to disturbances and management practices and their potential effects on ecosystem processes[11]. The first step in applying a trait-based approach is therefore to carefully select the traits most applicable to the ecological processes and research questions of interest. Trait selection is important for understanding the pathways of community responses and their associated implications[12]. When assessing the functional structure of a community, traits can be weighted by abundance or biomass, allowing for proportional representation[13,14], with abundance-weighting common practice in broad trait-based approaches[15].

Changes in species and traits with time since protection can produce novel functional configurations. Such novel configurations can sometimes produce the same ecosystem processes as previous communities, result in the loss of some functioning, or a new balance of functions and services can establish[16–18]. Key traits such as fish body size, trophic level, and life history strategies mediate the relationship between disturbance/recovery and abundance, biomass, and biomass production—all essential components for sustainable ecosystem functioning[19–23].

An assessment of changes over time in the traits of coral reef fish following establishment of marine reserves would enable a better understanding of the indicative impacts of protection on ecosystem functioning. In this paper, we apply a trait-based approach to a unique long-term dataset on high-compliance no-take marine reserves in Kenya, enabling a range of theory-based predictions to be evaluated (Supplementary Table S1). Specifically, we ask:

1. Do biomass and abundance trends vary over time in marine reserves?

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2. Does the abundance-based trait-space of the fish community change over time in marine reserves?
3. Do the relative abundances of individual trait categories progressively shift over time in marine reserves?

Materials and methods

Study sites. Kenya has four high compliance no-take marine reserves. Each of the reserves are regularly patrolled government national parks and differ in when they were legally established. Malindi Marine Park is the oldest reserve and was created in 1968, followed by Watamu Marine Park in 1972, Kisite Marine Park in 1973, and Mombasa Marine Park in 1991 (see map in[24]). The sizes of the reserves' closures vary. Mombasa is 6 km^2, Malindi is 6.3 km^2, Watamu is 10 km^2, and Kisite is 28 km^2; however, the amount of coral reef area within Kisite Marine park is ~ 10 km^2. Thus, the range in effective coral reef protected area is 6–10 km^2[25]. Malindi and Watamu are situated in close proximity. Malindi was excluded from the analyses of this study, because it was severely impacted by the 1998 bleaching event, with the fish community following lagged trends in benthic condition (Supplementary Fig. S2). Inclusion would bias the results towards benthic influence[26]. For the purposes of this paper, we were more interested in the effect of protection from fishing on the fish community, and as explained below, treated the reserves as a chronosequence (see "Marine protection chronosequence" section). The remaining three marine reserves provide a powerful dataset, spanning 44 years of protection from fishing and 732 ecological surveys.

Fish and benthic surveying. Visual censuses of fish were conducted by the same observer (TRM) during neap tides along two to five 5 × 100 m belt transects in each site. All surveyed sites in the parks were located in the shallow back-reef lagoon or leeward areas. Eight fish families were sampled at species level with abundance counted consistently across the full duration of monitoring from 1991 to 2018: Acanthuridae, Balistidae, Chaetodontidae, Diodontidae, Labridae (including Scarinae), Monacanthidae, Pomacanthidae, and Pomacentridae. These families include all of the trait categories explored in this analysis. However, some trait categories were less well represented than others, namely piscivores, pelagic species, and species with low levels of reef association. Species were counted using a discrete group sampling (DGS) method, whereby families or species with similar body shapes or behaviours were identified and counted during separate passes along a transect[24,27]. Total fish abundances (as well as trait-level abundances) were calculated as the mean number of fish/transect and standardised to the mean number of fish/ha. DGS survey dates and sites are presented in Supplementary Table S7. Benthic surveys were conducted on 9–27 10 m line transects at each site using the line-intercept method. Distances of benthic cover categories under the line were assigned to nine groups: hard coral, soft coral, algal turf, coralline algae, calcareous algae, fleshy algae, seagrass, sand, and sponge.

Biomass was estimated using a different method whereby fish were surveyed at the family level within two to six 5 × 100 m belt transects in each site (see[28] for further explanation of the two methods). Total lengths of individual fish were estimated and grouped into 10-cm size-class intervals. Total wet mass was estimated for each size-class using established length-mass relationships based on the centre point of the size-classes[29]. The families sampled in the species level abundance counts and used in the biomass analyses represented 74.2% of total biomass (in 2018). For the biomass over time model, individual site-year biomass values were used.

Fish traits. Seven species-level fish traits were evaluated in this paper: body length (size), diet, schooling behaviour (gregariousness), position in the water column, reef association, and length at maturity. These traits were carefully selected according to whether they were likely to respond to protection from fishing and affect ecosystem functioning[11] (see trait inclusion justification; Supplementary Table S1). The trait-based analysis was based on abundance data, as species level biomass estimates were not possible from the survey methodology, and the literature on trait-based ecology favours abundance-weighting[15]. Trait values were obtained from the Gaspar database[30], Fishbase[31], and FishLife[32]. Data were available for 216 out of 219 species surveyed in the nine families; therefore, three species were excluded from the analyses.

Data analysis. *Marine protection chronosequence.* To assess how the abundance, biomass, and functional space of the fish community changed over time with protection, the temporal parameter "time since closure" was derived for each of the marine reserves. This was done for each sample point within each reserve by calculating the number of years since the establishment of the marine reserve (the year of data collection minus the year at which the marine reserve was established) to assemble a chronosequence of the data. This method has been applied to the same data to create a time-series spanning several decades of marine protection[28].

