Parrotfish distribution and feeding behaviour in a fringing reef of Barbados

Jihane Benbahtane
Department of Biology
McGill University, Montreal
Submitted April 2021

A thesis submitted to McGill University in partial fulfillment of the requirements of the degree of Master of Science in Biology

Table of contents

Abstract

Coral reefs are among the most ecologically diverse and productive ecosystems in the world, but they are unfortunately subjected to a vast range of environmental disturbances and are declining globally. A better understanding of the ecological mechanisms that promote reef health and recovery is thus of prime importance. Reef ecologists are particularly interested in parrotfishes as a herbivorous group. Parrotfish species have been identified as keystone herbivores whose grazing action effectively removes macroalgae that compete for space with coral recruits, and can thus help maintain benthic equilibrium and prevent coral communities from shifting to macroalgae dominated states. Decades of research have demonstrated that parrotfish species are likely to have context-dependent grazing properties that change as a function of reef ecological dynamics. In this thesis, I examine the processes driving the spatial distribution of species in a parrotfish community, and investigate the factors influencing their feeding behaviour. In Chapter 1, I review the literature on parrotfishes to provide an overview of the different mechanisms underlying parrotfish distribution and feeding behaviour identified by previous research. In Chapter 2, I present the results of an empirical study I conducted on a parrotfish community across a fringing reef in Barbados. I first determined that there is little diversity in the benthic composition and that the reef is dominated by filamentous algae. I tested the hypothesis that species identity, ontogeny, and size influence feeding behaviour in five co-existing parrotfish species. I found that ontogeny, size, and species identity significantly influence feeding rate, but conclude that the respective effects of ontogeny and size cannot be teased apart. I also found that there was overall not much variation in food electivity between species and through ontogeny, as turf algae dominated the diet of all species and phases, most likely due to the lack of diversity in the benthos. I also tested the hypothesis that the spatial pattern of species abundance was related to the abiotic and biotic properties of the reef, and that this relation was modulated by feeding mode and body size. I found significant associations between species abundance and the reef's environmental structure, but that associations were only marginally mediated by feeding mode and body size. Additionally, I show that the choice of survey method has an impact on species abundance estimates for parrotfish species and discuss the importance of using multiple survey methods to account for method-specific biases that can alter results of studies on parrotfish ecological dynamics. In coral reef ecosystems, understanding the mechanisms of parrotfish herbivory is paramount since they can play a significant role in maintaining reef health. The research I present in this thesis highlights the

importance of studying how these mechanisms can be dependent on the ecological context of the study system.

Résumé

Les récifs coralliens font partie des écosystèmes les plus diversifiés et les plus productifs du monde sur le plan écologique, mais ils sont malheureusement soumis à une vaste gamme de perturbations environnementales et sont en déclin dans tous les océans à l'échelle globale. Une meilleure compréhension des mécanismes écologiques qui favorisent la santé et le rétablissement des récifs est donc primordiale. Les spécialistes s'intéressent tout particulièrement aux poissons-perroquets en tant que groupe herbivore. Les espèces de poissons-perroquets ont été identifiées comme des herbivores clés dont l'action de pâturage élimine efficacement les macroalgues qui rivalisent pour l'espace avec les recrues de corail. Les poissons-perroquets peuvent ainsi aider à maintenir l'équilibre benthique et empêcher les communautés coralliennes de passer à un état dominé par les macroalgues. Des décennies de recherche ont démontré que les espèces de poissons-perroquets sont susceptibles d'avoir des propriétés de pâturage qui changent en fonction de la dynamique écologique des récifs. Dans cette thèse, j'examine les processus déterminant la distribution spatiale des communautés de poissons-perroquets et j'étudie les facteurs qui influencent leur comportement alimentaire. Dans le Chapitre 1, je passe en revue la littérature sur les poissons-perroquets pour donner un aperçu des différents mécanismes sous-jacents à la distribution et au comportement alimentaire des poissons-perroquets identifiés par des recherches antérieures. Dans le Chapitre 2, je présente les résultats d'une étude empirique que j'ai conduite sur une communauté de poissons-perroquets à travers un récif frangeant de la Barbade. Je détermine d'abord qu'il y a peu de diversité dans la composition benthique et que le récif est dominé par les algues filamenteuses. Dans ce chapitre, je teste l'hypothèse que l'identité des espèces, l'ontogénie et la taille corporelle de cinq espèces de poissons-perroquets influencent le comportement alimentaire. J'observe que l'ontogénie, la taille et l'identité des espèces influencent de façon significative le taux d'alimentation, mais je conclus que les effets respectifs de l'ontogénie et de la taille ne peuvent pas être séparés. J'ai également constaté qu'il n'y avait globalement pas beaucoup de variation dans l'électivité alimentaire des espèces et à travers l'ontogénie, car les algues filamenteuses dominaient le régime alimentaire de toutes les espèces et toutes les phases, probablement en raison de la faible diversité du benthos. Je teste également l'hypothèse que la distribution spatiale d'abondance des espèces de poissons-perroquets est liée aux propriétés physiques et biologiques du récif, et que cette relation est modulée par le mode alimentaire et la taille corporelle. J'observe qu'il existe des associations significatives entre l'abondance des espèces et la structure environnementale du récif, mais que ces associations sont marginalement

modulées par le mode alimentaire et la taille corporelle. Finalement, je montre que le choix de la méthode de recensement a un impact sur les estimations de l'abondance des espèces de poissons-perroquets, et discute de l'importance d'utiliser plusieurs méthodes de recensement pour tenir compte des biais spécifiques à chaque méthode qui peuvent modifier les résultats des études sur la dynamique écologique des poissons-perroquets. Dans les écosystèmes des récifs coralliens, il est essentiel de mieux comprendre les mécanismes d’herbivorie des poissons-perroquets, puisqu’ils peuvent jouer un rôle important dans le maintien de la santé des récifs. La recherche que je présente dans cette thèse souligne l'importance d'étudier comment ces mécanismes peuvent dépendre du contexte écologique du système d'étude.

Acknowledgements

I would like to thank my supervisor, Dr. Virginie Millien, for helping me through this endeavour. I have learned and grown a lot throughout this project, and I owe a lot of it to her guidance and support. This has been an amazing experience, and I will always be grateful for being able to start my academic career under her care. I would also like to thank my co-supervisor, Dr. Henri Vallès, for sharing his wealth of knowledge on coral reef research and offering his indispensable support. Designing and conducting this study would simply not have been possible without him. My sincerest thanks to Rachel Rolland, my research assistant, who assisted in data collection, showed genuine interest and dedication in this work, and never complained despite the demanding requirements of this project. Thank you to my committee members, Dr. Frédéric Guichard, who offered valuable insight into the Bellairs reef system, and Dr. Brian Leung, who provided valuable insight for statistical analyses. Thank you also to the Millien lab for the much needed academic and moral support, and to Dr. Vallès's students at UWI Cavehill who showed me incredible hospitality. A special mention goes to the people at the Bellairs Research Institute, who took care of me, helped me with everything I needed for my research, and left me wanting to come back to Barbados to carry-on researching coral reefs in Holetown. Thank you to the Biodiversity, Ecosystem Services and Sustainability program for providing funding, allowing me to expand my research interests, and providing opportunities to collaborate with amazing scientists.

I also have to thank my family and friends, who always made me feel like I could accomplish anything and let me lean on their help at every step. To my parents and sister, thank you for always lifting me up and pushing me to give my 100% no matter what. No one accomplishes anything alone. This project is the result of years of labour on my part, but also of years of support, encouragement, and unconditional love from my loved ones. Last but not least, my niece, simply for being born during this stage of my life and providing comfort and warmth when I needed it the most.

Contribution of authors

Thesis format

This thesis comprises two main chapters: a literature review (Chapter 1), and the results of analyses of data I collected on my study system (Chapter 2) and on which I am the lead author**.**

Chapter 1 - The effect of parrotfish communities herbivory on coral reefs: A literature review

Jihane Benbahtane reviewed the literature and wrote the chapter. Dr. Virginie Millien and Dr. Henri Vallès reviewed the manuscript.

Chapter 2 - Spatial patterns of distribution and feeding behaviour in a parrotfish community in a Barbados reef

Jihane Benbahtane designed the observational study in collaboration with Dr. Henri Vallès, collected and analyzed the data, and wrote the manuscript. Dr. Virginie Millien and Dr. Henri Vallès contributed to the data analysis, wrote many of the R scripts used for the analyses, reviewed the manuscript, and supervised the project. Dr. Virginie Millien provided funding for the research.

General introduction

Coral reefs are considered one of the most important and diverse ecosystems, as they host an estimated 25% of all marine life, including over 4,000 species of fish, which depend on them as a habitat (Burke et al. 2011, Santos et al. 2014). Millions of people across the world rely on this ecosystem for food, income and coastal protection (Smith 1978, Done et al. 1996, Moberg and Folke 1999). Coral reefs are found in all oceans, both in deep and shallow waters, but stony reef-building corals are only found in shallow and clear waters in tropical and sub-tropical climates, which range within a belt 30 degrees north to 30 degrees south of the equator.

Across the world, however, the health of coral reefs is degrading at an alarming rate (Wilkinson 2000). Coral reefs are subjected to major stressors such as bleaching events, deteriorating water quality and overfishing, that lead to phase-shift reversals from coral-dominated reefs to algal-dominated ones (Hughes 1994, Arnold et al. 2010). Coral reefs in the Caribbean are of particular concern since trends of rapidly increasing rates of coral cover loss in favour of macroalgae have been observed for decades (Smith et al. 2018). Many factors have been attributed to these phase shifts, notably increases in nutrient concentrations, disease and bleaching events (Bellwood et al. 2006, Burkepile et al. 2013). In some reefs, algae overgrowth has also been attributed to declines in herbivorous species (Adam et al. 2015a). Herbivory can reduce and limit the abundance of algae species in coral reefs, thus decreasing the competition for space between algae and coral species (Ogden and Lobel 1978). For instance, mass mortality in the 1980s of the black sea urchin, *Diadema antillarum*, has been linked to the widespread algae overgrowth in the Caribbean since its grazing function has been found to be significant in reducing competition with corals (Carpenter 1988).

Parrotfish species have been identified as keystone herbivores in coral reefs, since their grazing action effectively removes macroalgae that compete for space with coral recruits (Adam et al. 2018). Reef ecologists are particularly interested in parrotfish species due to their ubiquity in reefs across the world as well as their morphologically unique feeding attributes, which allow these fishes to bite through reef carbonates and grind them into sand particles (Hoey and Bonaldo 2018), thus making them important bioeroders (Adam et al. 2015a). While the importance of parrotfish in promoting coral recruitment through their herbivory has generally been accepted, their involvement in promoting reef health and recovery has often been challenged (Russ et al. 2015, Russ et al. 2020). Indeed, relief of competition from algae on coral by herbivores as a facilitative process is considered a key paradigm in the study of reef ecology (Russ et al. 2015), but mechanisms driving the potential for herbivory to function as a facilitative process for coral recovery are still being uncovered. Further research is required to elucidate the intricate dynamics which influence the process of coral recovery and the role that parrotfishes play in it.

Thesis objectives

Given the importance of coral reefs for marine animals and the valuable resources they provide to people worldwide (Moberg and Folke 1999, Pauly et al. 2002, Burke et al. 2011, Santos et al. 2014), the alarming declines of coral reef communities are concerning. To better inform our conservation efforts in restoring degraded reefs, it is critical to understand the ecological mechanisms that regulate reef ecosystem dynamics. In this thesis, I focus on parrotfishes, a widespread keystone herbivore, and investigate their patterns of herbivory and distribution across a fringing reef of Barbados to further our understanding of the ecological mechanisms that mediate the interactions between parrotfishes and their habitat.

In the first chapter, I review the role that herbivory holds in coral reef ecosystems and subsequently focus on how parrotfishes fulfill that function. I then review the multiple factors that have been identified as drivers of parrotfish ecological function and conclude with an evaluation of the importance of research focused on parrotfish herbivory.

In the second chapter of this thesis, I present a case study on a parrotfish community in a fringing reef of Barbados. I studied the community structure, distribution and feeding behaviour of five species of parrotfishes. I show that feeding rate varied across species and with size and ontogeny, and that diet did not vary much within the parrotfish community. I collected data on reef benthic composition and topography to establish the relationship between patterns of parrotfish distribution and reef environmental structure. I also investigated how species traits mediate that relationship. I show that there were significant associations between species abundance and the environment, but that these associations were only marginally mediated by feeding mode and size. Additionally, I discuss the importance of considering the potential biases of different abundance survey methods when collecting species abundance data for studies of parrotfish ecology. I conclude this chapter by discussing the importance of the ecological context in determining whether parrotfish herbivory leads to top-down control of algae abundance in favour of coral communities.

Chapter 1 – The effect of parrotfish communities herbivory on coral reefs: A literature review

The role of herbivory in reef health and recovery

Coral reefs across the world have been observed to undergo phase-shifts from coral-dominated reefs to algae-dominated ones (Hughes 1994, Arnold et al. 2010). Although a natural phenomenon, the full recovery of coral reefs from these phase shifts is dependent on the ability of coral species to compete with algae species (Nyström et al. 2008). In several reefs, algae overgrowth has been linked to declines in herbivorous species (Adam et al. 2015a). Indeed, removal of herbivores from reef systems can result in substantial increase in macroalgae and decrease in coral cover (Miller 1998). Herbivory can not only reduce and limit the abundance of algae species in coral reefs (Ogden and Lobel 1978), but it can also increase the rate of recovery of coral reefs from phase shifts that occur after a major disturbance (Adam et al. 2015b).

Multiple communities of herbivorous organisms reside in coral reefs. *Diadema antillarum*, a large, highly mobile sea urchin, was once the most abundant herbivore on Caribbean reefs. In the early 1980s, populations across the Atlantic suddenly started dying off rapidly. Coral reefs began to experience excessive growth of macroalgae on the benthos, which killed countless coral colonies (Carpenter 1988, Hughes 1994). This die-off event of one of the most proficient herbivores in coral reef systems, although tragic, was meaningful in showcasing the potential positive effect that herbivory has on maintaining the ecological equilibrium of coral reefs (Lessios 2016).

Marine protected areas (hereafter MPAs) are one of the more important widespread conservation tools that allow the protection of marine organisms (Kelleher and Kenchington 1992) and represent an ideal study-system to test ecological questions and to quantify trophic links between organisms. Indeed, they emulate classic removal experiments (which are useful to identify presence of positive interactions) within natural settings and at larger scales through fishing regulations. MPAs have been extensively studied with the intent to assess whether their establishment generates a positive impact on marine ecosystems. One of the ways by which they do so is through increase in herbivore density and biomass. By protecting herbivorous communities, MPAs may thus have indirect positive effects on coral health by promoting macroalgae removal and resilience to phase shifts (McClanahan 2008).

Nevertheless, research on the efficacy of MPAs suggests that these dynamics are more complex than expected (Bozec et al. 2013, Graham et al. 2013). Therefore, it is reasonable to ask whether the removal of the disturbance of overfishing of herbivores through MPAs is sufficient to promote coral reef recovery and resilience to phase shifts. It is important to consider that MPAs, although having the potential to increase the density of herbivores in the reefs (Mumby and Harborne 2010, Humphries et al. 2014), are not often assessed in terms of their impact on effective grazing rates. In fact, one could predict that an increase in herbivore density should lead to increased overall herbivory in the ecosystem. However, some studies suggest that an increase in herbivore density does not always result in this expected development (Ferguson et al. 2017, McClanahan et al. 2011, Kramer and Heck 2007).

We can then ask the important and overlooked question: do MPAs increase grazing rates in herbivore communities? A search through the literature for studies that compared herbivory rates outside and inside of protected areas indicates that the efficacy of MPAs in promoting this ecological function in the reef is debatable (Table 1.1). Only three out of the six studies included in this review reported that MPAs had an overall significant positive effect on herbivory. In most cases, the positive effect of protection from fishing only occurred in certain specific contexts. For instance, Yabsley et al. (2016) reported that the effect of herbivore protection increased community-wide consumption of turf algae but not macroalgae, and that connectivity of the system to mangroves regulated the level of herbivory. Thus, results for these types of studies can greatly vary when investigating other biotic factors such as species identity and system connectivity. Furthermore, even for cases where a significant increase in grazing rates was reported, algal and coral cover were not consistently affected by protection from fishing and increase in herbivory (Table 1.1). We must consider that such positive effects are mostly indirect and mediated through interactions between multiple biotic and abiotic factors (Stachowicz 2001). Ecological context is thus likely of high importance in mediating the effect of herbivory on coral reef health.

The importance of grazers in maintaining the integrity of coral reefs has indeed been highly debated (Russ et al. 2015). Grazers such as parrotfishes are likely to have context-dependent grazing properties, which change as a function of reef ecological dynamics (Burkepile 2012). MPAs provide a compelling case study which showcases the ambiguity surrounding the reputation given to herbivorous fish as a key factor in phase-shift reversals. Data on parrotfish herbivory collected in MPAs or otherwise generally suggests that there is still much to learn about parrotfish communities.

Parrotfish: a keystone herbivore

Parrotfish are a very diverse group of herbivorous fish which display intricate coloration patterns and are equipped with fused beak-like jaws (Choat and Robertson 1975). Most species are protogynous hermaphrodites, allowing for fascinating patterns of female to male sex changes to occur within parrotfish populations (Choat and Robertson 1975). They can be observed on coral reefs all over the world, where they graze on various types of food such as algae, coral and sponge. Parrotfish species display multiple innovative morphological features allowing them to perform particular and significant ecological functions such as bioerosion and the removal of algae species in reefs (Wainwright and Price 2018, Smith et al. 2018). Their feeding activity is considered one of the most impactful ecological processes within reef ecosystems, as they can influence the benthic structure and composition in a way unparalleled by any other group of fish (Choat 1991, Mumby 2006, Wainwright and Price 2018).

Given that parrotfish are often the dominant herbivorous fishes across many reefs, they have been widely studied by ecologists, particularly because of their potential to regulate algae-coral dynamics (Adam et al. 2018). Indeed, there are many studies that focus on that specific ecological function, ranging from descriptive articles on anatomical features such as jaw morphology, to detailed reports of their feeding habits (Hoey and Bonaldo 2018). This extensive collection of literature allowed ecologists to divide parrotfish species into functionally defined clusters based on anatomical observations, diet analyses using jaw morphology, feeding observations, or gut content analysis (Smith et al. 2018). Excavators, scrapers and browsers are the three most commonly used feeding categories. The first one describes species of which the bite excavate substrates out in a short and powerful bout, with a general preference for short turf algae and crustose coralline algae, and includes species like *Scarus coelestinus* and *Sparisoma viride* (Adam et al. 2018, Bellwood and Choat 1990). The second category contains species with relatively weaker and more frequent bites that tend to eat short turf algae and endolithic algae, such as *Scarus vetula* and *Scarus taeniopterus* (Bellwood and Choat 1990). The third category describes species with soft bites which are used to tear into fleshy macroalgae and includes *Sparisoma aurofrenatum* and *Sparisoma rubripinne* (Adam et al. 2018). Yet, parrotfish are considered voracious creatures across all feeding categories, and their propensity to ingest large quantities of algae and other substrates in a single day branded this taxon as having a potential to promote reef health (Hoey and Bonaldo 2018). Many researchers have attributed the recovery of coral reefs from macroalgal to coral dominance to increased parrotfish abundance due to their protection from overfishing (Adam et al. 2015b). Nonetheless, the importance of parrotfish and other herbivores in maintaining the integrity of coral reefs has been highly debated (Russ et al. 2015, Bruno et al. 2019).

However, parrotfish are subjected to intense selective fishing in certain regions, and this pressure can interfere with herbivory mediated positive interactions on coral growth and persistence. These selective fishing practices, such as spear-fishing, target the more conspicuous and larger individuals (Russ 2002), which becomes an issue considering that functions of bioerosion and removal of macroalgae can only be fulfilled by larger individuals (Bellwood et al. 2012). For these reasons, parrotfish are widely regarded as keystone herbivores that require particular attention and for which the ecological function should be extensively studied.

The ecological function of parrotfishes as herbivores

Traditionally, studies on parrotfish herbivory have focused on the consequences of feeding in their reef ecosystem rather than on the factors driving their feeding behaviour, which has contributed to gaps in knowledge of parrotfish feeding modes. This lack of understanding of parrotfish ecology might be attributed to persistent use of stereotypical classifications of parrotfish species into fixed functional roles (excavators, scrapers, or browsers), with determined feeding preferences for different food resources. However, these classifications have been found to be more flexible than previously thought and can change with local ecological contexts (Smith et al. 2018). Indeed, there is increasing evidence pointing to more complex diets of parrotfishes than previously thought (Clements and Choat 2018). Recent investigations into parrotfish diets have shed light on the nutritional properties of the consumed substrates of these fishes, suggesting that a clearer understanding of the factors that drive their patterns of resource consumption is required (Clements and Choat 2018). We also need to consider that the composition of parrotfish communities will be different from one reef to the next, due to eco-evolutionary processes, or due to contemporary ongoing effects such as selective fishing. In general, parrotfish species are likely to have context-dependent grazing properties, which change as a function of reef ecological dynamics (Burkepile 2012). Therefore, the notion that the presence of herbivores such as parrotfish alone can help improve reef health through their grazing properties needs to be revisited. Indeed, understanding the variations in ecological function that individuals of the parrotfish guild can hold, depending on their species identity, ontogenetic phase and size is an important first step into investigating the relationship between parrotfishes and reef health. Moreover, beyond factors intrinsic to parrotfish communities, there are other variables to consider when trying to construct a comprehensive picture of the relationship between parrotfishes and coral reef health. For instance, structural and benthic complexity of the reef are likely to play a role in influencing these dynamics (Bozec et al. 2013). There is thus a need to review the functional role of parrotfishes in varying ecological contexts that are likely to alter their feeding patterns (Adam et al. 2015a).

