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Non-reef habitats in a tropical seascape: The effects of the surrounding seascape on coral reef fishes

A thesis submitted by

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Research presented and reported in this thesis was conducted withing the guidelines for research ethics outlines in the *James Cook University Code for Responsible Conduct of Research (2007), James Cook University Animal Welfare and Ethics Statement (2019), James Cook University Standard Practice and Guidelines (2007), James Cook University Health, Safety, and Environmental Management System (2017)*, and in accordance with the Memorandum of Agreement between James Cook University, Silliman University, and the Government of the Philippines.

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ABSTRACT

In tropical seascapes multiple habitats can function together as a larger network. While coral reef fishes are affected predominately by coral reef habitat, the surrounding habitat near coral reefs can influence reef fish populations and assemblages. Non-reef benthic habitats such as mangroves, seagrass, and macroalgal beds are important for foraging, spawning, and as nursery habitat for many coral reef fishes. The spatial configuration of non-reef habitats adjacent to coral reefs can therefore have a substantial influence on the distribution, abundance, and composition of reef fish. However, the relative importance of within-coral reef benthic habitat compared to the composition of surrounding habitats is poorly understood, especially in the Coral Triangle region.

To address this, my general aim of this thesis is to better understand how species of coral reef fish are influenced by and use non-reef habitats in the surrounding seascape. To achieve this, the specific aims of my thesis were to determine: (1) The relative effect of coral reef habitat and surrounding non-reef habitats adjacent to coral reefs on coral reef fish density and biomass; (2) which species of reef fish are most influenced by non-reef habitats, and how coral reef fish assemblages may vary depending on the adjacent seascape; (3) which species of reef fish are occupying non-reef habitats as juveniles; and (4) how spatial availability of habitat may alter habitat use patterns of fish species.

In **Chapter 1,** I investigated how different benthic habitats in a tropical seascape on the island around Siquijor in the Philippines influenced the presence, density, and biomass of coral reef fishes. My main aim was to understand the relative importance of different habitats across various spatial scales. A detailed seascape map generated from satellite imagery was combined with field surveys of fish and benthic habitat on coral reefs. I then compared the relative importance of local reef (within coral reef benthic composition) and adjacent habitat (distance to and area of multiple habitats in the surrounding seascape) for coral reef fishes. Overall, adjacent habitat variables were as important as local reef variables in explaining reef fish density and biomass, despite being included less often in final statistical models. For adult and juvenile wrasses (Labridae), and juveniles of some parrotfish taxa (*Chlorurus)*, adjacent habitat was more important in explaining fish density and biomass. Notably, wrasses were influenced positively by the amount of sand and macroalgae in the adjacent seascape. Adjacent habitat metrics with the highest relative importance were sand (positive), macroalgae (positive) and mangrove habitats (negative), and fish responses to these metrics were consistent across all fish groups evaluated. The 500-m spatial scale was selected most often in models for seascape variables. Local coral reef variables with the greatest importance were percent cover of live coral (positive), sand (negative), and macroalgae (mixed).

For **Chapter 2** I explored how coral reef fish assemblages responded to local scale benthic coral habitat and larger scale seascape features of multiple adjacent habitats. I examined the entire fish assemblage, and then refined my analyses to focus on parrotfishes and wrasses. I found that coral reef fish assemblages were influenced significantly by other benthic habitats in the surrounding seascape, and that different non-reef habitats can greatly alter species assemblages and diversity of fishes on coral reefs. Five distinct habitat types were identified in a hierarchical cluster analysis which incorporated both local benthic and seascape variables. These clusters represented distinct coral reef fish assemblages, and differed in coral reef fish species diversity. While the entire fish assemblage had distinct assemblages among clusters, parrotfish and wrasse assemblages showed some overlap among habitat clusters. Wrasses also had a much larger multivariate assemblage space compared to the more constrained parrotfish assemblages. Fish species identified as unique to a cluster type were often driven by their use of non-reef habitats adjacent to coral reefs. Despite fish being observed on coral reef habitat, non-reef habitat adjacent to coral reefs had a significant impact on the species assemblages observed on coral reefs, creating distinct reef fish assemblages, and contributing to fish diversity on coral reefs.

Juvenile fish often use alternative habitats distinct from those used by their adult phases. Parrotfishes are an integral group of coral reef fish assemblages, are targeted in reef fisheries, are sensitive to reef environmental disturbances, and have been documented as multiple-habitat users. Considering the abundance of research conducted on parrotfishes, very little is known about their ecology as juveniles at the species level due to their cryptic and variable coloration patterns, which make them difficult to identify. In **Chapter 3,** I collected juvenile parrotfishes in non-reef habitats (macroalgal beds, seagrass beds, and lagoons) adjacent to coral reefs and used DNA analysis to determine species composition. The results were then compared with data on adult parrotfish abundance from underwater visual census (UVC) surveys in coral reef and non-reef habitats. Collections identified 15 species of juvenile parrotfishes in non-reef habitats, and of these, 10 were also recorded in UVCs as adults. Informed by visual surveys of adults, 42% of the 19 parrotfish species observed as adults were classified as multi-habitat users based on their presence in coral reef and non-reef habitats. When accounting for the occurrence of species as juveniles in non-reef habitats, 93% of the species collected as juveniles would be considered multi-habitat users. Species identified as juveniles in non-reef habitats comprised 50% of the average adult parrotfish density on coral reefs and 58–94% of the average adult parrotfish density in non-reef habitats. The species richness of juveniles in non-reef habitats was greater than that of adults occupying the same habitats, and the most common adult species observed in UVCs were not collected as juveniles in non-reef habitats.

Finally, UVC suggested that 97% of juvenile parrotfish <10-cm total length were present in non-reef habitats compared to coral reefs. These results provide further evidence for potential ontogenetic movement across habitat boundaries for parrotfish species in a diverse and highly connected tropical seascape.

Characterizing habitat-use patterns of species across diverse seascapes improves our understanding of population dynamics and our ability to prioritize conservation zones more effectively. In **Chapter 4** I used stable isotope analysis to explore the diet and habitat-use patterns of species from two important reef fish groups: Parrotfishes (Scarinae) and rabbitfishes (Siganidae). My aims were to understand how fish species might be using different habitats at a relatively small spatial extent (16 km of coastline) within a highly connected seascape. Specifically, I investigated if a relationship existed between habitat use and availability of non-reef habitats by comparing stable isotopic signatures of fish between two reef sections that varied substantially in the amount of non-reef habitats present. I identified a clear trend in diet for parrotfishes relating to the degree of reliance on non-reef habitats. Dietary contribution switched from non-reef macroalgal sources (*Sargassum*) to coral reef sources (algal turf) as parrotfish species and life stages shifted from juveniles to adult life stages. Parrotfish juveniles are not consuming *Sargassum* directly, but instead are likely targeting epiphytes and invertebrates that feed on *Sargassum*. In this instance, *Sargassum* and algal turf isotopic signatures were used as indicators of habitats use, and not diet. For species reliant on coral reefs (*Siganus virgatus* and *Scarus dimidiatus* adults) there was similarity in isotopic signatures between reef sections that differed in the extent of adjacent non-reef habitat. Comparatively, species and life stages of parrotfishes with greater reliance on non-reef habitats showed considerable differences in isotopic signatures between reef sections with contrasting amounts of non-reef habitats. This suggests that their habitat use and/or diet may be influenced by available adjacent habitats. For the parrotfish *Scarus dimidiatus* there were clear transitions in isotopic dietary signatures from juvenile to initial phase (IP) sub-adults, and from IP sub-adults to terminal phase (TP) adults, suggesting dietary and habitat changes with ontogeny. Finally, there was a greater overlap in isotopic signatures between the rabbitfish species compared to the parrotfishes. Stable isotope analysis allowed for the examination of subtle patterns that may not be revealed by visual surveys, feeding observations, or gut content analysis. I demonstrated that the amount of available non-reef habitat can affect diet and habitat use patterns in coral reef fish.

In this thesis, I identified that incorporating spatial metrics that describe the surrounding seascape will capture more holistic patterns of fish-habitat relationships on coral reefs. I found that, although fishes are responding to benthic coral reef habitat, the surrounding seascape within 500-m of fish observations can have profound impacts on density, biomass, assemblage structure, diet, and diversity of coral reef fish. Furthermore, this is one of the few studies to quantify links between nursery and adult habitat in parrotfishes, highlighting the importance of including non-reef habitats in ecological studies for this iconic group of coral reef fish. Finally, I presented evidence to support the hypothesis that habitat-use patterns of fishes may be flexible and dependent on adjacent habitat available to them. My findings argue strongly for incorporation of multiple benthic habitats when exploring species patterns and designing marine reserves. This is especially important in regions where protection of reef fish habitat is an integral part of fisheries management but where protection of non-reef habitats is often overlooked.

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McClure EC, Hoey AS, **Sievers KT**, Abesamis RA, Russ GR (2020b) Relative influence of environmental factors and fishing on coral reef fish assemblages. Conservation Biology **https://doi.org/10.1111/cobi.13636**

Sambrook K, Andréfouët S, Aston EA, Bonin MC, Cumming GS, Duce S, **Sievers KT**, Hoey AS (in review) Relative importance of seascape versus within-habitat variables on the distribution of fishes in tropical seascapes. Estuarine, Coastal, Shelf Science

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CHAPTER 1: GENERAL INTRODUCTION

Understanding the mechanisms that shape the distribution and abundance of organisms is a central tenet of ecological theory (Odum 1959; Levin 1992). One of the strongest drivers of the distribution and abundance of organisms is the strong link to their habitat (Andrewartha and Birch 1954; MacArthur and Pianka 1966; Tews et al. 2004). An individual's habitat requirements are contingent on a suite of biological (e.g. food) and physical (e.g. temperature) drivers that are operating at multiple spatial and temporal scales, making observations and predictions of species-habitat relationships sometimes complex and difficult. When exploring the relationships between organisms and their habitat, historically, the focus was on metapopulation dynamics and processes such as extinction, colonization and population connectivity (MacArthur and Wilson 1967; Hanski and Gilpin 1991; Moilanen and Hanski 1998). Often evaluated within the context of habitat fragmentation and habitat loss, the spatial connectivity of habitats affecting species diversity, presence, and overall ecosystem function (Wiens 1994; Fahrig 2013). These approaches to species-habitat relationships engendered the sub-discipline of landscape ecology, which explores how the spatial dynamics of habitats in a landscape alters species patterns and processes (Turner 1989). The spatial connectivity and heterogeneity of habitat patches influences a wide range of ecological processes such as species colonization (Hanski 1998), species interactions (Bergin et al. 2000; Hovel and Lipcius 2001), energy flow (Heck et al. 2008), and nutrient transfer (Meyer and Schultz 1985). Yet, the paradigms developed from landscape ecology are not always directly transferrable to marine systems, particularly with respect to dispersal and movement. (Jones and Andrew 1992; Carr et al. 2003; Wedding et al. 2011b).

Seascape ecology is defined as the study of species-habitat relationships across a heterogeneous benthos, where multiple habitat patches across a seascape create a mosaic of patches which are presumed to affect the movement, distribution, and survival of animals (Grober-Dunsmore et al. 2009; Sheaves 2009; Boström et al. 2011; Berkström et al. 2012a; Pittman and Olds 2015). Seascape ecology is a landscape ecology approach to understanding species patterns in the marine environment, although not completely comparable. Seascape ecology can be partitioned into three attributes: 1. Patches, or the distinct habitats in space, 2. Boundaries, between the patches, and 3. Linkages, the exchange of organisms or materials among patches (Jones and Andrew 1992). Seascape connectivity explores how the configuration and composition of patches and boundaries affect the linkages across a seascape. Within seascape ecology, species patterns and connectivity are predominately focused on individuals during their post-settlement juvenile and adult stages across shallow water benthic habitats. Although larval dispersal is a major form of connectivity in marine systems (Jones et al. 2009), it is noticeably lacking in seascape ecology studies (Grober-Dunsmore et al. 2009; Boström et al. 2011; Pittman and Olds 2015). Seascape ecology, and especially seascape connectivity can be viewed as the complement of marine larval connectivity, but it should be stated, that future research should endeavor to combine larval and adult connectivity in seascape ecology (Brown et al. 2016).

While most marine research focuses on within-patch species-habitat relationships for a single habitat type, seascape ecology includes multiple habitat types to explore how the spatial configuration and composition of habitats may alter species connectivity. The inclusion of seascape structure (composition and spatial configuration) into seascape connectivity is lagging significantly behind that of landscape ecology due to the difficulties in explicitly measuring spatial patterns of organism movements and spatial patterns of submerged habitats (Grober-Dunsmore et al. 2009; Boström et al. 2011). However, within the last ten years, there has been a marked improvement in technologies to map and analyze marine systems (Pittman and Olds 2015), providing an opportunity to better quantify spatial patterns of habitats and to thus explore species-habitat dynamics across seascapes. Accounting for seascape structure when explaining distribution and abundance of marine species is the foundation of seascape ecology (Berkström et al. 2012a; Pittman and Olds 2015). Our knowledge of explicit spatial patterns of marine species is limited, and there is a pressing need to consider the surrounding habitat when describing local species patterns (Boström et al. 2011; Nagelkerken et al. 2015; Sheaves et al. 2015).

In tropical marine systems, coral reefs are one of the most prominent benthic habitats, accounting for the highest species diversity, and consequently the majority of research attention. But the tropical shallow water marine environment is often composed of multiple benthic habitat types (e.g., coral reef, reef flat, mangrove, seagrass beds, macroalgal beds) which comprise a diverse seascape mosaic. Each of these habitats is distinct and important in its own right, providing important ecosystem services such as storm buffering (Zhang 2012), carbon sequestration (Macreadie et al. 2014) and habitat structure for numerous organisms. Yet, rarely do habitats operate in isolation of one another, especially when they are in close proximity to each other. Accounting for the spatial connectivity of multiple habitats in a seascape can reveal nuanced relationships that link species patterns to processes.

1.1 CONNECTIVITY OF FISHES

In marine systems, species connectivity is predominantly focused on the larval stage of fishes and invertebrates (Almany et al. 2009; Jones et al. 2009). The larval stage has the greatest potential for movement, where, driven by oceanic currents, larvae can travel 100s of kilometers in distance (Christie et al. 2010; Green et al. 2015), facilitating networks of populations. Recruitment and settlement dynamics have been extremely well studied, especially in coral reef systems, and the connectivity of organisms driven by larval transport has widespread and significant consequences for population persistence and resilience in marine systems (Doherty and Williams 1988; Botsford et al. 2009; Gaines et al. 2010). Sometimes, tropical larvae will recruit to non-coral reef habitats, and settle onto other habitats in a seascape, such as mangroves, seagrass meadows, and macroalgal beds (Eggleston 1995; Harborne et al. 2006; Nakamura et al. 2009). Then, at some age or size, fishes will migrate back to coral reef habitats as adults, a process known as an ontogenetic habitat shift (Dahlgren and Eggleston 2000; Nagelkerken et al. 2002; Gillanders et al. 2003; Kimirei et al. 2013b). It has also been documented that fish species will migrate between habitats diurnally (Ogden and Buckman 1973), seasonally (Mellin et al. 2007), and tidally (Unsworth et al. 2007) to feed and spawn. While most marine connectivity research focuses on the larval stage, there is comparatively less known about post-settlement movement of fishes among benthic marine habitats, which is the predominant focus of seascape connectivity.

Fish are probably the strongest connectors across a seascape, with the ability to readily move among habitats (Sheaves 2009; Berkström et al. 2012a). Many coral reef fishes are increasingly acknowledged as having some reliance on benthic habitats other than coral reefs (Sambrook et al. 2019, 2020), which would reclassify them as multi-habitat users. The proximity, area, spatial arrangement, and diversity of non-reef habitats can play a role in determining coral reef fish assemblage structure, abundance, and species richness (Grober-Dunsmore et al. 2004, 2009; Dorenbosch et al. 2005), with affects on many food webs and ecosystem functions (e.g. trophic ecology and movement biology)In the US Virgin Islands, overall fish species richness, abundance of grunts (Haemulidae), and abundance of mobile invertebrate feeders were strongly influenced by the amount of seagrass area adjacent to coral reefs (Grober-Dunsmore et al. 2008). In Moreton Bay, Australia, the amount of mangrove area within 500-m of focal coral reefs was a significant predictor of abundance of *Lutjanis fulviflamma*, explaining 23% of the species variability (Olds et al. 2012a). In fact, as the proportion of mangrove habitat within marine reserves (permanent spatial closures to fishing) increased, the abundance of snappers (Lutjanidae), rabbitfish (Siganidae) and sweetlips (Haemulidae) also increased on coral reefs in Moreton Bay, Australia (Olds et al. 2013). Across the Caribbean, the density of adult fishes is positively influenced by the spatial proximity of seagrasses and mangroves, driven by the importance of non-reef habitats as shelter for juvenile fishes (Grober-Dunsmore et al. 2009; Boström et al. 2011).

Perhaps the greatest utility of non-reef habitats for some coral reef fishes is their nursery function. Nursery habitats are defined as such if they support the density, growth and/or survival of juvenile fishes and invertebrates, which then complete successful ontogenetic shifts to their adult habitats (Beck et al. 2001; Dahlgren et al. 2006). Nursery function is thus the process of supplying juveniles from discrete spatial units where juveniles reside, grow, and survive, and/or recruit to adult populations in large numbers.. (Dahlgren et al. 2006; Nagelkerken 2009; Sheaves et al. 2015). When adjacent non-reef habitats are available, their nursery contribution to coral reefs can be significant and widespread, affecting entire fish assemblages, fish diversity, and richness on coral reefs (Dorenbosch et al. 2005; Olds et al. 2012c). Non-reef habitats provide shelter and food for juveniles in an area with reduced predation levels (Dahlgren and Eggleston 2000), which largely drives the differentiation in habitat use between life stages. Direct links between non-reef habitats and coral reefs via ontogenetic migrations have been recorded for important fishery species (e.g. snappers) (Nakamura et al. 2008; McMahon et al. 2012; Kimirei et al. 2013b; Paillon et al. 2014), and herbivorous species (e.g. parrotfish and rabbitfish) (Cocheret De La Morinière et al. 2002; Davis et al. 2014, 2015) using stable isotope analysis. Driven by ontogenetic migrations, adjacent nursery habitats can have profound ecological consequences, replenishing coral reef fish populations, and improving coral reef resilience and potential recovery (Mumby and Hastings 2008; Nagelkerken et al. 2017). While multiple habitats are necessary and important to accommodate life histories that undertake ontogenetic migrations (Sheaves 2009), the degree to which the non-reef habitats are utilized as juvenile habitat is often dependent on abiotic factors such as tidal states and salinity (Igulu et al. 2014). The use of only one habitat type as a nursery is limiting, and, species often use multiple nursery habitats within a coastal seascape (Nagelkerken et al. 2000b; Sheaves et al. 2015). A fish's reliance on non-reef habitats is also contingent on the presence and spatial arrangement of the habitats themselves. It is important to emphasize that the use of nursery habitat is not obligatory for all species, as many reef fish species observed to use nursery habitats (e.g. snappers) are present in locations where no nursery habitats are available (i.e. isolated islands with only coral reef habitat) (McMahon et al. 2012). Nursery use is a complex process, and varies by situation. Viewing seascapes as interconnected mosaics of coastal ecosystems is however, likely to encourage more holistic perspectives of the roles of ontogenetic shifts in nursery habitat function.. Yet, we still lack some of the fundamental knowledge about the extent of reliance that fishes may have on non-reef habitats, the spatial relationship between fish and their habitats, and even which habitats are the most influential on fish distribution and abundance.

1.2 SEASCAPE CONNECTIVITY

The implicit assumption behind seascape connectivity is the movement of individuals between and among habitats within a seascape. Connectivity is driven by the movement capabilities of a species, and also the spatial configuration of the seascape. Both of these factors alter the scale at which species interact with their environment (Pittman et al. 2007). When considering the sedentary life stages (juvenile and adult), the physical connectivity of habitats (configuration), as well as the composition of habitats, are likely to have profound effects on species, by either facilitating or inhibiting movements (Nagelkerken et al. 2008).

Dispersal distance and home ranges of juvenile and adult coral reef fishes can vary substantially between species, life stage, and even vary among individuals within the same species (Kramer and Chapman 1999; Gillanders et al. 2003; Berkström et al. 2012a; Welsh et al. 2013; Green et al. 2015; Streit and Bellwood 2017). Therefore, the variability in seascape connectivity is driven strongly by the variability in species movement patterns and also by the spatial scale of cross-ecosystem linkages in seascapes, which are often shaped by biophysical processes. Because there is relatively little known about movement patterns and home range sizes of many coral reef fish, it is imperative to explore seascape connectivity and fish-habitat use patterns across multiple spatial scales (Pittman et al. 2004). The spatial scales at which species respond to the physical seascape are very species specific, but generally, larger spatial scales have been identified for more mobile species compared to smaller spatial scales for resident fishes (Knudby et al. 2010, 2013; Kendall et al. 2011). However, Pittman and Brown (2011) identified that the red hind grouper (*Epinephelus guttatus*) in the Caribbean responded to habitat (composition and configuration) at the 5-m scale, whereas the small three spot damselfish (*Stegastes planifrons*) responded at the 25-m scale. Despite their large body size, some groupers are highly site attached and tightly linked to the benthos, driving this small-scale response. Life stage can also alter the scale with which species are interacting with the seascape. For example, distribution and abundance of benthic juvenile fish is generally driven by factors operating at smaller spatial scales compared to adults (Grober-Dunsmore et al. 2007; Kendall et al. 2011; van Lier et al. 2018). Juveniles are often more tightly linked to benthic structure, which provides shelter from predation during this vulnerable life stage (Shulman and Ogden 1987). The spatial scale at which species are responding to the environment is therefore driven by a combination of inherent ecological characteristics such as morphology (Wainwright et al. 2002), species interactions (Rooker et al. 2018), and resource requirements (Carlson et al. 2017), but also the seascape configuration itself. In a highly fragmented seascape, species may travel greater distances than in a seascape that is continuous (Turgeon et al. 2010), or fragmentation can severely limit movement of individuals who may be reluctant to cross barriers between habitats, such as sand channels (Kendall et al. 2017). Home ranges and movements of fish species can be significantly altered by the seascape, and the scale with which fish interact with the surrounding environment can vary based on the seascape configuration itself. This is an especially important consideration when designing No Take Marine Reserves (NTMRs), where NTMRs are intended to protect species from fishing. Previous research has suggested that NTMRs should be at least twice the size of the focal species home range if conservation is the objective of the NTMR (Green et al. 2015). But if that home range size can be altered by the seascape, then the spatial connectivity of a seascape within and surrounding the NTMR must be considered when choosing the placement and size of the NTMR.