Functional space. A functional space based on fish traits within the marine reserves was constructed by carrying out a Principal Coordinates Analysis (PCoA). The PCoA was based on a Gower's distance matrix of species-level fish traits (size, diet, gregariousness, position in the water column, reef association, and length at maturity) for all years and sites using the R packages, "cluster"[33] and "ape"[34]. An abundance-weighted mean PCoA value for axes one and two was calculated for each site/year combination. A Pearson's correlation analysis between PCoA axes 1 and 2 values and community weighted mean (CWM) trait values shows the extent to which each of the traits were associated with the axes.

CWM trait values were calculated for each trait using the "FD" package[35] as:

$$CWM = \sum_{z=1}^{n} p_z x_z$$

where the site-level abundance of a species z in a given year is denoted as p_z, and x_z is the trait value of species z[36]. For each categorical or ordinal trait, the proportion of trait categories within a trait was calculated as:

$$proportional\_abundance\ i = \frac{\sum Abundance\ of\ species\ with\ attribute\ class\ i}{\sum Abundance\ of\ all\ species}$$

The proportional abundance of individual traits over time were weighted by total abundance in each sampling unit. For the continuous trait, length at maturity, the abundance-weighted mean value of that trait was modelled.

Covariates. Several covariates explaining variation in the trait space (Supplementary Fig. S6) were included in the global models. The first covariate controlled for in the models represented the benthic community of the sites. A Principal Component Analysis (PCA) was conducted on percentage cover of (1) hard coral, (2) macroalgae, (3) coralline algae, and (4) other calcareous algae across all sites. This produced a succinct multivariate value (PCA axis 1 explaining 50% of the variation) for each site/year that captured multiple aspects of the benthos and at the same time reduced the number of parameters needed to be included in the models. Rugosity, a measure of the structural complexity of the reef[37], was included as a covariate in the models separate to the PCA of the benthic community. The mean biomass (of the eight fish families) for each marine reserve per year was also calculated and used as a covariate. For years and sites where fish survey data were collected, but other covariate data (e.g. benthic, rugosity, biomass) were missing at random points across the time-series, a Generalized Additive Mixed Model (GAMM) of the covariate over time (calendar year), with reserve as a random effect, was conducted to impute missing data from fitted values. The models were fit with a Gaussian error distribution and followed model validation protocol described below.

The next covariate incorporated into the models was a time-series of Thermal Stress Anomalies (TSAs). TSAs were included in the models as they were associated with coral bleaching events. Moreover, McClanahan[38] showed that variation in TSA is associated with the biomass of certain fish families. Fish communities were expected to exhibit a lagged response to disturbances such as thermal stress[14]. TSA data from 1991 to 2018 for each marine park were extracted from The Coral Reef Temperature Anomaly Database (CoRTAD) hosted by NOAA Coral Reef Watch. TSAs were calculated for 4 km grid cells as the weekly sea surface temperature minus the maximum weekly climatological (long-term average) sea surface temperature[39]. The maximum TSA (magnitude) for each reserve in each year was selected for modelling. Therefore, the optimal time-lag for the effect of TSAs on fish functional space was assessed by lagging TSA values from 0 to 9 years and incorporating this lag into a GAMM model of the first PCoA axis. Lagged models were compared (for the same dataset years), and an optimal-fit lag of 4 years was selected to be included in the models, using the AIC selection procedure described below. The Granger Test, convergent cross-mapping and cross-correlation methods of detecting causality and time-lagged effects of covariates were trialled[14,40]. However, due to uneven time-steps in the time-series, a modelling approach for selecting the optimal thermal stress time-lag was favoured (e.g.[41]). The 4-year lag fits with previous findings showing that coral cover took approximately 4 years to return close to pre-1998 bleaching levels[42].

Oceanic productivity was estimated using chlorophyll a for the years 1997–2018, which were available from the Ocean Colour Climate Change Initiative dataset esa-cci-chla-monthly-v4-1 by the European Space Agency (http://www.esa-oceancolour-cci.org/). Daily data were averaged to get annual values at a 4-km resolution. For years prior to 1997, the average value of chlorophyll a for each park over the time-series was taken. Net Primary Productivity (NPP), another measure of oceanic productivity, was obtained as a static average value for the centre of each park from the Marine Socio-Environmental Covariates database[43].

An initial set of covariates including time since closure, calendar year, axis 1 of a benthic PCA, rugosity, chlorophyll a, NPP, TSA, and biomass were tested for collinearity using VIF values and checking the correlation matrices[44]. Biomass, calendar year, and NPP had VIF values > 3 and were therefore removed from models. All continuous covariates were scaled and centred to a mean of zero and standard deviation of one for model fitting.

Two modelling approaches were taken to explore community changes in biomass, abundance, and functional space (PCoA) over time. The first approach was to include the marine reserve (Mombasa, Kisite, Watamu) as a random effect. The second approach was to allow slopes and intercepts to vary by marine reserve. In applying these two approaches, we illustrate how the reserves form continuous patterns across the chronosequence and where they differ. For illustration purposes, all covariates aside from time since closure were held to their means, and partial residuals that account for covariate effects in the models (rather than raw data points) were presented. A summary of covariates can be found in Supplementary Table S2.