Context dependence of parrotfish herbivory

Early work on the ecological role of herbivores in the reef was centered around identification and classification of key herbivores. The initial predictions for the categorization of fish into distinct functional groups typically revolved around using phylogenetic information to determine these groups. For instance, one might predict that feeding preference and feeding rate would depend on physiological and morphological characteristics that are conserved within genera (Burkepile and Hay 2008). For parrotfishes in the Caribbean specifically, coral reef research contributed to the generalization that species in the *Sparisoma* genus mainly browse on macroalgae, while those in the *Scarus* genus primarily target turf algae (Randall 1967, Lewis 1985, McAfee and Morgan 1996).

For a certain time, these pioneering studies became the basis of how we consider parrotfish communities to be constructed. However, some of the early studies on the subject, such as McAfee and Morgan (1996), found slight variations in diet preference within the *Sparisoma* genera and hinted at a possibly more complex narrative. In the last decade or so, much of the research effort on identification of functional roles has been conducted with the prediction that there could be complementarity in functional roles at the species-level. For example, Mantyka and Bellwood (2007) used multiple-choice algal assays and remote stationary underwater digital video cameras to quantify the feeding preference of 6 species of herbivores. They found that there was a lesser amount of redundancy within functional groups of herbivores defined at the family or genus level than previously reported in the literature. Burkepile and Hay (2011) also identified patterns of complementarity as well as redundancy in ecological function between and within genera, indicating that species identity might be relevant when understanding functional roles of individual herbivores. Concurrently, accumulating research found evidence for context dependency for interspecific differences in parrotfish herbivory. Indeed, patterns of interspecific differences in diet selection seems to vary from one location to another. Cardoso et al. (2009) observed that all of the seven Caribbean species included in their study primarily consumed macroalgae, whereas previous studies conducted in different locations across the Caribbean reported that many of the same species have an aversion to macroalgae (e.g. Bruggeman et al. 1994, McAfee and Morgan 1996).

Even more rare in the literature are studies which consider intraspecific differences in herbivory within parrotfishes. Robertson and Warner (1978), and several other studies (e.g. Warner and Downs 1977, Choat and Robertson 1975) offer a detailed analysis of patterns in morphology across ontogenetic phases and discuss the possible implications of such intricate sexual transformations in parrotfishes. Despite the amassed knowledge on these processes, it is more difficult to find research that appropriately studies the potential intraspecific differences in feeding behaviour that could result from transitioning through life stages. The documented morphological and physiological differences between parrotfish life stages indicate that studying ontogenetic phases as a predictor of feeding behaviour could increase our understanding of context dependence of parrotfish herbivory. In an extensive examination of juvenile parrotfishes, Feitosa and Ferreira (2015) found that habitat use and feeding rates did not remain constant throughout the earlier developmental stages, and that this intraspecific variation also differed between species. Smith et al. (2018) observed feeding behaviour of parrotfishes in the Florida Keys to investigate variation based on ontogeny, benthic composition and parrotfish biomass. They found that preference for turf algae and fleshy algae differed significantly between ontogenetic groups for all identified functional groups in their study reefs. The aforementioned studies reveal a potentially significant knowledge gap in our understanding of how parrotfish ecological function works, yet studies on intraspecific variation in foraging behaviour remain still scarce in the literature on parrotfish herbivory.

Moreover, species identity and ontogenetic phase are not the only biological properties of parrotfishes documented as being of importance in the determination of their ecological function as herbivores in the reef. Studies which examine size as a predictor have predictably found that larger fishes remove a greater volume of substratum than smaller individuals (e.g. Bonaldo and Bellwood 2008, Bellwood et al. 2012, Lokrantz et al. 2008). However, most of these studies have typically focused on single species, or measured proxy properties of parrotfishes such as size of grazing scars to infer consumption rates. Very few studies use a multi-species approach to control for the effect of species identity, but those that did have yielded similar results which link larger parrotfish size to greater rates of substrate removal. Ong and Holland (2010) studied bioerosion rates and consumption of the reef's carbonate production in two species of parrotfishes with differing feeding modes, *Chlorurus perspicillatus* which is considered to be an excavator, and *Scarus rubroviolaceus* which is considered to be a grazer. They found that feeding mode did not affect consumption rate, and that size rather was a determinant factor in bioerosion capacity of individuals. A comparative analysis of parrotfish foraging behaviour conducted by Adam et al. (2018) found supporting evidence that fish size was a key factor in the magnitude of bioerosion impact for Caribbean parrotfishes as well. Jayewardene (2009) also determined that the degree to which parrotfish performed their algae removal function was also dependent on size, as they found that algal reduction rates were up to 30% higher for parrotfishes larger than 25 cm. Cumulatively, the available body of literature on the role of size in parrotfish ecological function indicates that individual fish size is a useful predictor of substrate consumption rate.

When gathered, research on the ecological function of parrotfishes as grazers provides valuable insight on the factors that may be determinant in mediating their feeding behaviour. Species identity, ontogenetic phase and size have been repeatedly identified as mediators of parrotfish herbivory. Therefore, future investigations into the impact of parrotfish grazing on reefs need to consider the variation in structure of parrotfish communities across reefs.

Reef and parrotfish ecological dynamics

We have seen that properties intrinsic to parrotfish communities can influence their feeding behaviour, however, parrotfishes are part of intricate ecological dynamics within the reef that can regulate their herbivory at a spatial level. There is in fact potential for several other factors such as habitat structure and benthic composition to introduce variability in the way parrotfish ecological function operates. Some studies have detected spatial or temporal variation in feeding behaviour (Bennett and Bellwood 2011, Lefèvre and Bellwood 2011), but relatively few studies have investigated the specific environmental factors this variation might be attributed to.

Ecosystem engineers often promote coexistence and biological diversity by providing various resources and structural refuge (Stachowicz 2001, Bruno and Bertness 2001). Corals are well-known ecosystem engineers that build intricate habitats for many organisms, and thus can generate mutually facilitative interactions which benefit both corals and their associated organisms (Bozec et al. 2013). In the case of parrotfish communities, high coral cover acts as a refuge from predators and a considerable food source (Harborne et al. 2012). It is also established that parrotfishes can reduce and limit the abundance of algae species in coral reefs through herbivory (Ogden and Lobel 1978), but can also drive the recovery of coral reefs from phase shifts which occur after a major disturbance (Adam et al. 2015b). This poses as a classic example of facilitation through refuge from competition under stressful environments, since herbivores decrease the interspecific competition for space that macroalgae exerts on coral species. Within parrotfish research, however, this facilitative interaction is often studied in a uni-directional and linear fashion, where the main focus of studies is the impact that the ecological function of parrotfish as grazers has on the resilience of coral species to being overtaken by algal species. However, emerging studies show that the structural quality and complexity of the habitat that corals provide to parrotfishes can greatly influence their abundance and community dynamics (Harborne et al. 2012). For instance, Howard et al. (2009) found that the abundance of parrotfishes was positively correlated with features of the habitat such as rugosity, substrate diversity and percent live coral cover. While studying a reef in Australia, Verges et al. (2012) found that the biomass of herbivorous fishes, as well as rates of herbivory varied significantly across reef habitats that differed in structural complexity.

A study conducted by Bozec et al. (2013) showed that the intensity of parrotfish grazing was highly dependent on the structural complexity of the reef, identifying a positive feedback between coral cover and herbivory. This finding corroborates the hypothesis that such positive interactions can be nested in and dependent on the positive effect of habitat forming species such as corals (Jones et al. 1997). The study also found that whether this structural-complexity/grazing relationship was asymptotic or linear depended on parrotfish community assembly and fishing regime (whether all parrotfishes were targeted or only one specific genera), and that the probability of phase shifts to macroalgae was significantly lower for the asymptotic model. Their model is a great example of how incorporation of multiple variables (the impact of fishing on herbivore diversity and structural feedback of corals) can help inform whether coral reef facilitation is likely to occur through protection of herbivores. Indeed, research on the ecological function of parrotfishes has to integrate data on the spatial structure and benthic community of the reef to really understand the ecological dynamics between parrotfishes and the habitat that shelters them.

Future directions

All things considered, there is a marked need to better understand the capacity that parrotfish community structure and reef structure have in mediating feeding behaviour of parrotfishes, as well as their impact on the resilience of coral reef communities to phase-shifts. We need to establish predictive and testable relationships between multiple biotic and abiotic factors and the ecological function of parrotfishes. Ideally, this area of research needs a robust theoretical framework that explains what the optimal conditions for herbivores to perform their ecological function are.

From there, researchers should explore building models that compute the multiple factors which alter the ecological function of herbivory and its effect on coral recovery to predict the outcome of management strategies. These models should consider interactions between parrotfish feeding behaviour, species identity, ontogeny and body size, as well as environmental stressors such as ocean warming, overfishing and nutrient run-off. Researchers should also take advantage of study systems such as MPAs to design straightforward studies that evaluate the role of these stressors in hindering any positive effect herbivory has on reef health, with overfishing being the best suited to be tested in such ecological settings. The potential of multivariate model frameworks in identifying these ecological patterns should be researched further to better understand the context dependence of parrotfish ecological dynamics and their role as promoters of reef health and recovery.

Linking Statement

Coral reefs provide critical and diverse ecosystem services to small island developing states like Barbados (Burke and Maidens 2004, Gill et al. 2019). With the increased demands for marine food resources, coral reef fisheries and other small-scale fisheries constitute a major economic support for coastal communities in Barbados, but also around the world (Gill et al. 2019). In the Caribbean, recent interest to implement policies that will reduce their reliance on the importation of food resources could have potential ramifications for the local fishing industry (McConney et al. 2017). Parrotfish fishing has been banned in some Caribbean countries such as Belize (ICRI 2013). On one hand, parrotfishes provide an important source of livelihood for many communities, but on the other they also provide an important ecological function that has been linked to reef health and recovery. It is thus essential to understand the mechanisms that drive parrotfish ecological function, so coral reef management and restrictions on fishing can be adequately implemented. Consequently, contributing to advancements in research on reef-parrotfish ecological dynamics is paramount.

In the first chapter of this thesis, I discussed the current debate surrounding the potential for reef herbivores, focussing on parrotfish species, to mitigate phase-shifts from coral dominated reefs to algae dominated ones. I reviewed studies that addressed this debate and contributed to the body of evidence for either side of this debate. I revisited the established and abundant research on the biological and ecological properties of parrotfishes as herbivores on coral reefs. I then considered the aspects of parrotfish ecology that are needed to be considered when investigating and defining the herbivorous ecological function of parrotfish communities, which appears to be highly context-dependent. Finally, the importance of parrotfishes for reef ecosystems and coastal communities was also discussed to contextualize the importance of research into parrotfish ecological function as a channel for reef conservation.

As coral reefs keep declining across all oceans, debates on the best management strategies to promote the recovery of reefs and to encourage coral recruitment are ongoing and remain unresolved (Arnold et al. 2010). The establishment of many Marine Protected Areas (MPAs) relies on the idea that a ban on or reduction of fishing will promote coral reef health through protection of herbivore diversity and density (McClanahan 2008). Some studies suggest focusing efforts on parrotfish conservation to help restore coral reefs, however, too little is known about the effect of varying ecological contexts on the parrotfish species' functional role as herbivores (Adam et al. 2015a). It is important to consider that the generalization that increase in herbivore density will positively regulate the ecological function of herbivores is simplistic and might overlook key mechanisms behind that process.

To better inform parrotfish and reef management, it is thus critical to understand what drives and influences patterns of distribution and herbivory in parrotfish communities. In chapter two, I present the results of an observational study on a parrotfish community in a protected coastal reef of Barbados. Our objective was to improve the understanding of how parrotfish biology, community structure, and reef benthic composition and topography determined species distribution across the reef as well as their feeding behaviour. To collect data relevant to this objective, we used a spatially explicit study design to perform feeding observations, species abundance surveys and assessments of the reef's benthic and topographical composition. Overall, the benthos across the reef was largely dominated by turf algae. We also found that diet did not vary much across species, or ontogeny, as all species fed preferably on turf algae, the most available and dominant food category in our system. However, feeding rates varied across species and with size. Finally, we found a significant association between environmental variables across the reef and species abundance that was marginally mediated by their feeding mode and body size. Together, these results speak to the context dependence of parrotfish herbivory.

Chapter 2 - Spatial patterns of distribution and feeding behaviour in a parrotfish community in a Barbados reef

Introduction

Coral reefs are one of the most important ecosystems in our oceans, as they represent one of the most ecologically diverse systems and provide a significant source of income and livelihood for many coastal communities across the world. They host an estimated 25% of all marine macro-organisms and are home to over 4,000 species of fishes (Santos et al. 2014, Burke et al. 2011). However, they are undergoing a global crisis of extinction due to their vulnerability to large-scale disturbances such as ocean acidification, nutrient run-off and overfishing. These stressors often lead coral reefs to shift from a coral-dominated state to an algae-dominated state (Hughes 1994). These rapid and dramatic changes in benthic cover are termed phase-shifts, and occur as a result of the cumulative detrimental effect of multiple abiotic and biotic stressors (Adam et al. 2015a). In the Caribbean, this phenomenon started to occur more frequently in the 1980s, with the global and gradual increase in severity of environmental degradation in marine ecosystems, and following the mass die off of the herbivorous sea urchin *Diadema antillarum.* The massive reduction in this once abundant and ubiquitous herbivore in Caribbean reefs was linked to the wide-spread triggering of phase-shifts (Hughes 1994). Herbivorous communities, which use reefs as habitats, effectively target a wide diversity of algal species, which helps coral reefs in their resilience against such disruptions (Adam et al. 2015a). This prompted researchers to investigate the relationship between algae overgrowth and reduction in herbivory, and many studies have found that algae overgrowth was related to decline in herbivorous species (Adam et al. 2015a). Researchers have found that the competitive pressure that algae exerts on coral species for space can be mitigated by the herbivorous species on reefs (Ogden and Lobel 1978).

Parrotfish species constitute another group of keystone herbivores that have been extensively studied in recent decades due to their ability to voraciously remove macroalgae (Adam et al. 2018). They can be found ubiquitously across many reefs and are often identified as the dominant herbivorous community in their ecosystem (Adam et al. 2018). Parrotfishes are characterized by various innovative morphological features and fulfill important and particular ecological functions such as bioerosion (Wainwright and Price 2018). They have usually been categorized into distinct functional groups based on anatomical observations and diet analyses across studies (Smith et al. 2018). These classifications, namely excavators, scrapers and browsers, have often been used to evaluate the grazing properties of parrotfish communities, and subsequently make predictions about their impact on the reef. However, these broad categorizations are not always definite in predicting their feeding behaviour, since parrotfishes are likely to have context-dependent grazing properties, which can change as a function of reef ecological dynamics (Burkepile 2012).

For instance, species identity was found to be indicative of a greater level of complementarity within functional groups than previously reported in the literature (Mantyka and Bellwood 2007). Researchers have indeed identified distinct patterns of functional complementarity and redundancy within genera, suggesting that species identity is important in determining functional roles (Burkepile and Hay 2011). Developmental stage was also found to be relevant in helping predict grazing patterns of parrotfishes (Feitosa and Ferreira 2015). In fact, Smith et al. (2018) investigated the variation in feeding behaviour of parrotfish species in relation to their ontogenetic phase and observed that preference for turf and fleshy algae differed significantly through life stages. Size was also identified as a reliable predictor of rate of consumption, as larger parrotfishes were consistently found to remove a greater volume of substratum than smaller parrotfishes (Bonaldo and Bellwood 2008, Lokrantz et al. 2008, Bellwood et al. 2012). Moreover, the capacity of individuals to perform their bioerosion function is also highly dependent on their size (Ong and Holland 2010, Adam et al. 2018).

Intrinsic biological properties of parrotfishes such as species identity, ontogenetic phase and size, are not the only factors that are likely to influence their herbivory. In fact, structural and benthic complexity was found to be of great significance in shaping their ecological function (Bozec et al. 2013). This is not a surprising finding, since coral cover acts as a refuge from predators and an important food source for many reef species, including parrotfishes (Harborne et al. 2012). Howard et al. (2009) also found that the physical features of reef habitats such as rugosity and diversity of the benthic community was highly correlated with parrotfish abundance.

Relief of competition from algae on coral by parrotfishes is considered a key paradigm in the study of reef ecology (Russ et al. 2015). However, in furthering this field of research, we should remain mindful that the ecological dynamics within reefs will not be consistent across reefs, and that they certainly are not static. Consequently, we need to also consider that the mechanisms that mediate the herbivorous function of parrotfishes may vary from one reef to the next. Investigations into the variation in functional role of parrotfishes thus need to adopt a multifactorial framework to allow the unveiling of ecological relationships between factors that are likely to alter their feeding patterns (Adam et al. 2015a). Integrating data on parrotfish community structure, environmental variables and spatial structure in reef ecology analyses can provide an integral stepping stone in increasing our understanding of reef-parrotfish dynamics.

Here, we present a multifactorial analysis of parrotfish spatial distribution and feeding behaviour in a fringing reef of Barbados. We first examine the interaction between feeding behaviour, species identity, ontogenetic phase and size. The literature on parrotfish diet suggests that food preference varies between species and across ontogenetic phases (e.g. Mantyka and Bellwood 2007, Feitosa and Ferreira 2015, Smith et al. 2018). We therefore expect that ontogeny influences food preference, and that this variation in diet will differ across species. Since larger individuals have been observed to have slower feeding rates (e.g. Bruggemann et al. 1994, van Rooij et al. 1996, Bonaldo et al. 2006, Afeworki et al. 2013), we also expect feeding rate to decrease with parrotfish size and through life stages, and that this change in feeding rate with size and ontogeny will vary across species.

Then, we examine the interaction between species abundance, environmental structure of the reef and parrotfish species trait. Since parrotfish species can vary in their habitat preference (Adam et al. 2015b), we expect individuals of different species to aggregate in distinct areas of the reef. We predict that the spatial distribution of individuals will be influenced by environmental variables, namely benthic cover and distance from shore (where distance from shore stands as a good proxy for topographic properties for the different areas in our study system). We also expect that species traits are modulating individuals' response to their environment (Brown et al. 2014), in particular that size and feeding behaviour are likely to impact species association with their habitat (Hoey and Bonaldo 2008, Yarlett et al. 2020). Here, we thus expect that fish size, genus and feeding mode will have an impact on how species abundance is influenced by the benthic community and topographic structure of the reef.

Methods

Study site

The study took place in the Northern reef in the Folkestone Marine Reserve and Park in Barbados (13°11'30.9"N 59°38'27.3"W), which is a fringing reef neighbouring the Southern Bellairs reef and is directly offshore from McGill University’s Bellairs Research Institute. We collected data on parrotfish abundance and spatial distribution across the reef, on the benthic composition and topographic characteristics of the reef, as well as on parrotfish feeding behaviour and community structure. To account for the fact that reefs are not homogeneous habitats, as they include separate topographical and ecological zones (Stearn et al. 1977), we set 18 quadrats (20 x 25m^2) in a regular grid, covering a total area of 9000 m^2. Each quadrat was set to be of an area of 500m^2 (Fig. 2.1) to be consistent with the range of average sizes of parrotfish territories (Mumby and Wabnitz 2002). All data collection was conducted within each quadrat, which allowed assessment of any spatial structure in the data across the reef.

The grid overlapped with three topographical zones of the reef (Fig. 2.1), as defined in Stearn et al.’s (1977) in-depth assessment of the physiography of the Northern reef. The “swash” topographical zone is characterized by a flat type of relief, which does not display much complexity in a 3D spatial frame, and ranges from 20 to 30m in width (Stearn et al. 1977). The depth of the zone at low tide ranges from 0 to 1m (Stearn et al. 1977). The “crest” zone is characterized by a sharper crest type of relief, which displays more complex and compact ridges, and extends seaward from the swash zone for about 40m (Stearn et al. 1977). The depth of the crest zone at low tide ranges from 1 to 3m (Stearn et al. 1977). The “coalesced spurs zone” is characterized by coalesced spurs and narrow grooves type of relief and ranges from 3 to 5 m in depth at low tide (Stearn et al. 1977). The “spurs and grooves” zone, which is characterized by wider spurs and grooves (Stearn et al. 1977), was not included in the layout of the grid due to the relatively lower abundance of parrotfish in that zone.

Environmental data

We conducted a topographical assessment of the reef to estimate the percent of each relief type found in the portion of the reef delineated by the grid (either flat relief, crest relief, coalesced spurs and grooves relief) in each of the 18 quadrats in the grid. We used the roving snorkeler survey technique (Fig. 2.2 A) to visually quantify the percent cover of relief type in each quadrat.