1.3 SEASCAPES AND MARINE RESERVES

Marine reserve networks are a priority focus of marine management systems with the intention to conserve and recover exploited populations (Gaines et al. 2010; Botsford et al. 2014). These networks generally span large spatial scales (10-100s of km) that reflect the known or perceived scale of movement of larvae transported in oceanic currents. Of course, NTMR networks are also strongly influenced by the legislative footprint, and the capabilities of the management authorities tasked with protections. However, placement of reserves within networks should also reflect the movement patterns of post-settlement life stages (juvenile and adult) across benthic habitats (Moffitt et al. 2009; Green et al. 2015; Brown et al. 2016). Incorporation of data on movement patterns of juvenile and adult fishes in simulation models can considerably improve model predictions of population persistence (Brown et al. 2016). Furthermore, combining both modes of connectivity (larval and adult) in conservation practices could drastically improve management outcomes (Brown et al. 2016). Population persistence declines substantially in models where movement of adults across a seascape is incorporated with larval models, because species are moving outside reserve boundaries more than previously accounted for (Moffitt et al. 2009; Grüss et al. 2011). However, we are currently lacking explicit information about the relationships between fishes and seascapes, and the addition of seascape connectivity in populations models would have substantial effects on reserve network design (Foley et al. 2010; Wedding et al. 2011b; Olds et al. 2016).

Identification of essential nursery habitats is critical for effective conservation and fisheries management of targeted species. The connectivity of non-reef habitats to coral reefs can alter the biomass, abundance and assemblage structure of fishes on adjacent coral reefs (Nagelkerken et al. 2000b; Mumby et al. 2004), and incorporation of seascape connectivity patterns into reserve design can provide better conservation outcomes. For example, Huijbers et al. (2013) used visual surveys and stable isotope data from the Caribbean to inform spatial simulation models which compared how seagrass bays contributed to population replenishment of fishes on coral reefs by acting as nursery habitats. They found that seagrass bays on the island of Curaçao were nursery habitats for the yellowtail snapper (*Ocyurus chrysurus*), and that adult distributions on coral reefs were best predicted by their spatial connectivity to nursery bays. Therefore, incorporating processes driven by seascape connectivity into population estimates improves prediction capabilities which can inform spatial management strategies like networks of marine reserves.

However, when examining seascape studies, a review in 2016 (Olds et al. 2016) revealed that only 21% of seascape studies include marine reserves, and only 5% of seascape studies evaluated the interactions between seascape and reserve effects. Accounting for seascape structure in reserve studies can reveal more nuanced effects of marine reserves (Huntington et al. 2010) and even identify seascape structure effects on target fish density (Olds et al. 2012c). Clearly, the connectivity of habitats in a seascape can shape ecological patterns (Gilby et al. 2017; Henderson et al. 2017b). This in turn can influence ecological processes such as herbivory and piscivory (Yabsley et al. 2016; Eggertsen et al. 2020), which can have cascading effects on the persistence and recovery of coral reef systems (Mumby and Hastings 2008).

1.4 MEASURING SEASCAPE CONNECTIVITY

Seascape ecology has matured considerably in the last 10 years, and with improved development in remote sensing techniques, more sophisticated analytical methods can be applied to marine habitat mapping. Enhanced habitat maps allow for a spatially explicit, multi-scale approach to describe species-habitat interactions at spatial scales that are more ecologically relevant to both the focal species, and to the management practices (Andréfouët and Riegl 2004; Mumby 2006; Mellin et al. 2009; Wedding et al. 2011a). There is ample evidence supporting the importance of small-scale, within-coral reef, habitat characteristics (e.g. coral cover) (Coker et al. 2014), and also large scale spatial metrics of the seascape (e.g. distance to mangroves) (Paillon et al. 2014) to reef fish dynamics. However, there is less of an understanding of the relative importance of these two spatial scales (local coral reefs vs seascape), because most studies focus on a single spatial scale. Yet, results from the studies that do explore the relative importance of habitat across multiple spatial scales find equivocal results that are dependent on the species in question, the life stage evaluated, and the spatial connectivity of the seascape (Grober-Dunsmore et al. 2008; Olds et al. 2012a; Eggertsen et al. 2019). Often, species-habitat studies are using an inappropriate spatial scale when describing patterns of distribution and abundance of organisms (Jackson and Fahrig 2015; Hale et al. 2019), and including information on the surrounding habitat provides for tighter integration of complex species processes such as feeding, spawning, and ontogenetic shifts which often occur across multiple habitat types (Harborne et al. 2006; Verweij et al. 2006).

1.5 AIMS AND THESIS OUTLINES

Incorporating the entire seascape provides a more holistic approach to quantifying species patterns and allows for better estimations of distribution, abundance, and complex processes of fish life cycles, such as ontogenetic shifts. While we have long understood the importance of multiple habitats in a tropical seascape, the relative effects of coral reef and non-reef habitats, especially at varying spatial scales, is poorly understood. This is especially important when developing spatial management strategies such as marine reserves and networks of such reserves, where representative protection of different habitats may be the most beneficial (Fernandes et al. 2005).

To address this, my general aim of this thesis is to better understand how species of coral reef fish are influenced by non-reef habitats in the surrounding seascape. To achieve this, the specific aims of my thesis were to determine: (1) The relative effect of within coral reef habitat and surrounding non-reef habitats on coral reef fish density and biomass; (2) which species may be most influenced by non-reef habitats, and how coral reef fish assemblages may vary depending on the adjacent seascape; (3) which fish species are occupying non-reef habitats as juveniles; and (4) how availability of habitat may alter species-habitat use patterns.

These aims were addressed in the following four chapters. **Chapter 2** investigated how common coral reef fish families responded to habitat effects across multiple spatial scales. It compared how coral reef benthic habitat and the spatial arrangement of different surrounding habitats in a seascape at multiple spatial scales affected the density and biomass of fishes on coral reefs. **Chapter 3** continued this multiscale approach to explore the fish assemblage structure on coral reefs. It compared fish assemblages between and among seascape types, and specifically focused on parrotfishes and wrasses, two species groups that had the greatest responses in the first chapter. **Chapter 4** focused on an economically and ecologically important taxon, parrotfishes, to describe juvenile habitat use. Parrotfish juveniles are extremely difficult to identify to the species level. Thus, I employed DNA analysis to identify small juvenile parrotfishes and compared juvenile habitat use to adult habitat use to understand potential ontogenetic shifts. **Chapter 5** then explored the concept of habitat availability and accessibility in driving fish habitat-use patterns. Stable isotopes were used to document dietary and habitat signatures of two common nominally herbivorous fish groups, parrotfish and rabbitfish. This approach allowed for a comparison between two reef sections that differed in the amount of non-reef habitats available, to understand whether species may be altering their habitat-use patterns based on habitat availability.

To conduct this study, I focused my research on Siquijor Island, a medium sized island in the Philippines. Siquijor is an ideal location for this work because it has a wide range of non-reef benthic habitats that vary in their abundance and spatial connectivity to coral reefs across the island. It is an excellent location for this research as it has a highly connected seascape, where non-reef habitats occur in close proximity to coral reefs, providing the greatest potential to observe non-reef habitat use by coral reef fishes. Furthermore, the Philippines has the highest density of No Take Marine Reserves (NTMR) in the world (Cabral et al. 2014), with 1,800 NTMRs nationwide, allowing for the ability to compare fished and NTMR sites on one island. Here, fishing occurs in both coral reefs and non-reef habitats, and understanding the importance of non-reef habitats on fish populations could provide realistic solutions to spatial management strategies on Siquijor.

CHAPTER 2: NON-REEF HABITATS IN A TROPICAL SEASCAPE AFFECT DENSITY AND BIOMASS OF FISHES ON CORAL REEFS

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2.1 ABSTRACT

Non-reef habitats such as mangroves, seagrass, and macroalgal beds are important for foraging, spawning, and as nursery habitat for some coral reef fishes. The spatial configuration of non-reef habitats adjacent to coral reefs can therefore have a substantial influence on the distribution and composition of reef fish. I investigate how different habitats in a tropical seascape in the Philippines influence the presence, density, and biomass of coral reef fishes to understand the relative importance of different habitats across various spatial scales. A detailed seascape map generated from satellite imagery was combined with field surveys of fish and benthic habitat on coral reefs. I then compared the relative importance of local reef (within coral reef) and adjacent habitat (habitats in the surrounding seascape) variables for coral reef fishes. Overall, adjacent habitat variables were as important as local reef variables in explaining reef fish density and biomass, despite being fewer in number in final models. For adult and juvenile wrasses (Labridae), and juveniles of some parrotfish taxa (*Chlorurus)*, adjacent habitat was more important in explaining fish density and biomass. Notably, wrasses were positively influenced by the amount of sand and macroalgae in the adjacent seascape. Adjacent habitat metrics with the highest relative importance were sand (positive), macroalgae (positive) and mangrove habitats (negative), and fish responses to these metrics were consistent across fish groups evaluated. The 500-m spatial scale was selected most often in models for seascape variables. Local coral reef variables with the greatest importance were percent cover of live coral (positive), sand (negative), and macroalgae (mixed). Incorporating spatial metrics that describe the surrounding seascape will capture more holistic patterns of fish-habitat relationships on reefs. This is important in regions where protection of reef fish habitat is an integral part of fisheries management but where protection of non-reef habitats is often overlooked.

2.2 INTRODUCTION

Fishes use multiple habitats for a variety of ecological reasons. In tropical coral reef ecosystems, non-reef habitats include, but are not limited to mangrove forests, seagrass meadows, and macroalgal beds. Though each habitat offers unique and essential ecosystem services, there is ample and increasing evidence that these non-reef habitats are important to coral reef fishes (Boström et al. 2011; Nagelkerken et al. 2015; Pittman and Olds 2015; Fulton et al. 2019) and, at least in some places, coral reef fisheries (Honda et al 2013; Fulton et al. 2020). Diel, tidal, and seasonal migrations of large-bodied fishes (Haemulids, Lutjanids, and Lethrinids) from coral reefs to seagrass and mangrove habitats to forage and spawn are well documented (Nagelkerken et al. 2000; Verweij et al. 2006; Appeldoorn et al. 2009; Huijbers et al. 2015; Honda et al. 2016). The recruits and juveniles of many reef fish species also use non-reef habitats as nursery grounds to reduce mortality due to predation (Dahlgren & Eggleston 2000; Beck et al. 2001; Adams et al. 2006; Lefcheck et al. 2019). Juveniles of many coral reef fishes reside in non-reef habitats, often in higher abundances than on coral reefs (Dorenbosch et al. 2005; Davis et al. 2014; Tano et al. 2017). In shallow water tropical seascapes, more than 600 species of coral reef fishes have been found to use adjacent non-reef habitat (Sambrook et al. 2019), yet we still do not understand the full extent of the reliance of coral reef fishes on adjacent non-reef habitats.

The distribution and assemblage structure of fishes on coral reefs can be significantly altered by the spatial configuration of non-reef habitats in the surrounding seascape. Mangroves in close proximity to coral reefs can increase the biomass of reef fishes in the Caribbean (Mumby et al. 2004), and dictate whether some species occur at all on coral reefs (Paillon et al. 2014). Area of adjacent seagrass can have positive relationships with coral reef fish density (Grober-Dunsmore et al. 2008; Davis et al. 2014). Some studies evaluating spatial connectivity patterns of multiple habitats in a seascape find seascape-level habitat metrics more influential in describing fish density, diversity, and biomass than within-patch characteristics of the coral reef (Pittman et al. 2004; Grober-Dunsmore et al. 2007; Mellin et al. 2009; Yeager et al. 2011; Martin et al. 2015). For example, coral reef fish abundance and distribution in Moreton Bay, Australia were influenced primarily by proximity to mangroves and seagrass, and only secondarily by local reef characteristics such as coral cover when patches were highly connected (Olds et al. 2012a). However, as a relatively new topic in marine systems, results comparing the relative importance of habitat types to fish density at different scales are equivocal, being location- and species-specific. While bottom up effects of coral reef benthic habitat are an essential driver in coral reef fish distributions (e.g. Russ et al. 2015), including surrounding habitat metrics is a necessary and productive avenue to improve our understanding of species-habitat interactions across diverse seascapes.

To counteract the uncertainty in species-habitat use patterns, adopting a hierarchical, multi-scale approach enables evaluation of species-habitat relationships at both the local (within patch) and seascape (across patches) scale (Mellin et al. 2009; Pittman and Brown 2011; Wedding et al. 2011b; Berkström et al. 2012a). Remote sensing technology and spatial analysis software have allowed for the development of marine habitat maps that describe diverse seascapes in high resolution across large spatial extents (Kendall and Miller 2008; Hedley et al. 2016; Roelfsema et al. 2018). This provides users with the flexibility to explore species-habitat relationships across multiple spatial scales, at spatial resolutions that are useful for ecological studies.

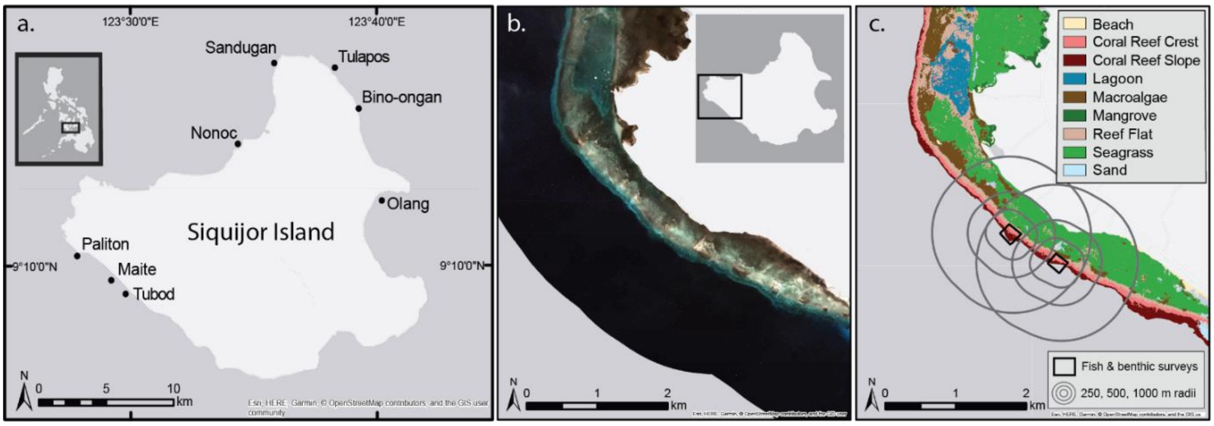
In the Philippines, coral reefs are often adjacent to or near large areas of seagrass beds, macroalgal beds, and/or mangrove stands. I use this system to explore how spatial connectivity of multiple habitats in a seascape affects coral reef fish. The Philippines is the northern tip of the Coral Triangle, and is considered a global biodiversity and conservation hotspot for shallow water reef fishes (Carpenter and Springer 2005), with the highest concentration of No-Take Marine Reserves (NTMR) in the world (Nañola et al. 2011; Horigue et al. 2012; Cabral et al. 2014). However, these NTMRs are mostly placed on coral reefs, often neglecting adjacent habitats (Weeks et al. 2010). I aim to understand fish-habitat relationships in a diverse model seascape, specifically focusing on coral reef fishes to explore: 1. The relative importance of local scale coral reef habitat and adjacent non-reef habitats on fish species presence, density, and biomass; and, 2. Which non-reef habitats and spatial connectivity metrics are the most important.

2.3 METHODS

2.3.1 Study Site

This study was conducted around Siquijor Island in the Visayan region of the Philippines (Fig. 2.1a). Shallow water benthic habitats of Siquijor include macroalgal beds, mangroves, and seagrass beds of varying spatial extent adjacent to fringing coral reefs. Seagrass meadows in Siquijor are composed of a diverse grouping of *Cymodocea rotundata, C. serrulata*), *Halodule pinifolia, H. uninervis, Thalassodendron ciliatum, Enhalus acroides, Halophila beccarii, H. minor, H. ovalis, H. spinulosa* and *Thalassia hemprichii* (Meñez et al. 1983). Macroalgal beds are characterized by *Sargassum* spp. when it is dominant and smaller red and green understory macroalgae when the *Sargassum* canopy has senesced seasonally. Mangrove habitats are patchily distributed around the island, composed mainly of *Rhizophora* spp. that were replanted between the mid 1980’s and early 1990’s (De Leon and White 1999), with some remaining natural stand of *Sonneratia* spp. and *Avicennia* spp. As of 2018 Siquijor had 12 NTMRs, providing an ideal location to evaluate the effects of non-reef habitat and NTMRs on coral reef fish presence, density, and biomass.

Figure 2.1. Survey sites and mapping process of submerged habitat on Siquijor Island. (a.) Map of sites (black circles) where fish and benthic assemblages were surveyed on coral reefs in April-July 2016. (b.) Satellite imagery from one area of western Siquijor Island (San Juan) from the Planet imagery at 3-m resolution showing the true color image. (c.) Map of classified habitats derived from satellite imagery including survey locations of coral reef substrate and fish, and radii scales (250, 500, 1000-m) from which spatial metrics of adjacent habitat types were calculated.



2.3.2 Fish and Habitat Surveys

Surveys of reef fish and benthos were conducted in April – July 2016 at eight locations around Siquijor Island (Fig. 2.1a), with paired NTMR and control (open to fishing) sites, totalling to 16 sites. Location selection was based on distance to non-reef habitat, accessibility, coral reef habitat type, and NTMR compliance. Underwater visual censuses (UVC) were conducted to quantify the fish and benthic communities on coral reefs. At each location, three or four transects were surveyed along both the coral reef slope and reef crest per site, representing 6 or 8 transects per location, and totalling to 108 transects across all locations. The number of replicate transect surveys was determined by the NTMR size. Along a 50-m by 5-m transect, large mobile reef fish (>10 cm TL) were counted and sized to the nearest centimetre. On the return swim, smaller (≤ 10 cm TL) reef fish species were recorded within a 2-m width. Biomass of fishes was calculated using published length-weight relationships (Kulbicki et al 2005). For benthic surveys, substratum was identified at 50-cm intervals along the 50-m transect and was classified based on substrate (rock, sand, rubble, coarse sand) and benthic cover (abiotic, crustose coralline algae, epilithic algal matrix, macroalgae, soft coral, hard coral, other) (Table 2.1). Macroalgae and soft coral were identified to genus when possible. Hard coral was identified to genus and classified into growth form (fragile, robust). The ‘other’ category included sessile invertebrates such as sponges, tunicates, and gorgonians. Structural complexity was estimated visually on a 0-5 scale following methods used in Wilson et al. (2007). In general terms, 0 = flat, 5 = highly complex structure.

Table 2.1. Predictor variables used for model analysis with their mean, minimum, and maximum values from coral reef surveys and spatial analysis output. Variables are separated by scale category (local reef or adjacent habitat). * denotes radii measures were only reported for the 500-m radius because that radius was selected most often in model selection. Values were also calculated for 250 and 1000-m spatial radii.

Variable	Unit	Mean	Minimum	Maximum
Local Reef Category				
Rubble	% Cover	24	0	91
Sand	% Cover	16	0	83
Macroalgae	% Cover	10	0	38
Epilithic Algal Matrix (EAM)	% Cover	32	5	87
Soft Coral	% Cover	8	0	38
Hard Coral	% Cover	26	1	81
Fragile Coral	% Cover	11	0	61
Robust Coral	% Cover	15	1	47
Depth	Meters	9.6	2.9	17.5
Structural Complexity	Scale 0-5	2.7	0	5
Adjacent Habitat Category				
Distance to Shore	Meters	209	63	477
Distance to Seagrass	Meters	88	5	650
Distance to Macroalgae	Meters	35	5	100
Distance to Mangrove	Meters	2,380	104	8,200
Coral Reef Area within 500-m*	% Area	26	13	41
Macroalgal Area within 500-m*	% Area	14	5	41
Mangrove Area within 500-m*	% Area	2	0	10
Reef Flat Area within 500-m*	% Area	11	1	24
Seagrass Area within 500-m*	% Area	32	0	58
Sand Area within 500-m*	% Area	12	1	20

2.3.3 Habitat Mapping

Remotely sensed satellite imagery paired with *in-situ* georeferenced habitat data were used to create a marine benthic habitat map. Images from the GeoEye and PlanetScope satellite sensors were acquired from the Digital Globe Foundation, and Planet, respectively. The GeoEye satellite provides a spatial resolution of 1.84-m and Planet provides a 3-m resolution, both across four spectral bands of blue, green, red, and near-infrared (NIR) (Fig. 2.1b). Both sensors were necessary to acquire complete coverage of the island. Pre-processing of imagery was conducted using the software ENVI (v. 5.3, Harris Geospatial Inc.). Band ratios were calculated to provide additional unique spectral signatures for benthic habitat classes (Phinn et al. 2012; Roelfsema et al. 2013). Band ratios were: blue to red (B/R), blue to green (B/G), and red to NIR (R/NIR). After pre-processing, classification of imagery into habitat types was conducted using the maximum likelihood classification tool in ArcGIS, v. 10.4.1.

Feature classes were a combination of biotic and geomorphological features: seagrass meadows, macroalgal beds, reef flat, reef crest, reef slope, lagoon, sand, mangrove forest, and beach (Fig. 2.1c). Georeferenced habitat data points (n=500) collected *in-situ* in 2016-2018 informed the maximum likelihood classification, with 70% of points used for training, and the remaining 30% used for validation of the classified map. The map was then manually reviewed and edited for obvious errors, smoothed using the majority filter in ArcGIS, and converted to polygons for spatial analysis. Map validation identified 72% accuracy of habitat classification using the maximum likelihood method.

2.3.4 Spatial Analysis

Fish and benthic survey locations were overlaid onto the classified habitat map to calculate spatial statistics of the seascape surrounding each site (n = 16). Adjacent habitats used for spatial analysis were seagrass, macroalgae, sand, reef flat, and mangroves. For each location, distance to the nearest habitat type was measured using edge-to-edge distance between survey sites and each habitat. Because reef fish species respond to benthic habitat at varying spatial scales, I used a multi-scale approach to measure the area of each habitat (Grober-Dunsmore et al. 2009). Buffer zones surrounding each survey site were calculated at three different spatial scales (250, 500, 1000-m) (Fig. 2.1c). Buffers were clipped by shore and deep-water features to only represent shallow water habitat. The proportion of each habitat within each buffer zone was calculated as the area of habitat divided by the total area of the clipped buffer. These data were then incorporated with the benthic survey data on coral reefs for further analysis (Table 2.1). Global Moran's I was calculated for the 500-m habitat spatial scale to evaluate any potential spatial autocorrelation. Spatial data was not significantly spatially autocorrelated for the 500-m scale (Moran's I = 0.370, p = 0.24).