Modelling. All research questions were addressed using GAMMs with the R package "mgcv"[45] to model changes of respective variables of interest over time since closure of the marine parks. GAMMs were favoured over other modelling tools, because they allow for the detection of non-linear patterns discovered in this dataset with exploratory analyses and typically present in time-series data[46]. A backwards selection process, whereby each variable was eliminated until all variables left in the model were significant ($p < 0.05$), was used to select the optimal model, as determined by AIC scores (optimal model < 2 AIC from other models). Where models did not differ more than 2 AIC, the simplest model with the fewest parameters was selected. Smoother functions for continuous covariates were fit with cubic regression splines[47]. The number of knots (k) in a smoother determines the "wiggliness" of the smoother parameter's curve[48]. This number was estimated by comparing Estimated Degrees of Freedom (EDF) values to k and through a generalized cross validation technique. The number of knots was restricted to four for the time since closure parameter, in order to allow for polynomial relationships and to detect a range of non-linear trends, but also to restrain the flexibility of model fits for ease of interpretation and to limit computation time[49]. An ARMA(1,0) residual autocorrelation structure was added to the models to account for dependent values on preceding years within the same site[50]. The need for an autocorrelation structure was assessed visually using the autocorrelation function (ACF)[44]. For the biomass model with the marine reserve as a random effect, a residual variation structure, VarPower, was also incorporated. Optimal model equations and outputs can be found in Supplementary Tables S3–S5.

All models were validated following protocols outlined in Zuur and Ieno[44]. Significant outliers, as determined by Cook's Distance, were removed to ensure they did not over-influence results[44] (but see Supplementary Fig. S5). Model assumptions were checked by plotting model residuals against fitted values as well as covariates included and excluded from the models. Biomass and abundance data were log-transformed and trait proportions were logit-transformed in order to normalise the residuals (as in[49,51]), after trialling the use of different distribution families[52]. Biomass, abundance, and proportional trait models had a Gaussian distributed error term, while PCoA and length at maturity (logged cm) had a Gamma distributed error term. All data analysis was conducted using R Version 3.6.3.[53].

Results

Biomass and abundance models.

Biomass and abundance both increased over time since the cessation of fishing, while holding other covariates to their means (Fig. 1). However, while the slope of biomass was close to log-linear (EDF = 1.330, $R^2 = 0.255$), with the rate of increase slowing just after 20 years of closure, the abundance curve was relatively flat to 17 years, and then steeply increased to a peak at 35 years (EDF = 2.68, $R^2 = 0.83$; Supplementary Table S3). When the slope of the biomass curve was allowed to vary by marine reserve, the marine reserve trends remained very similar to the global trend. However, when the slope of the abundance curve was allowed to vary by marine reserve, only Mombasa had a significant, positive trend (EDF = 2.28, $R^2 = 0.74$, $p < 0.001$). Kisite's abundance slope was not significant when looked at independently ($p = 0.20$), but in the hierarchical global model, it appears to drive the steep increase in the overall trend, whereas, Watamu flattens the curve (Supplementary Table S3). Importantly, the overlap between abundance values in Kisite and Mombasa around 20 years of closure, indicates that this increase was more likely due to time since closure, rather than Kisite having a higher abundance of fish than Mombasa. There was a mass bleaching event in 1998, which corresponded to 7 years of closure for Mombasa, 25 years of closure for Kisite, and 26 years of closure for Watamu, but this does not appear to have an overall effect on the recovery trajectory of fish abundances in each of the reserves included in this analysis (Fig. 1b.; Supplementary Fig. S1).

Functional space.

The first two PCoA axes captured 75% of the variation in the trait space of the 216 species assessed in this analysis (Fig. 2a). The top five trait categories most positively associated with axis 1 of the fish community PCoA are bottom-dweller, large length at maturity, solitary, invertivorous (mobile invertebrate feeders), and medium reef association. The most negatively associated traits with PCoA axis 1 were planktivorous, low in the water column, medium group, high reef association, and 7.1–15 cm sized fish (Fig. 2b). The top five traits most positively associated with PCoA axis 2 were 7.1–15 cm sized fish, high reef association, small group forming, bottom dweller, and invertivorous (mobile invertebrate feeders). The most negatively associated traits with PCoA axis 2 were 15.1–30 cm, medium reef association, 50.1–80 cm, medium group forming, and pelagic (Fig. 2c).

Both PCoA axes' 1 and 2 mean community values had a negative relationship with time since closure of the marine parks, while holding other covariates to their means (Fig. 3), and the time smoother was significant for both axes (Axis 1, $p = 0.01$; Axis 2, $p = 0.03$). However, a greater proportion of the variance was described in the model by PCoA 1 ($R^2 = 0.75$) compared to PCoA 2 ($R^2 = 0.44$) (Supplementary Table S3). This indicated a shift from solitary bottom dwellers, with large lengths at maturity, and invertivorous diets, towards medium size group forming, high to medium level of reef association fish found low in the water column, sized 7–15 cm, with planktivorous diets. These traits were mostly represented by species in Pomacentridae, with *Chromis dimidiata, Chromis viridis, Neopomacentrus azysron*, and *Pomacentrus caeruleus* largely driving the trends (Supplementary Fig. S3). While the overall axis trends decreased, when the slopes were allowed to vary by marine park, we see a difference in trends between Kisite and Watamu. The PCoA axis 1 values for Kisite decreased significantly over time ($p < 0.001$), while the PCoA axis 1 values for Watamu do not change significantly over time ($p = 0.908$). For PCoA axis 2, Kisite increased over time ($p = 0.012$), while Watamu decreased over time ($p < 0.001$). However, the PCoA axis 1 model explained more variance ($R^2 = 0.645$; deviance explained = 67%) than the PCoA axis 2 model ($R^2 = 0.48$; deviance explained = 50.2%).