To assess benthic cover composition across the reef, we laid 20 photoquadrats (50 x 50cm, taken at distance of 1m) in each of the 18 quadrats in the grid, for a total of 360 photos of the benthos (Fig. 2.3). The data from the topographic assessment of the reef (percent of relief type per quadrat) was used to determine the proportion of the 20 photoquadrats that should be laid on a specific relief type to assess the benthic cover composition across the reef (e.g. if 25% of the quadrat is composed of flat topography, 25% of the photoquadrats would be laid out on flat relief).

Using the CPCe (Coral Point Cover with Excel extensions) software (Kohler and Gill 2006), we determined the proportion of each food type on the reef, that were classified into the following broad categories (Fig. S1 in Supplementary material): turf algae, macroalgae, coralline algae, coral, sponge, and sargassum. Short (less than 2 cm in height) macroscopic filamentous algae was assigned to the turf algae category, while longer vegetation was classified as macroalgae. Hard coloured (white, gray, pink, orange, red, yellow, blue or green) crustose algae were classified as coralline algae (hereafter CCA). The sargassum category corresponded to yellow/brown free-floating invasive algae of the *Sargassum* genus. We determined the percent cover of each food category by laying 20 points randomly across each photo and assigned the appropriate identification label for food category for each of those points. We then aggregated the total number of points across the 20 photoquadrats within each quadrat and calculated the percentages for the cover of each food category.

Sponges were only found in one quadrat within the sampling grid and with negligible cover (<1%) and were not considered ecologically relevant to the parrotfish in this reef since instances of feeding on sponge were rare. Therefore, it was not included in analyses involving benthic cover data. Sargassum was only detected in two quadrats within zone C. Also, since it is a free-floating algae and wave-action prevented it from accumulating in quadrats closer to the shore, it was not included in analyses involving benthic cover data.

Species abundance data

Multiple survey methods exist to assess fish species abundance within a reef, and the choice of a method over another is rarely explained by investigators. Within investigations of parrotfish ecological roles in a reef, it is rare for researchers to explicitly consider the potential biases of using a particular method over another to assess parrotfish abundance. In most studies, except in those investigating method biases, data collected using only one method of species abundance surveys are reported and used for subsequent analysis (e.g. Smith et al. 2018, Ruthenberg et al. 2019).

Therefore, to account for potential method biases, we used two different sampling methods to assess parrotfish abundance and distribution across our study site. We conducted roving snorkeler surveys and stationary point surveys (Fig. 2.2) within each quadrat in the sampling grid. We carried out two roving snorkeler surveys and two stationary point surveys, for four independent abundance assessments in total. The roving snorkeler surveys consisted of a snorkeler swimming in a zig-zag pattern within each quadrat for five minutes to note down every parrotfish sighted during that time (Fig. 2.2 A). The stationary point survey consisted of a snorkeler rotating around a fixed point located at the center of each quadrat for five minutes to note down every parrotfish sighted within a 7m radius during that time (Fig. 2.2 B). All surveys were conducted between 10am and 2pm, when parrotfish are known to be most active (Adam et al. 2015b). Each survey took two hours to complete and was conducted at a one week interval in the span of a month on May 20th, May 27th, June 3rd and June 10th 2019. For each parrotfish sighted, we noted down its species identity, ontogenetic phase and size. To estimate parrotfish size, surveyors trained every day for a week prior to starting the first survey using a PVC pipe that was taped every 5 cm as a reference for the length of objects underwater. The PVC pipe was repeatedly placed at different depths of the reef to allow surveyors to get used to the diffraction effect of water. Size was then visually estimated by the surveyor.

Feeding observations

The species of parrotfishes included in the study were the five most abundant parrotfish species found on this reef (Fig. S2 in Supplementary material): the princess parrotfish (*Scarus taeniopterus*), queen parrotfish (*Scarus vetula*), redband parrotfish (*Sparisoma aurofrenatum*), stoplight parrotfish (*Sparisoma viride*), and yellowtail parrotfish (*Sparisoma rubripinn*e). Two species present on the reef were excluded from the study due to their much lower abundance, namely the redtail parrotfish (*Sparisoma chrysopterum*) and the striped parrotfish (*Scarus iseri*).

To assess the feeding behaviour of individual fishes, we followed every target individual for 10 minutes and recorded its location within the sampling grid, species identity, ontogenetic phase and size before starting every focal observational study. We let the fish acclimate to the presence of the snorkeler for 3 minutes before starting surveys to limit the effect of human presence on their behaviour. During each survey, we recorded the total number of bites, number of bites per food category, number of bites per relief type and time spent within a quadrat.

We used Manly's alpha electivity index (α) to assess the preference for each food type for each fish recorded during the focal observational surveys. Manly's alpha electivity index is calculated with the following formula:

$$\alpha_i = \frac{r_i}{n_i}\frac{1}{\sum(r_j/n_j)}$$

where α_i is Manly's alpha for food type i, r_i is the proportion of food type i bitten by an individual, and n_i is the proportion of food type i found on the reef (Manly et al. 1972). Manly's index is calculated for each food type (i) in reference to the summation of the proportion of all food types in the individual's diet (r_j) to the proportion of all food types in the environment (n_j). This index therefore accounts for changes in the abundance of other food categories due to consumption by parrotfish as well as the change in abundance of the food category of interest. Since we recorded the location of the target parrotfish while feeding within the sampling grid, we used data on the benthic cover in the quadrat where the fish spent most of its time feeding to determine the parameters for proportion of food type in the environment (n_i, n_j). For most parrotfish, the time spent feeding in their feeding quadrat was above 70% and only two individuals had a 50/50 time ratio between two quadrats. For these individuals we used benthic cover data across both quadrats. Since we calculated electivity indices for four benthic cover categories (turf algae, macroalgae, CCA and coral), electivity values of 0.25 represent the null expectation of equal selectivity for each food category based on its availability in the environment.

Statistical analysis

All statistical analyses were carried out using the R program version 3.6.3 (R Core Team 2020) through the RStudio platform version 1.3.1073-1.

Reef structure

To analyse the structure of the benthic cover across the sampling grid, we considered the percent cover of turf algae, macroalgae, CCA and coral with an arcsin transformation in our analyses. We first performed a Multivariate Analysis of Variance (MANOVA) using the *stats* package (R Core Team 2020) on the benthic cover data to test if it varied across zones (zones A, B and C) within the sampling grid (see Fig. 2.1 B). In this analysis, the response variable was the percent cover of each benthic category within each quadrat and the explanatory variable was reef zone. Next, we ran a Principal Component Analysis (PCA) to assess the variation in benthic cover across quadrats within the sampling grid using the *ade4* package (Dray and Dufour 2007).

Effect of method choice on abundance estimates

We first built a Generalized Linear Mixed-Effect Model (GLMM) with a poisson distribution and a log link to determine whether method type had an effect on species abundance estimates across the quadrats within the grid using the *lme4* package (Bates et al. 2015). In our model, method and species were included as fixed effects, while quadrat was added as a random effect. We used the interaction term between method and species to evaluate if an effect of method was consistent across species. We then calculated Spearman's correlation coefficients between abundance estimates counted at each quadrat using the two different methods for each species to assess whether abundance estimates were correlated between methods for each species.

For all subsequent analyses, we used species abundance data collected using stationary point surveys since we found differences in species abundance estimates between methods and found that stationary point surveys yielded the maximum abundance value across all species (see Results for Effect of method on fish abundance estimates).

Feeding behaviour

We first built a linear model that included species and phase as explanatory variables and individual fish size as the response variable to determine whether phase and size were correlated for each species. To determine if feeding rate varied across species, phase and size, we first built a general linear model (GLM) with a negative binomial distribution and a log link which included phase and species as explanatory variables, and the total number of bites within the 10 minute time-frame of the feeding observations as the response variable. For this analysis, we categorized ontogenetic phases into non-terminal phase individuals (juvenile and initial phase) and terminal phase individuals. We then built a second GLM which included size with a log transformation and species as explanatory variables and the total number of bites within the feeding observation time as the response variable. We did not include the ontogenetic phase and size in the same model as diagnostic tests revealed a VIF > 6 for this variable due to its high correlation with fish size (see Results for Feeding behaviour). Finally, to determine if and how electivity varied across species, we made bar charts with the means of electivity indices and their 95% confidence intervals for the four food categories per species, and visually assessed whether the 95% confidence interval crossed the null expectation of equal selectivity for each food category ($\alpha = 0.25$). We used the same method to determine if electivity varied across ontogenetic phases.

Reef structure and parrotfish abundance

To assess if fish abundance significantly differed between species and across zones, we first performed a MANOVA on the species abundance data to test if it varied across zones (zones A, B and C) within the sampling grid. In this analysis, the response variable was the abundance of each parrotfish species within each quadrat and the explanatory variable was reef zone.

We then used a fourth corner analysis to quantify the individual and combined effects of environmental data and species traits (parrotfish size, genus and feeding mode - i.e. scraper, browser or excavator) on species distribution across the reef. The fourth corner approach allowed us to test for the effect of environmental variables and of species-specific traits, as well as of the interaction between these two types of variables (i.e. the fourth corner). For this analysis, we built a series of three Generalized Linear Latent Variable Models (GLLVMs) with increasing complexity using the package *gllvm* (Niku et al. 2020). The environmental data were a scaled matrix of variables describing the benthos composition (percent cover of turf, macroalgae, CCA, and coral) and distance from shore of the quadrats (distance from shore stood as a good proxy for topographic complexity in our system). Size data were obtained from abundance surveys and feeding modes were attributed to species using information from Bellwood and Choat (1990), Bruggeman et al. (1996) and Adam et al. (2018). *Scarus taeniopterus* and *Scarus vetula* were categorized as scrapers, *Sparisoma aurofrenatum* and *Sparisoma rubripinne* as browsers, and *Sparisoma viride* as an excavator. All three models were run with species abundance across quadrats as a response variable and a negative binomial family with a log link. We included a random row effect in our models to account for the difference in relative abundance of species across quadrats (Niku et al. 2019). The first model included only two latent variables that account for variation in species abundance due to ecological variables we did not explicitly measure in this study. In the second model, we added our environmental data as an explanatory variable. Finally, in the third model, we included both environmental data and species trait data (parrotfish size, genus and feeding mode) as explanatory variables, as well as their interaction to account for a possible effect of a trait x environment interaction (i.e. the fourth corner) on the patterns of species abundance. We used the traces of the estimated residual covariance matrix from each model to quantify the amount of variation in the data that is attributed to environmental variables and their species traits (Niku et al. 2019, Warton et al. 2015). Finally, we used a likelihood ratio test to determine whether adding species trait data to the model significantly improved its fit at explaining variation in species abundance in relation to the environment (Niku et al. 2019).

Results

Reef structure and benthic cover

All zones (zone A, B and C) within the sampling grid were almost completely dominated by turf algae (> 91% cover) (Fig. 2.4). Percent cover of turf algae was greater within quadrats closer to the shore (zone A), where most of the topography consists of flat relief (Fig. 2.5, Table 2.1). CCA was the second most abundant benthic cover category across the reef (> 5.75% cover) (Fig. 2.4). CCA percent cover was greater in quadrats that were further from shore (zone B and zone C), and not much was found close to shore (Fig. 2.5, Table 2.1). The reef hosted relatively little coral or macroalgae (< 1.02% and < 1.30% cover, respectively) (Fig. 2.4). Macroalgae percent cover was greater in quadrats that were further from shore, especially on the northernmost side of the reef (although not significant, Table 2.1), whereas coral was generally more spread out (Fig. 2.5). Sponges were only found in one quadrat within the sampling grid and sargassum was only detected in two quadrats within zone C (Fig. 2.5).

The first two axes of the PCA showing variation in benthic cover among quadrats cumulatively explain 90.7% of the variance in benthic cover across the sampling grid (Fig. 2.6). The first axis captured variation in CCA and turf algae cover, and the second axis captured variation in coral and macroalgae cover. The PCA showed a gradient in benthic cover composition, where quadrats in zone A (quadrats A1 to A6) and quadrat C1 overall hosted more turf algae than other quadrats (Fig. 2.6).

Effect of method choice on abundance estimates

We found an overall significant effect of the survey method on parrotfish abundance regardless of species identity ($X^2 = 8.43$, $p < 0.0037$). There was also a significant effect of species on parrotfish abundance ($X^2 = 976.12$, $p < 2.2e-16$). However, there was no significant interaction between method and species ($X^2 = 1.97$, $p = 0.74$), indicating that the difference in abundance estimates between the two methods was consistent across species.

Spearman's correlation coefficients of the fish abundance at each quadrat across the sampling grid estimated from the two methods were significant for *Scarus taeniopterus* ($r_s = 0.74$, $p < 0.00048$) and *Sparisoma viride* ($r_s = 0.71$, $p < 4.45e-05$), but not for *Scarus vetula* ($r_s = 0.0078$, $p = 0.98$), *Sparisoma aurofrenatum* ($r_s = 0.37$, $p = 0.13$) and *Sparisoma rubripinne* ($r_s =0.45$, $p = 0.19$) (Fig. 2.7). Finally, across all species, the stationary point survey method yielded the maximum abundance value (Fig. S3 in Supplementary Materials). Given these cumulative results, further analyses were carried using abundance data from the stationary point surveys.

Parrotfish community structure

On average, a total of 365 parrotfish individuals (378 during the first survey and 352 during the second survey) of various species, size classes and ontogenetic phases were detected during the stationary points surveys (Table 2.2). Most parrotfish detected during the surveys were initial phase individuals belonging to the second size class (Table 2.2).

Scarus vetula was the dominant parrotfish species across all zones (zone A, B and C) within the sampling grid (Fig. 2.8). *Sparisoma viride* was the second most abundant species in the reef, but was found mainly in zones B and C (Fig. 2.8). *Sparisoma viride* and *Sparisoma rubripinne* were the only species to significantly vary in abundance across zones (Table 2.3). Both these species were found in relatively lower abundance in zone A, but increased in abundance in zones B and C (Fig. 2.8-9). *Sparisoma viride* seemed to aggregate on the quadrats furthest from shore (B1 to B6, C1 to C6). In addition, *Scarus taeniopterus* seemed to aggregate on the southewestern quadrats (A1 to A3, B1 to B3), although such aggregation was not statistically significant. (Fig. 2.9, Table 2.3). Finally, there was no clear pattern of spatial aggregation for *Scarus vetula*, *Sparisoma aurofrenatum* and *Sparisoma rubripinne* (Fig. 2.9).

Feeding behaviour

We recorded feeding data for a total of 85 individual fish: 22 *Scarus taeniopterus*, 16 *Scarus vetula*, 18 *Sparisoma aurofrenatum*, 19 *Sparisoma viride*, and 10 *Sparisoma rubripinne* (Table 2.4). We were unable to identify and record feeding data for juvenile *Sparisoma rubripinne* individuals within the reef (Table 2.4).

We found that fish size significantly differed across species (df = 4, F = 72.27, p < 2.2e-16) and phase (df = 2, F = 399.46, p < 2.2e-16). The best fitted GLM that included feeding rate as the response variable was the one which included ontogenetic phase and species as explanatory variables, rather than size and species (AIC = 866.035, AIC = 872.065, respectively). Bite rate significantly varied across species as *Scarus taeniopterus* and *Scarus vetula* had a greater mean bite rate (0.26 ± 0.09 s^{-1} and 0.26 ± 0.13 s^{-1}, respectively) than *Sparisoma aurofrenatum*, *Sparisoma viride* and *Sparisoma rubripinne* (0.13 ± 0.06 s^{-1}, 0.13 ± 0.06 s^{-1} and 0.14 ± 0.04 s^{-1}, respectively) (Table 2.5, Fig. 2.10). Bite rate also significantly varied with size within species (Table 2.6, Fig. 2.11). Bite rate decreased with size for all species except for *Sparisoma rubripinne* (Fig. 2.11). Overall, all species fed disproportionally more on turf algae given its abundance across the reef ($\alpha > 0.25$ for all species, Fig. 2.12). All species fed disproportionally less on macroalgae as well as on coral, except for *Sparisoma viride* (Fig. 2.12). *Sparisoma viride* did not exhibit any partiality for either coral nor CCA, and *Scarus taeniopterus* fed more on CCA given its abundance across the reef. Finally, parrotfishes preferentially fed on turf algae throughout ontogeny ($\alpha > 0.25$ for all phases, Fig. 2.13) and fed proportionally less on coral and macroalgae. Terminal phase and juvenile individuals did not exhibit any partiality for CCA.

Reef structure and parrotfish abundance

To ensure that our species trait and environmental data were independent, we did not consider food preference in our GLLVM models, a variable calculated using the abundance of benthos cover types available across the reef. The addition of environmental variables in our second model from our first model, which included only latent variables as explanatory variables, reduced the trace from 1.774 to 0.833, which indicates that the environmental data account for approximately 53.04% of the covariation in abundance between species. The abundance of *Scarus taeniopterus* was negatively correlated with macroalgae (Fig. 2.14). The abundance of *Sparisoma viride* was positively correlated with distance from shore and negatively correlated with turf algae (Fig. 2.14). The likelihood ratio test between our second and third GLLVM models (where the second model included environmental data in addition to two latent variables and the third model included environmental and species trait data as explanatory variables and their interaction) revealed that the simpler model (model two) had a better fit ($p < 0.001$). The addition of species traits and of the interaction between species traits and environmental variables in our third model reduced the trace from 1.774 (from our first model) to 0.832, which indicates that the environment, species traits and their interaction account for approximately 53.12% of the covariation in abundance between species. This is only 0.8% higher than for the second model, which explained 53.04% of the covariation in abundance between species. Phylogeny (species genus) did not have a significant effect on species association to their environment (Fig. 2.15). Scrapers were less abundant than browsers in quadrats where more macroalgae was found, whereas excavators were more abundant than browsers in quadrats further away from shore (Fig. 2.15). Moreover, larger fish were more abundant in quadrats where there was more macroalgae (Fig. 2.15).

Discussion

Benthic community composition

In our study system, we did not find much diversity in benthic cover across the reef. Indeed, not much coral was found on the reef (less than 1.02% cover overall) as most of the benthic cover was dominated by turf algae (more than 91% cover overall). We expected coral cover to be low in the sampling zone closest to the shore (zone A), since it is a shallow flat habitat, dominated by rubble and sand, which offers little protection from sediment disturbance from wave-action and is therefore not an ideal environment for coral to establish (Thornborough and Davies 2011). However, coral cover was low even in deeper areas where the topography was more complex (sampling zones B and C). Moreover, we noticed that most of the area in the reef was covered in short filamentous vegetation and that there were very few patches of macroalgae (less than 1.30% cover overall). Our results then differ from the literature on parrotfish and reef ecological dynamics that suggests that presence of parrotfishes can lead to an increase in coral cover (Mumby 2006). In our system, parrotfish abundance was found to be very high on the reef (365 individuals counted on average with the stationary point surveys), but turf algae was still dominant on the benthos.

Multiple studies have documented diversity of coral reef communities and the degradation of corals in Barbados in the past decades (Lewis 1960, Stearn et al. 1977, Mah and Stearn 1986, Tomascik and Sander 1987, Bell and Tomascik 1994). The historical patterns of loss of live coral cover on the West coast of Barbados has been attributed to a combination of multiple stressors such as anthropogenic activities, hurricanes, but also eutrophication (Tomascik and Sander 1987, Bell and Tomascik 1994). Tomascik and Sander (1987) measured coral cover and species composition of multiple reefs on the West coast of Barbados along a eutrophication gradient and found that reduction in coral species diversity through removal of more vulnerable species was related to levels of eutrophication. Additionally, eutrophication in these reefs benefited macrophytic algae at the expense of coralline algae cover (Allard 1994, Mann 1994). Although the impacts of eutrophication and nutrient loading in our study system has not been explicitly measured, it is reasonable to hypothesize that they play a significant role in the lack of benthic diversity and the dominance of turf algae. The low cover of coral and CCA could be related to the fact that the Folkestone Marine Reserve and Park is in the vicinity of a watershed which runs off into the Caribbean sea, and through which pollution from agriculture, hotels, land-clearing and sewage is poured into the ocean water (Tosic et al. 2009). The Bellairs reef system is located 600m north-west of this watershed (Tosic et al. 2009). Tosic et al. (2009) studied the impact of the watershed's nutrient loading from chronic flush events into Holetown's coastal waters. They found high mean nutrient concentrations across the Bellairs reef system after flush events, which corresponded to nutrient concentrations recorded in the watershed.

Competitive interactions between slow-growing corals and faster growing algae can be altered by nutrient enrichment in favour of algal growth (Hughes 1994). Indeed, nutrients such as phosphorus and nitrogen can inhibit coral larval settlement and coral calcification (Ward and Harrison 1997, Hoegh-Guldberg et al. 1997), which could explain low coral cover in the reef, despite the presence and high abundance of parrotfishes. Moreover, high abundance of parrotfishes leads to increase in grazing intensity, which has been shown to limit the growth of epilithic communities to an early successional stage dominated by cyanobacteria (Sammarco 1983, Wilkinson and Sammarco 1983). Miller et al. (1999) tested the effect of nutrient enrichment and herbivory on dominance of algal taxonomic groups in coral reefs of Florida and found that an addition of fertilizer increased turf algae cover, but not macroalgae cover, and especially benefited *Scytonema* spp. which are a type of filamentous cyanobacteria. Therefore, the impact of grazing on turf abundance might be outweighed by, or exacerbate the positive feedback from nutrient run-offs by increasing cyanobacteria abundance in algal turfs.