2.3.5 Statistical Analysis

Boosted regression trees (BRT; Elith et al. 2008) were used to evaluate how benthic habitats at different spatial scales affected coral reef fishes using the gradient BRT method from the gbm package. BRTs are an excellent tool to understand the relative influence of multiple predictor variables, with the advantage of handling multi-collinearity and non-linearity among predictor variables (De'ath 2007). Fish groups were analysed in terms of density and biomass, or presence/absence, using Poisson, Gaussian, and Bernoulli distributions, respectively. Fish groups at the family level were selected to allow for more robust analysis compared to species or functional level data which would have only allowed for presence absence. Presence/absence was used for species groups with too few observations for density and biomass analysis (Lutjanidae and Serranidae). In total, 32 BRT models were run on fish groups with the greatest number of observations at the family level: Labridae (wrasses, excluding parrotfishes), Lutjanidae (snappers), Serranidae (groupers), Pomacentridae (damselfishes), Chaetodontidae (butterflyfishes), and Acanthuridae (surgeonfishes) (Table 2.2). Parrotfishes (Labridae, subfamily Scarinae) were run at the level of genus for two different feeding-type groups, *Scarus* and *Chlorurus*, where Scarus are scrapers and Chlorurus excavators. *Hipposcarus* was included in the 'Scarus' group and *Cetoscarus* was included in the 'Chlorurus' group based on their feeding modes. Models for juvenile reef fish density were only possible for wrasses, and the parrotfish groups *Scarus* and *Chlorurus,* due to the lack of juveniles observed from other families. Fish groups were also separated by coral reef zones, i.e. reef crest and slope.

To identify the scale at which reef fish responded to the seascape, a BRT was run for each adjacent habitat type at all three spatial scales (250, 500, 1000 m) for each response variable. The 'best' scale for each habitat type was selected as the radius with the highest relative importance, and only that scale was included for further analysis. Variables with correlation values greater than 0.8 (e.g. hard coral, fragile coral, robust coral) were run in a BRT, and only the variable with highest relative importance was selected for the remaining analysis. Full models were then run with these pre-selected variables with an interaction depth of 3 and bag fraction of 0.75 using the gbm.step method in the gbm package, and were calibrated for best results by altering the learning rate to achieve the optimal number of iterations between 1000-10000 trees, based on a 10-fold cross-validation procedure. The gbm.simplify process was used to reduce the number of variables by an iterative backwards stepwise removal of the least influential variables using k-fold cross validation until the change in predictive deviance was minimized. The simplify process selected the nine most influential variables, and NTMR status was the tenth variable to evaluate any reserve effect. To account for stochasticity and incorporate uncertainty values for relative importance, models were bootstrapped (sampling with replacement) 100 times. Error in relative importance and deviance explained values were measured by 95% confidence intervals from the bootstrapping process. Cross validation deviance (CV deviance) was calculated by subtracting the CV deviance from the null deviance and dividing by the null deviance. Mean relative importance was used as an indicator for variable importance. Because models had 10 variables, relative importance values greater than 10% were considered influential as they were selected more frequently than expected by chance. The mean relative importance was summarised only for influential variables (>10% relative importance) and compared between variables categories (local reef vs. adjacent habitat) (Table 2.1). Here, I define "local reef" as the small-scale benthic habitat characteristics of a coral reef, whereas "adjacent habitat" describes larger scale spatial metrics of multiple habitat types across a seascape. Wilcoxon ranked tests for non-parametric data were used to compare the mean relative importance between local reef and adjacent habitat categories across all models, at the level of reef zones (crest and slope), fish life stages (juvenile and adult), and for each fish group.

Table 2.2. Summary of each reef fish group with model parameters selected for bootstrap boosted regression tree analysis using the gbm step method. Mean trees and Mean CV deviance are reported values from the bootstrap (sample and replacement) process with their upper and lower 95% confidence limits.

Model	Species Group	Stage	Metric	Level	Ave Trees	95% CI Trees	Ave CV Deviance	95% CI CV Deviance
1	Surgeonfishes	Adult	Biomass	Crest	4406	573,10000	0.51	0.15,0.87
2	Surgeonfishes	Adult	Biomass	Slope	7123	800,10000	0.27	0.07,0.74
3	Surgeonfishes	Adult	Density	Crest	4457	873,10000	0.71	0.45,0.87
4	Surgeonfishes	Adult	Density	Slope	8444	992,10000	0.50	0.07,0.89
5	Butterflyfishes	Adult	Biomass	Crest	3376	450,10000	0.61	0.35,0.89
6	Butterflyfishes	Adult	Biomass	Slope	6317	600,10000	0.34	0.07,0.75
7	Butterflyfishes	Adult	Density	Crest	6904	2595,10000	0.63	0.45,0.73
8	Butterflyfishes	Adult	Density	Slope	3444	400,9702	0.60	0.29,0.85
9	*Scarus*	Adult	Biomass	Crest	7947	1245,10000	0.31	0.06,0.59
10	*Scarus*	Adult	Biomass	Slope	6716	892,10000	0.31	0.02,0.57
11	*Scarus*	Adult	Density	Crest	6861	1390,10000	0.29	0.02,0.58
12	*Scarus*	Adult	Density	Slope	8614	1100,10000	0.33	0.02,0.59
13	*Scarus*	Juvenile	Density	Crest	2972	523,9760	0.69	0.45,0.84
14	*Scarus*	Juvenile	Density	Slope	2265	400,9155	0.52	0.23,0.74
15	*Chlorurus*	Adult	Biomass	Crest	3134	300,10000	0.41	0.07,0.74
16	*Chlorurus*	Adult	Biomass	Slope	4145	397,10000	0.46	0.15,0.78
17	*Chlorurus*	Adult	Density	Crest	2720	300,9160	0.35	0.1,0.64
18	*Chlorurus*	Adult	Density	Slope	3789	621,10000	0.48	0.06,0.82
19	*Chlorurus*	Juvenile	Density	Crest	3691	261,10000	0.31	0.02,0.65
20	*Chlorurus*	Juvenile	Density	Slope	1404	205,9895	0.24	0.01,0.6
21	Wrasses	Adult	Biomass	Crest	7712	4206,10000	0.71	0.42,0.91
22	Wrasses	Adult	Biomass	Slope	5296	370,10000	0.64	0.35,0.89
23	Wrasses	Adult	Density	Crest	7577	2407,10000	0.28	0.06,0.52
24	Wrasses	Adult	Density	Slope	4792	600,10000	0.51	0.09,0.78
25	Wrasses	Juvenile	Density	Crest	4264	1182,9730	0.62	0.35,0.85
26	Wrasses	Juvenile	Density	Slope	4955	1250,10000	0.49	0.16,0.79
27	Damselfishes	Adult	Density	Crest	3306	300,9976	0.55	0.17,0.86
28	Damselfishes	Adult	Density	Slope	2847	423,6126	0.74	0.36,0.95
29	Snappers	Adult	Presence	Crest	4431	1340,10000	0.29	0.07,0.56
30	Snappers	Adult	Presence	Slope	1744	650,3347	0.44	0.22,0.72
31	Groupers	Adult	Presence	Crest	1719	450,4076	0.50	0.26,0.8
32	Groupers	Adult	Presence	Slope	1373	371,4008	0.40	0.18,0.71

2.4 RESULTS

For all 32 BRT models explaining reef fish presence, density, or biomass, 62.2% of the influential variables were local coral reef variables, 36.3% were adjacent habitat metrics, and 1.5% were NTMR variables. The mean relative importance of influential variables (>10% relative importance) between local reef and adjacent habitat were similar (16.9, 15.9 respectively; Fig. 2.2a) and not statistically different (Wilcoxon rank sum test, W=2306, p = 0.248) (Table 2.3). For surgeonfish, local reef variables had significantly higher mean relative importance in determining density and biomass compared to adjacent habitat (Wilcoxon rank sum test, W=11, p = 0.011) (Fig. 2.2b). In contrast, the mean relative importance of adjacent habitat was significantly higher for wrasses (Wilcoxon rank sum test, W=104, p = 0.008). The remaining taxa had no significant differences in mean relative importance between the two habitat categories. Juvenile fish density (represented by *Chlorurus, Scarus*, and wrasses combined) had significantly higher mean relative importance for adjacent habitat variables (Wilcoxon rank sum test, W=78, p = 0.022) (Fig. 2.2c). For wrasses, both juvenile and adult density had greater mean relative importance for adjacent habitat variables (Fig. 2.2d).

Individual variables with the highest mean relative importance were adjacent habitat metrics of sand and macroalgae (Fig. 2.3). Both adjacent sand and macroalgae had a consistently positive relationship with fish taxa responses, where the greatest change occurred between 10-20% coverage in the surrounding seascape. The most selected radius for adjacent habitat variables was the 500-m spatial scale for all habitats except seagrass, which was dominated by the 1000-m spatial scale (Table 2.4). Local coral reef variables were found to strongly affect reef fish presence, density, and biomass, and were included 1.7 times more frequently than adjacent habitat variables. Specifically, live coral cover (selected in 69% of models, Fig. 2.3) was a consistent, strong, and positive predictor of coral reef fish presence, density and biomass for most models. Percent cover of sand (56%), and depth (47%) were also influential local reef variables with sand having a negative effect and depth having mixed effects.

For juvenile fish, adjacent habitat variables had higher relative importance compared to local coral reef variables (Fig. 2.2c). Wrasse and *Chlorurus* juveniles were most influenced by adjacent sand in the seascape (positive relationship), and adjacent macroalgal habitat (positive) (Appendix A, Table S2.1). *Scarus* juveniles were strongly positively influenced by percent fragile coral but were secondarily influenced by the adjacent habitat variables distance to mangrove (positive relationship) and amount of sand within 500-m (positive relationship). Across all juvenile BRT models, percent cover of sand at the local reef scale was the most frequently selected variable (5 of 6 models) with a negative relationship, followed by a positive relationship with percent cover of fragile coral (4 of 6 models).

Wrasses were the only fish group to have higher relative importance of adjacent habitat spatial metrics for both adults and juveniles (Fig. 2.2d). For wrasses, the most influential variables were adjacent macroalgae, adjacent sand, and distance to mangrove, all with positive relationships to wrasse density and biomass (Fig. 2.4) (Appendix A Table S2.1, models 21-26). However, local reef variables did have the greatest inclusion rate in wrasse models, where the percent cover of sand (negative relationship), and percent live coral cover (mixed relationships) were selected most frequently. *Scarus* juvenile density was positively affected by fragile coral cover at the local reef scale, but adult density and biomass was predominantly influenced by macroalgal cover at the local reef scale (mixed effects), and negatively influenced by distance to mangrove and seagrass (Appendix A Table S2.1, models 9-14). In *Chlorurus* models (models 15-19), live coral cover on the local reef positively influenced adults, whereas juveniles were positively influenced by the amount of adjacent sand in the surrounding seascape. The area of seagrass in the surrounding seascape was also a common predictor in *Chlorurus* models, appearing in three of six models with a negative response to area of adjacent seagrass. For snapper presence (models 29-30), influential variables were almost all local reef. For surgeonfish (models 1-4), NTMR size was included as an influential predictor, positively affecting density and biomass of fish on the reef crest and was the only fish group to have an NTMR variable selected as influential. For damselfish density (models 27-28), the reef crest model was influenced by depth, whereas the reef slope model was influenced by distance to seagrass and mangrove. For grouper presence (models 31-32) on the reef crest there was high importance of adjacent habitat variables (e.g. distance to seagrass, and area of mangrove), whereas on the reef slope, the presence of groupers was influenced by local coral reef variables. Finally, for butterflyfishes (models 5-8), mangrove variables were present in all models, with a negative influence on density and biomass of fish.

Figure 2.2. Relative importance of variables with high influence (>10% relative importance) comparing the difference between scale categories of adjacent habitat (blue) and local reef habitat (grey), and No Take Marine Reserve (NTMR) effect (green) for models describing density, biomass, and presence of coral reef fish. Boxplots show medians and quartiles, dots are outliers. * Indicates significance of relative influence between scale categories based on Wilcoxon rank sum tests. Values at the top of each plot show the number of times each variable was included in the model (n) and the mean relative importance value (x̅) of the variable categories across models for (a.) all models combined, (b.) separated by fish taxa, (c.) life stage, and (d.) for juvenile and adult wrasses.

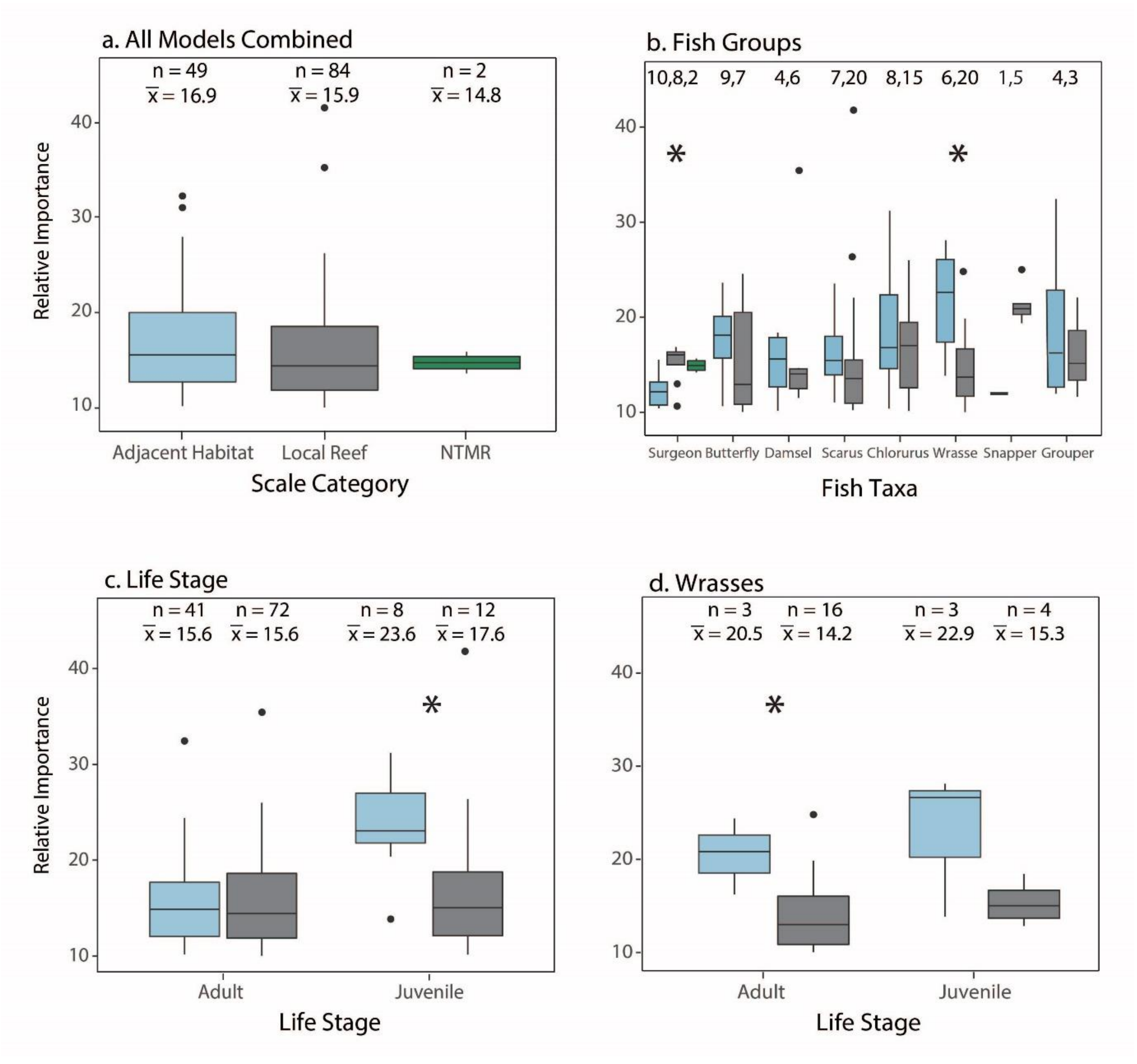


Figure 2.3. Mean relative importance of variables with high influence (>10% relative importance) across all 32 reef fish models analyzed for density, biomass, and presence of coral reef fish. Dots represent means and bars represent upper and lower standard deviation. Colors indicate the scale category for adjacent habitat (blue), local reef (grey), or no-take marine reserve (green). Values on the left hand side of the graph represent the number of times that variable was used in a model, symbols (+ or -) on the right hand size indicate the direction of the relationship when obvious.

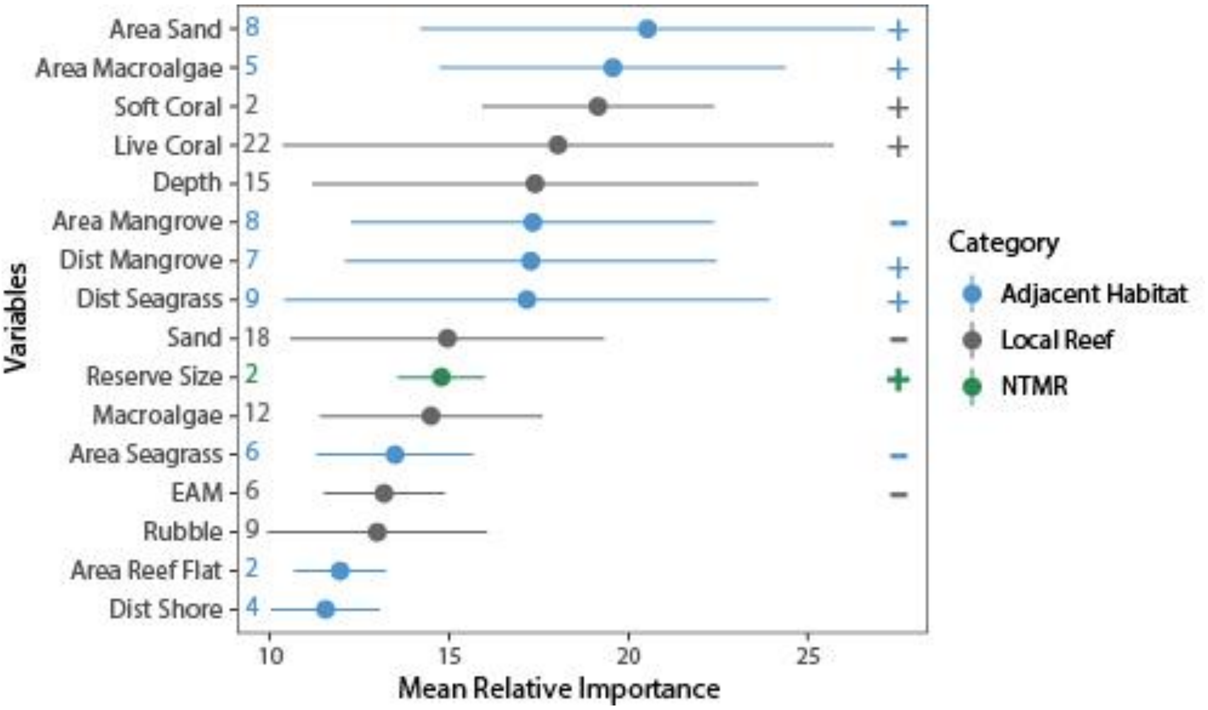
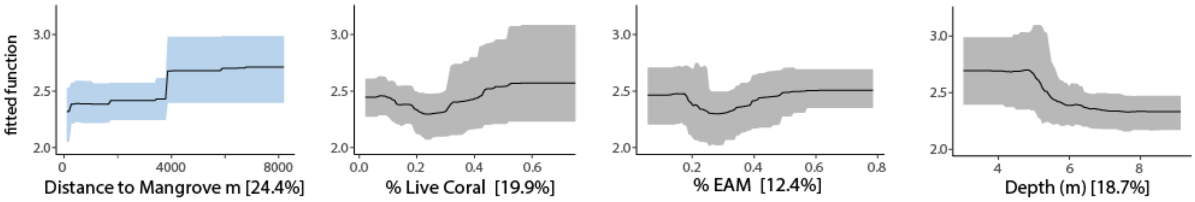
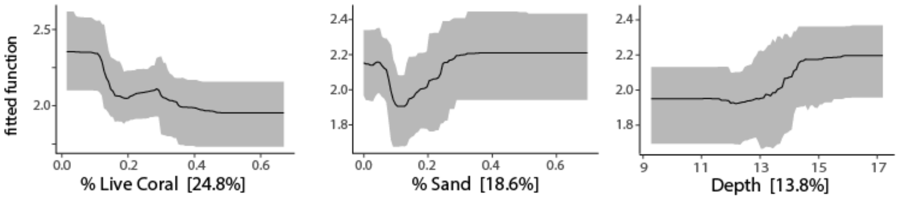


Figure 2.4. Partial dependence plots from boosted regression tree (BRT) bootstrap analysis for wrasse adult density on crest (a) and slope (b), and wrasse juvenile density models on the crest (c) and slope (d) and with the relative importance of each variable in brackets [%]. Partial plots present the relationship of each variable when all other variables are at their mean. Center line is the mean and ribbons are 95% confidence intervals for 100 bootstrap runs. Blue ribbons are for adjacent habitat variables, and grey are for local reef variables. For each model, only partial plots with high relative importance (>10%) are shown.

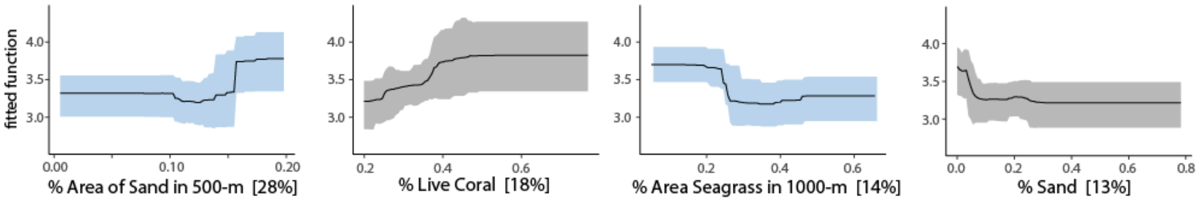
a. Wrasse adult density on crest



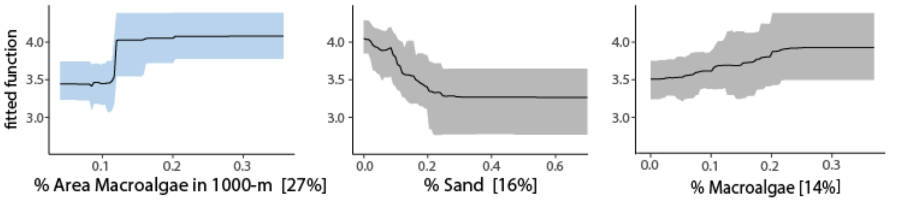
b. Wrasse adult density on slope



c. Wrasse juvenile density on crest



d. Wrasse juvenile density on slope



2.5 DISCUSSION

Overall, reef fish presence, density, and biomass were affected primarily by local within-reef attributes and were secondarily influenced by adjacent habitat in the seascape. Although local reef variables were selected most often in models, the mean relative importance for influential variables was similar between adjacent habitat and local reef. This implies that reef fishes in this seascape are responding to features beyond their immediate vicinity, and that adjacent habitat measures of the seascape at the scale of hundreds of meters are important to consider. Other research comparing the influence of local coral reef and adjacent habitats on coral reef fishes have found that seascape scale habitat can be more important than local reef habitat (Yeager et al. 2011; Knudby et al. 2011; Kendall et al. 2011; Olds et al. 2012a; Henderson et al. 2017). In high connectivity seascapes, fish assemblages can be more similar between coral reefs and non-reef habitats compared to more isolated seascapes (van Lier et al. 2018), and many species traditionally classified as coral reef dwellers are also found in other non-reef habitats (Evans et al. 2014; Sambrook et al. 2019). Here, I find that on coral reefs, juvenile *Chlorurus* and wrasses were more strongly influenced by adjacent habitat metrics than local reef factors. For adjacent habitat, the relative amount of sand and macroalgae in the surrounding seascape were the strongest predictors of reef fish density and biomass, with seagrass and mangrove habitat having less of an effect.