Shifts in trait proportions and means.

Individual trait proportions enable a clearer understanding of the mechanisms behind shifts in the multivariate trait space. We found that the majority of trait categories exhibited some change over time with protection (Fig. 4). Within the first 20 years of protection, a significant shift towards the increasing dominance of fish in the size-class 7–15 cm is observable, particularly increasing after 17 years, likely driving the overall abundance trend. The 15–30 cm size-class declined over time, while there was a slight increase in the proportion of fish in the 30–50 cm size-class between the beginning and end of the chronosequence, likely driving the overall biomass trend (Fig. 4a).

Planktivores, the most dominant diet category, become more proportionally abundant over time with protection (Fig. 4b). When holding all other model covariates to their means, the rate of increase in proportional abundance steepens after 20 years of protection and declines again after 30 years of protection (EDF = 2.60). Sessile invertebrate feeders, piscivores, and macroalgal feeders also increased, while detritivores, omnivores, and mobile invertebrate feeders decreased (Fig. 4b).

The proportion of pelagic fish recorded in the survey sites within the marine parks was consistently lower than both bottom-dwellers and fish low in the water column, likely due to the location of the survey sites on

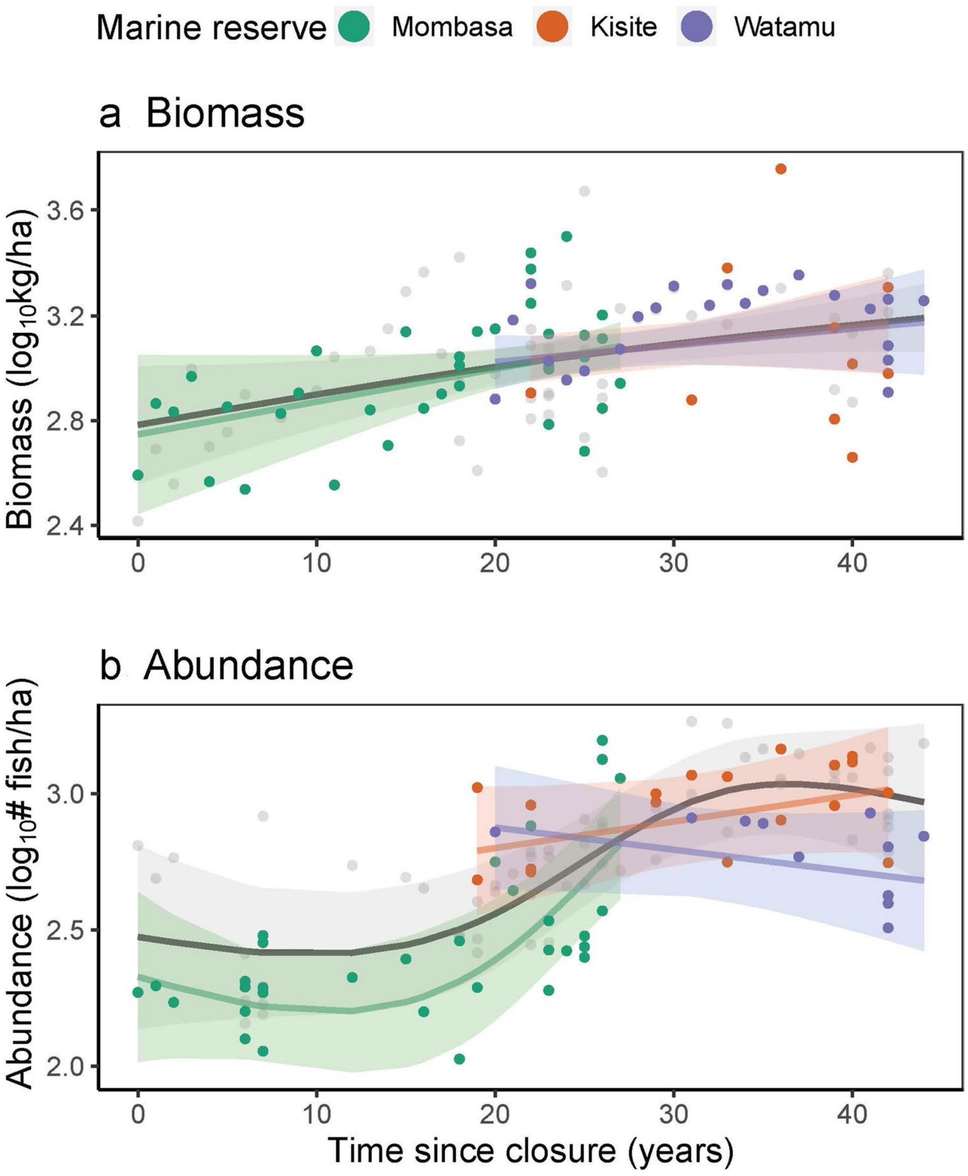

Figure 1. Modelled changes in (**a**) mean biomass (logged) and (**b**) mean abundance (logged) over time since closure of the marine parks, holding other covariates to their means, with 95% confidence intervals shaded. Points are partial residuals for the models with colours corresponding to the marine reserve, where Mombasa = green, Kisite = orange and Watamu = purple. The model with marine reserve as a random effect is illustrated in grey.

lagoonal back reefs. However, an increase in the dominance of fish low in the water column over bottom dwellers is observable after 20 years of protection, which corresponds to the first recordings of Watamu and Kisite marine reserves in the chronosequence (Fig. 4c). The random effect term "marine reserve" however, was not significant in the model, suggesting the patterns were more likely attributable to time since closure across the chronosequence (Supplementary Table S4).