Parrotfish distribution and feeding behaviour

Feeding behaviour analyses revealed that *Scarus taeniopterus* and *Scarus vetula* had higher mean bite rates than other species. In comparison, *Sparisoma aurofrenatum*, *Sparisoma viride* and *Sparisoma rubripinne* had mean bite rates 50% lower. We also found that feeding rate decreased with body size for most species, which is consistent with previous research on the effect of size on feeding rate (Bruggemann et al. 1994, Afeworki et al. 2013, Hoey 2018). Hoey (2018) has suggested that for some species that decrease in feeding rate with increase in size, this trend is consistent across broad spatial scales, indicating this species-specific feature of parrotfish herbivory can be generalized across locations. We did not observe this trend for *Sparisoma rubripinne*, which is most likely due to the lack of data for smaller bodied individuals as we were not able to identify any juveniles of that species (Table 2.2). Studies on the relationship between body size and feeding rate have attributed the decrease in bite rate with size to larger individuals, mainly terminal phase males, spending more time surveying their environment to protect their territory and chase away conspecifics, which leaves less time for feeding (Bruggemann et al. 1994, van Rooij et al. 1996, Bonaldo et al. 2006, Afeworki et al. 2013). We indeed found that feeding rate for terminal phases individuals was lower than for initial phase individuals and juveniles, which is consistent with what has been previously reported in the literature (Bruggemann et al. 1994, van Rooij et al. 1996, Bonaldo et al. 2006, Afeworki et al. 2013). However, as fish size increases with ontogenetic phase, it is not possible to tease apart the relative contribution of these two factors to the variation in bite rate.

Furthermore, we found that turf algae was the dominant food of interest for all species in our study system. As we found that turf algae also dominated benthic cover across the reef, these results raise the question of whether higher feeding on turf algae over other foods is a consequence of targeted feeding or simply of over-availability of turf algae. From what is known of parrotfish nutritional needs, their rapid growth rates are likely to require consumption of protein rich resources, such as cyanobacteria, which has one of the highest concentrations of protein among parrotfish food resources (Clements and Choat 2018). Moreover, Clements and Choat's (2018) review of the literature on parrotfish nutrition, based on gut content analyses, stable isotope analyses and tissue fatty acid analyses, revealed that the diet of parrotfishes consists mainly of protein-rich microorganisms and cyanobacteria. Therefore, if the turf algae dominating the benthic community of our study system is indeed rich in protein-filled cyanobacteria, it is very likely that all parrotfish species included in our study exhibit an actual preference for turf algae. This would contradict what has been reported for the diets of many *Sparisoma* species, which are typically believed to preferentially feed on macroalgae (Clements and Choat 2018). Also, a study by Goecker et al. (2005) showed that *Sparisoma radians* sampled different food items before starting to target the most protein-rich resources available, implying that the sense of taste was an important mechanism in choice for food items. In line with our own observations, the results from this study support the hypothesis that parrotfish may adopt a preference for the most abundant protein-rich resource in their environment. However, these inferences remain speculative and more in-depth research on species-specific nutritional needs is required to identify patterns of feeding preferences. We also note the need to interpret these results with caution since the other benthic components (macroalgae, CCA and coral) in the reef were rare, and that the variation in the electivity metrics could simply reflect sampling error for the rare benthic categories.

We recorded species-specific patterns of spatial aggregation in the parrotfish community. *Scarus taeniopterus* aggregated in the southwestern corner of the reef, where a higher abundance of turf algae and lower abundance of macroalgae was found, and *Sparisoma viride* aggregated in areas furthest from the shore, where turf algae was relatively less abundant. We found a few significant species-specific correlations between environmental variables and abundance for both *Scarus taeniopterus* and *Sparisoma viride*, where the abundance of the former was negatively correlated with macroalgae and the abundance of the latter was negatively correlated with turf algae. Additionally, we found that the abundance of *Sparisoma viride* was positively correlated with distance from shore. These results mirror reports from previous studies which have shown that environmental variables influence parrotfish distribution and grazing patterns (Howard et al. 2009, Nash et al. 2012, Bozec et al. 2013, Carlson et al. 2017, Yarlett et al. 2020). Nonetheless, we acknowledge that the lack of diversity in benthic composition in our study system hinders our interpretation of these results and that we may be missing other important environmental drivers of parrotfish distribution.

Moreover, we found that species traits marginally accounted for associations between environmental variables and species abundance, indicating that feeding mode and size may not be the most important factors in mediating these associations. Therefore, we may be missing important factors in our model to explain patterns of parrotfish distribution and their species-specificity. Notably, we did not consider the effect of competition in our models, and how it can modulate interactions between species abundance and environmental structure. It is possible that the degree of pressure of competitive interactions experienced by parrotfishes depends on species identity and their tendencies for antagonistic behaviour (Bellwood 1985, Nash et al. 2012). For instance, Davis et al. (2017) found that both patterns of space use and herbivory for one species of parrotfish were influenced by competitive pressure from the surrounding herbivorous fish community.

We found that scrapers were less abundant than browsers where macroalgae cover was higher, excavators were more abundant than browsers further from shore, and larger fish were more abundant where macroalgae cover was higher. However, the integration of species traits in our fourth corner analysis did not improve model fit by a consequential amount. This result contradicts some studies that have reported that feeding behaviour and size were associated with how parrotfishes are distributed in their habitat (Hoey and Bonaldo 2008, Nash et al. 2012, Carlson et al. 2017, Yarlett et al. 2020). For instance, a study by Carlson et al. (2017) reported that grazing patterns of the parrotfish *Chlorurus microrhinos* and their abundance were related to the abundance of mixed algal turfs, which was their preferred resource, as the intensity of grazing was higher where turf algae was dominant. Also, Nash et al. (2012) found that the level of coral cover influenced feeding behaviour for one species of parrotfish in the system.

Effect of method choice on species abundance estimates

An additional result of note is the difference in parrotfish abundance estimates obtained from using different survey methods. Although strip transects have been the most commonly used method in ecological surveys to assess abundance and diversity of fish in coral reef communities (Edgar et al. 2004), there is a wide variety of methods that are used across studies of reefs (Edgar et al. 2004, Dickens et al. 2011). Unless reef ecologists are interested in specifically studying the effect of survey method choice on fish abundance estimates, it is not common practice to compare methods within studies which examine parrotfish ecological dynamics. However, reef ecologists need to select census methods according to the study design and the hypotheses that are being tested (Edgar et al. 2004).

For instance, stationary point surveys are useful to assess the area at a 360° angle, which is why it was chosen over classic strip transects for the gridded quadrat design of our study. Still, because it has been shown that different techniques to assess the same fish community are likely to yield different results (e.g. Kulbicki and Sarramégna 1999, Rassweiler et al. 2020), we tested the variation in abundance data collection with another method. The roving method was chosen as an alternative method to assess parrotfish abundance because it allows the surveyor to scan the entire area of the sampling quadrat, which could potentially make the detection of more evasive individuals easier. Ultimately, we found that there was a significant difference in parrotfish abundance estimates when using these two different survey methods. Stationary point surveys yielded higher maximum abundance values than roving snorkeler surveys and this difference was consistent across species (see Fig. S3 in Supplementary material).

Some studies have reported that presence and movement of divers can drive fish to steer away from surveyors (Stanley and Wilson 1995, Dickens et al. 2011). The cause for these diver effects is not entirely known, but Dickens et al.'s (2011) investigation of diver biases in underwater visual census revealed that vision might be the main stimulus for fish that encounter divers. Therefore, since stationary point surveys require little movement on the part of the diver, they are less likely to generate deterring diver effects that would lead to reduced ability of surveyors to count individuals (Stanley and Wilson 1995, Dickens et al. 2011) than a method that requires more movement such as the roving snorkeler method.

Limitations

In this study, which focuses on parrotfish behaviour, the taxonomic resolution at which we collected data on the food items targeted by parrotfish was relatively low, as the categories used did not account for the species identity of the different benthic organisms observed. We used broad categorizations such as turf algae or macroalgae, which can be problematic since it can limit our inferences about reef structure and the drivers of feeding patterns. These broad categorizations may have reduced our ability to detect patterns of benthic diversity as well as patterns of diversity in parrotfish diet. Indeed, algal turfs are very heterogenous and host a wide variety of organisms such as rhodophytes, chlorophytes, phaeophytes and cyanobacteria (Connell et al. 2014, Harris et al. 2015). Identification of the algal community at the species level within the assigned broad categories could have helped in identifying the nutritional value of the food consumed and could have thus better informed our research on parrotfish herbivory. However, achieving higher taxonomic resolution is very time consuming and requires input of specialized experts, and the approach used in this study has been successfully used in the past by Cardoso et al. (2009) in the same system.

We also did not evaluate the effect of important biotic factors known to influence patterns of parrotfish feeding and distribution. For instance, we did not collect data on interspecific interactions such as competition and territoriality, which can be important in determining parrotfish distribution and how they utilize their habitat (Nash et al. 2012). For instance, Davis et al. (2017) found that the feeding rate for *Chlorurus spilurus* was affected by interference competition and predation risk, while habitat use was influenced by exploitative competition with the herbivorous community. Including such variables in our fourth corner analysis would have allowed us to paint a more comprehensive picture of the ecological context within which the herbivory of the parrotfish in our study system functions.

Conclusion

In coral reef ecosystems, understanding the mechanisms of parrotfish herbivory is paramount since they play a significant role in maintaining reef health (Mumby 2006, Adam et al. 2015a). Multiple studies have reported that herbivorous fish communities promote coral reef health and recovery (e.g. Lewis 1986, Mumby 2006, Smith et al. 2010). However, in our study system, there was little diversity in benthic cover across the reef and low coral cover despite the high abundance of parrotfishes. We found that most of the benthos was covered in turf algae, which could be related to the proximity of the reef to a waterway through which nutrients run-off in the ocean (Tosic et al. 2009). The high abundance of parrotfishes could also contribute to the benthic turf dominance by promoting cyanobacteria growth in algal turfs through their grazing action. The results from this study suggest that top-down control of algae abundance by parrotfish does not apply to all coral reefs that are protected from herbivore removal. As in previous studies, we found that ontogeny had an effect on bite rate (Bruggemann et al. 1994, van Rooij et al. 1996, Bonaldo et al. 2006, Afeworki et al. 2013), although it is impossible to completely dissociate the ontogenetic effect from the effect of size on bite rate due to these variables' collinearity. We also found that turf algae dominated feeding preference across the parrotfish community, possibly due to targeted feeding or the low benthic diversity in the reef. This lack of diversity in feeding preference challenges the idea that parrotfish species have static pre-determined dietary preferences. All things considered, this research presents strong supporting evidence that local context plays a very important role in mediating the effects of parrotfish herbivory on coral reef benthic communities.

Tables and figures

Table 1.1. Summary of studies used in the review of MPA effects on herbivory. Reported in the table are the authors' assessment of the differences between grazing rates, algal cover and coral cover in fished areas versus protected areas. A positive effect was reported when protection from fishing significantly increased the variable of interest (herbivory, algal cover, coral cover).

Study	Effect on herbivory	Effect on algal cover	Effect on coral cover
Ferguson et al. (2017)	No significant effect	Not reported	Not reported
Yabsley et al. (2016)	Positive effect	Negative effect	Not reported
McClanahan et al. (2011)	No significant effect	No significant effect	No significant effect
McClanahan (2008)	Positive effect	No significant effect	No significant effect
Kramer and Heck (2007)	No significant effect	No significant effect	No significant effect
McClanahan et al. (1994)	Positive effect	No significant effect	Not reported

Table 2.1. MANOVA testing for the effect of sampling zone across the reef on percent cover per benthic category. Benthic cover data were arcsin-transformed. Significant p-values are highlighted in red.

	Predictor	Sum of Squares	*df*	Mean square	*F*	*p*
Turf	Zone	0.24	2	0.12	7.42	0.00057
	Residuals	0.24	15	0.016	-	-
Macroalgae	Zone	0.023	2	0.012	2.94	0.084
	Residuals	0.059	15	0.0039	-	-
CCA	Zone	0.10	2	0.052	6.02	0.01
	Residuals	0.13	15	0.0086	-	-
Coral	Zone	0.0087	2	0.0044	1.66	0.22
	Residuals	0.039	15	0.0026	-	-

Table 2.2. Number of individuals recorded during stationary point surveys by ontogenetic phase and size class for each species, averaged over two surveys. On average, a total of 365 individuals were sighted during the surveys (378 during the first survey and 352 during the second survey).

	Juvenile	Initial			Terminal		
Species	Size class 1	Size class 1	Size class 2	Size class 3	Size class 2	Size class 3	Total
Scarus taeniopterus	2.5	1.5	14.5	2.5	6	7	34
Scarus vetula	5.5	38.5	109	4	1.5	48	206.5
Sparisoma aurofrenatum	4.5	2	9.5	5	0.5	5.5	27
Sparisoma viride	2.5	3	40	0	-	11	76.5
Sparisoma rubripinne	-	-	4.5	13.5	-	3	21
Total	15	45	177.5	45	8	74.5	365

Table 2.3. MANOVA testing for the effect of sampling zone on abundance per species. Significant p-values are highlighted in red.

	Predictor	Sum of Squares	*df*	Mean square	*F*	*p*
Scarus taeniopterus	Zone	15.44	2	7.72	0.51	0.61
	Residuals	225.67	15	15.04	-	-
Scarus vetula	Zone	20.11	2	10.06	0.34	0.72
	Residuals	440.17	15	29.34	-	-
Sparisoma aurofrenatum	Zone	3	2	1.5	0.32	0.73
	Residuals	71	15	4.73	-	-
Sparisoma viride	Zone	508.33	2	254.17	11.21	0.0011
	Residuals	340.17	15	22.68	-	-
Sparisoma rubripinne	Zone	27	2	13.5	3.97	0.041
	Residuals	51	15	3.4	-	-

Table 2.4. Number of individuals sampled during feeding behaviour observations by ontogenetic phase and size class for each species.

	Juvenile	Initial			Terminal		
Species	Size class 1	Size class 1	Size class 2	Size class 3	Size class 2	Size class 3	Total
Scarus taeniopterus	3	4	7	2	2	4	22
Scarus vetula	3	2	5	2	-	4	16
Sparisoma aurofrenatum	3	3	6	1	-	5	18
Sparisoma viride	4	4	5	2	-	4	19
Sparisoma rubripinne	-	-	6	3	-	1	10
Total	13	13	29	10	2	18	85

Table 2.5. Generalized linear model of the effect of species and phase on bite rate (total number of bites within the 10-minute time frame of the feeding observations). Below we present the contrasts between the different factor levels and their significance. Significant p-values are highlighted in red.

Contrasts	Estimate	Standard Error	*z ratio*	*p*
Scarus taeniopterus – *Scarus vetula*	0.045	0.116	0.393	0.995
Scarus taeniopterus – *Sparisoma aurofrenatum*	0.686	0.114	6.046	1.482e-08
Scarus taeniopterus – *Sparisoma viride*	0.735	0.112	6.558	5.454e-10
Scarus taeniopterus – *Sparisoma rubripinne*	0.696	0.137	5.066	4.034e-06
Scarus vetula – *Sparisoma aurofrenatum*	0.641	0.123	5.229	1.692e-06
Scarus vetula – *Sparisoma viride*	0.689	0.121	5.693	1.2471e-07
Scarus vetula – *Sparisoma rubripinne*	0.650	0.145	4.495	6.823e-05
Sparisoma aurofrenatum – *Sparisoma viride*	0.048	0.119	0.407	0.994
Sparisoma aurofrenatum – *Sparisoma rubripinne*	0.009	0.143	0.064	1
Sparisoma viride – *Sparisoma rubripinne*	-0.039	0.141	-0.278	0.999
Non-terminal phase – Terminal phase	0.418	0.093	4.503	6.685e-06

Table 2.6. Generalized linear model of the effect of species and size on bite rate (total number of bites within the 10-minute time frame of the feeding observations). Below we present the contrasts between the different factor levels and their significance. Significant p-values are highlighted in red.

Predictor and Contrasts	Estimate	Standard Error	*z ratio*	*p*
Size	-0.223	0.063	-3.560	3.710e-04
Scarus taeniopterus – Scarus vetula	-0.055	0.122	-0.453	0.991
Scarus taeniopterus – Sparisoma aurofrenatum	0.724	0.118	6.140	8.251e-09
Scarus taeniopterus – Sparisoma viride	0.677	0.116	5.829	5.567e-08
Scarus taeniopterus – Sparisoma rubripinne	0.543	0.143	3.804	1.344e-03
Scarus vetula – Sparisoma aurofrenatum	0.779	0.131	5.933	2.969e-08
Scarus vetula – Sparisoma viride	0.733	0.126	5.811	6.186e-08
Scarus vetula – Sparisoma rubripinne	0.599	0.149	4.021	5.549e-04
Sparisoma aurofrenatum – Sparisoma viride	-0.047	0.125	-0.375	0.996
Sparisoma aurofrenatum – Sparisoma rubripinne	-0.180	0.151	-1.198	0.753
Sparisoma viride – Sparisoma rubripinne	-0.134	0.146	-0.915	0.891

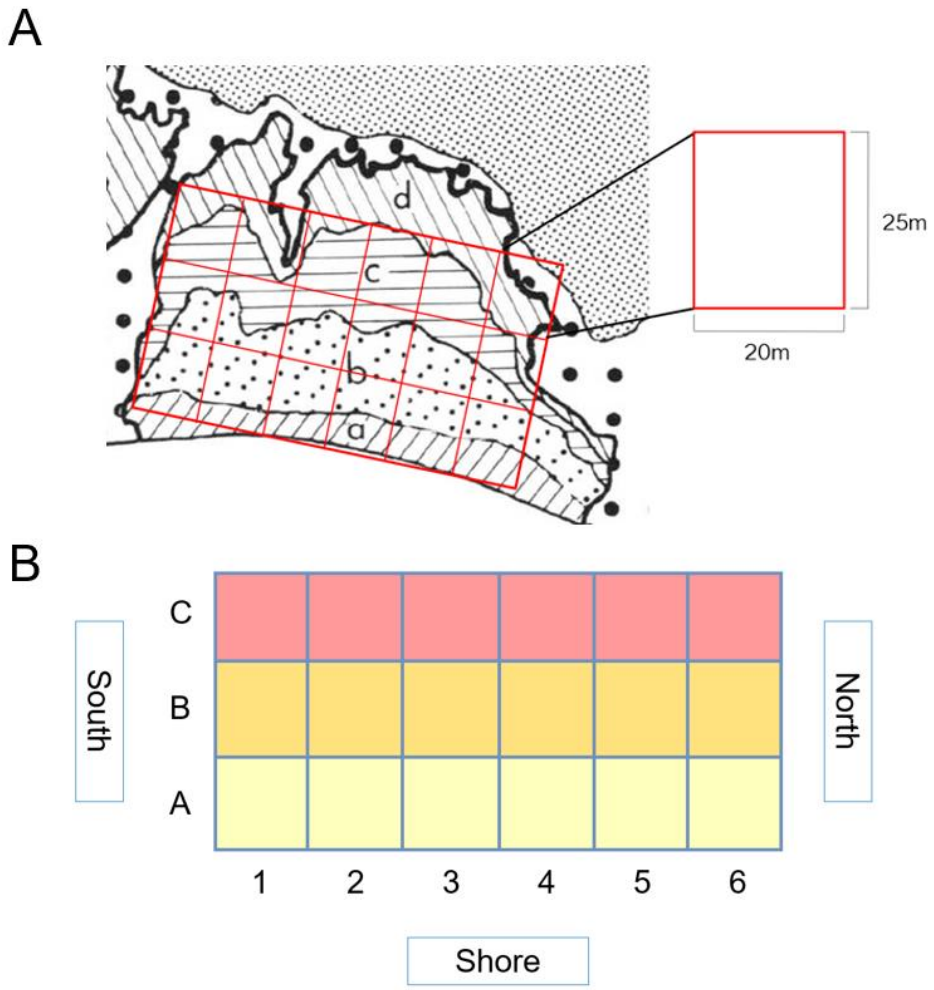

Figure 2.1. Layout of the sampling grid consisting of 18 quadrats covering the Northern reef in the Folkestone Marine Reserve and Park. (A) Topographical mapping of the different zones in the reef: a – Swash zone, b – Crest zone, c – Coalesced spurs zone, d – Spurs and grooves zone. The spurs and grooves zone was not included in the study due to the low abundance of parrotfishes. The sampling grid is shown to overlap with the topographical mapping in an approximative fashion. Figure modified from Stearn et al. (1977). (B) Numerical designation of the 18 quadrats within the sampling grid. Sampling zones were divided in three (zone A, B and C) and are differentiated by colour on this figure.