One of the most influential habitats in my models was sand, where sand adjacent to coral reefs had a positive effect on fish, while sand at the local reef scale had a negative effect (e.g. Fig. 2.4). Adjacent sand in the seascape had the highest average relative importance of any habitat metric, with a consistent, positive change in density and biomass of reef fish when sand was between 10-20% of the total area of a seascape. In Siquijor, sand in the seascape was in the back reef areas, on the reef slope, and as large sand patches interspersed throughout the seascape. I hypothesize that a low amount of sand cover between 10-20% may represent the presence of transition zones to other important habitats. These transition zones, or ecotones, have their own unique contribution that mediates species distributions and interactions, and can be an important seascape predictor (Pittman et al. 2007; Valentine et al. 2007; Vanderklift et al. 2007). An alternative hypothesis would be an isolation effect, where sand patches adjacent to coral reefs reduce the overall area of preferred habitat, thus concentrating fish on coral reefs. At small spatial scales, isolated reefs can have increased densities of fishes (Chittaro 2002; Belmaker et al. 2005), and sandy habitat adjacent to coral reefs can alter movement of fishes (Turgeon et al. 2010). Contrastingly, sand at the local reef scale had a negative relationship with fish density and biomass. Although some taxa may benefit from the presence of sand and rubble at a local scale (e.g. parrotfishes and wrasses) (Russ et al. 2015, 2017), other taxa which are more reliant on the reef structure itself may respond negatively to sand and rubble (e.g. damselfishes and butterflyfishes) (Russ and Leahy 2017). However, responses to sand on transects can be taxon-specific, where species responses vary even within the same family (Russ et al. 2017, 2018, Lowe et al. 2019). Here, the opposing relationship of sand cover at different spatial scales underpins the importance of employing a multi-scale approach to describing fish-habitat relationships.

Interestingly, I found that fishes were negatively associated with mangrove and seagrass habitats, where density and biomass of fishes on coral reefs were highest when these habitats were farther away and made up less of the seascape. This is counter to other seascape studies which show increased coral reef fish presence and biomass with increased spatial connectivity to seagrass and mangrove habitat (Nagelkerken et al. 2002; Mumby et al. 2004; Verweij et al. 2006; Olds et al. 2013). In this Philippine system, the tidal regime makes these habitats inaccessible for significant periods of time, which may limit their use by coral reef fishes. Indeed, the importance of mangroves has been shown to be strongly tidally influenced (Lee et al. 2014), and mangroves play a larger role for juvenile fishes in regions where mangrove stands are permanently inundated (Igulu et al. 2014). Philippine mangrove systems have been considerably altered, by cutting, coastal development, and planting (Primavera and Esteban 2008). While planting can increase the extent of mangrove stands, it may come at a cost to their ecological function if mangrove species are planted in unsuitable habitats (e.g. *Rhizophora* spp. planted on seagrass beds) (Primavera and Esteban 2008; Lee et al. 2014). Potentially, planted mangrove habitats in my study seascape may not sufficiently mimic natural ecological systems, partially accounting for the negligible effects of adjacent mangroves on fish dynamics on coral reefs.

For juvenile wrasses and juveniles in the parrotfish genus *Chlorurus*, adjacent non-reef habitat metrics had a significantly higher mean relative importance. I believe that the present study is one of the first examples to show that the surrounding seascape influences juveniles of some fish genera on coral reefs. Non-reef habitats are sometimes important nursery grounds for coral reef fish (Nagelkerken et al. 2000c; Cocheret De La Morinière et al. 2002; Adams et al. 2006; Sheaves et al. 2015)**.** Higher densities of juvenile reef fishes in non-reef habitats compared to coral reefs implies their nursery value to coral reef fish populations (Nagelkerken et al. 2000a; Kimirei et al. 2015; Tano et al. 2017). Non-reef habitats are suggested to be optimal nursery habitat for juveniles due to reduced predation risk (Dahlgren and Eggleston 2000; Valentine et al. 2007; Dorenbosch et al. 2009), and often greater availability of food resources (Kramer et al. 2015; Tano et al. 2016). Coral reefs with high spatial connectivity to adjacent habitats may be benefitting from ontogenetic habitat shifts of fishes from adjacent non-reef nursery habitat. Exploring the relative abundance of juveniles on both coral reef and non-reef habitats would further validate these hypotheses and should be explored in more detail.

Juvenile wrasse and juvenile *Chlororus* densities on coral reefs had a positive relationship with macroalgae and sand in the surrounding seascape. In my study system, macroalgal beds occur around the entire island, and I suggest that for Siquijor, macroalgal beds may be critical juvenile nursery habitat for some coral reef fish species. Recent evidence suggests that *Sargassum* dominated macroalgal beds harbor significantly greater densities of juvenile fishes compared to other non-reef habitat such as seagrass (Tano et al. 2017; Eggertsen et al. 2017; Fulton et al. 2019). However, for fishes, the ecological importance of sand in the seascape is less clear. Some parrotfish species are known to occasionally forage in sandy areas (Russ 1984) and have been shown to preferentially associate with sand and soft unvegetated habitat during the juvenile stage (Mellin et al. 2007). Comparatively, *Scarus* juveniles were strongly influenced by the amount of live fragile coral cover on reefs (e.g., branching *Acropora* and *Porites*) rather than by adjacent habitat. Juvenile *Scarus* parrotfish have been one of the more conspicuous taxa observed in non-reef habitats (Gullström et al. 2011; Tano et al. 2017; Sambrook et al. 2019), but have also been shown to associate with small branching pocilloporid corals (Bellwood and Choat 1989) and dead coral skeletons in back reef habitats (Wilson et al. 2010). Perhaps the discrepancy between species within the parrotfish family (*Chlorurus* and *Scarus*) is demonstrating multiple post-settlement habitat selection strategies and/or multiple ontogenetic habitat shifts. Though research has detailed how ontogenetic shifts occur by changes in diet (Bellwood 1988; Chen 2002), home range (Welsh et al. 2013; Streit and Bellwood 2017), and habitat use (Dahlgren and Eggleston 2000), further research must explore how habitat use patterns and ontogenetic shifts may be modified by the habitat availability and spatial configuration of the seascape.

Wrasses were the only fish group to show a significantly greater relative importance of adjacent habitat variables than local reef variables for both juveniles and adults. The amount of adjacent macroalgae and sand in the seascape were both positively correlated with wrasse density and biomass on coral reefs (Fig. 2.4). Wrasses have been highlighted as a group with a high prevalence for multi-habitat use (Sambrook et al. 2019) and can respond to seascape level spatial dynamics (Staveley et al. 2017). van Lier et al. (2018) showed greater overlap in wrasse assemblage structure between coral reefs and macroalgal beds when macroalgal beds were close to coral reefs with *Thalassoma* generalists identified as driving this response. Generalist species are more versatile in their diet and ability to use different habitats, and generalist wrasse species are more likely to move across a wider range of benthic resources compared to their specialist counterparts (Berkström et al. 2012b, 2014). This plasticity may allow individuals to take advantage of nearby non-reef habitats such as macroalgal beds, which can have higher abundances of epifauna, small crustaceans, and copepods, potential dietary sources for many tropical wrasses (Berkström et al. 2012b; Kramer et al. 2015; Tano et al. 2016). Nonetheless, live coral cover was also an important factor affecting wrasses, selected as an influential predictor in 5 out of 6 BRT models. Thus, my results indicate that both local reef variables such as live coral cover, as well as adjacent habitat variables influence density of wrasses. Indeed, wrasses in the Philippines have been shown to correlate with benthic dynamics, mirroring long-term changes in benthic substrata (Russ et al. 2017b). However, those responses were taxon-specific, varied, and occurred on small offshore Philippine islands with little to no shallow adjacent non-reef habitats.

In a complex island seascape in the Philippines, density, biomass, and presence of coral reef fishes were driven by both local reef habitat on coral reefs, and adjacent habitats in the surrounding seascape. Adjacent habitats were the primary driver for some fish taxa (e.g. wrasses) including their juveniles. I found that coral reef fishes responded to adjacent habitats across multiple spatial scales but measuring the surrounding seascape at a 500-m scale obtained the best model results. Employing a multi-scale approach better explained reef fish patterns and incorporation of multiple adjacent habitats across an island seascape may offer deeper insights into the structuring of coral reef fish assemblages. This is especially relevant for regions like the Philippines where non-reef habitats are heavily impacted by coastal development, fishing pressure, and pollution, and where juvenile fishes are often the direct or incidental targets of fisheries. When considering management strategies that are spatially focused, such as NTMRs, adopting a multi-scale seascape level approach would consider other non-reef habitats that can often be overlooked in the management process (Weeks et al. 2010).

Interestingly, surgeonfishes were the only species group to include influential NTMR effects in models. Results of surgeonfish responses to NTMRs in the Philippines have been varied (Abesamis et al 2014, Russ et al. 2018). Yet, very few studies have focused on the interaction between seascapes and NTMR effects (Olds et al. 2016) and this topic should be pursued further.

Developing NTMR networks to improve reserve performance and region-wide resilience has been a major focus in recent years (Gaines et al. 2010; Weeks et al. 2014). Incorporating non-reef habitats in the establishment of NTMR networks could better conserve populations for species of reef fish with ontogenetic migrations (Grüss et al. 2011; Green et al. 2015). Accounting for ecological processes such as ontogenetic habitat shifts and movement patterns could greatly increase the conservation potential of NTMRs to improve fish species diversity, abundance, and biomass (Brown et al. 2016; Engelhard et al. 2016; Olds et al. 2016). For fishes that utilize non-reef habitats, adjacent habitats can even outweigh the NTMR effect for adult fish biomass on coral reefs (Nagelkerken et al. 2012), or act synergistically with NTMRs to improve NTMR outcomes (Olds et al. 2012b). Indeed, non-reef habitats in the Philippines were identified as priority conservation areas to "optimize tradeoffs between biodiversity and fishery targets" (Weeks et al. 2010). With the improved ability to obtain satellite imagery and map habitats, incorporating simple metrics such as distance to adjacent habitats and total area of multiple habitats is now much more attainable. I argue that including habitat metrics across multiple spatial scales to describe reef fish patterns, dynamics, and functions should be considered when feasible, and is especially critical in diverse seascapes.

CHAPTER 3: CORAL REEF FISH ASSEMBLAGES INFLUENCED BY MULTIPLE ADJACENT NON-REEF HABITATS ACROSS A SEASCAPE

3.1 ABSTRACT

In tropical seascapes multiple habitats can function together as a larger network. While coral reef fishes are predominately affected by coral reef habitat, the surrounding adjacent habitat near coral reefs can influence coral reef fish assemblages. Here, I explore how coral reef fish assemblages respond to local scale (within coral reef) benthic habitat and larger scale (surrounding seascape) features of multiple habitats on Siquijor Island in the Philippines. I examined the entire fish assemblage, and then refined my analyses to focus on parrotfishes and wrasses. I find that coral reef fish assemblages are influenced significantly by other adjacent habitats in the surrounding seascape, and that different non-reef habitats can greatly alter species assemblages and diversity of fishes on coral reefs. Five distinct habitat types were identified in cluster analysis which incorporated both local-scale benthic and larger-scale adjacent seascape variables. The five clusters were defined by 1. Rubble and epilithic algal matrix (EAM), 2. Coral cover and area of adjacent macroalgae, 3. Area of adjacent mangrove and sand habitat, 4. Soft coral cover and area of adjacent seagrass, and 5. Area of coral reef and area of reef flat. These clusters contained unique coral reef fish assemblages, and differed in overall fish species diversity. While the entire fish assemblage had distinct structure among clusters, parrotfish and wrasse assemblages showed some overlap between habitat clusters. Fish species identified as unique to a cluster type were often driven by their use of non-reef habitats adjacent to coral reefs. Despite fish being observed on coral reef habitat, non-reef habitat adjacent to coral reefs had a significant impact on the species assemblages observed on coral reefs, creating unique reef fish assemblages and contributing to fish diversity on coral reefs.

3.2 INTRODUCTION

Understanding the spatial scale which organisms use habitats has been a fundamental component of ecology (MacArthur and Wilson 1967, Moilanen and Nieminen 2002; Tischendorf et al. 2003), affecting population dynamics, distribution, abundance, and community structure (Ault and Johnson 1998; Fahrig 2003). The influence of surrounding habitats has gained renewed interest in marine systems with improved abilities to map marine systems (Grober-Dunsmore et al. 2009; Wedding et al. 2011b). While still a relatively nascent field, seascape ecology explores how the spatial distribution of habitats affect species patterns and processes (Pittman et al. 2004; Boström et al.

2011). Specifically, a point of focus has been estimating the relative effects of within-coral reef habitat features, and surrounding habitat spatial configuration on fish biomass, density, diversity, and assemblage structure (Chittaro et al. 2005; Mumby and Hastings 2008; Olds et al. 2012a; Pittman and Olds 2015). While coral reef benthic characteristics are well known to alter coral reef fish populations (Pratchett et al. 2011; Coker et al. 2014; Russ et al. 2015a), the effect of other adjacent habitats across larger spatial scales is widely appreciated, but highly variable both among species and seascapes.

There has long been acknowledgement of the importance of multiple habitats for fishes (Ogden and Buckman 1973; Shulman and Ogden 1987; Nagelkerken et al. 2000c, 2000b), but only recently has this topic gained widespread attention. For habitats across a seascape to impact fishes, the assumption is that species can move across habitat boundaries, use other habitats, and have the capabilities to move relatively large distances (100-1000 meters). Therefore, spatial metrics such as proximity and total area are expected to have the greatest effects on populations and assemblages (Fahrig 2013). However, the scale at which species respond to the seascape is still relatively unknown (Berkström et al. 2012a; Jackson and Fahrig 2012), varies for different species (Pittman and Brown 2011; Johnson et al. 2013), and can be location or region specific (Igulu et al. 2014). Many fishes, such as emperors and grunts, travel diurnally from coral reef habitat to seagrass beds to feed (Nagelkerken et al. 2000a; Appeldoorn et al. 2009). Perhaps the greatest benefit of non-reef habitats towards coral reef fishes is the potential nursery function (Beck et al. 2001; Adams and Ebersole 2002; Nagelkerken et al. 2015; Sheaves et al. 2015). Non-reef habitat adjacent to coral reefs can harbor greater densities of juvenile fishes (Nagelkerken et al. 2000c), many of which ontogenetically shift to coral reef habitats as adults. Movement of fishes between habitats are direct connectivity links contributing to ecosystem processes such as nutrient transport (Meyer and Schultz 1985), trophic transfers (Harborne et al. 2016), and population replenishment (Nakamura et al. 2008).

Incorporating spatial characteristics of multiple habitats at the seascape scale reveals more nuanced effects of other drivers, such as marine reserves (Huntington et al. 2010; Olds et al. 2012a, 2013), ecological processes like herbivory (Verweij et al. 2006; Mumby and Hastings 2008; Yabsley et al. 2016; Martin et al. 2018), and fish assemblage structure (Olds et al. 2012a; Henderson et al. 2017a). In tropical systems, the most conspicuous non-reef benthic habitats are mangroves, seagrass beds, and macroalgal beds. Mangroves are well known to harbor higher densities of juveniles and can contribute to increased biomass of certain fishes on coral reefs (Nagelkerken et al. 2000b, 2012; Lefcheck et al. 2019). But the importance of mangroves are most pronounced in places like the Caribbean where mangroves do not experience much tidal change, compared to the Indo-Pacific where mangroves are often exposed at low tide (Igulu et al. 2014; Kimirei et al. 2015). Seagrass beds are well studied with respect to their connectivity to coral reef habitats, affecting the presence, density, and diversity of fish species on coral reefs (Nakamura et al. 2003; Dorenbosch et al. 2005; Grober-Dunsmore et al. 2007), and altering coral reef fish feeding patterns (Davis et al. 2014; Eggertsen et al. 2020). Macroalgal beds have recently been reviewed and identified as an important tropical habitat (Fulton et al. 2019, 2020), and there is increasing evidence supporting the nursery importance of this habitat (Eggertsen et al. 2017). Many tropical seascape studies focus on coral reef and one other non-reef habitat. Some studies evaluate both mangroves and seagrass within the context of coral reefs. But very few evaluate the effects of seagrasses, mangroves, and macroalgal beds (Sambrook et al. 2020).

This study investigated how seagrass, mangroves, and macroalgal beds affected the coral reef fish assemblage structure in a highly connected seascape. I used a multi-scale approach to explore the relative effect of within-coral reef metrics and seascape level non-reef adjacent habitat availability on the entire coral reef fish assemblage, parrotfishes, and wrasses. Parrotfishes are well documented multi-habitat users and are present in non-reef habitats as juveniles (Dorenbosch et al. 2005; Sambrook et al. 2019; Sievers et al. 2020b, Chapter 2). Wrasses have also demonstrated significant responses to the spatial arrangement of multiple habitats in a seascape, with altered assemblage structure (Vanderklift et al. 2007; van Lier et al. 2018), increased densities when non-reef habitats are near coral reefs (Sievers et al. 2020b, Chapter 2), and use of non-reef habitats as juveniles (Evans et al. 2014). I tested my questions in a highly connected and diverse seascape on the island of Siquijor in the Philippines, where the potential to explore the effect of multiple habitats is available. Specifically, I sought to identify 1. How coral reef habitat and spatial variables of multiple habitats adjacent to coral reefs influence coral reef fish assemblages,, 2. Identify which species are most strongly driven by the adjacent seascape, 3. Explore whether fish diversity on coral reefs is influenced by the surrounding seascape.

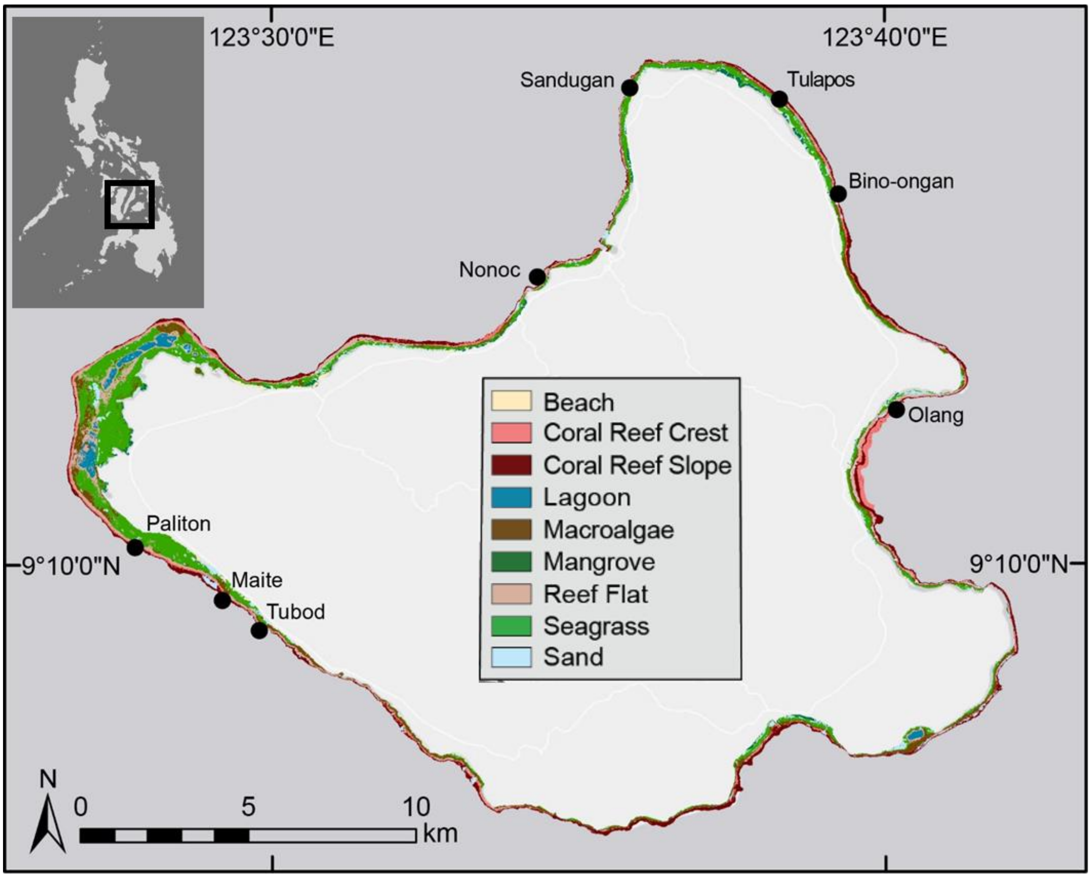
3.3 METHODS

3.3.1 Study Site

The island of Siquijor in the Philippines was the study area for this work (Fig. 3.1). This island is characterized by a range of submerged benthic habitats that vary in local diversity and total area surrounding the island. Shallow water benthic habitats include coral reef, reef flat, macroalgal beds, seagrass beds, and mangroves. Corals reefs surround the entire island, and the other non-reef habitats adjacent to coral reefs (seagrass beds, macroalgal beds, mangroves) vary in their distribution (Fig. 3.1). Eight locations around the island were selected for surveys as they represented a range of available non-reef habitat diversity and total area as well as had established no take marine reserves (NTMR)

(Fig. 3.1). This allowed us to evaluate any potential fish assemblage differences driven by NTMR effects.

Figure 3.1. Map of Siquijor Island with classified habitat map indicating types of submerged habitats. Black dots indicate locations of fish and benthic habitat surveys conducted on coral reef. For each location, a fished and no take marine reserve (NTMR) site was surveyed.



3.3.2 Fish and Habitat Surveys

Surveys of coral reef fishes and benthic habitat occurred in April – July 2016 at eight locations around Siquijor Island, and are the same data used in Chapter 2 of this thesis. Each location had a paired NTMR and fished site, where paired sites were no more than 500-m from one another, and every attempt to match similar benthic habitat between sites (NTMR vs Fished) were made. In total, this gave us 16 sites to explore assemblage responses to coral reef and adjacent habitat. Surveys of fish and benthic habitat were conducted only on coral reef habitat. At each site, three to four transects were placed at both the coral reef crest (5-8 m depth) and coral reef slope (10-15 m depth), resulting in 6-8 transects per site. In total, there were 108 transects across the island. For fish surveys, large mobile reef fishes were identified, counted, and had their length estimated to the nearest centimeter on a 50-m*5-m transect. On the return swim, smaller reef fish (<10 cm TL) were identified and counted on a 2-m wide belt. For benthic surveys, substrate was identified every 50-cm along the 50-m transect, and classified based on substrate type (rock, sand, rubble) and benthic cover (abiotic, crustose coralline algae, epilithic algal matrix (EAM), macroalgae, soft coral, hard coral, other). Macroalgae and soft coral was identified to genus when possible. Hard coral was identified to genus, and classified into growth form (fragile, robust). The ‘other’ category included sponges, tunicates, and gorgonians. Structural complexity was also estimated on a 0-5 scale where 0 represented flat and 5 equated to highly complex structure (Wilson et al. 2007).