Medium group-forming species, initially equally as dominant as solitary and small group (3–20 individuals) forming species become more dominant over time. All trends for schooling categories were linear or close to linear (EDF between 1.000031 and 1.000505). While large (> 50 individuals) groups increase over time, solitary, pairing, and small group (3–20 individuals) forming fish species decrease (Fig. 4d).

Patterns of change observed in levels of reef association were similar to those found for position in the water column. Fish with low levels of reef association were proportionally less abundant in the surveys than those with medium and high association across the time series, due to similar issues with sampling design that resulted in few pelagic fish being detected; Fig. 2a highlights the proximity of these two traits within the functional space. A switch from the dominance of medium to high levels of reef association can be observed after 20 years of protection (Fig. 4e).

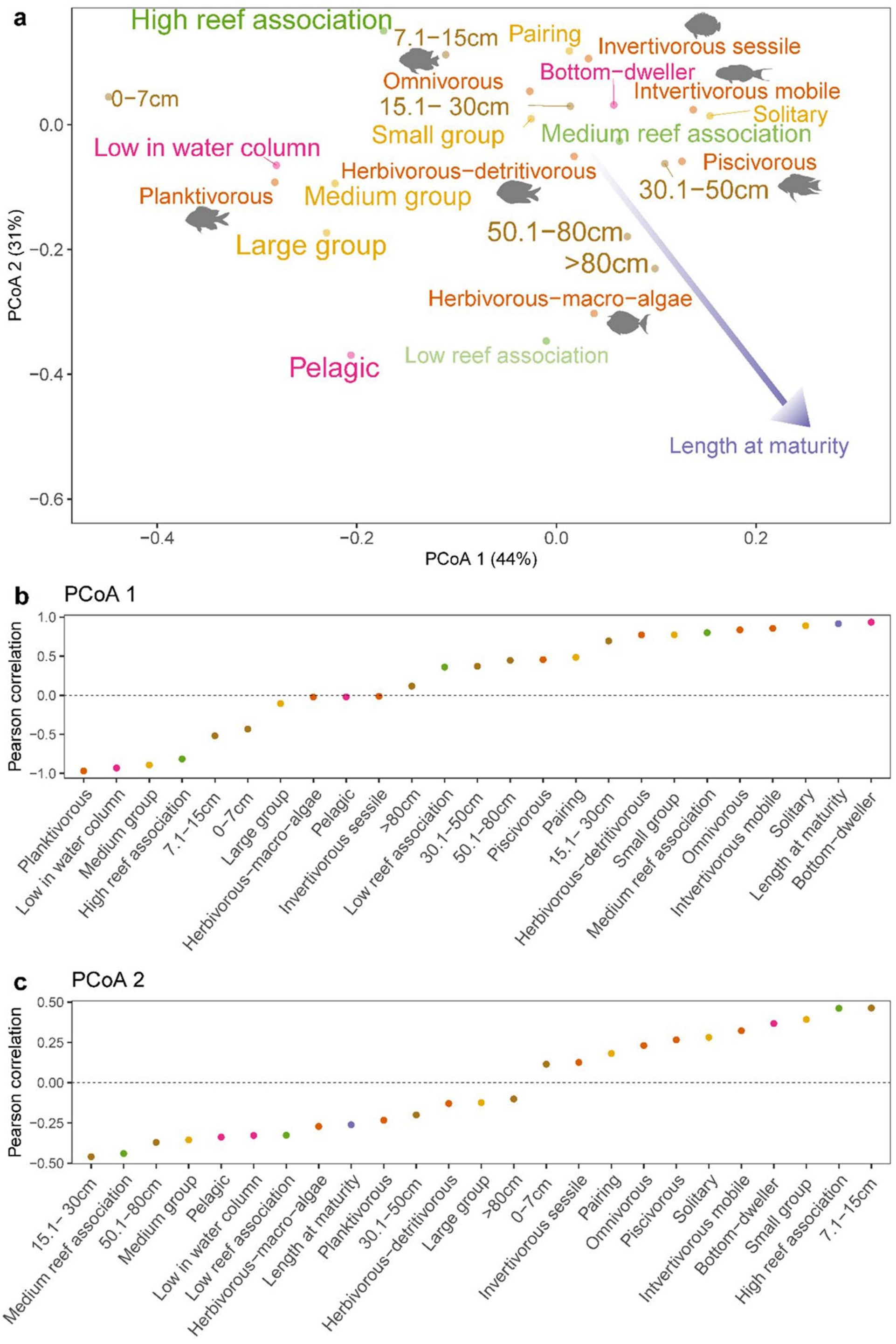

Figure 2. (**a**) Functional space of Kenyan marine parks across all sites and years spanning the chronosequence. Traits included: size, diet, gregariousness, position in the water column, reef association, length at maturity. Traits grouped by colour: purple = length at maturity, green = reef association, yellow = gregariousness, pink = position in the water column, brown = size, and orange = diet. A colour and size gradient are applied to each ordinal trait, increasing in size and opacity along the gradient. (**b**) Pearson correlation between community weighted mean values of trait categories and PCoA axis 1 and c) PCoA axis 2.