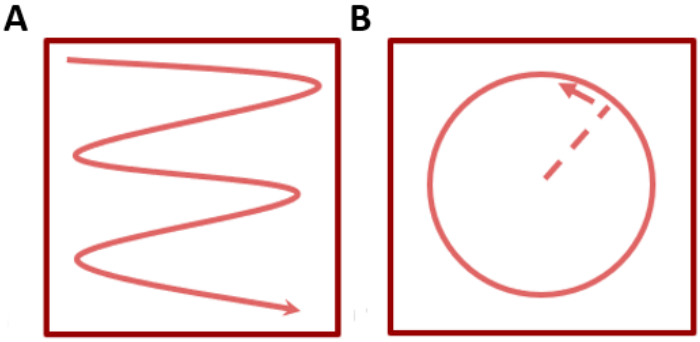

Figure 2.2. Visual representation of (A) roving snorkeler survey and (B) stationary point survey within each 20x25m quadrat.

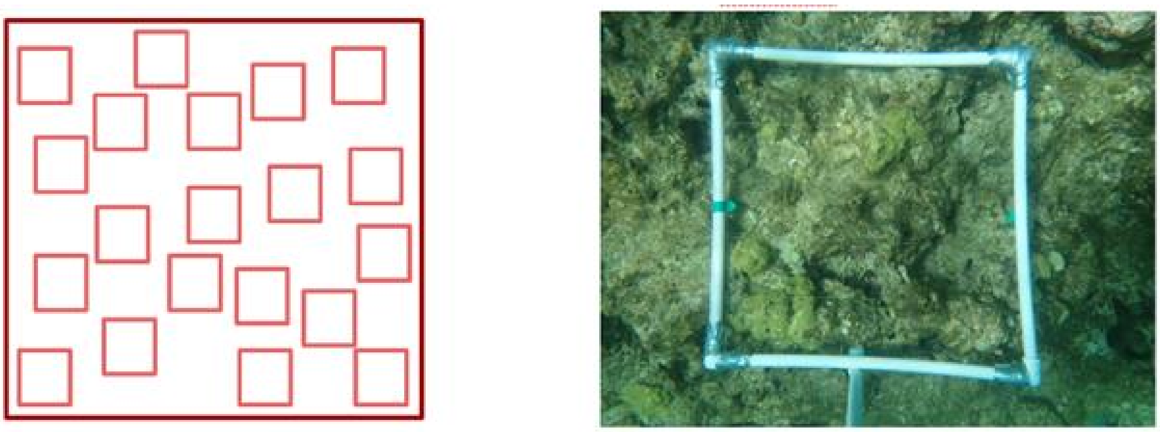

Figure 2.3. (A) Visual representation of the layout for photoquadrats used for benthic cover assessments within the 20x25m sampling quadrats. The bigger red square represents a sampling quadrat. Each smaller square in pink represents a photoquadrat. A total of 20 photoquadrats were randomly placed within each sampling quadrat while still considering the proportion of topographic relief type within sampling quadrats to determine the proportion of photoquadrats that should be set on the different reliefs. Figure is not to scale. (B) Picture showing one of the 50 x 50 cm photoquadrats.

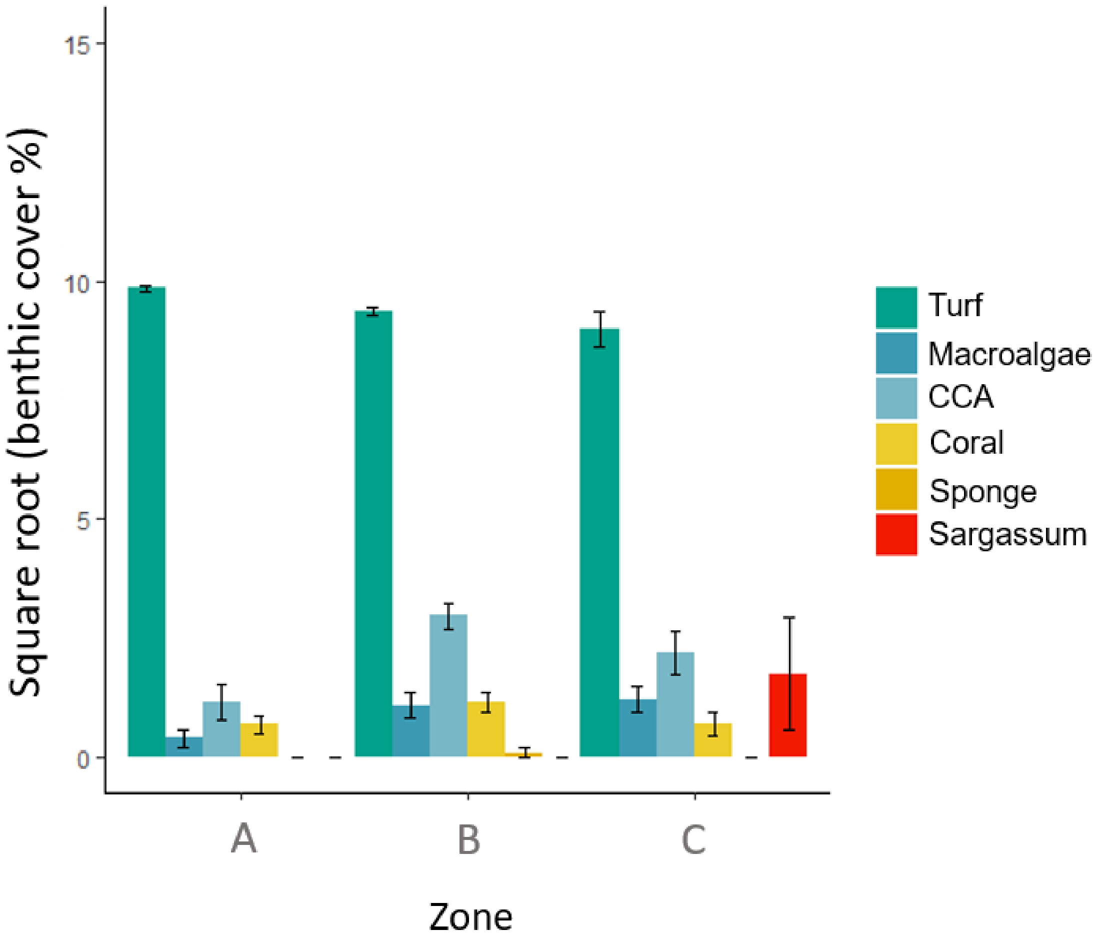

Figure 2.4. Mean proportion of cover per benthic cover category (+SE) on the reef in zone A, zone B, and zone C. Proportion of cover per benthic cover category was averaged across all 6 quadrats within each zone. Sargassum and sponge were present only in a single zone (zone C and zone B, respectively). Only turf and CCA percent cover varied significantly across zones. Data was square-root transformed for better visualization.

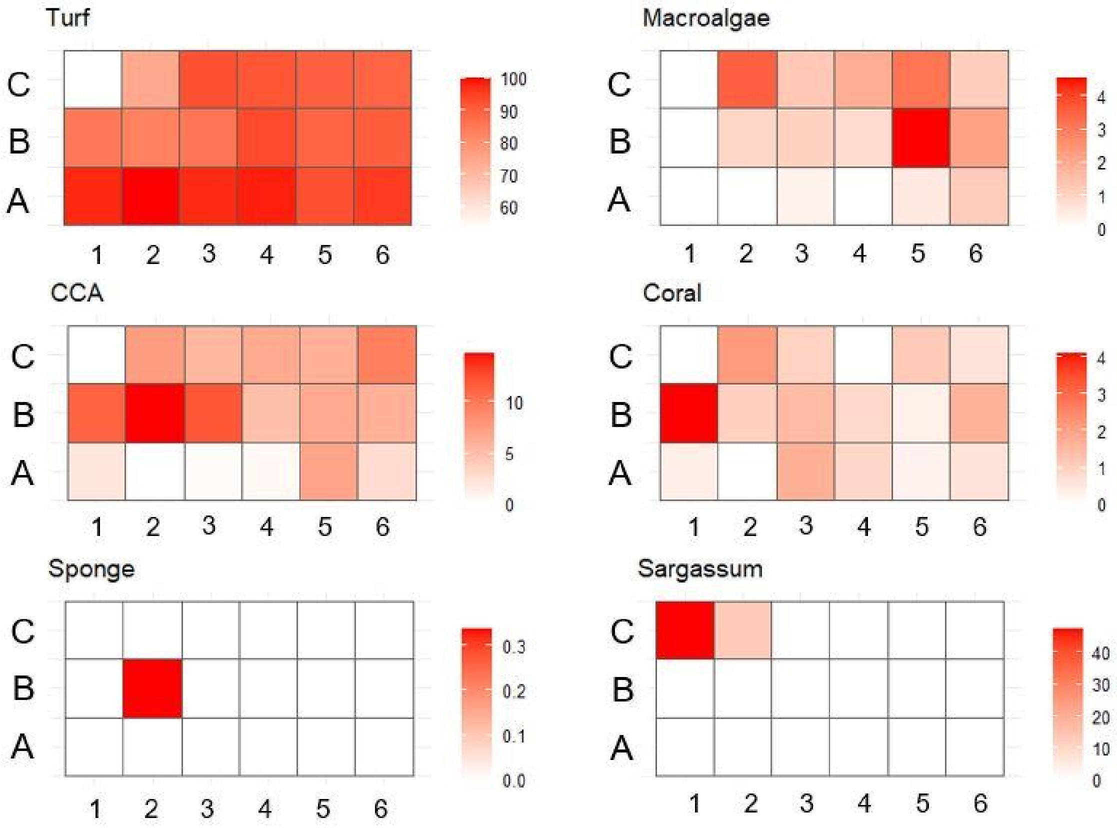

Figure 2.5. Variation in percent cover for each benthic cover category across the quadrats of the sampling grid. Gradient is relative to the total percent cover for each benthic cover category across the sampling grid and goes from white (low percent cover) to red (high percent cover). As such, the scale of percent cover varies for each benthic cover category.

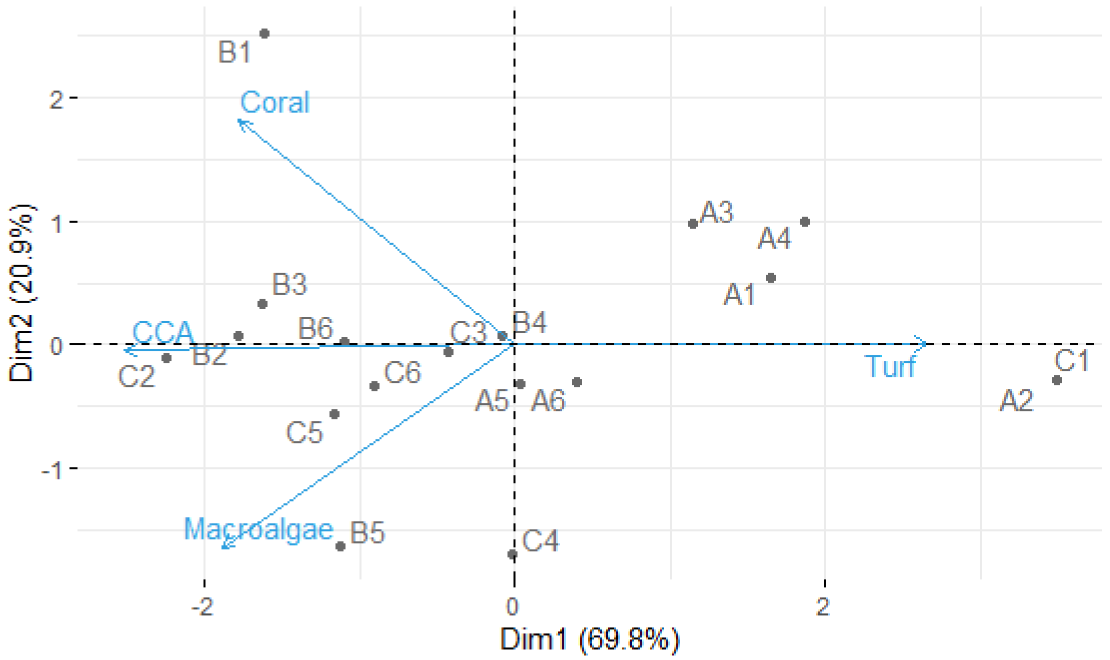

Figure 2.6. Biplot of the first two components of a Principal Component Analysis showing the variation in benthic cover and topographical composition of each quadrat within the sampling grid. Each point is a quadrat and each arrow represents an environmental variable. The first two components explain a total of 90.7% of the variation in benthic cover across the sampling grid. The PCA shows a gradient in benthic cover composition, where quadrats in zone A and quadrat C1 overall hosted more turf algae than other quadrats.

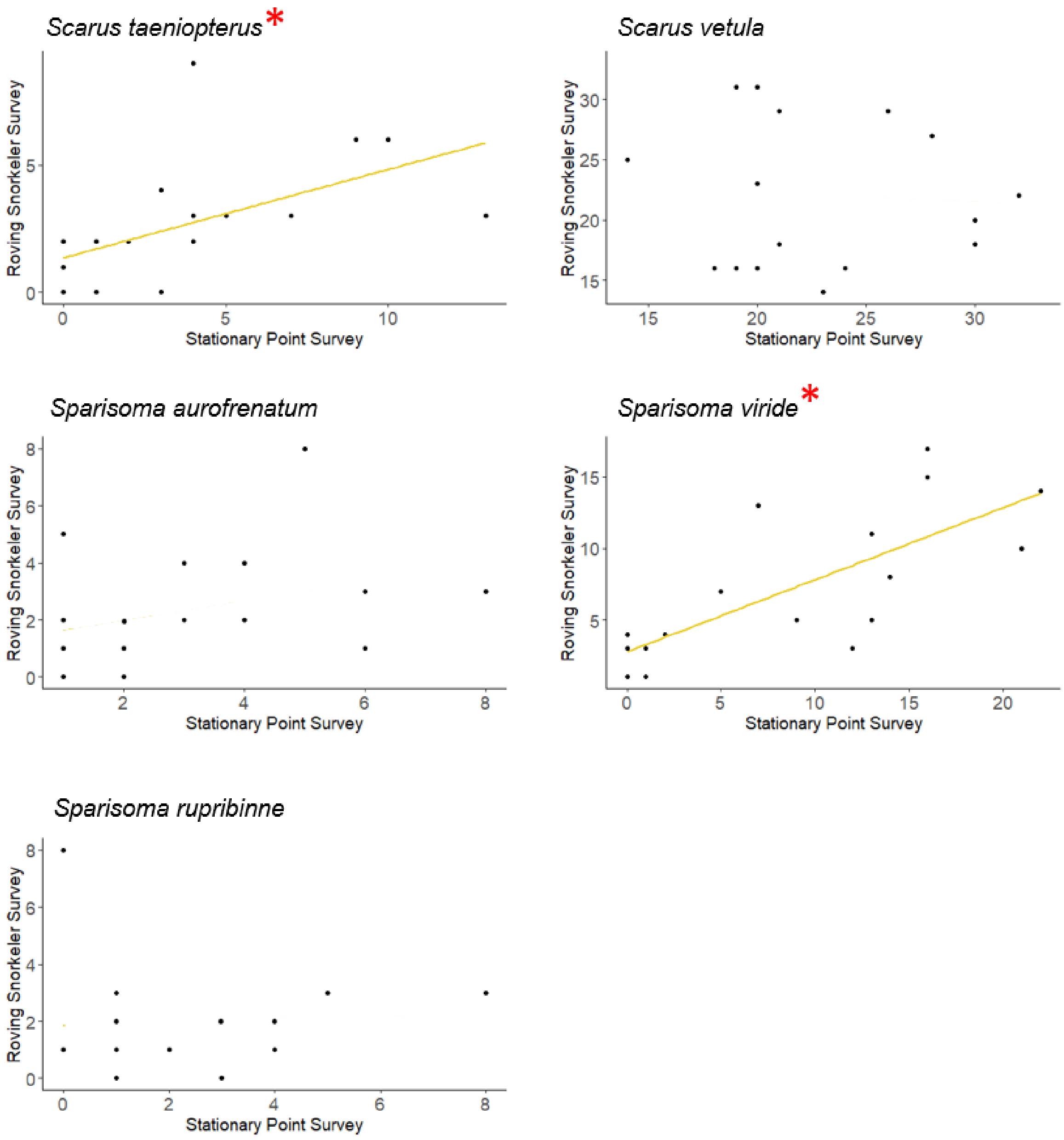

Figure 2.7. Scatter plots of the abundance estimates for each sampling quadrat for each parrotfish species collected using two different sampling methods (stationary point surveys and roving snorkeler surveys). A best fit regression line is also shown to help delineate trends, when significant. Species for which correlation between abundance estimates is significant are denoted with an asterisk.

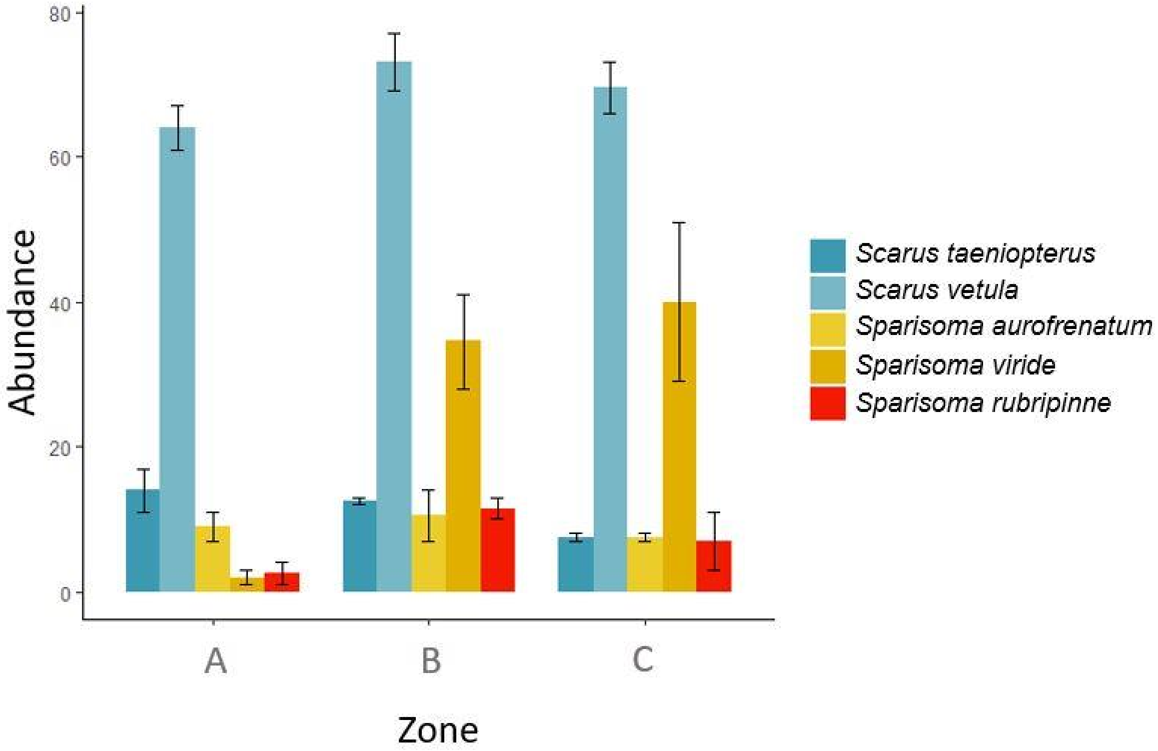

Figure 2.8. Abundance (+ SE, averaged across two surveys) of five species of parrotfishes within the reef in zone A, zone B, and zone C. Abundance data was collected with stationary point surveys. Abundance was summed for each species across all 6 quadrats within each zone. *Sparisoma viride* and *Sparisoma rubripinne* abundance significantly varied across zones.