3.3.3 Spatial Analysis

Spatial data of habitats across the Siquijor seascape were calculated using satellite derived habitat maps. Methodology of the habitat classification process is detailed in Sievers et al. (2020b, Chapter 2). Briefly, habitat was classified using the maximum likelihood classification method in ArcGIS, informed by geo-referenced habitat data points collected *in-situ*. Submerged benthic habitats classified were macroalgal beds, seagrass beds, mangroves, reef flat, coral reef, lagoon, and sand. Total area (km^2) of each of the habitat types was measured within 500-m of each coral reef fish survey site. The 500-m scale was selected, as it was previously identified as the most relevant spatial distance in describing fish abundance and biomass patterns in this location (Sievers et al. 2020b, Chapter 2). Global Moran’s I was calculated for habitats within 500-m of each survey site to evaluate potential spatial autocorrelation among sites and locations. Spatial data were not significantly spatially autocorrelated (Moran’s I = 0.370, p =0.24).

3.3.4 Statistical Analysis

To evaluate how fish communities are affected by small scale within coral reef habitat features (benthic coral reef transect data) and seascape wide habitat availability (total area of different adjacent habitat types) I used a series of redundancy analyses (RDA) and multidimensional scaling (MDS) analyses. All predictor variables were explored for normality and transformed if needed. Secondly, a correlation-based RDA using the *vegan* package v. 2.5.6 in R was performed on all predictor variables (benthic and seascape) to visualize general trends in variable relationships using transformed and standardized data. A hierarchical clustering using the *pvclust* package v.2.2.0 (Suzuki and Shimodaira 2011) was then conducted on the predictor habitat variables (benthic and seascape) using the standardized values also used for the RDA. *Pvclust* assess uncertainty in hierarchical cluster analysis and allows for bootstrapping and calculated probability analyses to assign p-values to the clusters. P-values were calculated using 10,000 multi-scale bootstrappings, and clusters were considered significant when the approximately unbiased (AU) p-value was greater than 0.95. To incorporate those hierarchical clusters into assemblage analyses, a K-means partial clustering process was conducted using the k-means function in the *cluster* package v. 2.1.0 (Rai and Singh 2010). The k-means cluster number was informed by cluster numbers identified in the hierarchical clustering. All 108 transects were assigned to a cluster type that described both its benthic habitat features and seascape habitat availability.

To explore how fish assemblages differed with relation to the unique habitat clusters, MDS analysis based on Bray-Curtis dissimilarity was used. MDS analyses were run for: 1. All fish species, 2. Parrotfishes (SubFamily: Scarinae), and 3. Wrasses (Family: Labridae). Parrotfishes and wrasses were selected as they demonstrated the strongest responses to seascape variables at the population level (Sievers et al. 2020b, Chapter 2). Fish species density per 1000-m^2 was fourth root transformed and standardized using Wisconsin standardization. nMDS was also used to explore patterns in fish assemblages between fished and NTMR sites. To evaluate which species and habitat variables were significantly driving these responses, envfit was run for species scores and environmental scores (habitat data) to explore which variables were best correlated across MDS ordination. Significant species and habitat variables were identified using the permutation feature in envfit to calculate a p-value, and only habitat variables and fish species scores that were significant ($p<0.05$) were plotted. Fish assemblage differences between habitat clusters and also fishing effects (NTMR versus fished) was tested using a one-way PERMANOVA for each fish group (permutations = 999) using the adonis function in the *vegan* package v. 2.5.6 using fourth root transformed and Wisconsin standardized data. To assess significant differences in assemblages between clusters, pairwise comparisons were conducted using the pairwise.adonis function from the *pairwiseAdonis* v. 0.0.1 which uses Bray-Curtis distance measures and Bonferroni corrections to compare clusters.

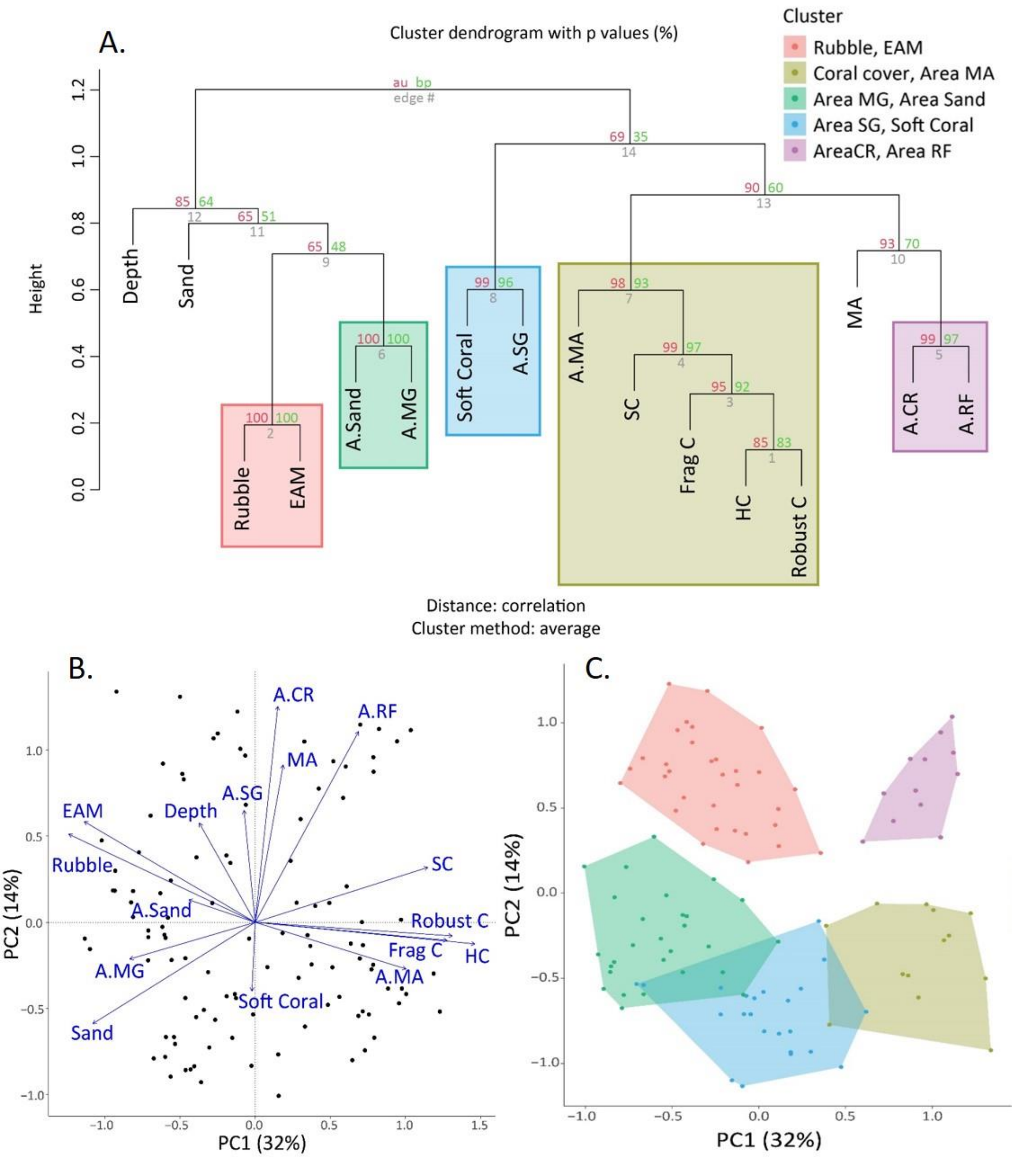
To describe which individual fish species are driving assemblage differences between habitat clusters, a percentage similarity analysis (SIMPER) was used to identify the dissimilarity among assemblages across habitat clusters. SIMPER analysis was conducted in R with 999 permutations which provide p-values to identify species significantly driving differences between assemblages. The permutation results are less influenced by species with high variability in density or very high abundances which might otherwise give them high contributions even though they do not differ among groups. Species that were repeatedly observed in the top of the contribution list and also had significant p-values were selected as fish species significantly driving differences between clusters. I then explored if there were consistencies in cluster comparisons, where certain fish species were repeatedly observed as significantly unique to that cluster compared to all other clusters.

Finally, to explore any effect on the diversity of fishes among the habitat clusters, I calculated a Shannon-Wiener diversity index for each fish species group (all species, parrotfishes, wrasses). I then explored the effect of habitat clusters on fish diversity using generalized linear models with glm in the *MASS* package v. 7.3.51.5, using the habitat clusters as the predictor and the Shannon-Wiener index values as the response. *Post-hoc* multiple comparison Tukey tests were used to identify differences in fish species diversity between clusters. Additionally, fish diversity was compared between fished and NTMR sites.

3.4 RESULTS

A total of 5,297 fishes from 248 species were recorded on coral reef habitat, with 52 wrasse species and 19 parrotfish species observed (Appendix B Table S3.1). Redundancy analysis (RDA) of habitat variables (benthic and seascape) and hierarchical clustering revealed clear habitat clusters typifying sites (Fig. 3.2). The first and second RDA axes explained 32% and 14% respectively of the total variation in the habitat dataset. This was confirmed by the hierarchical cluster analysis which identified five significant habitat clusters (Fig. 3.2). These clusters were sometimes described by coral reef benthic variables only or adjacent seascape variables only, but some were a mixture of both habitat scales. The first cluster, Rubble/EAM, was characterized by percent cover of rubble and percent cover of epilithic algal matrix (EAM) on benthic transects from coral reef surveys, representing degraded coral reef habitat (Fig. 3.2, Fig. 3.3). The second cluster was characterized by percent live coral cover on transects, structural complexity of coral reef habitat, and area of macroalgae within 500-m of survey transects (Coral/A.MA). Areas with the highest coral cover had low amounts of adjacent non-reef habitats, where macroalgal habitat was the dominant adjacent habitat. The third cluster was characterized by the area of sand and area of mangrove habitat within 500-m of coral reef surveys sites (A.MG/A.Sand). The fourth cluster was characterized by area of seagrass within 500-m of surveys, and percent cover of soft coral on coral reef transects (A.SG/Soft Coral). The final cluster was characterized by the total area of coral reef and large expanses of reef flat within 500-m of survey sites, representing consolidated substratum of reef (A.CR/A.RF). Although this cluster also has very large expanses of seagrass, it was classified as area of coral reef and area of reef flat because of its high amounts of both of these habitats, and relatively even distribution of benthic habitat types on coral reef. Statistical analysis identified these clusters as unique, and we acknowledge that all habitat types are present within each cluster.

Figure 3.2. (A) Cluster dendogram of the classification analysis of within reef benthic habitats and seascape level measures of non-reef habitats into groups using hierarchical cluster analysis. At each branch, the left value (red) is the Approximately Unbiased (AU) p-value, and the right value (green) is the Bootstrap Probability (BP) p-value. The AU value is used to cluster, where clusters with AU > 95% are significant. (B) Redundancy analysis (RDA) showing the variation in habitat variables along two principle components. Dots are transects and vectors are plotted variables. (C) is the RDA grouped by the clusters identified in the hierarchical cluster analysis. A.MG = area of mangrove, A.MA = area of macroalgae, A.CR = area of coral reef, A.RF = area of reef flat. SC = structural complexity. Frag C = fragile coral. HC = hard coral. Robust C = robust coral. MA = macroalgae.



When exploring how fish assemblages differed between the habitat clusters, there were diverse differences between the comparisons depending on which assemblage was evaluated (Fig. 3.4). Results evaluating the differences between fished and NTMR sites revealed weakly significant differences in fish species assemblages, explaining only 3-4% of the total variation. Furthermore, no fish diversity effects were observed between fished and NTMR sites. Therefore, NTMR results will not be presented for the remaining results and discussion. The primary factor separating clusters, and consequently species, seemed to be live hard coral cover, or lack thereof, resulting in EAM and rubble (Fig. 3.4, column C). The secondary effects were adjacent seascape level variables that measure total area of habitat types within 500-m of coral reef surveys. When exploring all species observed (n=248 species), there was clear separation between the clusters, with only slight overlap for the Rubble/EAM and Area Seagrass/Soft Coral cluster (Fig. 3.4.1A). Because there were so many species in this analysis, the significant species were further refined to ones with a significance of $p<0.001$ (Fig. 3.4.1B). When examined in conjunction with the environmental vectors (Fig. 3.4.1C), there seemed to be clear separation between environmental vectors. Species most influenced by live hard coral cover were *Chaetodon lunulatus, Zebrasoma scopas, Bodianus mesothorax,* and *Chromis retrofasciata*. The species with the longest vector towards rubble, EAM, and sand was *Pomacentrus amboinensis*, and *Halichoeres scapularis*. Species most correlated with the area of mangrove and area of seagrass were *Pomacentrus coelestis, Plectorhinchus sp., Anampses sp, Halichoeres crysus,* and *Stethojulis interrupta*. Species most aligned with area of macroalgae within 500-m of survey sites were *Ctenochaetus striatus*, *Scarus niger, Cephalopholis argus,* and *Thalassoma hardwicke*. The pairwise PERMANOVA comparisons also revealed that species assemblages were significantly different among all five habitat clusters (Table 3.1). SIMPER results revealed slightly different fish species drivers when evaluating unique dissimilarities between habitat clusters (Table 3.2, Appendix B Table S3.2). For the cluster characterized by the amount of mangrove and sand within 500-m of coral reef surveys (A.MG/A.Sand), fishes typifying this habitat were *Ctenochaetus striatus, Acanthurus nigrofuscus,* and *Plectrohincus sp*. For the cluster characterized by area of coral reef and area of reef flat (A.CR/A.RF), the species unique to these sites were *Pterocaesio tile, Caesio caerulaurea, Caesio teres, and Naso vlamingii*. Species unique to the Rubble/EAM cluster were *Ctenochaetus binotatus*, and *Naso minor*. Fish species that characterized the cluster typified by live hard coral cover and area of macroalgal habitat within-500 of reef survey sites (Coral/A.MA) were *Naso lituratus, Zebrasoma scopas,* and *Naso unicornis*. And finally, for clusters identified by the area of seagrass within 500-m and soft coral cover (A.SG/Soft Coral), there was largely a lack of unique species on these transects compared to other clusters, but occasionally had *Chaetodon baronessa* listed as a significant species.

Figure 3.3. Average (mean) and variation (standard deviation) of cover or area of habitat variables within each cluster type. The left column (blue) is the mean percent cover of benthic coral reef habitat variables observed on coral reef transect surveys. The right column (green) is the mean total area of habitat types within 500-m of fish survey locations.

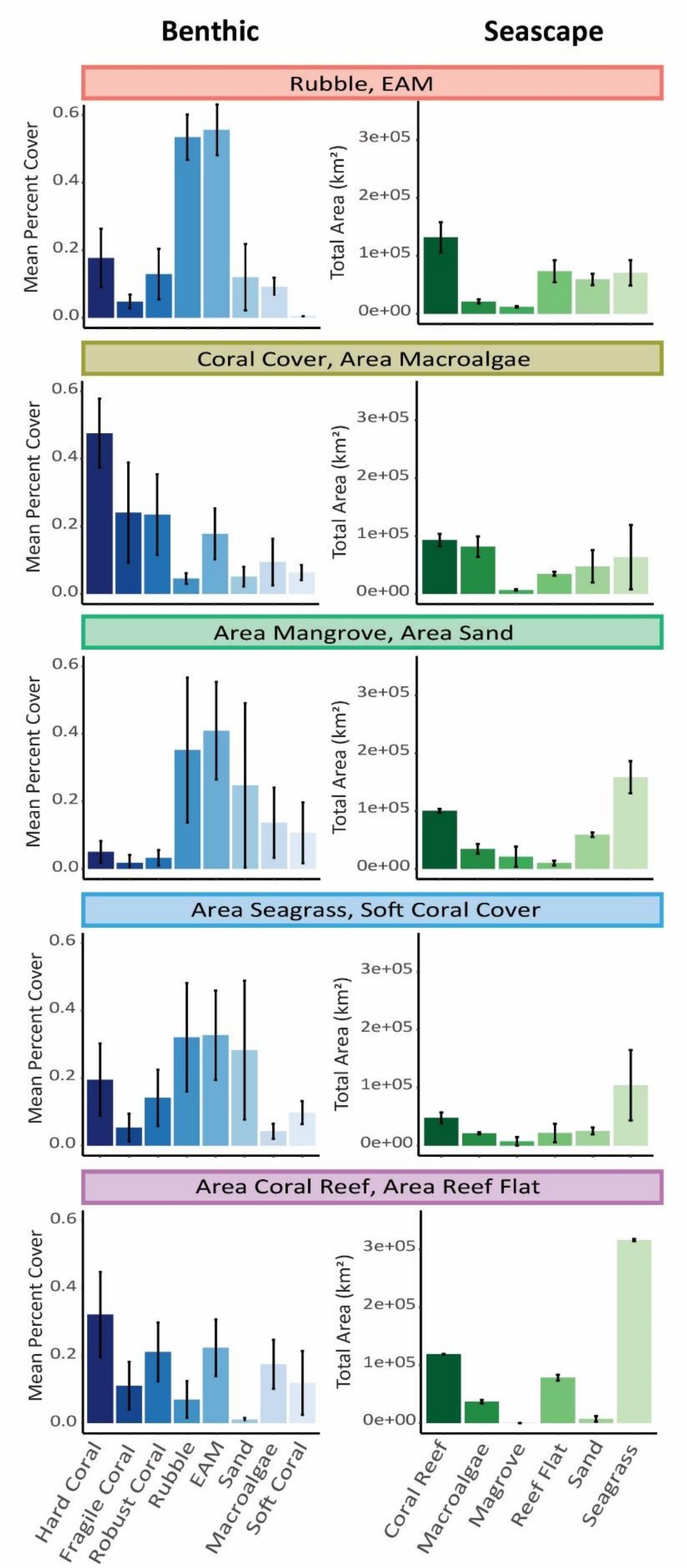
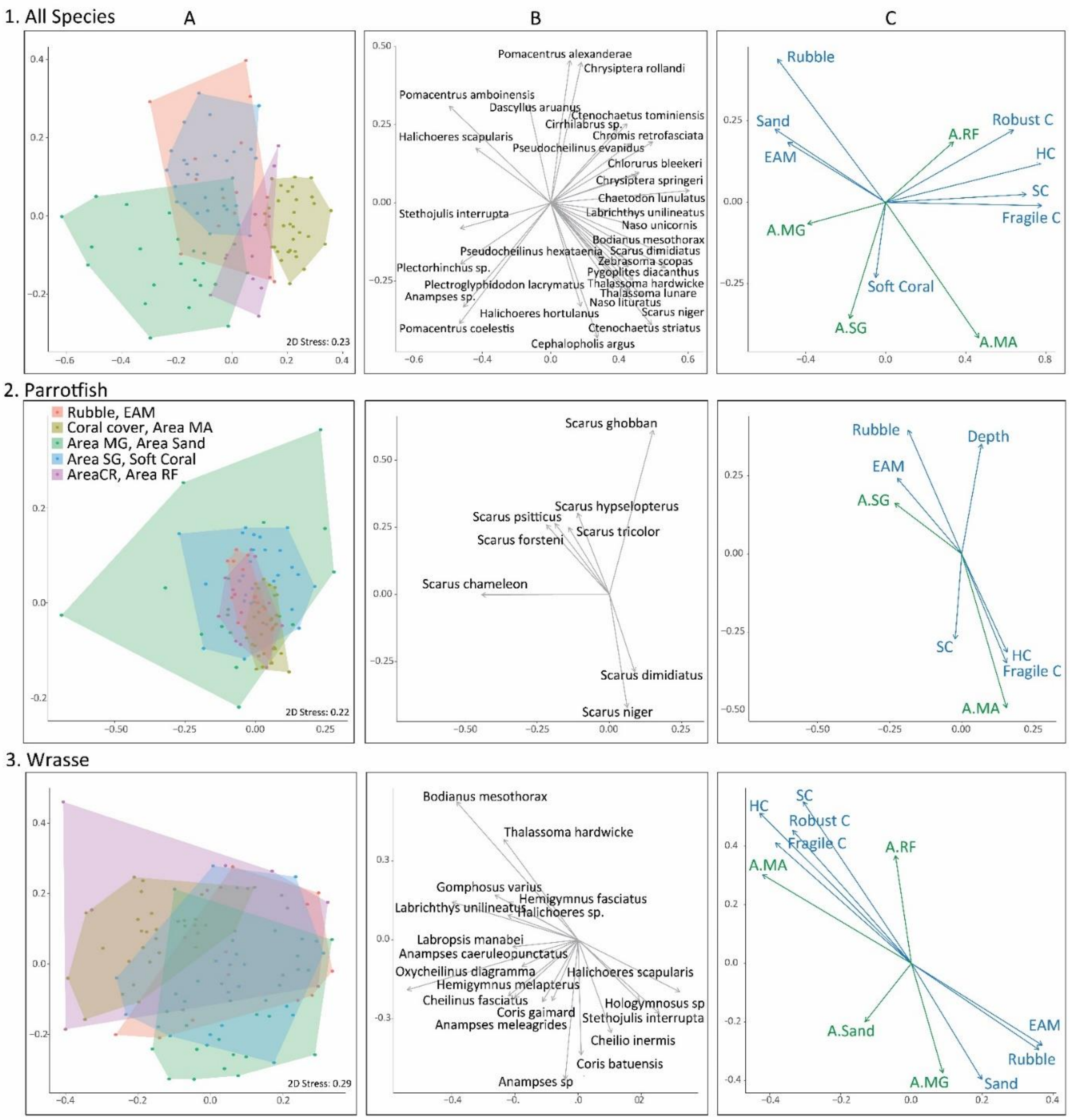


Figure 3.4. Fish assemblage results for all species observed (row 1), Parrotfish (row 2), and Wrasses (row 3). Column A displays the nonmetric multidimensional scaling (MDS) analysis depicting similarities in fish assemblage structure among habitat cluster types. MA = macroalgae, MG = mangrove, SG = seagrass, CR = coral reef, RF = reef flat. Column B displays the vectors of individual fish species with significant ($p<0.05$) correlations resulting from the envfit analysis. Column C displays habitat variables significantly ($p<0.05$) correlated to fish assemblage structure. Blue vectors and variables are within-habitat benthic variables describing coral reef habitat, and the green vectors are the seascape level variables describing the area of different habitat types.