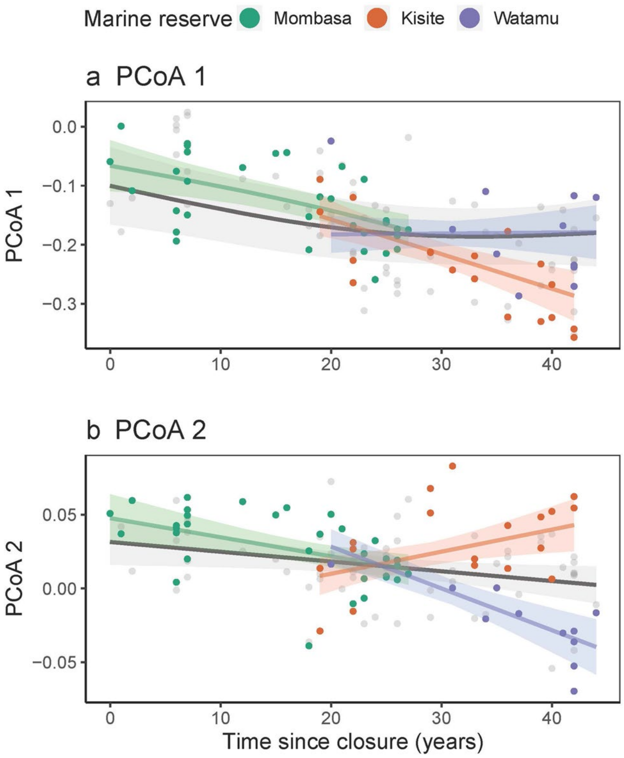

Figure 3. Modelled changes in (**a**) PCoA 1 and (**b**) PCoA 2 over time since closure of the marine parks, holding other covariates to their means, with 95% confidence intervals shaded. Points are partial residuals for the models with colours corresponding to the marine reserve, where Mombasa = green, Kisite = orange and Watamu = purple. The model with marine reserve as a random effect is illustrated in grey.

The last trait assessed was an abundance-weighted mean of the continuous measure, length at maturity. Mean length at maturity did not significantly change over time (Fig. 4f), but this was likely due to the retrospective allocation of lengths at maturity at the species level, as intraspecific data on this were not available over time (see model outputs in Supplementary Table S5).

Discussion

Developing our understanding of the mechanisms by which marine reserves affect ecosystem functioning is critical to identifying how, when, and if marine ecosystems recover from fishing[54]. We illustrate a shift in functional space over time with protection towards communities numerically dominated by fish in the size-class 7–15 cm, with a planktivorous diet, found low in the water column, forming medium-large schools, and with a high level of reef association. These findings were based on species' trait abundances, and while both overall biomass and abundance increased over time, their patterns of increase differed.

The difference in shape between the biomass and abundance curves reflected community shifts occurring at the level of species' traits. While the slope of the biomass curve increased steeply immediately following protection, the abundance curve did not follow suit until nearly 20 years of closure, when the rate of increase in biomass began to decline. The number and size of larger fish (e.g. 30–50 cm) increased early in the chronosequence, while the abundance of small, more proportionally abundant fish (e.g. 7–15 cm) did not increase significantly until 20 years of closure. This shift appeared to be largely driven by Kisite, which did not have as much absolute change in hard coral cover following the 1998 bleaching event as Watamu and Mombasa[55]. Kisite's benthic PCA had a positive relationship with axis 2 of the fish community functional space, for which the 7–15 cm size class trait was strongly correlated (Supplementary Fig. S10). This was reflected in Kisite's deviation from the overall trend in PCoA 2. Kisite marine reserve is located further offshore than the other two reserves, had less coral cover than the other reserves prior to 1998, and has less market gravity than both Mombasa and Watamu[56]. It is possible that these factors interacted to create a greater buffer against fish community change driven by disturbance to the benthos. After time since closure, thermal stress and benthic composition explained the most variance in the functional space models (Supplementary Fig. S7).

Because the fish trait size bins were somewhat arbitrary, as size is a continuous trait, and the 7–15 cm and 15–30 cm categories were sequential, the patterns observed were not easily distinguishable from those driven by shifts in species composition, a consequence of using an interspecific trait-based approach[10]. However, a sensitivity analysis revealed that even when the most abundant species in the 7–15 cm size-class, *Chromis dimidiata*, was removed, the same trends persisted (Supplementary Fig. S4). Larger bodied fish were likely to be driving overall biomass trends, while small fish were likely to be driving the overall abundance trends and appeared to be