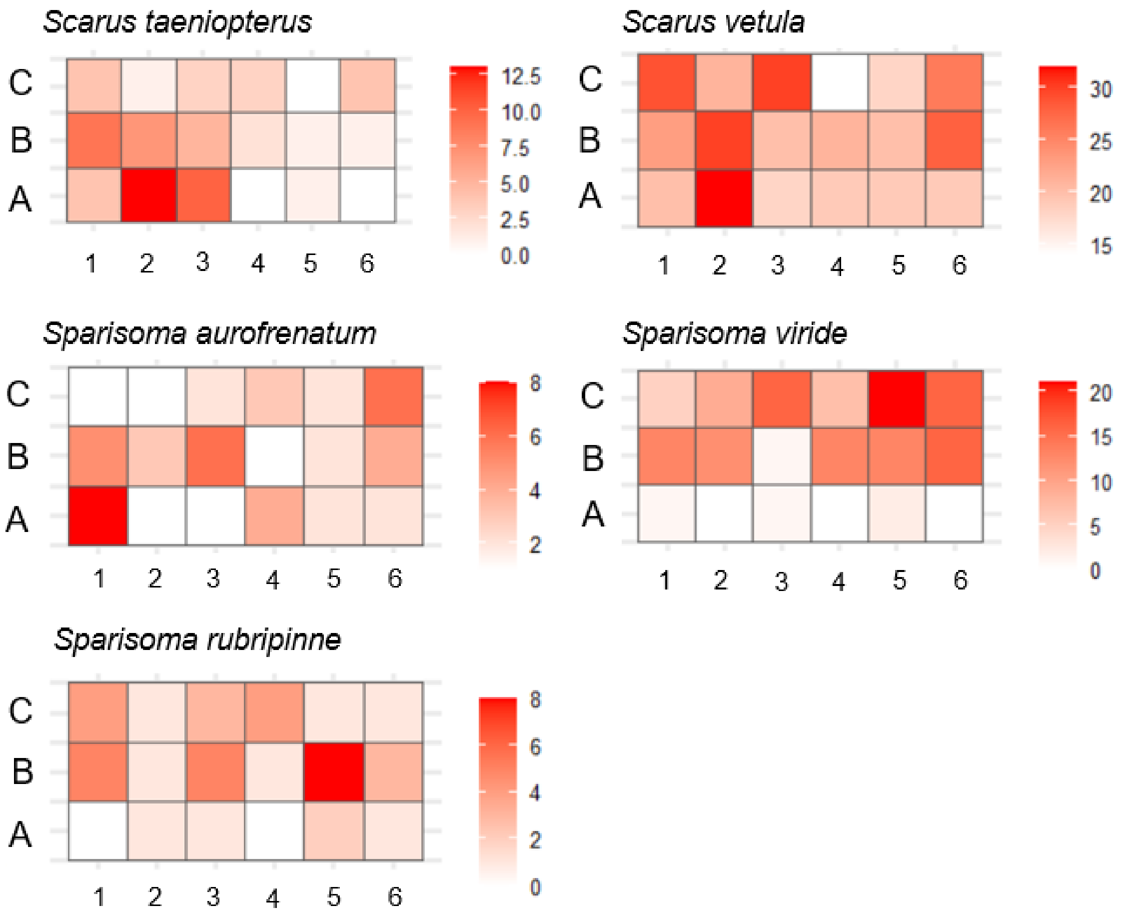

Figure 2.9. Variation in parrotfish abundance in each quadrat across the sampling grid for each species. The gradient scale represents the number of individuals and is relative to the total abundance for each species and goes from white (low abundance) to red (high abundance). Abundance data were collected during stationary point surveys.

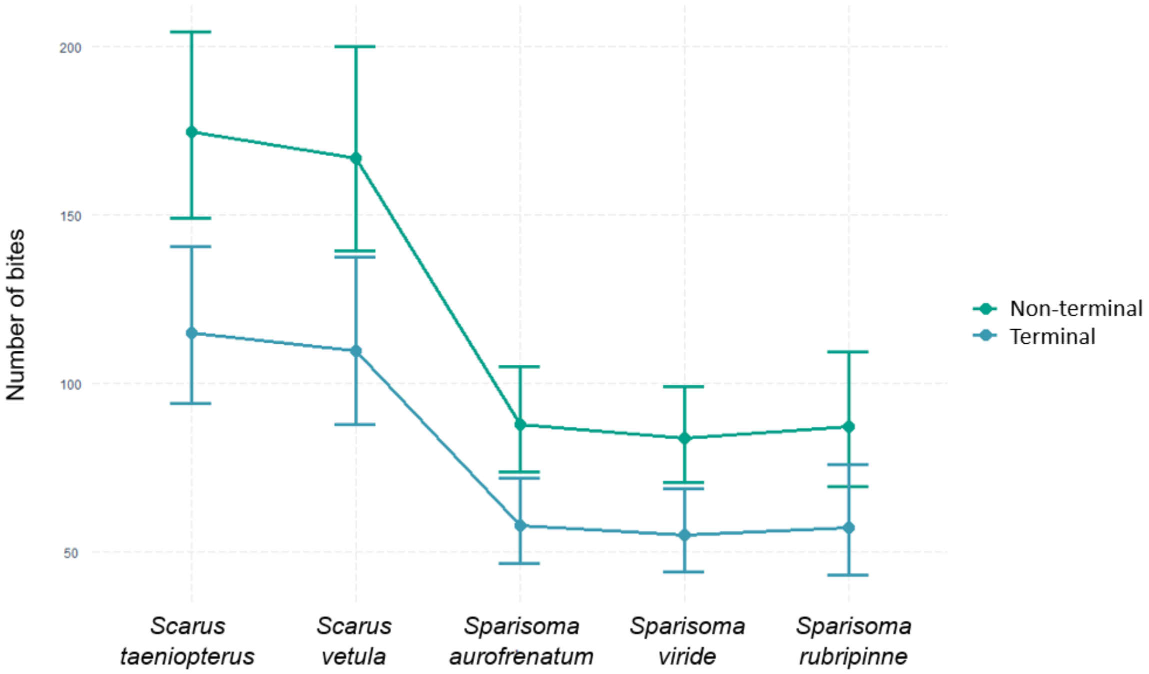

Figure 2.10. Variation in bite rate with ontogenetic phase for each species. Data were collected from feeding behaviour observations. We categorized ontogenetic phases into non-terminal phase individuals (juvenile and initial phase) and terminal phase individuals. Bite rate significantly varied with phase and species. Scarus taeniopterus: n = 22, Scarus vetula: n = 16, Sparisoma aurofrenatum: n = 18, Sparisoma viride: n = 19, Sparisoma rubripinne: n = 16.

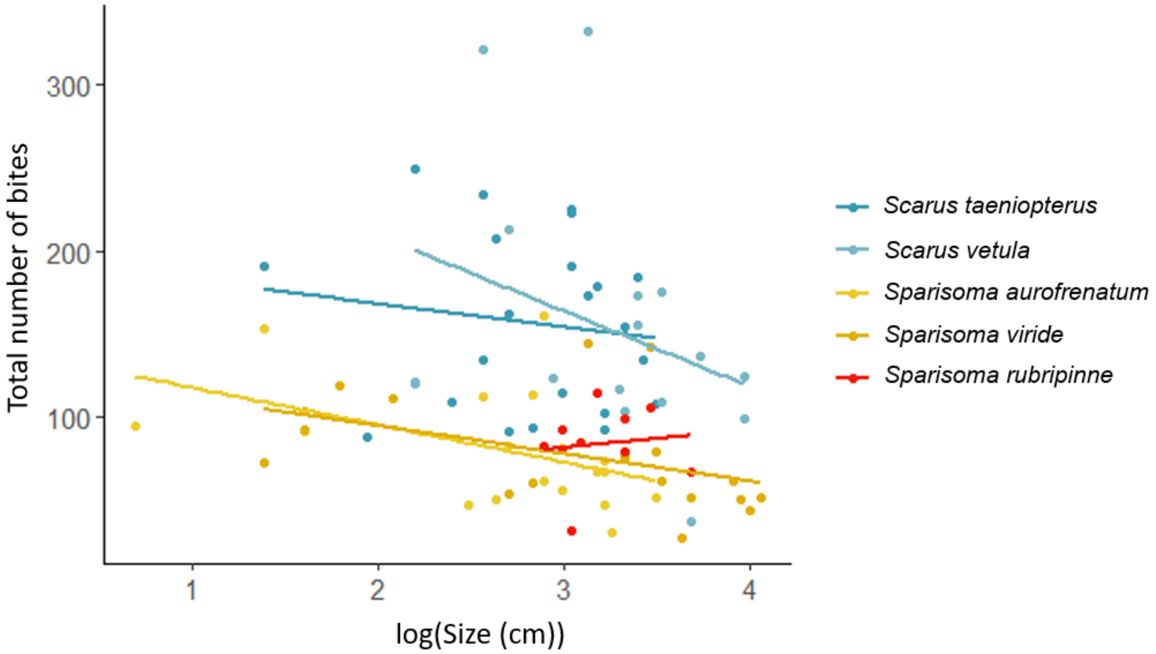

Figure 2.11. Variation in bite rate (total number of bites within the 10 minute feeding observations) with size for each species. Data were collected from feeding behaviour observations. Size data were log-transformed. Bite rate significantly varied with size and species. Bite rate decreased with size for all species except for *Sparisoma rubripinne*. *Scarus taeniopterus*: n = 22, *Scarus vetula*: n = 16, *Sparisoma aurofrenatum*: n = 18, *Sparisoma viride*: n = 19, *Sparisoma rubripinne*: n = 16

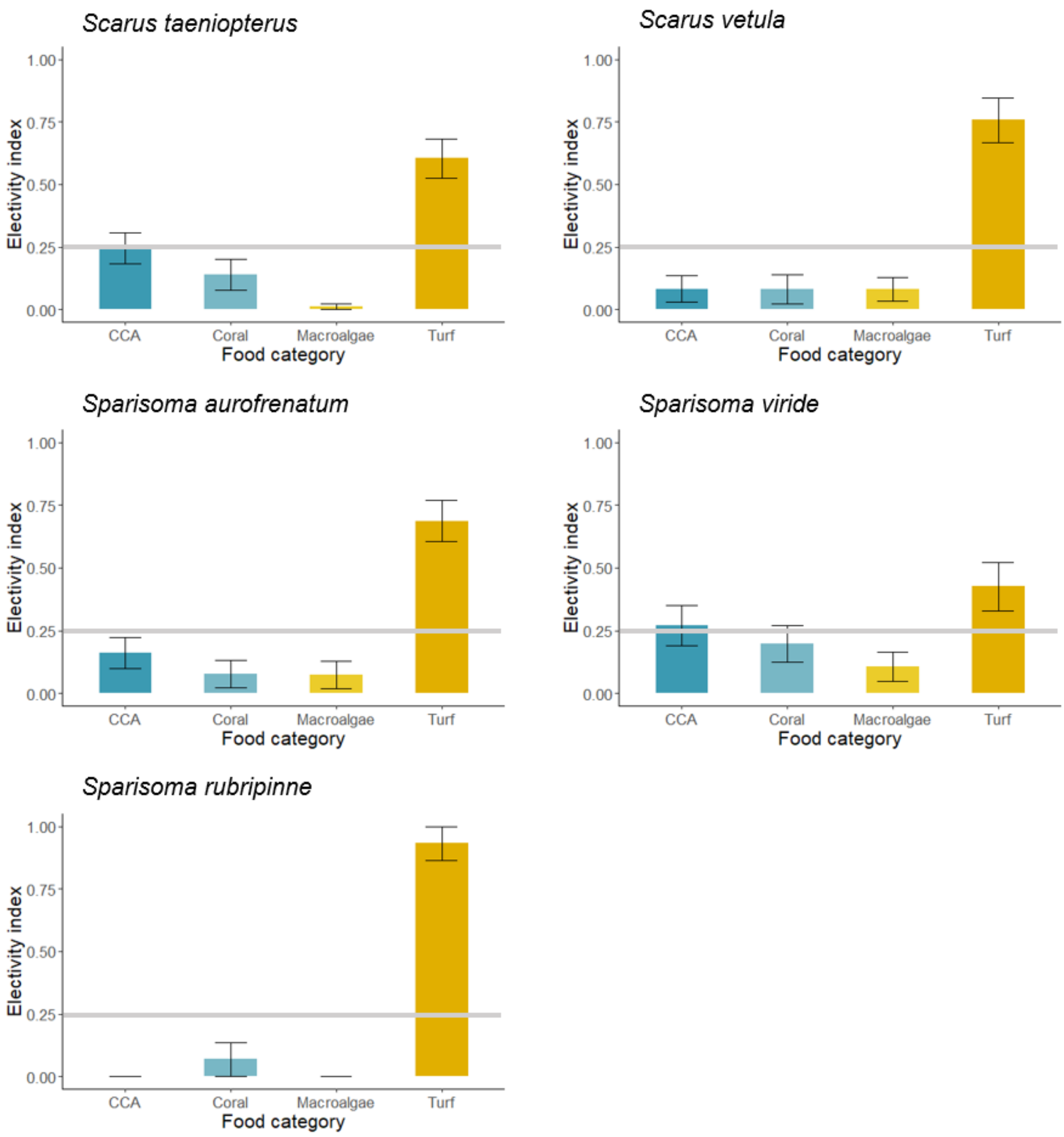

Figure 2.12. Electivity (α) for each food category for each species of parrotfish (+SE). Data were collected from feeding behaviour observations. Electivity indices were obtained by converting the proportion of bites taken on each diet item to Manly's electivity index. Grey line at α = 0.25 is the null expectation of equal selectivity for each food category based on its availability in the environment. Values above the grey line indicate preference for a particular food category, values below indicate avoidance. *Scarus taeniopterus*: n = 22, *Scarus vetula*: n = 16, *Sparisoma aurofrenatum*: n = 18, *Sparisoma viride*: n = 19, *Sparisoma rubripinne*: n = 16. Diet across all species was dominated by turf algae.

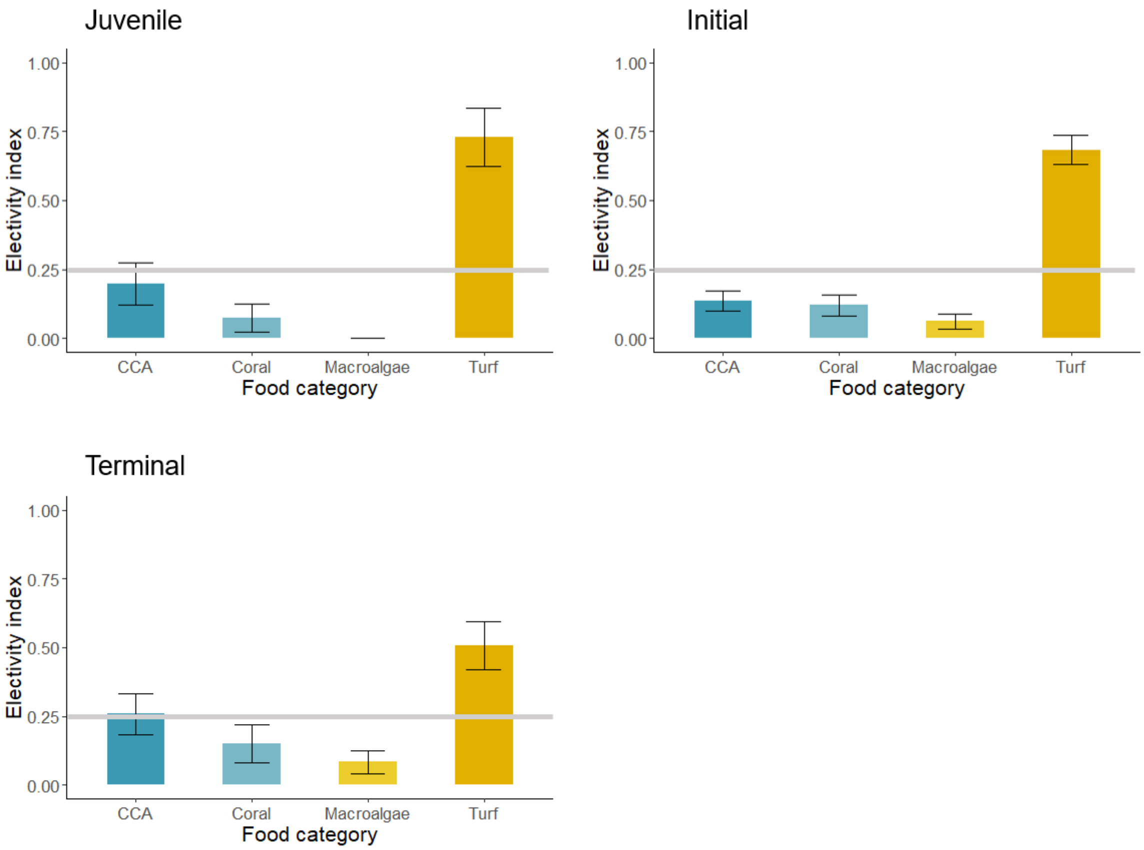

Figure 2.13. Electivity (α) for each food category for each ontogenetic phase (+SE). Data were collected from feeding behaviour observations. Electivity indices were obtained by converting the proportion of bites taken on each diet item to Manly's electivity index. Grey line at α = 0.25 is the null expectation of equal selectivity for each food category based on its availability in the environment. Values above the grey line indicate preference for a particular food category, values below indicate avoidance. Juvenile: n = 13, Initial: n = 52, Terminal: n = 20. Diet across all phases was dominated by turf algae.

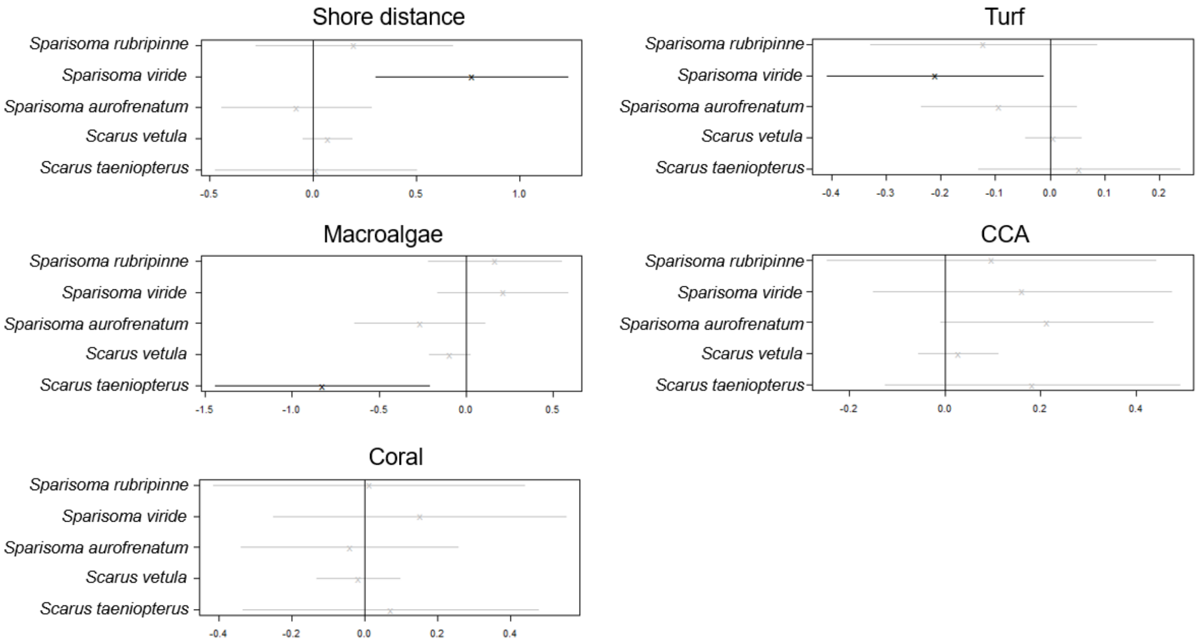

Figure 2.14. Correlation between environmental variables and species abundance. The model included two latent variables and five environmental variables. Significant estimates are highlighted in black.

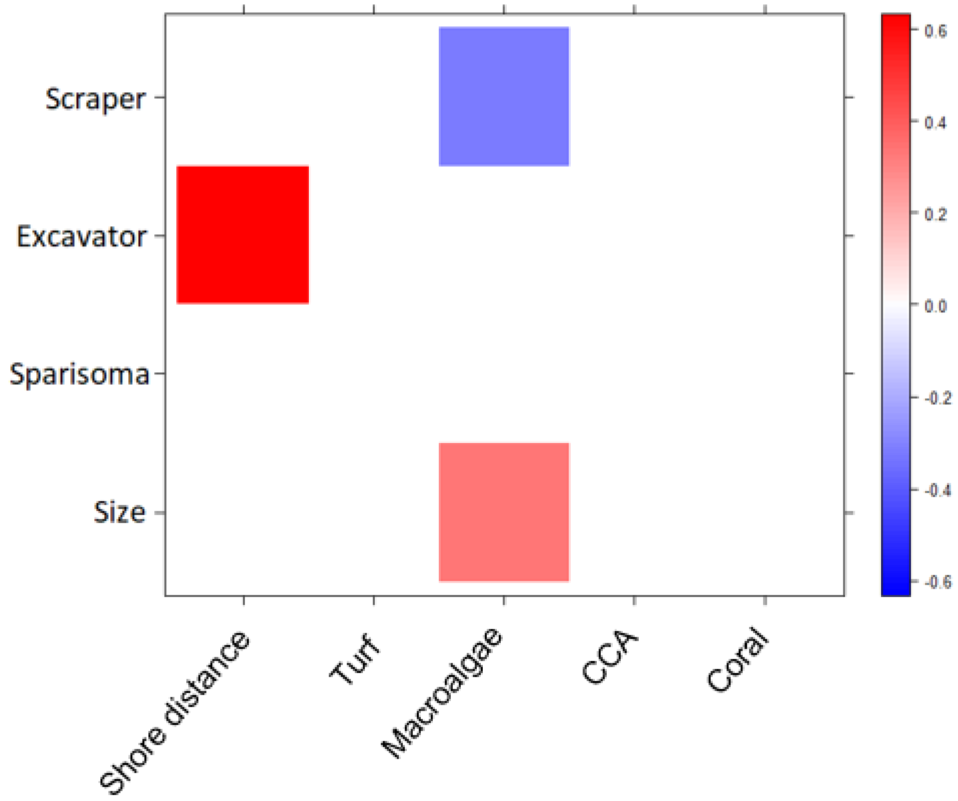

Figure 2.15. The effect of the interaction between environmental variables and species traits (fourth corner) on species abundance. The model included two latent variables and five environmental variables, as well as parrotfish average size, feeding mode and genus. Red colours represent positive interactions and blue colours represent negative interactions. Dark shading represents strong interaction while light shading represents weak interactions. Only significant estimates are shown. The colour scale indicates the values of the fourth-corner coefficients.