For parrotfishes (Subfamily: Scarinae), the clusters were very different in MDS space compared to the all species analysis (Fig. 3.4.B1). The clusters were noticeably more constrained in MDS space except for the cluster area of mangrove and sand (A.MG/A.Sand) which had a very large cluster space compared to the other clusters. The pairwise PERMANOVA results revealed that four of the 10 comparisons of the clusters were not statistically different from one another and that three habitat clusters were similar to each other (Table 3.1). Area of coral reef and reef flat (A.CR/RF), area of seagrass and soft coral cover (A.SG/Soft Coral), and the Rubble/EAM clusters had fish assemblages not statistically different from one another. From the PERMANOVA results, *Scarus dimidiatus* and *Scarus niger* were tightly aligned with live coral cover metrics and area of macroalgae (Fig. 3.4.3B). *Scarus ghobban, Scarus hypselopterus, Scarus psittacus, Scarus forsteni* and *Scarus tricolor* were associated with the cover of rubble, sand, and EAM on transects. Interestingly, the *Scarus chameleon* vector was strongly extending along the first MDS axis which seems to be related to the area of mangrove and sand cluster. From the SIMPER analysis, the species which are most unique to the area of mangrove and sand cluster were *Chlorurus spp, Scarus chameleon,* and *Scarus hypselopterus* (Table 3.2). The parrotfish species representing area of coral reef and reef flat sites were *Chlorurus microrhinos,* and *Scarus psittacus*. The rubble and EAM cluster was described by *Chlorurus bowersi,* and *Chlorurus bleekeri*. The live coral cover and area of macroalgae cluster was described by *Scarus spp., Scarus dimidiatus, Scarus niger,* and *Chlorurus bleekeri.* Lastly, the area of seagrass and soft coral cover was described by *Scarus tricolor, Scarus ghobban,* and *Scarus rivulatus*.

When evaluating the wrasse assemblages, clusters were more spread across MDS space compared to the parrotfish clusters (Fig. 3.4.3A). The PERMANOVA pairwise comparisons identified that the rubble and EAM cluster was most similar to other clusters (Table 3.1). There was strong separation in MDS space between significant environmental variables, where one grouping was live hard coral cover, structural complexity, area of macroalgae, and area of reef flat (Fig. 3.4.3C). Whereas in the opposite direction there was rubble, EAM, sand, and area of mangrove habitat. Fish species most significantly associated with the live coral and area of macroalgae group were *Bodianus mesothorax, Thalassoma hardwicke,* and *Labrichthys unilineatus*. Species most strongly correlated with rubble, EAM and area of mangrove were *Halichoeres scapularis, Stethojulis interrupta,* and *Coris batuensis. Oxycheilinus diagramma* was diametrically and strongly opposed to those groups. The SIMPER analysis again revealed distinct species driving differences between habitat clusters (Table 3.2). The area of mangrove and sand cluster was characterized by *Anampses spp, Anampses meleagrides,* and *Cheilinus chlorurus.* The area of coral reef and reef flat cluster was distinguished by *Bodianus dictynna, Coris gaimard,* and *Gomphosus varius.* The Rubble/EAM cluster was differentiated by *Coris batuensis, Hemigymnus melapterus, Novaculichthys taeniourus, Oxycheilinus celebicus,* and

Cheilinus fasciatus. The cluster with live coral cover and area of macroalgae was described by *Bodianus mesothorax, Labrichthys unilineatus,* and *Cheilinus oxychephalus.* Finally, the area of seagrass and cover of soft coral cluster was described by *Choerodon sp., Cheilio inermis, Epibulis brevis,* and *Cheilinus trilobatus.*

Table 3.1. Pairwise post-hoc comparison tests from PERMANOVA analysis comparing fish assemblage structure between cluster types for all species, parrotfishes, and wrasses. Bold values are significant (p<0.05) highlighting differing fish assemblages. P-values are bonferroni adjusted p-values. A.MG/A.Sand is the area of mangrove and area of sand cluster. Rubble/EAM is the cluster defined by rubble and the epilithic algal matrix (EAM). Coral/A.MA is the cluster for live coral cover and area of macroalgae. A.SG/Soft Coral is the cluster for the area of seagrass and soft coral cover. A.CR/A.RF is the cluster for the area of coral reef and area of reef flat habitats. Bolded values are significant (p<0.05) for differing assemblages.

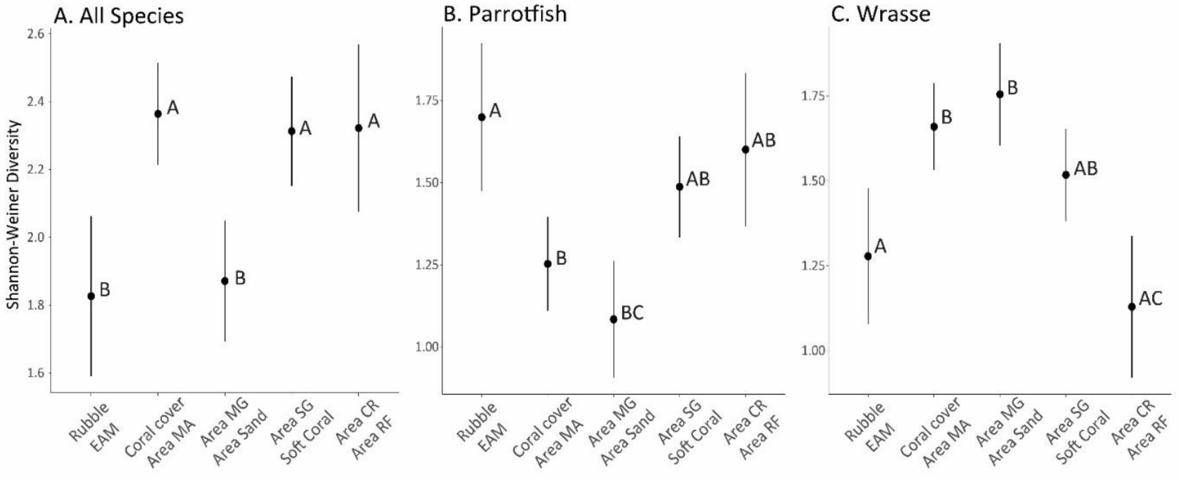
ALL.SPECIES	**All Species**	**Parrotfish**	**Wrasse**
A.MG/A.Sand vs Rubble/EAM	**0.01**	**0.02**	0.08
A.MG/A.Sand vs Coral/A.MA	**0.01**	**0.01**	**0.01**
A.MG/A.Sand vs A.SG/Soft Coral	**0.01**	**0.03**	**0.01**
A.MG/A.Sand vs A.CR/A.RF	**0.01**	0.34	**0.01**
Rubble/EAM vs Coral/A.MA	**0.01**	**0.01**	**0.01**
Rubble/EAM vs Area.SG/Soft Coral	**0.01**	0.16	0.43
Rubble/EAM vs A.CR/A.RF	**0.01**	1.0	0.37
Coral/A.MA vs A.SG/Soft Coral	**0.01**	**0.01**	**0.01**
Coral/A.MA vs A.CR/A.RF	**0.01**	**0.01**	**0.03**
A.SG/Soft Coral vs A.CR/A.RF	**0.02**	0.07	**0.01**

Shannon-Weiner diversity differed significantly between habitat clusters for all three species groups analyzed (Fig. 3.5). Richness and evenness were also evaluated, where richness followed the same trends observed for diversity, and evenness showed some significant differences between clusters, and thus I have decided to present only diversity results here. When evaluating the entire fish assemblage, diversity was high for three clusters, with lower diversity for the clusters Rubble/EAM cluster and the A.MG/A.Sand cluster. For parrotfish, there was more nuanced diversity results, but the highest diversity was observed on the sites characterized by Rubble/EAM, with the lowest on sites typified by A.MG/A.Sand. Wrasses, interestingly, showed an opposite diversity response compared to parrotfishes, where the highest wrasse density was from habitat clusters A.MG/A.Sand and Coral Cover/A.MA, with the lowest diversity for A.CR/A.RF.

Table 3.2. Fish species results from the percentage similarity analysis (SIMPER) identifying species uniquely attributed to each habitat cluster. Species are selected from the entire SIMPER output and species listed here are only species that were significant in the SIMPER output and were repeatedly selected as describing that habitat cluster across all cluster comparisons.

Cluster	**All Species**	**Parrotfish**	**Wrasse**
Area Mangrove Area Sand	*Ctenochaetus striatus* *Acanthurus nigrofuscus* *Plectorhinchus sp.*	*Chlorurus sp.* *Scarus chameleon* *Scarus hypselopterus*	*Anampses sp.* *Anampses meleagrides* *Cheilinus chlorurous*
Area Coral Reef Area Reef Flat	*Pterocaesio tile* *Caesio caerulaurea* *Caesio teres* *Naso vlamingii*	*Chlorurus microrhinos* *Scarus psittacus*	*Bodianus dictynna* *Coris gaimard* *Gomphosus varius*
Rubble EAM	*Ctenchaetus binotatus* *Naso minor*	*Chlorurus bowersi* *Chlorurus bleekeri*	*Coris batuensis* *Hemigymnus melapterus* *Novaculichthys taeniourus* *Oxycheilinus celebicus* *Cheilinus fasciatus*
Coral Cover Area Macroalgae	*Naso lituratus* *Zebrasoma scopas* *Naso unicornis*	*Scarus sp.* *Scarus dimidiatus* *Scarus niger* *Chlorurus bleekeri*	*Bodianus mesothorax,* *Labrichthys unilineatus* *Cheilinus oxychephalus*
Area Seagrass Soft Coral	*Chaetodon baronessa* mostly lack thereof	*Scarus tricolor* *Scarus ghobban* *Scarus rivulatus*	*Choerodon spp* *Cheilio inermis* *Epibulus brevis* *Cheilinus trilobatus*

Figure 3.5. Shannon-Weiner diversity estimates (fitted values 95% confidence intervals) in habitat clusters for (A) all species, (B) parrotfish, and (C) wrasse.



3.5 DISCUSSION

Coral reef fish assemblages are primarily influenced by local scale benthic structure, but are secondarily influenced by other benthic habitat types in the surrounding seascape. Unlike most studies, this work explores the relative influence of within coral reef metrics and seascape level metrics from multiple habitats types on coral reef fish assemblages, rather than focusing on the effect of only one adjacent non-reef habitat (Gillanders et al. 2003; Kimirei et al. 2011). Five distinct habitat clusters significantly influenced the entire coral reef fish assemblage, as well as wrasse and parrotfish assemblages, with analyses identifying species unique to each habitat cluster. Fish species diversity differed significantly between habitat clusters, and wrasses and parrotfishes had opposing diversity relationships between clusters. While it is well known that within-coral reef benthic habitat drives species patterns and assemblages (Pratchett et al. 2011; Coker et al. 2014; Russ et al. 2015a; McClure et al. 2020a), the effects of multiple habitats at a seascape scale are understudied. Here I demonstrate that non-reef habitats within 500-m of coral reef habitat can affect fish assemblage structure and species diversity of fishes on coral reefs. This has profound implications for the management and protection of coral reefs, as my results support broader incorporation of multiple benthic habitats in marine reserve management practices.

My findings suggest that incorporating a combination of within coral reef benthic habitat and seascape level habitat metrics are best at describing coral reef fish assemblages in a diverse seascape. This was observed in the MDS analysis which included both coral reef benthic and adjacent seascape variables as significantly correlated with fish assemblages. Some studies show seascape level metrics as the primary influence for species assemblages (Olds et al. 2012a), while others observe a secondary influence of seascape context (Grober-Dunsmore et al. 2008; Davis et al. 2014). Species groups, as well as life stage seem to alter the order in which habitat scales are prioritized, and a combination of fine and broad scale metrics are likely the best predictors (Berkström et al. 2013b; Berkström 2020). For juvenile wrasses in non-reef habitats such as macroalgal beds or seagrasses, within-patch metrics (e.g. canopy structure) are the primary factor affecting density and abundance, but adults were more influenced by seascape level metrics such as patch area and isolation (van Lier et al. 2018). It is therefore critical to consider the focal habitat of interest with respect to the species and life stage evaluated. I focused on adult fishes on coral reefs, but juveniles emerged in two notable instances. *Plectorhinchus sp. (*sweetlips*), and Scarus sp. (*parrotfish) juveniles were classified as spp. because they were juveniles and were identified as unique species for some of the habitat clusters. These two examples were listed as unique for clusters which also described the surrounding habitats. *Plectorhinchus sp.* was identified as unique to the cluster represented by the amount of mangrove and sand in the surrounding seascape (A.MG/A.Sand) and was also correlated with area of mangrove in the RDA analysis. *Plectorhinchus* (Family: Haemulidae), known as sweetlips, are from the grunt family, and juveniles have been observed in seagrass beds, albeit rarely (Nakamura et al. 2003; Vanderklift et al. 2007; Berkström et al. 2012a). Other species of grunts are well known to use non-reef habitats, predominately seagrass beds, for foraging and as nursery habitat (Nagelkerken et al. 2008; Berkström et al. 2012a, 2020; Sambrook et al. 2019). Although the use of mangroves has been recorded in only a few species of this genus (*P. gibbosus,* and *P. albovittatus*) (Igulu et al. 2014; Olds et al. 2014), here I find that reef sites with closer proximity to mangroves had uniquely higher numbers of juvenile *Plectorhinchus*, indicating that mangrove may be an important nursery habitat for *Plectorhinchus* species in this region. *Scarus sp.* (Subfamily: Scarinae) was listed as a unique species in the habitat cluster describing the live coral cover and the area of macroalgal habitat (Coral/A.MA). Macroalgal beds have previously been identified as important for driving parrotfish species patterns in this area (Sievers et al. 2020b, Chapter 2), specifically for juvenile parrotfishes (Sievers et al. 2020a, Chapter 4). Macroalgal habitat has recently been recognized as an important habitat in a tropical seascape, and as potential nursery grounds for many coral reef species (Tano et al. 2017; Fulton et al. 2020), which my results corroborate. While some species and life stages might be more associated with fine-scale within coral reef metrics, it is important to consider the context with which you explore these relationships, and consider the potential connectivity occurring across a seascape.

When examining the entire fish assemblage, there were clear and distinct fish assemblages between habitat clusters. From the RDA, some species were highly correlated with individual habitat variables such as *Pomacentrus amboinensis* with rubble on reefs, *Ctenochaetus striatus* with the area of macroalgal within 500-m of reefs, and *Chaetodon lunulatus* with the cover of fragile coral on reefs. These tight correlations are likely driven by species feeding ecology. For example *Chaetodon lunulatus* predominately feeds on branching *Acropora* coral species when on front reef locations like the crest (Berumen et al. 2005). Interestingly, compared to the taxon analysis (parrotfishes and wrasses), the RDA analysis for all fish species showed a more diverse spread of significant habitat variables. The parrotfish and wrasse RDA results generally split along two axes which were separated out by live coral cover and degraded reefs (rubble, sand, EAM), with seascape variables also splitting along these groupings. However, the all species analysis seemed to have a wider separation of variables, where more seascape variables were in unique sections of the multivariate space. For example, in the cluster described by the area of mangrove and area of sand habitat nearby, *Ctenochaetus striatus* and *Acanthurus nigrofuscus,* two conspicuous and abundant species observed on coral reefs. *C. striatus* is a common detritivore (Russ et al. 2018), and *A. nigrofuscus* is a herbivore which feeds on turf algae (Hart and Russ 1996). Mangrove habitats are soft sediment habitats which experience tidally driven changes that transport organic material and detritus from estuarine and intertidal systems out onto submerged reef habitats (Bouillon et al. 2008; Lee et al. 2014). Potentially, here, coral reefs near mangroves have higher levels of detritus and nutrients, which support growth of turf algae. Another detritivore, *Ctenochaetus binotatus* was identified as unique for the Rubble/EAM cluster, which has shown clear correlations with cover of dead substrata over long periods (Russ et al. 2018). Not so apparent was the addition of *Naso minor* for this cluster. *Naso minor* is a mid-water reef associated nominally planktivorous species which has been anecdotally recorded to feed on benthic algae (Randall 1986). Perhaps *N. minor* was associated with this habitat as it is less tightly coupled to benthic habitat compared to some of the other coral reef fishes. The cluster typified by large expanses of reef flat (A.CR/A.RF) identified a few fusilier species (Caesionidae) and *Naso vlamingii* as unique to this cluster for the all species analysis. The reef sites in this cluster also had relatively steep slopes, which is likely a main attractor for these midwater, mobile, reef-associated species. *Caesios* are highly mobile, but require structurally complex reef slope structure to sleep (Russ et al. 2017a), and *Naso vlamingii* is a moderately mobile species, but highly territorial (Russ et al. 2003; Abesamis and Russ 2005). Perhaps *Naso vlamingii* needs large areas of reef to reduce density dependent competition. For the cluster characterized by live coral cover and adjacent macroalgal habitat, three herbivorous fishes, *Naso lituratus, Zebrasoma scopas,* and *Naso unicornis* were identified as unique to this habitat cluster. These species are abundant grazers and browsers, where the two *Naso* species feed on fleshy brown macroalgae (Choat et al. 2002; Hoey and Bellwood 2010). *Naso unicornis* has been shown to travel hundreds of meters to foraging areas (Meyer and Holland 2005) to consume fleshy macroalgae (Bierwagen et al. 2017). This association creates another line of evidence linking macroalgal and coral reef habitats. Across and entire coral reef fish assemblage, there are strong and unique correlations with habitats beyond the coral reef, emphasizing the importance of including multiple habitats across a seascape.

For parrotfishes, assemblages were tightly clustered in MDS space, and assemblages were more similar to each other compared to the analysis of the entire fish assemblage. Fish assemblages from three clusters, area of seagrass and soft coral cover (A.SG/Soft Coral), rubble and EAM (Rubble/EAM), and area of coral reef and reef flat (A.CR/A.RF) were statistically similar to each other. The cluster defined by the area of mangrove and sand had a very large assemblage space compared to the other clusters, and also had the lowest parrotfish diversity. Although mangrove habitats can be important parrotfish habitat in the Caribbean (Mumby et al. 2004; Serafy et al. 2015) and east Africa (Dorenbosch et al. 2005; Lugendo et al. 2006), mangroves seems to be less influential in the Coral Triangle (Igulu et al. 2014; Sambrook et al. 2019), especially for parrotfishes. The benthic composition of the coral reef in the mangrove cluster was similar to other clusters (e.g. Rubble/EAM), suggesting that the effect of parrotfish diversity and assemblage structure was driven by the area of mangrove and sand in the adjacent seascape, rather than the local benthic habitat. If the surrounding seascape did not have an impact on fishes, one would expect the parrotfish assemblage to be similar between the mangrove/sand cluster and the rubble/EAM cluster. However, there are stark differences in the assemblage structure and diversity of these two clusters, indicating that seascape level effects have a substantial effect on parrotfish assemblages. The mangrove and sand cluster was characterized by *Scarus chameleon,* a species with relatively low abundances (Gust 2002), that uses a variety of reef habitats (Choat and Randall 1986), and is not strongly associated with the benthos (Gust 2002). *Scarus chameleon* was observed in non-reef habitats (Sievers et al. 2020a, **Chapter 4**), but relatively little is published about *S. chameleon* habitat use patterns. The remaining habitat clusters had relatively small MDS space. Perhaps the small assemblage space is due to the lower number of species in this taxon (n=19) compared to wrasses (n=52). Another explanation is the highly specialized feeding modes within parrotfish taxon, where they target microautotrophs (Clements et al. 2017; Nicholson and Clements 2020), and are tightly linked to the benthic composition (Russ et al. 2015b). The three compact assemblage spaces were the habitat clusters describing benthic coral reef habitat (Rubble/EAM and Coral/A.MA) or coral reef area (A.CR/A.RF). Although the benthic composition varies substantially between these groups, I hypothesize that parrotfishes are so tightly linked to their benthic food resource needs that species in these clusters target the necessary food sources irrespective of its abundance, and thus maintain similar assemblage structure. For example, adult *Chlorurus microrhinos,* a parrotfish species highly associated with the reef, will change their feeding behavior and home range dependent on the availability of resources to maintain their highly selective resource requirements (Carlson et al. 2017). However some species do change their feeding behaviors based on the structural connectivity of surrounding habitats (e.g. distance to seagrass). Eggertsen *et al.* (2020) observed increased bite rates for *Scarus ghobban* when near seagrass beds. I indeed found a similar response, where *Scarus ghobban* was unique to the cluster described by the area of seagrass. *Chlorurus microrhinos,* and *Scarus psittacus* were most unique to the habitat cluster describing area of coral reef and reef flat habitat. *Chlororus microrhinos* is rare in this region (Russ et al. 2015b), but is highly site associated to the coral reef crest (Welsh and Bellwood 2012a; Fox and Bellwood 2014). *Scarus psittacus* is also a species recorded to have widespread habitat use (Choat and Randall 1986; Sievers et al. 2020a, Chapter 4) and is commonly found on the crest, off crest, and especially the back reef area near sandy and rubble areas in this region (Russ, pers. obs.). At the assemblage level, I find evidence that the entire parrotfish assemblage is affected by the surrounding seascape, and although assemblages are tightly clustered when describing coral reef habitat, unique species characterizing clusters are driven by both coral reef benthic composition and non-reef habitats in a seascape. Results here provide further evidence that parrotfish diversity is linked to the presence and diversity of non-reef habitats in a highly connected seascape.Wrasses had much larger assemblage area in nMDS space compared to parrotfishes, while still exhibiting differences in species composition among habitat cluster types. Wrasses are a diverse group of fishes with varied feeding and swimming strategies (Fulton and Bellwood 2002; Wainwright et al. 2002). While wrasses respond to changes in benthic composition (Fulton and Bellwood 2002; Russ et al. 2017b; Lowe et al. 2019), they seem to be less tightly coupled to the benthic habitat (Green 1996; Lowe et al. 2019), potentially explaining the larger assemblage space. The two habitat clusters with the highest wrasse diversity were represented by the area of mangrove and sand within 500-m of coral reef habitat, and the cluster defined by live coral cover and area of macroalgae. While the diversity measures were similar between these two clusters, the wrasse assemblages were distinctly different. This only emphasizes the diversity in the wrasse taxa, and their varied habitat use and resource requirements. It is interesting to note that *Thalassoma* spp. did not appear in any of the SIMPER analyses. *Thalassoma hardwicke* was listed as significantly correlated to live coral and structural complexity, which corroborates relationships found on the Great Barrier Reef (Lowe et al. 2019) but is contrary to the responses observed for *Thalassoma* spp. from other islands in the Philippines (Russ et al. 2017b). The lack of *Thalassoma* spp. in the SIMPER analysis is likely because this genus is abundant, highly mobile (Wainwright et al. 2002), and a habitat generalist (Berkström et al. 2014), allowing them to be evenly distributed across all habitat clusters.