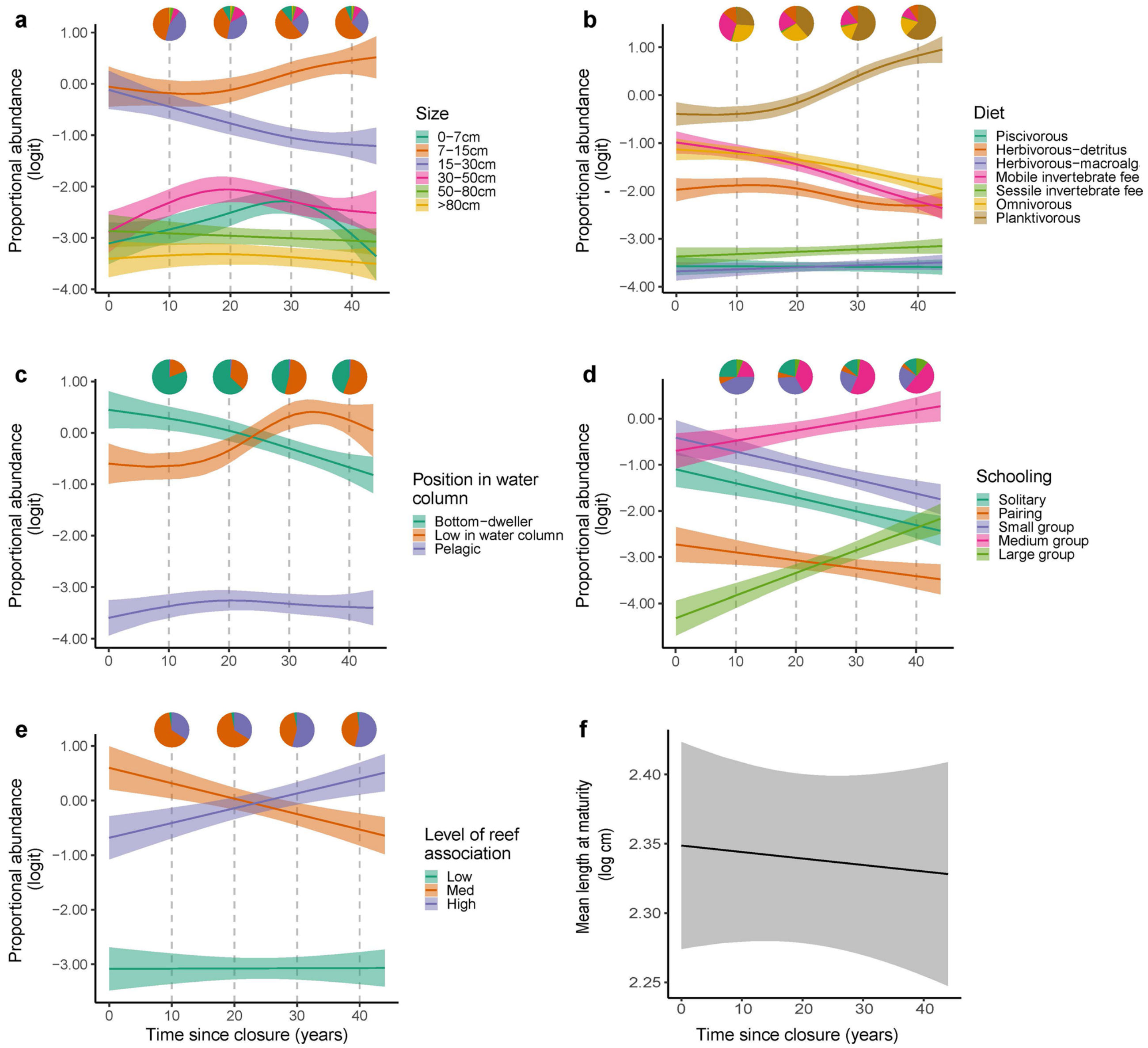

Figure 4. Modelled changes in proportional abundance of trait categories (**a**–**e**; (**a**) Size, (**b**) Diet, (**c**) Position in the water column, (**d**) Schooling, (**e**) Level of reef association) and mean values (**f** Mean length at maturity) of coral reef fish traits over a chronosequence of time since closure of marine parks, holding other covariates to their means, with 95% confidence intervals. Colours of the curves indicate the trait categories. Vertical dashed lines indicate 10 year marks in the chronosequence for which average trait category proportional abundances are illustrated in pie charts.

responding in sequence and contrary to the ecological succession expectation that small fish will respond more rapidly than large fish[57]. Perhaps the deviation from expectation occurs because fish in the 30–50 cm size-class were disproportionately targeted in Kenyan fisheries[58], and therefore, they increase rapidly when released from predation. Smaller fish, in contrast, respond to slower contextual changes in the food web.

We hypothesised that there would be a decrease in smaller size-classes and an increase in larger size-classes, as fishing exploitation has been shown to increase the steepness of the slopes of coral reef fish size spectra, due partly to the effects of predation release[59]. Increased predation in reserves may therefore be expected to drive a reduction in smaller size-classes and an increase in larger size-classes. However, previous research has demonstrated that piscivores are not disproportionately caught in Kenyan fisheries, and therefore they do not experience the rapid recovery following protection that might lead to a decrease in smaller fish (Fig. 4)[58]. In geographies where piscivores are a more prominent component of the fish community, these patterns may differ. Similar work evaluating shifts in the biomass of trophic groups indicated that the overall trophic level of fish within Kenyan marine parks was decreasing over time as slow-growing herbivores come to dominate the biomass[29]. It may be that these small to modest-size urban parks are not large enough to support the space requirements of large piscivores[60]. Therefore, the responses observed here may only be applicable to these types of modest-size closures of < 10 km^2.