General conclusion

In this thesis, I first reviewed the extensive literature on the biological and ecological properties of parrotfishes as herbivores on coral reefs. I discussed the ongoing debate on the potential for parrotfishes to promote reef health and recovery through their grazing action. I thus focused my review on the factors that have been repeatedly identified in parrotfish research as important mediators of their ecological function. I examined the research addressing the role of species identity, ontogeny and size in parrotfish feeding behaviour. I also reviewed the results from studies that have investigated the role of environmental structure of the reef on parrotfish distribution and feeding behaviour. I then concluded that the established knowledge on parrotfish points to highly context-dependent mechanisms driving their capacity to fulfill their ecological function as herbivores

In our study of parrotfishes in a fringing reef of Barbados, located in a Marine Protected Area, we presented meaningful results on the dependence of parrotfish ecological function on the ecological context of the system. Notably, we found a relatively high abundance of parrotfishes and of large individuals within our study system, which hosted seven species of parrotfishes (two rare species, *Sparisoma chrysopterum* and *Scarus iseri*, were not included in our analyses). This supports the notion that protection from fishing can help preserve parrotfish communities and prevent loss of larger individuals in the community (Vallès et al. 2014, Vallès et al. 2015). These results are noteworthy, since the impact of parrotfish grazing and bioeroding activity increases with their size (Bonaldo et al. 2014). However, we also found almost complete dominance of turf algae in a reef that used to have significant levels of coral and CCA cover (Stearn et al. 1977) and is protected from fishing. These results speak to the historical degradation of the reefs of Barbados caused and exacerbated by deterioration in water quality and eutrophication, following the increase in urbanization and tourism in recent decades (Tomascik and Sander 1987, Bell and Tomascik 1994). The almost complete dominance of turf algae on the reef, coupled with the strong presence of parrotfishes, provides supporting evidence that parrotfish herbivory does not always positively impact coral communities (Mumby 2009, Russ et al. 2015, Carlson et al. 2017). Together, these results suggest that the potential for Marine Protected Areas to restore coral communities and prevent phase-shifts to algae dominated states in Barbados is hindered by environmental stressors unrelated to fishing pressure, but still highlight the importance of protection from fishing in preserving coral reef fish communities.

We also examined how species, size and phase influenced feeding rate and preferences. We found that bite rate varied significantly across species, and decreased with body size of individual fishes, mirroring the results from previous studies (Bruggemann et al. 1994, Van Rooij et al. 1996, Hoey 2018). We also found a significant effect of ontogeny on feeding rate, mirroring previous studies (Bruggemann et al. 1994, van Rooij et al. 1996, Bonaldo et al. 2006, Afeworki et al. 2013), but we recognize that its effect cannot be completely dissociated from the effect of body size.

In our investigation of parrotfish distribution across the reef, we detected patterns of spatial aggregation in two species, *Scarus taeniopterus* and *Sparisoma viride*, but not in the other three species. We also found species-specific associations with benthic composition and topography, marginally mediated by feeding mode and size, where abundance of *Sparisoma viride* was negatively associated with turf algae cover and positively correlated with distance from shore, and abundance of *Scarus taeniopterus* was negatively correlated with macroalgae cover. Although previous research has shown that environmental variables influence parrotfish distribution and grazing patterns (Howard et al. 2009, Nash et al. 2012, Bozec et al. 2013, Carlson et al. 2017, Yarlett et al. 2020), we also recognize that the species-specific nature of these responses, as well as the lack of diversity in benthic composition in our study system, suggest that we may be missing some key environmental drivers in explaining parrotfish distribution. For instance, data on predation risk, competition and territoriality, which have all been shown to influence parrotfish distribution and feeding behaviour (Nash et al. 2012, Adam et al. 2015b, Davis et al. 2017, Skinner et al. 2019), should be integrated in future studies to tease apart the main factors driving these mechanisms. Moreover, little is known about parrotfish macronutrient intake (Clements and Choat 2018), but knowledge of parrotfish nutritional needs should be further investigated and integrated in analyses of feeding behaviour and associations between benthic composition and parrotfish distribution.

While there is a wealth of research on parrotfish ecological function, there are relatively few studies such as our own that explore multiple drivers of herbivory and species distribution, as well as their interaction. Our study is also an example of how spatially explicit study designs can improve our understanding of these mechanisms. We used a grid-like design with quadrats of areas that allowed us to assess benthic composition and feeding behaviour at an ecologically relevant scale for parrotfishes, since the quadrat areas approximated parrotfish territory size. Overall, the results of our study speak to the variable nature of parrotfish feeding behaviour and indicate that generalized categorizations of parrotfish feeding modes need to be reconsidered within the ecological context of study systems. This research improves our understanding of the relationship between parrotfish ecological function and reef recovery in Barbados and can consequently inform local conservation efforts in preserving coral reef communities.

References

Adam, T., Burkepile, D., Ruttenberg, B., & Paddack, M. (2015a). Herbivory and the resilience of caribbean coral reefs: Knowledge gaps and implications for management. *Marine Ecology Progress Series*, 520, 1-20.

Adam, T., Kelley, M., Ruttenberg, B., & Burkepile, D. (2015b). Resource partitioning along multiple niche axes drives functional diversity in parrotfishes on Caribbean coral reefs. *Oecologia*, 179(4), 1173-85.

Adam, T.C., Duran, A., Fuchs, C.E., Roycroft, M.V., Rojas, M.C., Ruttenberg, B.I., & Burkepile, D.E. (2018). Comparative analysis of foraging behavior and bite mechanics reveals complex functional diversity among Caribbean parrotfishes. *Marine Ecology Progress Series*, 597, 207-220.

Allard, P. (1994). *Changes in coral community structure in barbados : effects of eutrophication and reduced grazing pressure.* (Master's Thesis, McGill University). eScholarship. https://escholarship.mcgill.ca/concern/theses/6d56zx44v

Afeworki, Y., Zekeria, Z. A., Videler, J.J., & Bruggemann, J.H. (2013). Food intake by the parrotfish scarus ferrugineus varies seasonally and is determined by temperature, size and territoriality. *Marine Ecology Progress Series*, 489, 213–224.

Afeworki, Y., Videler, J.J., Tekle, F.Y., Kibrom, H.E., & Bruggemann, H. (2017). Alternative male mating tactics of the endemic red sea parrotfish scarus ferrugineus. *Journal of Fish Biology*, 91(2), 679–685.

Arnold, S., Steneck, R., & Mumby, P. (2010). Running the gauntlet: Inhibitory effects of algal turfs on the processes of coral recruitment. *Marine Ecology Progress Series*, 414, 91-105.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1-48. doi:10.18637/jss.v067.i01.

Bell, P.R.F., & Tomascik, T. (1994). The demise of the fringing coral reefs of Barbados and of regions in the Great Barrier Reef (GBR) lagoon-impacts of eutrophication. *Oceanographic Literature Review*, 8, 688.

Bellwood, D.R. (1985). *The functional morphology, systematics and behavioural ecology of parrotfishes (family Scaridae)*. [PhD dissertation, James Cook University]. ResearchOnline.

Bellwood, D., & Choat, J. (1990). A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. *Environmental Biology of Fishes*, 28, 189-214.

Bellwood, D., Hoey, A., Ackerman, J., & Depczynski, M. (2006). Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. *Global Change Biology*, 12(9), 1587-1594.

Bellwood, D., Hoey A., & Hughes, T. (2012). Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. *Proceedings of the Royal Society B: Biological Sciences,* 279, 1621–1629.

Bennett, S., & Bellwood, D.R. (2011). Latitudinal variation in macroalgal consumption by fishes on the Great Barrier Reef. *Marine Ecology Progress Series*, 426, 241−252.

Bonaldo, R.M., Krajewski, J.P., Sazima, C., & Sazima, I. (2006). Foraging activity and resource use by three parrotfish species at Fernando de Noronha Archipelago, tropical West Atlantic. *Marine Biology*, 149, 423–433.

Bonaldo R.M., & Bellwood D.R. (2008). Size-dependent variation in the functional role of the parrotfish Scarus rivulatus on the Great Barrier Reef, Australia. *Marine Ecology Progress Series*, 360, 237–244.

Bonaldo, R.M., Hoey, A.S., & Bellwood, D.R. (2014). The ecosystem roles of parrotfishes on tropical reefs. *Oceanography and Marine Biology - An Annual Review*, 52, 81–132.

Bozec, Y., Yakob, L., Bejarano, S., & Mumby, P. (2013). Reciprocal facilitation and non-linearity maintain habitat engineering on coral reefs. *Oikos*, 122(3), 428-440.

Brown, A.M, Warton, D.I, Andrew, N.R., Binns, M., Cassis, G., & Gibb, H. (2014). The fourth-corner solution – using predictive models to understand how species traits interact with the environment. *Methods in Ecology and Evolution*, 5, 344–352.

Bruggemann, J.H., Kuyper, M.W.M., Breeman, A.M. (1994). Comparative analysis of foraging and habitat use by the sympatric Caribbean parrotfish Scarus vetula and Sparisoma viride (Scaridae). *Marine Ecology Progress Series*, 112, 51–66.

Bruggemann, J.H., van Kessel, A.M., van Rooij, J.M., & Breeman, A.M. (1996). Bioerosion and sediment ingestion by the Caribbean parrotfish *Scarus vetula* and *Sparisoma viride*: implications of fish size, feeding mode and habitat use. *Marine Ecology Progress Series*, 134(1-3), 59–71.

Bruno, J.F., & and Bertness, M.D., (2001). Habitat modification and facilitation in benthic marine communities. In: Bertness, M.D. et al. (Eds.), *Marine community ecology* (pp. 201–218). Sinauer.

Bruno, J.F., Cote, I.M., & Toth, L.T. (2019). Climate change, coral loss, and the curious case of the parrotfish paradigm: why don't Marine Protected Areas improve reef resilience? In: Carlson, C.A., & Giovannoni, S.J. (Eds.), Annual Review of Marine Science Vol 11 (pp. 307-334).

Burke, L.M., & Maidens, J. (2004). Reefs at risk in the Caribbean. World Resources Institute.

Burke, L.M., Reytar, K., Spalding, M., & Perry, A. (2011). Reefs at Risk Revisited. World Resources Institute.

Burkepile, D. (2012). Context-dependent corallivory by parrotfishes in a caribbean reef ecosystem. *Coral Reefs: Journal of the International Society for Reef Studies*, 31(1), 111-120.

Burkepile, D.E. & Hay, M.E. (2008). Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proceedings of the National Academy of Sciences USA*, 105, 16201−16206.

Burkepile, D.E., & Hay, M.E. (2011). Feeding complementarity versus redundancy among herbivorous fishes on a caribbean reef. *Coral Reefs*, 30(2), 351–362.

Burkepile, D., Allgeier, J., Shantz, A., Pritchard, C., Lemoine, N., Bhatti, L., & Layman, C. (2013). Nutrient supply from fishes facilitates macroalgae and suppresses corals in a caribbean coral reef ecosystem. *Scientific Reports*, 3(1).

Cardoso, S.C., Soares, M.C., Oxenford, H.A., & Côté, I.M. (2009). Interspecific differences in foraging behaviour and functional role of Caribbean parrotfish. *Marine Biodiversity Records*, 2, e148.

Carlson, P.M., Davis, K., Warner, R.R., & Caselle, J.E. (2017). Fine-scale spatial patterns of parrotfish herbivory are shaped by resource availability. *Marine Ecology Progress Series*, 577, 165–176

Carpenter, R.C. (1988). Mass mortality of a Caribbean sea urchin: immediate effects on community metabolism and other herbivores. *Proceedings of the National Academy of Sciences USA*, 85, 511−514.

Choat, J.H. (1991). The biology of herbivorous fishes on coral reefs. In: P.F. Sale (Ed.), *The Ecology of Fishes on Coral Reefs* (pp. 120–155). Academic Press, San Diego.

Choat, J.H., & Robertson, D.R. (1975). Protogynous hermaphroditism in fishes of the family Scaridae. In: R. Reinboth (Ed.). *Intersexuality in the Animal Kingdom* (pp: 263–283). Springer-Verlag, Heidelberg.

Clements, K.D. & Choat, H. (2018). Nutritional ecology of parrotfishes. In Hoey, A.S., & Bonaldo, R.M. (Eds.), *Biology of Parrotfishes* (pp. 42-68). Boca Raton, FL: CRC Press.

Connell, S.D., Foster, M.S., & Airoldi, L. (2014). What are algal turfs? Towards a better description of turfs. *Marine Ecology Progress Series*, 495, 299–307.

Davis, K., Carlson, P.M., Bradley, D., Warner, R.R., & Caselle, J.E. (2017). Predation risk influences feeding rates but competition structures space use for a common pacific parrotfish. *Oecologia*, 184(1), 139–149.

Dickens, L.C., Goatley, C.H.R., Tanner, J.K., & Bellwood, D.R. (2011). Quantifying relative diver effects in underwater visual censuses. *PLOS ONE,* 6(4): e18965.

Done, T.J., Ogden, J.C., Wiebe, W.J., & Rosen, B.R. (1996). Biodiversity and ecosystem function of coral reefs. In: Mooney, H.A., Cushman, J.H., Medina, E., Sala, O.E., Schulze, E.-D. (Eds.), *Functional Roles of Biodiversity: A Global Perspective*. SCOPE 1996, John Wiley and Sons.

Dray, S., Dufour, A. (2007). The ade4 Package: Implementing the Duality Diagram for Ecologists. *Journal of Statistical Software*, 22(4), 1–20.

Edgar, G.J., Barrett, N.S., & Morton, J. (2004). Biases associated with the use of underwater visual census techniques to quantify the density and size-structure of fish populations. *Journal of Experimental Marine Biology and Ecology*, 308(2), 269-290.

Feitosa, J.L.L, & Ferreira, B.P. (2015). Distribution and feeding patterns of juvenile parrotfish on algal-dominated coral reefs. *Marine Ecology*, 36, 462–474.

Ferguson, A. M., E. S. Harvey, & N. A. Knott. (2017). Herbivore abundance, grazing rates and feeding pathways on Australian temperate reefs inside and outside marine reserves: How are things on the west coast? *Journal of Experimental Marine Biology and Ecology*, 493, 49–56.

Gill, D.A., Oxenford, H.A., Turner, R.A., & Schuhmann, P.W. (2019). Making the most of data-poor fisheries: Low cost mapping of small island fisheries to inform policy. *Marine Policy,* 101, 198-207.

Goecker, M.E., Heck Jr., K.L., & Valentine, J.F. (2005). Effects of nitrogen concentrations in turtlegrass Thalassia testudinum on consumption by the bucktooth parrotfish Sparisoma radians. *Marine Ecology Progress Series*, 286, 239–248.

Graham, N., Bellwood, D., Cinner, J., Hughes, T., Norström, A., & Nyström, M. (2013). Managing resilience to reverse phase shifts in coral reefs. *Frontiers in Ecology and the Environment*, 11(10), 541-548.

Harborne, A. R., Mumby, P. J., & Ferrari, R. (2012). The effectiveness of different meso-scale rugosity metrics for predicting intra-habitat variation in coral-reef fish assemblages. *Environmental Biology of Fishes*, 94(2), 431–442.

Harris, J.L., Lewis, L.S., & Smith., J.E. (2015). Quantifying scales of spatial variability in algal turf assemblages on coral reefs. *Marine Ecology Progress Series*, 532, 41–57.

Hoegh-guldburg, O., Takabayashi, M., & Moreno, G. (1997). The impact of long-term nutrient enrichment on coral calcification and growth. *Proceedings of the 8th International Coral Reef Symposium*, 1, 861–866.

Hoey, A.S., & Bonaldo, R. (Eds.). (2018). Biology of parrotfishes. Boca Raton, FL: CRC Press.

Hoey, A.S. (2018). Feeding in parrotfishes: the influence of species, body size, and temperature. In Hoey, A.S., & Bonaldo, R.M. (Eds.), *Biology of Parrotfishes* (pp. 119-133). Boca Raton, FL: CRC Press.

Howard, K.G., Schumacher, B.D., & Parrish, J.D. (2009). Community structure and habitat associations of parrotfishes on Oahu, Hawaii. *Environmental Biology of Fishes*, 85(2), 175–186.

Hughes, T.P. (1994). Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*, 265, 1547–1551.

Humann, P., & DeLoach, N. (2014). Reef fish identification: florida, caribbean, bahamas (Fourth, Ser. Reef set, bk.1). New World Publications.

Humphries, A.T., McClanahan, T.R. & McQuaid, C.D. (2014). Differential impacts of coral reef herbivores on algal succession in Kenya. *Marine Ecology Progress Series*, 504, 119–132.

ICRI, 2013. Recommendation on addressing the decline in coral reef health throughout the wider Caribbean: the taking of parrotfish and similar herbivores. Adopted at 28th General Meeting of the International Coral Reef Initiative. International Coral Reef Initiative, Belize.

Jayewardene, D. (2009). A factorial experiment quantifying the influence of parrotfish density and size on algal reduction on Hawaiian coral reefs. *Journal of Experimental Marine Biology and Ecology*, 375(1–2), 64-69.

Jones, C. G., Lawton, J. H., & Shachak, M. (1997). Positive and negative effects of organisms as ecosystem engineers. *Ecology*, 78, 1946–1957.

Kelleher, G., Kenchington, R. A., & Great Barrier Reef Marine Park Authority. (1992). Guidelines for establishing marine protected areas (Ser. A marine conservation and development report). IUCN in collaboration with Great Barrier Reef Marine Park Authority.

Kohler, K.E., & Gill, S.M. (2006). Coral Point Count with Excel extensions (CPCe): A visual basic program for the determination of coral and substrate coverage using random point count methodology. *Computers and Geosciences*, 32(9), 1259-1269, doi:10.1016/j.cageo.2005.11.009.

Kramer, K.L., & Heck, K.L. (2007). Top-down trophic shifts in Florida Keys patch reef marine protected areas. *Marine Ecology Progress Series*, 349, 111–123.

Kulbicki, M., & Sarramégna, S. (1999). Comparison of density estimates derived from strip transect and distance sampling for underwater visual censuses: a case study of Chaetodontidae and Pomacanthidae. *Aquatic Living Resources*, 12(5), 315-325.

Lefèvre, C.D., & Bellwood, D.R. (2011). Temporal variation in coral reef ecosystem processes: herbivory of macroalgae by fishes. *Marine Ecology Progress Series*, 422, 239−251.

Lessios, H.A. (2016). The great Diadema antillarum die-off: 30 years later. *Annual Review of Marine Science*, 8(1), 267-283.

Lewis, J.B., 1960. The coral reefs and coral communities of Barbados, W.I. *Canadian Journal of Zoology*, 38, 1133-1145.

Lewis, S.M. (1985). Herbivory on coral reefs: algal susceptibility to herbivorous fishes. *Oecologia*, 65, 370–375.

Lewis, S.M. (1986). The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecological Monographs*, 56, 183–200.

Lokrantz, J., Nyström, M., Thyresson, M., & Johansson, C. (2008). The nonlinear relationship between body size and function in parrotfishes. *Coral Reefs*, 27, 967–974.

Mah, A.J., & Stearn, C.W. (1986). The effect of Hurricane Allen on the Bellairs fringing reef, Barbados. *Coral Reefs*. 4, 169-176.

Manly, B.F.J., Miller, P., & Cook, L.M. (1972). Analysis of a selective predation experiment. *American Naturalist*, 106, 719−736.

Mann, G.S. (1994). *Distribution, abundance and life history of the reef coral Favia fragum (Esper) in Barbados: effects of eutrophication and of the black sea urchin Diadema antillarum (Philippi)*. [Master's Thesis, McGill University]. eScholarship. https://escholarship.mcgill.ca/concern/theses/5m60qs924

Mantyka, C.S., & Bellwood, D.R. (2007). Macroalgal grazing selectivity among herbivorous coral reef fishes. *Marine Ecology Progress Series*, 352, 177–185.

McAfee, S.T., & Morgan, S.G. (1996). Resource use by five sympatric parrotfishes in the San Blas Archipelago, Panama. *Marine Biology*, 125, 427–437.

McClanahan, T. R. (2008). Response of the coral reef benthos and herbivory to fishery closure management and the 1998 ENSO disturbance. *Oecologia*, 155, 169–177.

McClanahan, T., Nugues, M., & Mwachireya, S. (1994). Fish and sea urchin herbivory and competition in kenyan coral reef lagoons: The role of reef management. *Journal of Experimental Marine Biology and Ecology*, 184(2), 237-254.

McClanahan, T. R., N. A. Muthiga, & R. A. Coleman. (2011). Testing for top-down control: Can post-disturbance fisheries closures reverse algal dominance? *Aquatic Conservation: Marine and Freshwater Ecosystems*, 21, 658–675.