Some wrasse species selected as unique to a habitat cluster are clearly responding to within coral reef benthic characteristics. For example, *Novaculichthys taeniourus*, the rockmover wrasse, was associated with the Rubble/EAM cluster, and *Labrichthys unilineatus,* a corallivore (Berkström et al. 2012b), with the Coral/A.MA cluster. However, many species seem to have a correlation with the surrounding seascape. *Coris gaimard* was correlated with the area of sand in the MDS, and uniquely described the cluster area of coral reef and reef flat (A.CR/A.RF). *C. gaimard* has previously shown low associations to any coral reef benthic type (Fulton and Bellwood 2002; Kramer et al. 2016), and therefore might be more strongly associated with the surrounding habitat at larger spatial scales. *Cheilio inermis* was characteristic of the habitat cluster area of seagrass and soft coral cover (A.SG/Soft Coral). *C. inermis* has higher densities on reefs close to seagrass habitats (Dorenbosch et al. 2005; Shibuno et al. 2008), in seagrass beds as potential predators (Gullström et al. 2011; Tano et al. 2017; Wilson et al. 2017), as well as using seagrass beds as juveniles (Wilson et al. 2010). Both *Cheilinus chlorurus* and *Anampses* spp. were described in the cluster area of mangrove and sand (A.MG/A.Sand). These two species have inconsistent responses to within-coral reef benthic characteristics (Lowe et al. 2019), and *C. chlorurus* has one of the largest foraging distances (Fulton and Bellwood 2002), suggesting their potential to use multiple habitats across a connected seascape. Wrasses clearly respond to non-reef habitats, and the spatial arrangement of habitat can alter the assemblage structure in the western and eastern Indian Ocean (Dorenbosch et al. 2005; Olds et al. 2014; van Lier et al. 2018), and here in the Philippines. Now, we must further explore the extent with which wrasses are reliant on other habitats, and how they may connect important habitats within a seascape.

Whether a species or assemblage responds to within-coral reef or surrounding habitat depends heavily on the context of the seascape, which species are being evaluated and which life stages are observed. Ultimately, fishes are responding to the habitat at multiple spatial scales, and in a highly connected seascape, like my study system on Siquijor, all habitats within 500-m of sites should be considered as potentially influential. Among the five habitat clusters, coral reef benthic composition was similar between many of them (e.g. Rubble/EAM, and A.MG/A.Sand). If within coral reef benthic characteristics were the only drivers of fish assemblages, one would expect fish assemblage and diversity to be similar. However, the differences between clusters were apparent and significant across the entire assemblages and for wrasses and parrotfishes, implying the importance of the surrounding non-reef habitats. Considering non-reef habitats and coral reefs habitats as a holistic interconnected seascape will provide better estimations of the drivers of fish assemblages and improve conservation potential.

CHAPTER 4: UNRAVELLING SEASCAPE PATTERNS OF CRYPTIC LIFE STAGES: NON-REEF HABITAT USE IN JUVENILE PARROTFISHES

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4.1 ABSTRACT

Juvenile fish often use alternative habitats distinct from their adult phases. Parrotfishes are an integral group of coral reef fish assemblages, are targeted in fisheries, are sensitive to reef disturbances, and have been documented as multiple-habitat users. Considering the abundance of research conducted on parrotfishes, very little is known about their juvenile ecology at the species level due to their cryptic and variable coloration patterns. I collected juvenile parrotfishes in non-reef habitats (macroalgal beds, seagrass beds, and lagoons) in the Philippines and used DNA analysis to determine species composition. The results were then compared with data on adult parrotfish abundance from underwater visual census (UVC) surveys in coral reef and non-reef habitats. Collections identified 15 species of juvenile parrotfishes in non-reef habitats, and of these, 10 were also recorded in UVCs as adults. Informed by adult surveys, 42% of the 19 parrotfish species observed as adults were classified as multi-habitat users based on their presence in coral reef and non-reef habitats. When accounting for the occurrence of species as juveniles in non-reef habitats, 93% of the species collected as juveniles would be considered multi-habitat users. Species identified as juveniles in non-reef habitats comprised 50% of the average adult parrotfish density on coral reefs and 58–94% in non-reef habitats. The species richness of juveniles in non-reef habitats was greater than that of adults occupying the same habitats, and the most common adult species observed in UVCs was not collected as juveniles in non-reef habitats. Finally, UVC suggested that 97% of juvenile parrotfish <10-cm total length was present in non-reef habitats compared to coral reefs. These results provide further evidence for ontogenetic movement across habitat boundaries for parrotfish species in a diverse and highly connected tropical seascape. This is one of the few studies to quantify links between nursery and adult habitat in parrotfishes, highlighting the importance of including non-reef habitats in ecological studies of an iconic group of coral reef fish.

4.2 INTRODUCTION

Juvenile fish often use alternative habitats distinct from their adult phases. This strategy is assumed to increase juvenile survival, which contributes to adult populations. These alternative habitats are defined as nursery habitats (Beck et al. 2001; Nagelkerken et al. 2015; Sheaves et al. 2015; Lefcheck et al. 2019). In tropical seascapes, juvenile fish often use non-coral reef habitats such as seagrass, macroalgal beds, lagoons, and mangroves (Nagelkerken et al. 2000c; Adams et al. 2006; Dahlgren et al. 2006; Lefcheck et al. 2019; Fulton et al. 2020). Non-reef habitats can have reduced predation levels compared to coral reefs but often at the cost of reduced growth rates (Dorenbosch et al. 2009; Grol et al. 2011). This fitness trade-off is a key element driving nursery habitat use, where juveniles use habitats adjacent to coral reefs before moving to coral reefs as adults (Kimirei et al. 2013b), otherwise known as ontogenetic habitat migrations. For ontogenetic shifts to occur, the benefit of the unidirectional shift must outweigh the risk associated with the migration or change (Dahlgren and Eggleston 2000; Gillanders et al. 2003; Galaiduk et al. 2017).

Ontogenetic shifts often occur in conjunction with morphological and size changes. For example, juvenile parrotfish less than 10 cm in total length (TL) feed predominately on small crustaceans (Bellwood 1988) and, then, switch to scraping or excavating coral and hard substrata to consume endolithic and epiphytic protein-rich microorganisms as adults (Clements et al. 2017). This dietary shift is facilitated by morphological changes of the mouth, jaw, and intestine (Chen 2002), allowing individuals to shift from carnivory to “herbivory”. Morphological changes can thus influence habitat use patterns, where ontogenetic movement is driven by resource needs. Ontogeny also displays shifts in mobility or home range sizes. Fish are more likely to move greater distances (Streit and Bellwood 2017) or to have increased home ranges (Welsh et al. 2013; Huijbers et al. 2015) as body size increases and as an individual’s resource needs change. Ontogenetic shifts, especially ones driven by changes in habitat needs, can be spatially linked, as physical migrations may occur across habitat boundaries.

The spatial arrangement of habitats within a seascape can modify ontogenetic processes. While resource requirements are fundamental to driving ontogenetic habitat use, the strength of the connection between nursery habitats and coral reefs is contingent on the spatial arrangement of the seascape as well as on the individual species’ movement capabilities. Firstly, non-reef habitats must be present. Secondly, the spatial proximity of habitats in a seascape must be great enough that fishes can reasonably move between and among different habitats. The use of non-reef habitats is not necessarily obligatory and is more likely opportunistic, whereby fishes exploit non-reef habitats when available (Kimirei et al. 2011; van Lier et al. 2018). Nagelkerken et al. (2008) showed that French grunts on coral reefs had dietary signatures from seagrass habitats only when seagrasses were close to coral reefs. In a small island system in Mozambique, 8 km or more of separation between seagrass nursery habitats and coral reefs resulted in a steep reduction in fishes on coral reefs that use seagrass nursery habitat (Berkström et al. 2020). Individuals may be deterred by natural barriers such as sand or deep trenches (Turgeon et al. 2010; Hitt et al. 2011), and the link between nursery and adult habitats can only occur if species are capable of migrating across habitat boundaries. The linkages between non-reef habitats and coral reef habitats are therefore strongly dependent on the spatial arrangement of the habitat in a seascape. However, the flexibility in the use of non-reef habitats as nurseries has not been explored in detail. It is critical for us to understand the scope and degree to which species use non-reef habitats as nurseries to gain a more accurate understanding of habitat-use patterns for fishes across multiple life stages.

Seagrass beds, macroalgal beds, mangroves and lagoons are all considered potential nursery habitats in tropical seascapes for a wide range of fish species (Nagelkerken et al. 2002; Adams et al. 2006; Lugendo et al. 2006; Kimirei et al. 2011; Berkström et al. 2012a; Sheaves et al. 2015). Macroalgal beds, often dominated by *Sargassum*, have recently been confirmed as important habitat for the juveniles of a substantial number of near-shore fish species (Fulton et al. 2020). Research in macroalgal beds at the seascape level is limited, and we lack a complete understanding of the strength of connections between macroalgal beds and coral reefs. Furthermore, the list of species identified in non-reef habitats that may have previously been considered “coral reef” species is growing (Sambrook et al. 2019). Multi-habitat use patterns exist across a diverse group of fish families (Nakamura et al. 2008; Gullström et al. 2011; Berkström et al. 2012a; Honda et al. 2016), but only within the last decade has a more holistic approach been applied to exploring species patterns across multiple habitats.

Parrotfishes (Family: Labridae, subfamily Scarinae*)* are abundant, incredibly diverse, highly exploited by fisheries, contribute to key ecological processes on coral reefs, and are thus extremely well studied (Bellwood et al. 2012; Bonaldo et al. 2014; Taylor et al. 2014). They are well documented as multiple habitat users, often recorded in adjacent non-reef habitats (Dorenbosch et al. 2005; Igulu et al. 2014; Fulton et al. 2019; Sambrook et al. 2019). However, parrotfishes are notoriously difficult to identify to the species level, with a wide range of coloration patterns that change with body size and sex. Initial phase sub-adults and terminal phase adults are fairly accurately identified, but identifying the juvenile phases of parrotfish to the species level is very difficult due to their varied and often cryptic coloration patterns (Bellwood and Choat 1989). Most research describes parrotfish juveniles as only “*Scarus spp*.” when exploring juvenile habitat patterns (Grober-Dunsmore et al. 2007; Tano et al. 2016; Eggertsen et al. 2017; Bradley et al. 2019), but see (Feitosa and Ferreira 2014). Typical studies may be dealing with 2–3 dozen species of parrotfishes, especially in the Indo-Pacific. Because of this, we lack the fundamental resolution to appropriately describe nursery use patterns in parrotfishes, inhibiting our ability to directly link juvenile and adult habitat use at the species level(Nagelkerken et al. 2008). This is especially concerning for a taxonomic group as well studied as parrotfishes.

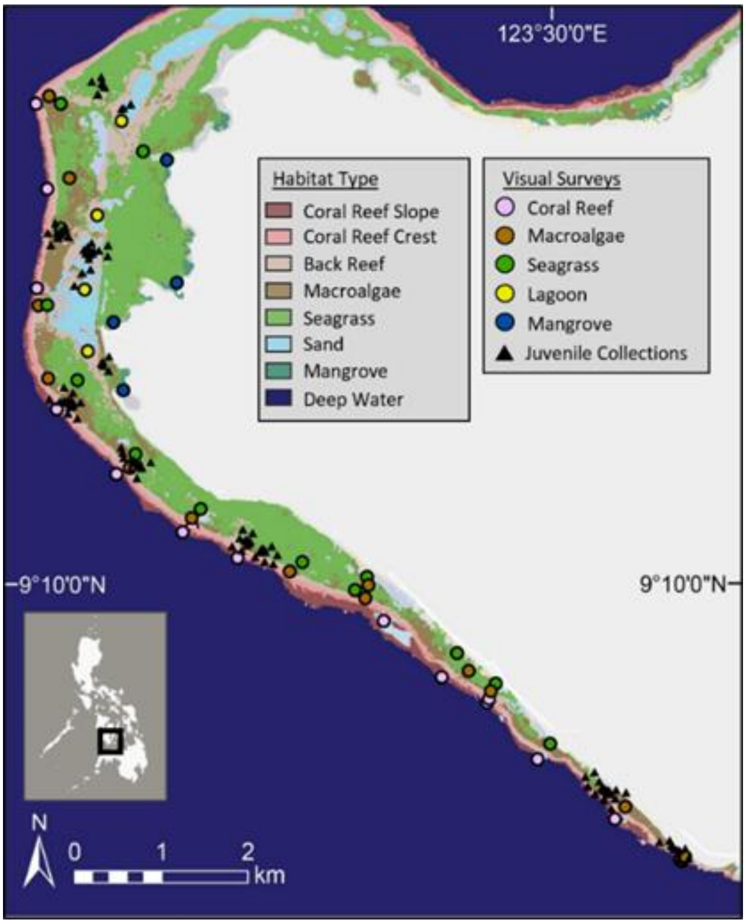
Here, I used DNA analysis to determine the species composition of juvenile parrotfishes in non-reef habitats. I then compared the data with visual survey data of adult parrotfishes in coral reef and non-reef habitats to compare and contrast juvenile and adult habitat use patterns. DNA analysis allows for the identification of small (<10 cm TL) juvenile fishes to the species level across the family (Weigt et al. 2012). My objectives are to explore potential nursery habitat use of parrotfish juveniles, to identify which non-reef habitats are important, and to determine which parrotfish species potentially undergo ontogenetic habitat shifts between juvenile and adult phases. With the identification of juvenile parrotfish using DNA, I can begin to explicitly describe diverse habitat use patterns for an important and highly diverse group of reef fish.

4.3 METHODS

4.3.1 Study Site

Research was conducted on the southwestern side of Siquijor Island (Figure 4.1), in the Visayan region of the Philippines. This area is characterized by a mosaic of sub-tidal and inter-tidal benthic habitats extending up to 1 km off the coastline. Non-reef habitats include lagoons, macroalgal beds, seagrass beds, and mangrove stands adjacent to fringing coral reef habitat. Lagoons on Siquijor are characterized by deeper areas that are predominately sand with patches of seagrass and small corals. Macroalgal beds are composed of *Sargassum* species when seasonally present and with understory red, brown, and green algae that dominates when *Sargassum* senesces. Seagrass beds are characterized by a diverse set of seagrasses from the genera *Cymodocea, Halodule, Thalassodendron, Enhalus, Halophila,* and *Thalassia* with patchy sand, coral, and macroalgae interspersed. Mangrove habitats are patchily distributed across the island and are mainly composed of *Rhizophora spp.* that were planted in the early 1990s (de Leon and White 1999), with some remaining natural stands of *Sonneratia* and *Avicennia spp.* This region in the Philippines was selected specifically because it has extensive seagrass and macroalgal beds very close to coral reefs. It therefore presents an opportunity to evaluate multi-habitat use patterns in a seascape that may facilitate ontogenetic movement between different habitats.

Figure 4.1. Map of the western section of Siquijor Island in the Philippines: coloured circles mark the centroid of the sites surveyed within each habitat. Black triangles mark the collection locations for juvenile parrotfishes.



4.3.2 *Fish Surveys and Fish Collections*

Fish surveys were conducted in April 2015 at 52 sites distributed across five habitat types (coral reef, seagrass bed, macroalgal bed, lagoon, and mangroves) on the south western side of Siquijor Island (Figure 4.1). Underwater visual census (UVC) was conducted using replicate circular plots with a diameter of 10 m (78.5-m^2) in all sites except those in mangroves. The minimum distance between sites was 50 m. Each circular plot was surveyed in one complete rotation, being careful not to miss faster moving and smaller species. Sites in mangroves were surveyed using replicate belt transects 20 m in length and 5 m wide. Total area differed between habitat types, and thus, the number replicate plots was determined by available habitat. The numbers of replicate plots for coral reef, macroalgal bed, seagrass bed, lagoon, and mangrove were 96, 60, 44, 16, and 15, respectively. Fishes were identified to the species level when possible, and their total lengths (TLs) were estimated to the nearest centimetre and classified as either adult or juvenile. Because smaller parrotfishes are extremely difficult to correctly identify at the species level during surveys, parrotfish individuals under

10-cm TL were classified as juvenile and identified as a generic "*Scarus spp*." for the analysis. A number of parrotfish were confidently identified to the species level as juveniles during surveys due to their distinct juvenile coloration patterns (Bellwood and Choat 1989). Namely, *Cetoscarus ocellatus, Chlorurus microrhinos, Scarus dimidiatus,* and *Scarus niger*. The data analysis also explored treating these species separately from the generic "S*carus spp.*" analysis.

Habitat-use patterns for adult parrotfish were classified based on observations from circular plot surveys. If an adult parrotfish species was observed in the coral reef habitat only, they were classified as coral reef exclusive. If a species was observed in any non-reef habitat (seagrass beds, macroalgae, and/or lagoon) but not coral reefs, they were classified as non-reef habitat users. If species were observed in any one of the non-reef habitats as well as coral reef habitat, they were classified as multi-habitat users.

To examine which species of parrotfishes were using non-reef habitats as juveniles, small juvenile parrotfishes were collected in March 2018. Collections were focused in seagrass beds, macroalgal beds, and lagoon areas, and GPS locations were recorded for all collections (Figure 4.1). Collections were attempted in mangrove habitats, but no juveniles of parrotfish or rabbitfish were observed. Parrotfishes less than 10-cm TL were targeted by snorkelers using small hand nets and barrier nets. Once captured, fish were immediately transported to the boat and put on an ice slurry. Fish were stored in a −20 °C freezer in a laboratory in Dumaguete City, Negros Oriental, awaiting further processing, which was conducted in July 2018. For DNA analysis, caudal fin clips were taken from frozen fish samples and stored in 5-mL vials containing 95% ethanol. Total length (TL) and weight (g) were recorded for each fish. Vials were then shipped to James Cook University in Townsville, Australia for the remaining laboratory analysis.

4.3.3 DNA Sequencing

DNA extraction from caudal fin clips was performed with the Isolate II kit (Bioline) for genomic mitochondrial DNA following the manufacturer's instructions. The cytochrome oxidase subunit I (COI) gene for fish was selected and amplified using the COI primers identified in Ward et al. (Ward et al. 2005) for FishF2 -5'TCGACTAATCATAAAGATATCGGCAC3', and FishR2-5'ACTTCAGGGTGACCGAAGAATCAGAA3'. PCR amplification was performed for a total volume of 25 µl, with 13.625 µl ultrapure water, 5 µl GoTaq 5× PCR buffer, 2.5 µl dNTPs (10 mM), 2.5 µl MgCl2 (25 mM), 0.125 µl Taq DNA polymerase, 0.125 µl each primer (100 µM), and 1 µl DNA template. Fragments were amplified using the thermal regime detailed in Ward et al. (Ward et al. 2005) for two minutes at 95 °C; then 35 cycles of 30 s at 94 °C, 30 s at 54 °C, 60 s at 72 °C, and 10 min at 72 °C; and then held at 4 °C. The PCR products were visualized and inspected with 0.8% agarose gel with gel green, before shipment for sequencing. Forward and reverse gene fragments were sequenced at Macrogen Inc. facilities in Seoul, South Korea.

Table 4.1. Criteria to assign confidence to species identification based on DNA sequence quality, percent match with sequence to databanks, and quality of databank references: these criteria were evaluated, and sequences were given a final confidence score (high, medium, and low).

	High	**Med**	**Low**
DNA Sequence Quality			
High Quality Bases	>95%	80–95%	<80%
Alignment	>90%	50–90%	<50%
Ambiguities	<5	5-15	>15
Sequence Match on Databank			
% Similarity	>98%	90–98%	<90%
Databank References			
Peer review and accessibility	Published, accessible	Published, not accessible	Not published, not accessible
Photo	Yes	No	Wrong photo
Collection Details (e.g., lat/long, collector, and identifier)	Full details	Minimal details	No details
Consistency of top hits	Top 10 all same species	5 of 10 top hits same species	Mix of species for top 10 hits

4.3.4 Analysis of Sequences

Sequences were evaluated and edited using the software Geneious Prime (v.2020.1). Reverse and forward sequence ends were manually trimmed, and pairwise alignments were used to create a consensus sequence. Pairwise identity, number of ambiguities, and quality scores were evaluated and inspected within Geneious software to identify any potential sequence issues. When consensus alignment sequences were of poor quality, cleaned forward or reverse sequences would be used for a Basic Local Alignment Search Tool (BLAST) on GenBank (https://www.ncbi.nlm.nih.gov/genbank/) in addition to consensus sequences. The top GenBank hits for each BLAST were scrupulously checked. Additionally, all sequences were run against the Barcode of Life Data (BOLD) Systems (https://www.boldsystems.org/) website, and results from both GenBank and BOLD were carefully examined and assigned a confidence level for accuracy of species identification (Costa et al. 2012). Parrotfish can be difficult to identify correctly based on morphology and colour of their terminal phases, and further assessments of top GenBank and BOLD hits were necessary as misidentification of species in this subfamily were found to be common. Considerations to select the most accurate species identification are listed as follows: quality of DNA sequences (quality score, alignment score, and ambiguities), percent similarity between sequenced DNA and databank sequence, databank reference information accessibility and/or a peer reviewed publication, photo associated with databank reference collection, details of collection (location, collector, and associated tags), and consistency of species identification for top hits. Based on these criteria, confidence measures of high, medium, and low were given to the final species identification (Appendix C Table S4.1, Table 4.1).

4.4 RESULTS

A total of 1724 parrotfish individuals from 19 species were recorded (Table 4.2) during UVCs in coral reef, macroalgal bed, seagrass, and lagoon habitats. No parrotfishes were observed in the mangrove habitat, and thus, the mangrove habitat was excluded from analysis. I am confident that I have captured a large proportion of parrotfish species richness in my surveyed area and that these results compare with others from the region (Stockwell et al. 2009; Russ et al. 2015b; McClure et al. 2020b) (Appendix C Table S4.1).

A total of 241 juvenile individuals were collected from non-reef habitats spanning the length of southwestern Siquijor (Figure 4.1). Of these juveniles collected, 27 were easily identified as *Scarus dimidiatus,* as they were slightly larger individuals, and were differentiated from other species by their characteristic yellow body and vertical black bars on the dorsal side (Bellwood and Choat 1989). These *S. dimidiatus* samples were therefore not included in DNA analysis. Fin clips of the remaining individuals (n = 214) were sent for sequencing, and 209 of those sequences were of good enough quality to BLAST for species identification (Appendix C Table S4.2). Most BLASTS were run with consensus alignments, but 34 alignments were of low quality. Thus, the higher quality forward or reverse sequences were used instead (Table 4.2). From the 209 samples used for species identification, 112 (52%) were graded as high-confidence identifications, 82 (38%) were graded as medium confidence, and 15 (7%) samples were graded with low confidence (Table 4.3). Phylogenetic agreement of species further confirmed species identifications (Appendix C Figure S4.1). Most juveniles were collected from macroalgal habitat (n = 197), with much fewer collected from seagrass (n = 11) or lagoon (n = 28) habitats (Table 4.2).

I identified 15 parrotfish species (subfamily: Scarinae) or species sets based on collection of juveniles (Table 4.3), 14 by DNA results and one by observation (*S. dimidiatus*). The two species sets were *Chlorurus japanesnsis/capistratoides* (n = 1), and *Chlorurus bleekeri/bowersi* (n = 6). I retained these identifications as a potential of two species because top hits from GenBank and BOLD were a mix of the two species. I felt that they were appropriate to present as such, as the two species in each set were highly phylogenetically related (Siqueira et al. 2019). For the remaining results and discussion, *C. bleekeri/bowersi,* and *C. japanensis/capistratoides* will each represent one “species” in the following results.