The four most economically valuable fish families in Kenya, including Lutjanidae (Snappers), Lethrinidae (Emperors), Siganidae (Rabbitfishes), and Serranidae (Groupers), were not included in the list of eight families surveyed for the full duration of the chronosequence. The species list for this study comprised of mid-value and bycatch families that are more common in the fisheries (e.g. Scarinae)[61] and contribute most to fish biodiversity. They make up the bulk of the abundance and biomass. Thus, the functional importance of the trait shifts observed in this study should be interpreted through the lens of the mass-ratio hypothesis—whereby it is the more abundant traits or species that have the greatest functional impact[62]. For example, for diet, the most abundant trait class (planktivores) became even more abundant with protection. Where the abundance of mainly small planktivores adds up to produce large proportions of the biomass, systems can be said to be "middle-driven". These middle-driven trophic pyramids have been found to exist at high levels of biomass, regardless of protection regime[63,64]. Planktivores provide important pelagic subsidies to a reef, increasing overall productivity and playing a key role in nutrient cycling[65]. Many planktivores are also dependent on reef structure for recruitment and predator avoidance[66,67]. Their abundances have been shown to decline with coral bleaching and the loss of structural complexity and increase with protection from fishing[68,69]. Some planktivorous families, such as the Pomacentridae, are considered "bycatch" in Kenyan fisheries and are not specifically targeted. The increase in the proportional abundance of planktivores could therefore primarily be linked to the recovering habitat within protected areas[70,71].

Evolutionarily, shifts to planktivory are linked to increasing schooling behaviour[72]. Our analysis showed that these trait categories, which tend to cluster, were both increasing over time with protection. An increase in the abundance of fish exhibiting gregarious behaviour has implications for functional processes related to how much fish consume. For example, Michael et al.[73] found that both herbivory rates and the amount of algae consumed by three studied species were higher when individuals fed in monospecific groups. Social aggregations should theoretically lead to more protection, and therefore the increased ability to forage[74]. However, resource competition among those in the group can also lead to less overall consumption. It has been demonstrated that for a planktivorous species, this trade-off between protection and competition is mediated by the availability of resources[75].

Competition within groups also affects life history characteristics dependent on environmental stochasticity, so that individuals in larger groups tend to have slower growth rates[76]. Interestingly, however, we did not see a significant positive response to protection in the length at maturity trait. This may be due to the interspecific approach taken in the analysis that doesn't account for changes in the phenotypic plasticity of individuals and evolutionary adaptations inherited in specific populations over time[77,78]. Again, the patterns here may also be a function of the limited space of the closures that could exclude long-lived and late-reproducing species. These closures should not be viewed as undisturbed systems but rather islands within fished seascapes[79]. Nevertheless, given the interspecific approach, we would expect that considering the overall PCoA abundance trends towards smaller or moderate-sized species, these species would have smaller lengths at maturity. This is because length at maturity, like many traits, is highly correlated with size[80].

The trait-based analyses presented in this paper were abundance-weighted. This provides a species-level approach to compliment previous family-level studies weighted by biomass investigating the Kenyan marine park system[29,81]. If intraspecific or species-level body sizes were available to evaluate biomass-weighted trends, it is possible that different patterns could emerge, with implications for ecosystem functioning. For example, families such as Labridae (Scarinae) and Acanthuridae have been shown to dominate the biomass of marine reserves in Kenya over time with protection from fishing[28]. These families consist of herbivorous and large-bodied fish, and their functional impact has been demonstrated in experiments[82]. Abundance-based metrics may not reflect the dominance of these groups as much as biomass-based metrics. Therefore, it is necessary to interpret these results as a component of a multi-faceted approach to understanding ecosystem processes as a function of both abundance and biomass. Furthermore, directly measuring ecosystem processes (e.g. herbivory, predation, etc.) would also provide a fuller picture[9].

Increases in fish biomass, abundance, and the proportion of functionally important traits over time with high compliance protection is expected to represent recovery from fishing pressure[83,84]. However, this recovery is taking place in the context of a changing climate and a dynamic ocean[26,85]. While we see an increase in the biomass and abundance of fish in Kenya's marine reserves, species and traits have not necessarily recovered, in that they have not returned to historic compositional "baselines"[86]. Incorporating the concept of a novel ecosystem into conservation moves away from the de facto goal of restoration to ecological baselines[17]. In this paper, we demonstrate how fish traits respond over time to the establishment of marine reserves. The resulting community after 44 years of protection appears to still be changing and not approaching a plateau. While some traits have become more dominant over time (e.g., 7–15 cm, planktivores), other traits (e.g., high gregariousness, high reef association) have started to surpass those that were previously dominant. This highlights the importance of interpreting patterns within the context in which marine reserves are situated, the dynamic nature of recovery, and the potential for novel trait configurations to shape the provision of altered ecosystem functions and services[87].

Data availability

The data and code used for this study will be made available on https://github.com/Jeneen/trait_time_series.

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Author contributions

J.H.H. did the data curation, data analysis, and wrote the first draft of the manuscript. T.M. collected the field data. N.G. and T.M. helped to conceive the project, provided supervision, data analysis suggestions, and editorial comments. All authors contributed to the article and approved the submitted version.

Competing interests

The authors declare no competing interests.

Additional information

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