McConney, P., Phillips, T., Nembhard, N., & Lay, M. (2017). Caribbean fisherfolk engage the small-scale fisheries guidelines. In: Jentoft, S., Chuenpagdee, R., Barragán-Paladines, M., Franz N. (Eds.), *The Small-Scale Fisheries Guideline*s. MARE Publication Series, vol 14. Springer, Cham.

Miller, M.W. (1998). Coral/seaweed competition and the control of reef community structure within and between latitudes. *Oceanography and Marine Biology: An Annual Review*, 36, 65–96.

Miller, M.W., Hay, M.E., Miller, S.L., Malone, D., Sotka, E.E., & Szmant, A.M. (1999). Effects of nutrients versus herbivores on reef algae: a new method for manipulating nutrients on coral reefs. *Limnology and Oceanography*, 44(8), 1847–1861.

Moberg, F., & Folke, C. (1999). Ecological goods and services of coral reef ecosystems. *Ecological economics*, 29(2), 215-233.

Mumby, P.J. (2006). The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. Ecological Applications, 16, 747–769.

Mumby, P.J. (2009). Phase shifts and the stability of macroalgal communities on caribbean coral reefs. *Coral Reefs*, 28(3), 761–773.

Mumby, P.J., & Wabnitz, C.C.C. (2002). Spatial patterns of aggression, territory size, and harem size in five sympatric caribbean parrotfish species. *Environmental Biology of Fishes*, 63(3), 265–279.

Mumby, P.J. & Harborne, A.R. (2010) Marine reserves enhance the recovery of corals on Caribbean reefs. *PLoS One*, 5, e8657.

Nash, K.L., Graham, N.A.J., Januchowski-Hartley, F.A., & Bellwood, D.R. (2012). Influence of habitat condition and competition on foraging behaviour of parrotfishes. *Marine Ecology Progress Series*, 457, 113–124.

Niku, J., Hui, F.K.C., Taskinen, S., & Warton, D.I. (2019). gllvm: Fast analysis of multivariate abundance data with generalized linear latent variable models in r. Methods in Ecology and Evolution, 10(12), 2173–2182. https://doi.org/10.1111/2041-210X.13303

Niku, J., Brooks, W., Herliansyah, R., Hui, F.K.C., Taskinen, S., Warton, D.I., & van der Veen, B. (2020). gllvm: Generalized Linear Latent Variable Models. R package version 1.2.3. https://CRAN.R-project.org/package=gllvm

Nyström, M., Graham, N.A.J., Lokrantz, J., & Norström, A.V. (2008). Capturing the cornerstones of coral reef resilience: linking theory to practice. *Coral Reefs*, 27(4), 795-809.

Ogden, J.C. & Lobel, P.S. (1978). The role of herbivorous fishes and urchins in coral reef communities. *Environmental Biology of Fishes*, 3, 49−63.

Ong, L., & Holland, K. (2010). Bioerosion of coral reefs by two Hawaiian parrotfishes: Species, size differences and fishery implications. *Marine Biology*, 157, 1313-1323.

Pauly D., Christensen, V., Guénette, S., Pitcher, T.J., Sumaila, R.U., Walters, C.J, Watson, R., & Zeller, D. (2002). Towards sustainability in world fisheries. *Nature,* 418, 689−695.

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Randall, J.E. (1967). Food habits of reef fishes of the West Indies. *Studies in Tropical Oceanography*, 5, 665–847.

Rassweiler, A., Dubel, A.K., Hernan, G., Kushner, D.J., Caselle, J.E., Sprague, J.L., . . . Miller, R.J. (2020). Roving divers surveying fish in fixed areas capture similar patterns in biogeography but different estimates of density when compared with belt transects. *Frontiers in Marine Science*, doi:http://dx.doi.org/10.3389/fmars.2020.00272.

Robertson, D.R., & Warner, R.R. (1978). Sexual patterns in the labroid fishes of the Western Caribbean, II, the parrotfishes (Scaridae). *Smithsonian Contributions to Zoology*, 1–26.

Russ, G.R. (2002). Marine reserves as reef fisheries management tools: Yet another review. In: Sale, P. (Ed.), *The Ecology of Fish on Coral Reefs* (pp. 421–444). San Diego, California: Academic Press.

Russ, G.R., Questel, S.L., Rizzari, J. &, Alcala, A. (2015). The parrotfish-coral relationship: refuting the ubiquity of a prevailing paradigm. *Marine Biology*, 162, 2029−2045.

Russ, G.R., Rizzari, J.R., Abesamis, R.A., & Alcala, A.C. (2020). Coral cover a stronger driver of reef fish trophic biomass than fishing. *Ecological Applications*, e02224.

Ruttenberg, B.I., Adam, T.C., Duran, A., & Burkepile, D.E. (2019). Identity of coral reef herbivores drives variation in ecological processes over multiple spatial scales. *Ecological Applications: A Publication of the Ecological Society of America*, 29(4), 01893.

Santos, H.F., Carmo, F.L., Duarte, G., Dini-Andreote, F., Castro, C.B., Rosado, A.S., et al. (2014). Climate change affects key nitrogen-fixing bacterial populations on coral reefs. *ISME J.*, 8, 2272–2279.

Sammarco, P.W. (1983). Effects of fish grazing and damselfish territoriality on coral reef algae. I. Algal community structure. *Marine Ecology Progress Series*, 13, 1–14.

Skinner, C., Newman, S.P., Box, S., Narozanski, A., & Polunin, N.V.C. (2019). Chronic spearfishing may indirectly affect reef health through reductions in parrotfish bite rates. *Journal of Fish Biology*, 94(4), 585–594.

Smith, S.V. (1978). Coral-reef area and the contribution of reefs to processes and resources of the world’s oceans. *Nature,* 273, 225–226.

Smith, J.E., Hunter, C.L., & Smith, C.M. (2010). The effects of top-down versus bottom-up control on benthic coral reef community structure. *Oecologia*, 163(2), 497–507.

Smith, K., Quirk-Royal, B.E., Drake-Lavelle, K., & Childress, M. (2018). Influences of ontogenetic phase and resource availability on parrotfish foraging preferences in the Florida Keys, FL (USA). *Marine Ecology Progress Series*, 603, 175-187.

Stachowicz, J. (2001). Mutualism, facilitation, and the structure of ecological communities: Positive interactions play a critical, but underappreciated, role in ecological communities by reducing physical or biotic stresses in existing habitats and by creating new habitats on which many species depend. *Bioscience*, 51(3), 235-246.

Stanley, D.R., & Wilson, C.A. (1995). Effect of scuba divers on fish density and target strength estimates from stationary dual-beam hydroacoustics. *Transactions of the American Fisheries Society*, 124, 946–949.

Stearn, C.W., Scoffin, T.P., & Martindale, W. (1977). Calcium carbonate budget of a fringing reef on the West coast of Barbados. *Bulletin of Marine Science*, 27(3), 479-510.

Thornborough, K.J., & Davies, P.J. (2011). Reef Flats. Encyclopedia of Modern Coral Reefs. Springer.

Tomascik, T., & Sander, F. (1987). Effects of eutrophication on reef-building corals : ii. structure of scleractinian coral communities on fringing reefs, barbados, west indies. *Marine Biology : International Journal on Life in Oceans and Coastal Waters*, 94(1), 53–75.

Tosic, M., Bonnell, R.B., Dutilleul, P., & Oxenford, H.A. (2009). Runoff water quality, land use and environmental impacts on the Bellairs Fringing Reef, Barbados. In: Yang, Y. (Ed.), *Remote Sensing and Geospatial Technologies for Coastal Ecosystem Assessment and Management*. (pp. 521-553). Springer.

Vallès, H., & Oxenford, H.A. (2014). Parrotfish size: a simple yet useful alternative indicator of fishing effects on Caribbean reefs? PLoS One 9(1), e86291.

Vallès, H., Gill, D., & Oxenford, H. A. (2015). Parrotfish size as a useful indicator of fishing effects in a small caribbean island. *Coral Reefs :Journal of the International Society for Reef Studies*, 34(3), 789–801.

van Rooij, J.M., Kroon, F.J., & Videler, J.J. (1996). The social and mating system of the herbivorous reef fish Sparisoma viride: one-male versus multi-male groups. *Environmental Biology of Fishes*, 47, 353–378.

Verges, A., Tomas, F., & Ballesteros, E. (2012). Interactive effects of depth and marine protection on predation and herbivory patterns. *Marine Ecology Progress Series*, 450, 55–65.

Wainwright, P., & Price, S. (2018). Innovation and diversity of the feeding mechanism in parrotfishes. In: Hoey, A.S. & Bonaldo, R.M. (Eds.), *Biology of Parrotfishes* (pp. 26-41). Boca Raton, FL: CRC Press.

Ward, S., & Harrison, P.L. (1997). The effects of elevated nutrient levels in the settlement of coral larvae during the ENCORE experiment, Great Barrier Reef, Australia. In: Lessios, H.A., Macintyre, I.G (Eds.), *Proceedings of the Eighth International Coral Reef Symposium*. (pp. 891–896). Smithsonian Institute Press, Balboa, Panama.

Warner, R.R., & Downs, I.F. (1977). Comparative life histories: Growth vs reproduction in normal males and sexchanging hermaphrodites of the Striped parrotfish Scarus croicensis. *Proceedings of the Third International Coral Reef Symposium,* 1, 275-281.

Warton, D.I., Blanchet, F.G., O’Hara, R.O.O., Taskinen, S., Walker, S.C., & Hui, F.K.C. (2015). So many variables: joint modeling in community ecology. *Trends in Ecology and Evolution*, 30, 766–779.

Wilkinson, C. (2000). Status of Coral Reefs of the World: 2000. Australian Institute of Marine Science, Townsville, Australia.

Wilkinson, C.R., & Sammarco, P.W. (1983). Effects of fish grazing and damselfish territoriality on coral reef algae. II. Nitrogen fixation. *Marine Ecology Progress Series*, 13, 15–19.

Yabsley, N.A., Olds, A.D., Connolly, R.M., Martin, T.S.H., Gilby, B.L., Maxwell, P.S., . . . Schlacher, T.A. (2016). Resource type influences the effects of reserves and connectivity on ecological functions. *Journal of Animal Ecology*, 85, 437–444.

Yarlett, R.T., Perry, C.T., Wilson, R.W., & Harborne, A.R. (2020). Inter-habitat variability in parrotfish bioerosion rates and grazing pressure on an indian ocean reef platform. *Diversity*, 12(381).

Supplementary material

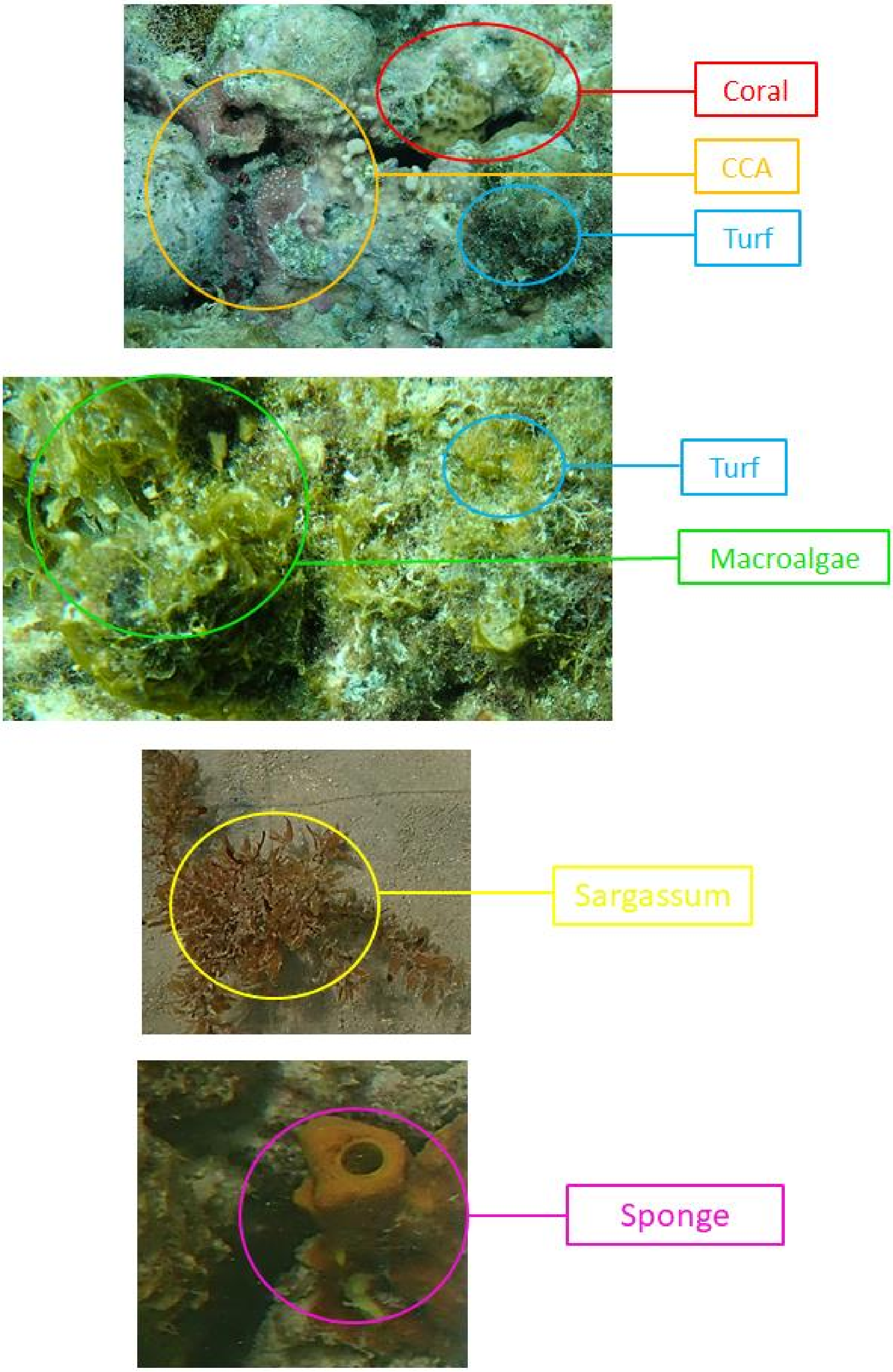

Figure S1. Sample images of the different benthic cover categories found in the reef. CCA = coralline algae.

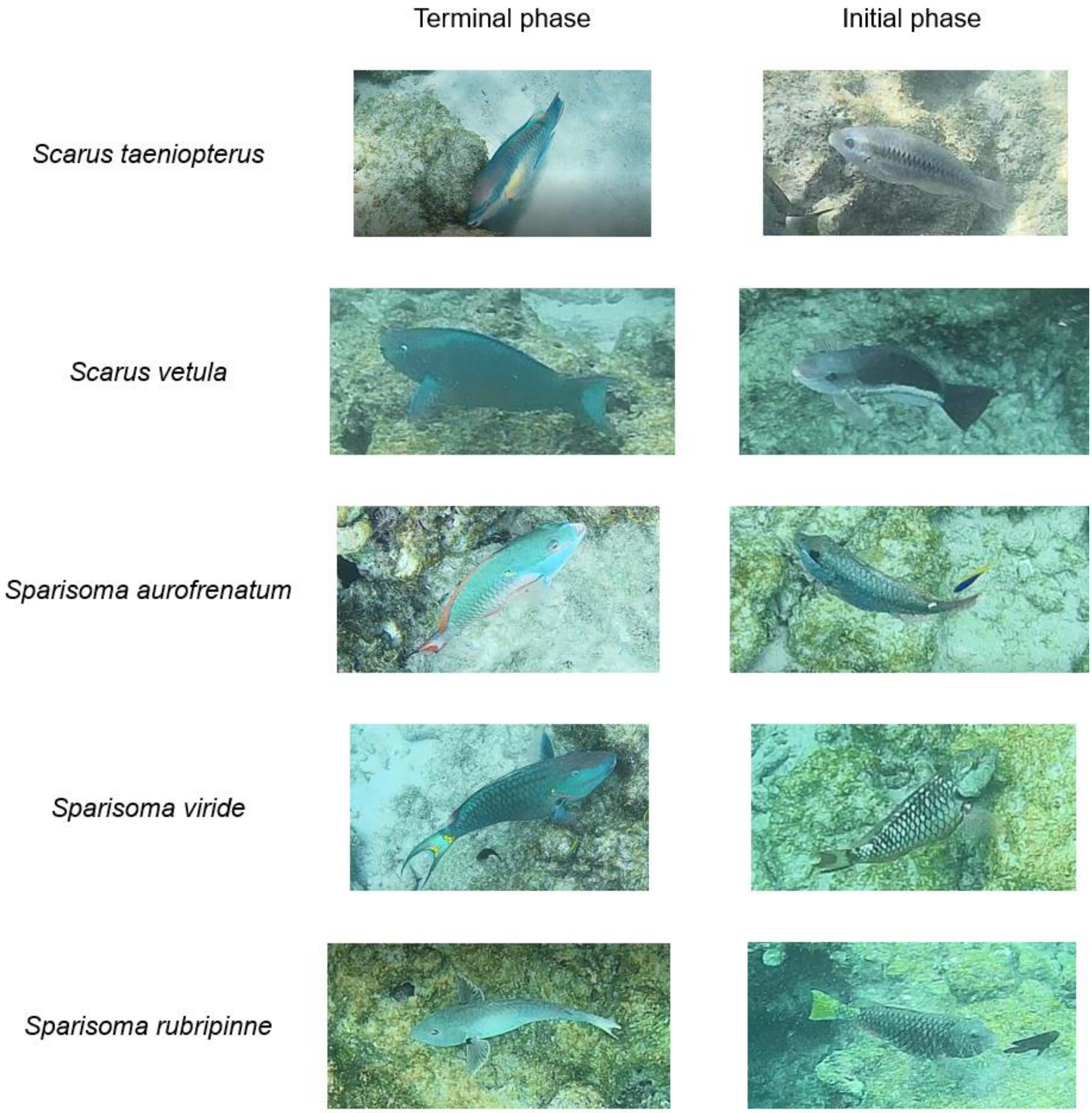

Figure S2. Images of the parrotfish species included in our study extracted from footage recorded during data collection.

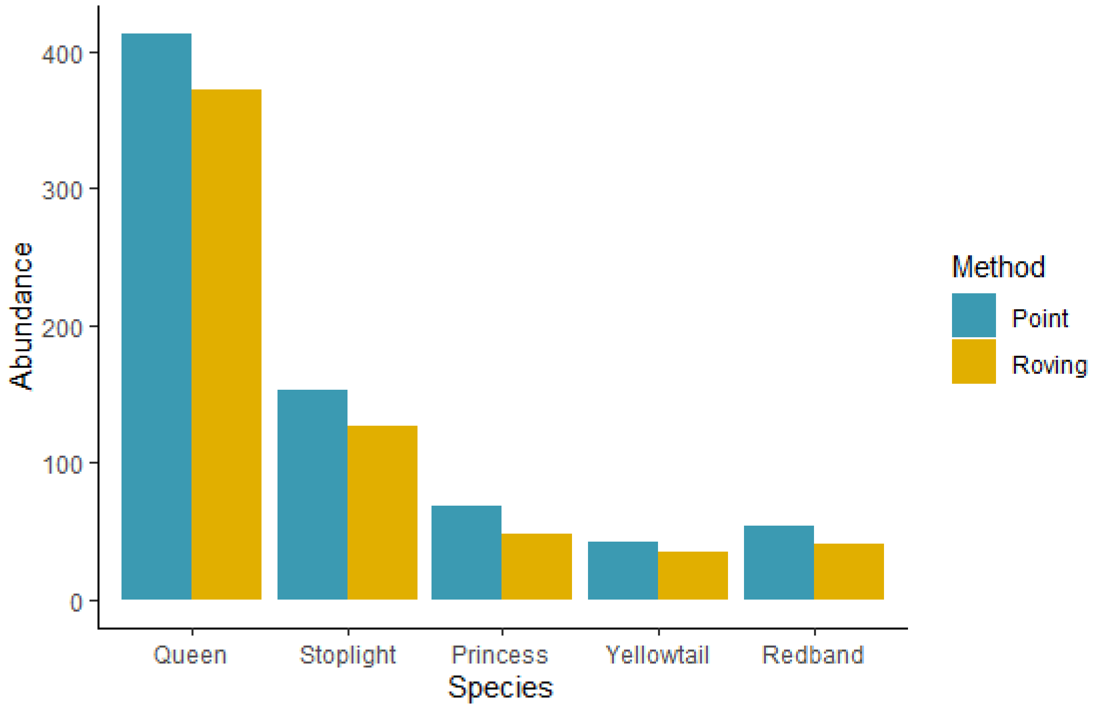

Figure S3. Total abundance estimates (summed over two replicates per survey method) for each species obtained from two different survey methods. Point = Stationary point method, Roving = Roving snorkeler method. Queen = *Scarus vetula*, Stoplight = *Sparisoma viride*, Princess = *Scarus taeniopterus*, Yellowtail = *Sparisoma rubripinne*, Redband = *Sparisoma aurofrenatum*.