Table 4.2. Parrotfish (family: Labridae, subfamily: Scarinae) species identified by DNA analysis of juveniles collected in non-reef habitats and species observed as adults on underwater visual census surveys across multiple habitats: 1 = present in surveys or collections, 0 = not observed or identified. Data is separated by juveniles and adults and then also recorded by habitat type. Total count is the total number of each species collected as juveniles in non-reef habitats. All = observed in any habitat on visual surveys, CR = Coral Reef, MA = Macroalgal bed, SG = Seagrass, and LAG = Lagoon.

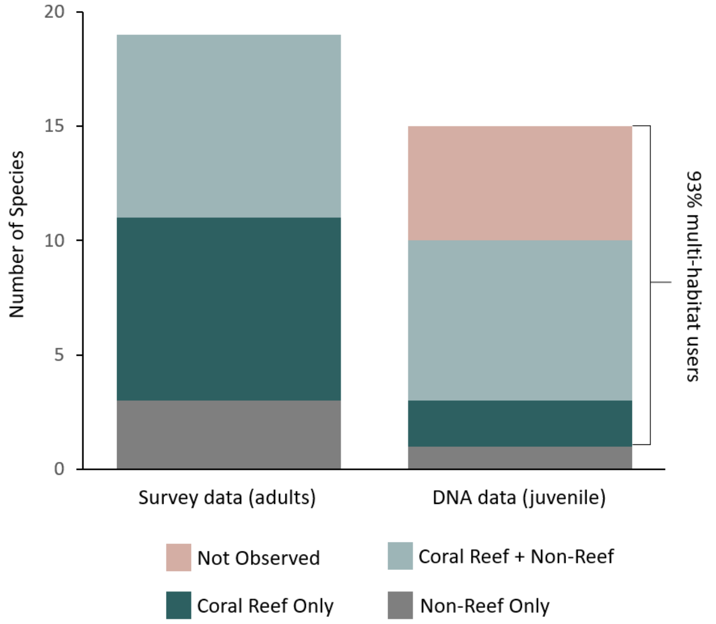
		Adult Presence					**Juvenile Presence**				**Juvenile Count**		
	Species	**All**	**CR**	**MA**	**SG**	**LAG**	**All**	**MA**	**SG**	**LAG**	**MA**	**SG**	**LAG**
1	*Calotomus carolinus*	1	0	0	1	0	0	0	0	0	0	0	0
2	*Calotomus spinidens*	1	0	1	1	0	1	1	0	0	4	0	0
3	*Cetoscarus ocellatus*	1	1	0	0	0	0	0	0	0	0	0	0
4	*Chlorurus bleekeri*	1	1	1	0	1	1	1	0	1	2	0	1
5	*Chlorurus bowersi/bleekeri*	0	0	0	0	0	1	1	0	0	6	0	0
6	*Chlorurus japanensis/capistratoides*	0	0	0	0	0	1	1	0	0	1	0	0
7	*Chlorurus spilurus*	1	1	1	0	1	1	1	0	0	4	0	0
8	*Hipposcarus longiceps*	1	1	0	0	0	0	0	0	0	0	0	0
9	*Leptoscarus vaigiensis*	1	0	1	0	0	0	0	0	0	0	0	0
10	*Scarus altipinnis*	1	1	0	0	0	0	0	0	0	0	0	0
11	*Scarus chameleon*	1	1	1	1	1	1	1	0	0	2	0	0
12	*Scarus dimidiatus*	1	1	0	0	1	1	1	1	1	2	5	20
13	*Scarus flavipectoralis*	1	1	1	0	1	1	1	0	0	1	0	0
14	*Scarus forsteni*	1	1	0	0	0	0	0	0	0	0	0	0
15	*Scarus ghobban*	1	1	0	0	1	1	1	1	0	1	2	0
16	*Scarus hypselopterus*	1	1	1	1	1	0	0	0	0	0	0	0
17	*Scarus niger*	1	1	0	0	0	0	0	0	0	0	0	0
18	*Scarus psittacus*	0	0	0	0	0	1	1	1	1	105	1	1
19	*Scarus quoyi*	1	1	0	0	0	1	1	1	1	19	2	2
20	*Scarus rivulatus*	1	1	0	0	0	1	1	0	1	41	0	3
21	*Scarus rubroviolaceus*	0	0	0	0	0	1	1	0	0	7	0	0
22	*Scarus schlegeli*	1	1	1	0	0	1	1	0	0	1	0	0
23	*Scarus spinus*	0	0	0	0	0	1	0	0	1	0	0	0
24	*Scarus tricolor*	1	1	0	0	0	0	0	0	0	0	1	1
	Total	19	16	8	4	7	15	14	4	6	197	11	28

Table 4.3. Juvenile parrotfish collections and confidence associated with species identification accuracy: Total length (TL) range is the minimum and maximum TLs for each species.

Count	Species	High	Med	Low	Total	TL Range (mm)
1	*Scarus psittacus*	80	24	3	107	18–51
2	*Scarus rivulatus*	1	35	8	44	13–57
3	*Scarus dimidiatus*	27			27	32–98
4	*Scarus quoyi*	15	6	2	23	17–87
5	*Scarus rubroviolaceus*		7		7	24–75
6	*Chlorurus bowersi/bleekeri*		4	2	6	21–39
7	*Calotomus spinidens*	4			4	36–42
8	*Chlorurus spilurus*	4			4	22–67
9	*Chlorurus bleekeri*	1	2		3	29–38
10	*Scarus ghobban*	2	1		3	46–118
11	*Scarus chameleon*		2		2	29–38
12	*Scarus flavipectoralis*	2			2	31
13	*Chlorurus japanensis/capistratoides*		1		1	29
14	*Scarus schlegeli*	1			1	39
15	*Scarus spinus*	1			1	21
	Grand Total	112	82	15	209	

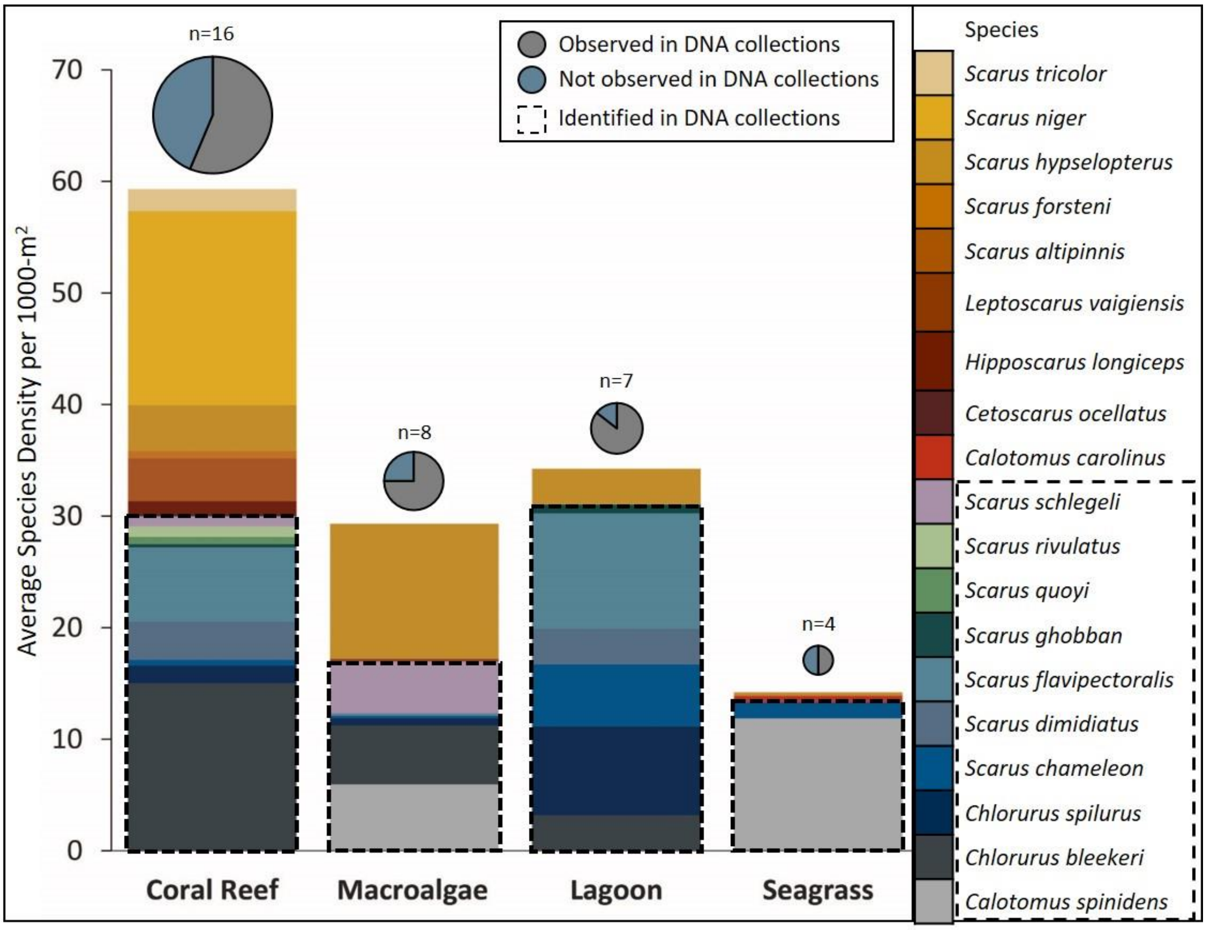
Of the 15 juvenile parrotfish species identified, 10 were also observed on UVC circular plots as adults and five juvenile species were not observed as adults on any circular plot in any habitat. In total, UVC surveys of adult parrotfish recorded 19 species across seagrass, macroalgae, lagoon, and coral reef habitats (Table 4.2). Of the 19 adult parrotfishes observed on surveys, eight (42%) were coral reef exclusive habitat users, eight (42%) were multi-habitat users, and three (16%) were non-reef habitat users (Figure 4.2). Categorizing the 15 juvenile species by their adult habitat use patterns (based on adult surveys) indicated that two (13%) species of juveniles collected in non-reef habitats were coral reef exclusive habitat users, one (7%) species was a non-reef exclusive habitat user, seven (47%) were multi-habitat users, and five (33%) species were not observed on any visual census observations in any habitats (Figure 4.2). However, if we reconsider my classification, species originally classified as coral reef exclusive species but observed in non-reef habitats as juveniles would hence be multi-habitat users. Additionally, juveniles collected in non-reef habitat but not observed as adults in any habitat likely occupy another habitat not surveyed, and could also be classed as a multi-habitat user. With this reclassification, 93% of species collected as juveniles could then be considered multi-habitat users. This contrasts adult surveys, where only 42% of species were classified as multi-habitat users.

Figure 4.2. Habitat use classification for parrotfish species: classification colours are based on observations from adult parrotfish surveys across all habitat types. Classification of adults observed on surveys (left) and juveniles collected in non-reef habitats (right): Coral Reef only (dark green) are species only observed as adults on coral reef habitat, Coral Reef + Non-Reef (light green) are species observed as adults on both coral reef and any non-reef habitat, Non-Reef only (grey) are adults observed only in non-reef habitats, and Not Observed (beige) are species identified with DNA analysis from juvenile collections in non-reef habitats but not seen as adults on visual surveys in any habitat.



On coral reefs, 16 parrotfish species were observed as adults and nine (56%) of those species were collected as juveniles in non-reef habitats (Figure 4.3, Table 4.2). Those nine species make up 50% of the total average density of parrotfishes on coral reefs. For macroalgal beds, eight species were observed as adults on surveys and six (75%) were collected as juveniles (Figure 4.3). Those six species make up 58% of the total average density of parrotfish adults in macroalgal habitat. For lagoons, juveniles collected represented six (85%) of the seven adult parrotfish species observed. Those six species make up 91% of the total average density of adult parrotfishes seen in a lagoon habitat (Figure 4.3). Finally, for adults observed in a seagrass habitat, only four parrotfish species were observed as adults, and I captured two (50%) of those species in my juvenile collections. Those two species represented 94% of the total average density of adults in seagrass beds (Figure 4.3).

Figure 4.3. Average density of adult parrotfish species observed in visual census surveys within each habitat type: the colours represent different species. Dashed boxes on each bar outline the species identified in DNA analysis from juvenile collections in non-reef habitats. Pie graphs represent the total number of species observed in each habitat type, separated by whether the species were observed in DNA collections of juveniles in non-reef habitats (grey) or not observed in collections (blue). Size of the pie graph portrays total number (n) of species observed as adults within each habitat type.



The species composition and richness of juveniles collected in seagrass, macroalgae, and lagoon habitats were different from those for adults observed in UVC surveys of these habitats (Figure 4.4). Overall, juvenile identifications were dominated by *Scarus psittacus* (45.3%), *Scarus rivulatus* (18.6%), and *Scarus dimidiatus* (11.4%) (Table 4.2). In comparison with adult survey data, *S. rivulatus* was identified in coral reef habitat only, *S. dimidiatus* was observed in coral reef and lagoon habitats, and *S. psittacus* was not observed on any habitat as an adult. In seagrass habitat, I identified four species as juveniles and observed four species as adults (Figure 4.4). In macroalgal habitat, 14 species were identified as juveniles and eight were recorded as adults. In lagoon habitat, six species were identified as juveniles compared to seven species as adults. Furthermore, the species composition looks vastly different between adult and juveniles in the same habitats (Figure 4.4). For macroalgal habitats, adults were dominated by *Scarus hypselopterus* and juveniles in macroalgae were dominated by *Scarus psittacus.* In lagoon habitats, adults were dominated by *Scarus flavipectoralis* and *Chlorurus spilurus* whereas juveniles were dominated by *Scarus dimidiatus*. In seagrass habitat, adult parrotfishes were dominated by *Calotomus spinidens* (Table 4.2), compared with *Scarus dimidiatus* for the juveniles (Figure 4.4). Interestingly, for all non-reef habitats, the most common adult observed on surveys was not collected as juveniles in their respective habitats.

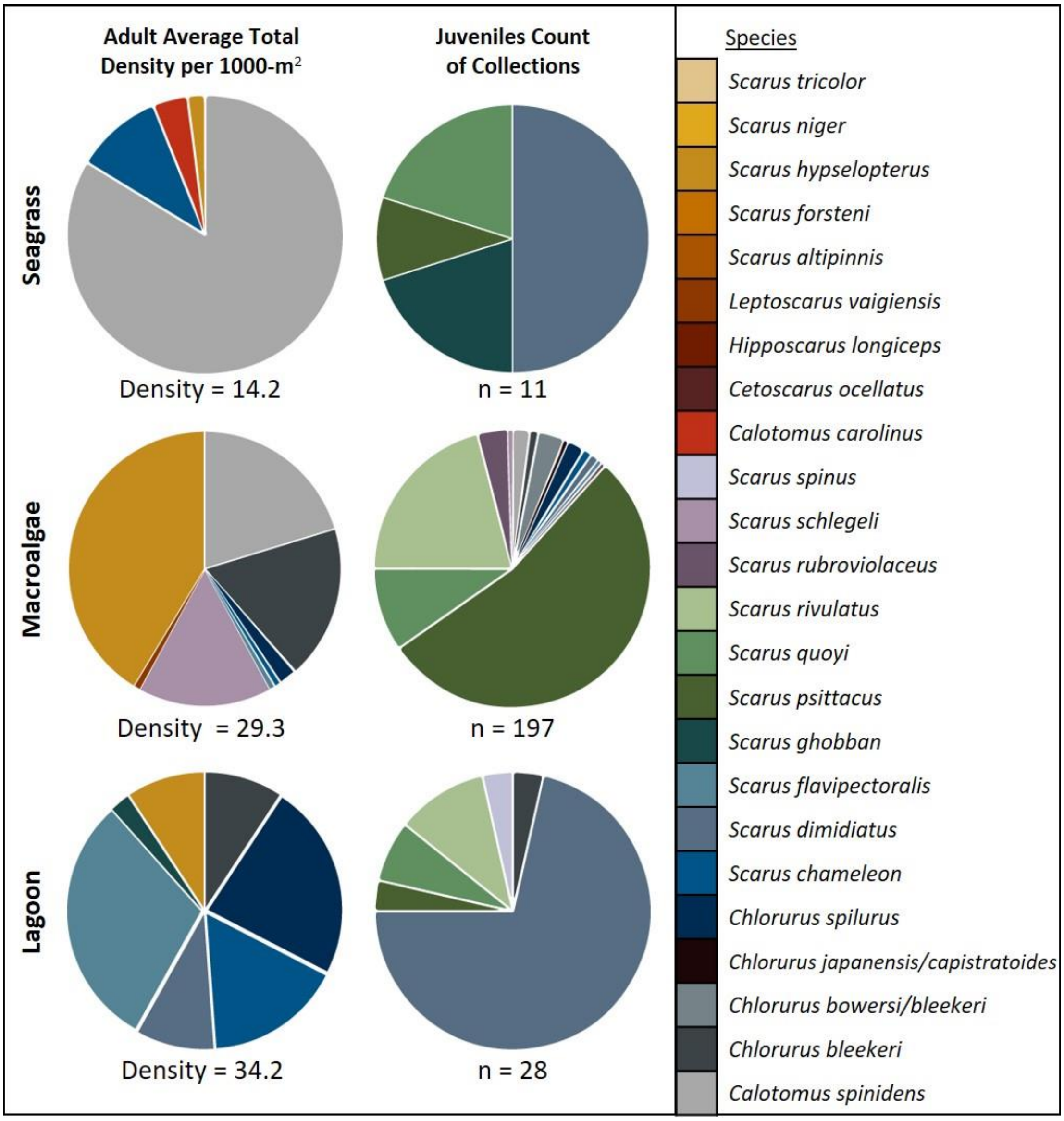
There were nine parrotfish species that were observed as adults and not captured as juveniles in non-reef habitats with the collections (Table 4.2). These were *Calotomus carolinus, Cetoscarus ocellatus, Hipposcarus longiceps, Leptoscarus vaigiensis, Scarus altipinnis, Scarus forsteni, Scarus hypselopterus, Scarus niger,* and *Scarus tricolor.* Six of those nine species are coral reef exclusive habitat users based on UVC.

Table 4.4. Presence (1) from visual census in different habitats for parrotfish species with unique coloration patterns that enable confident identifications at the juvenile stage: shaded cells represent juveniles which were also identified from DNA analysis during collections in non-reef habitats. CR = Coral Reef, MA = macroalgal bed, LAG = lagoon, and SG = seagrass.

	Juvenile				Adult			
Species	**CR**	**MA**	**LAG**	**SG**	**CR**	**MA**	**LAG**	**SG**
Cetoscarus ocellatus	1				1			
Chlorurus microrhinos	1							
Scarus dimidiatus	1		1		1		1	
Scarus niger	1		1		1			

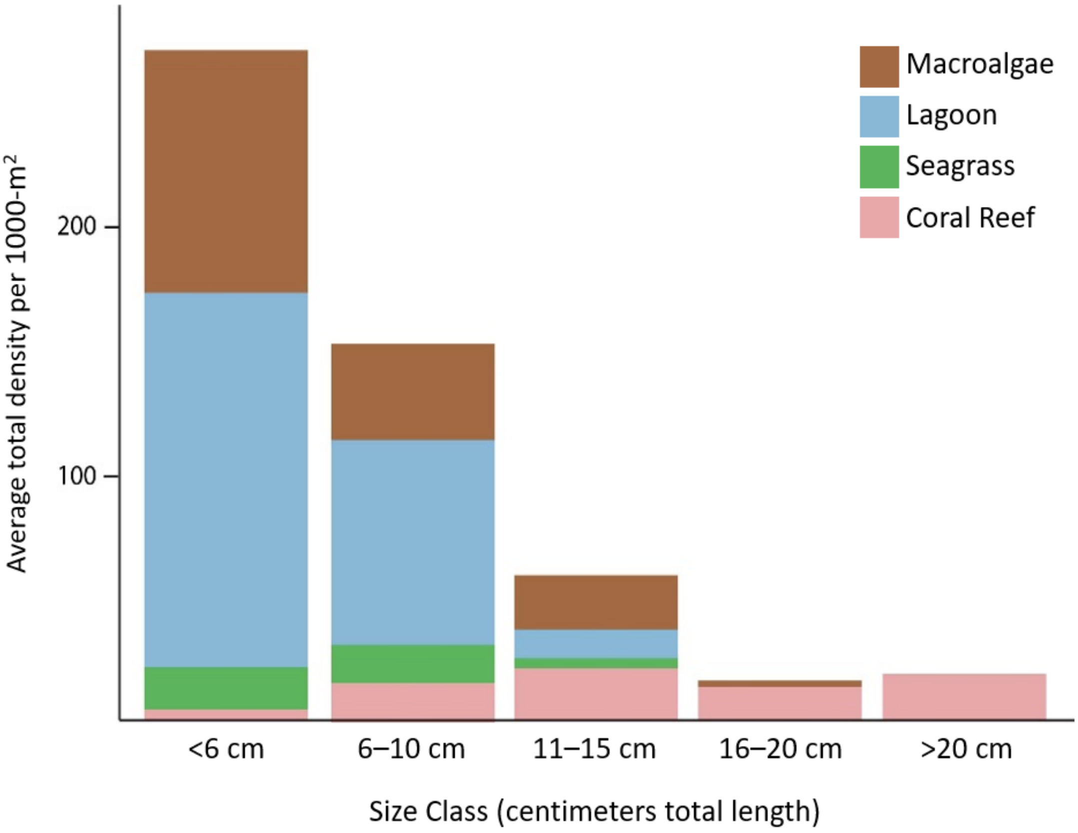
For parrotfish species that are distinct and visually identifiable as juveniles (*Cetoscarus ocellatus*, *Chlorurus microrhinos, Scarus niger,* and *Scarus dimidiatus*), visual surveys revealed subtle patterns (Table 4.4). *Cetoscarus ocellatus* and *Chlorurus microrhinos* were observed only on coral reefs, with only one observation each as juveniles. *Scarus dimidiatus* was observed as juveniles on coral reefs and lagoon habitats, which is consistent with the adult surveys and juvenile collections. *Scarus niger* was the most abundant species as adults on coral reefs (Appendix C Table S4.3, and Figure 4.4) and was observed as a juvenile mostly on coral reefs, but two observations were recorded for *Scarus niger* in the lagoon habitat.

Figure 4.4. Comparing parrotfish species composition between seagrass habitat (top), macroalgal bed habitat (middle), and lagoon habitat (bottom) for adults identified on surveys (left) and juveniles identified through DNA analysis (right): adults are presented as the average total density per 1000-m^2. Juveniles are reported as the total number of individuals collected (n) in each habitat.



UVC surveys showed that parrotfish less than 10-cm TL were 34 times more abundant in non-reef habitats compared to coral reefs and that non-reef habitats had 97% of all parrotfish individuals less than 10-cm TL (Figure 4.5). Lagoon was the primary habitat for small parrotfish individuals, followed by macroalgal beds. It is important to note that the variability of observations in lagoons was very high (Appendix C Table S4.4). As fish get bigger, the proportion of fish observed in non-reef habitats decreases, and larger parrotfishes (>15-cm TL) were almost exclusively present in the coral reef habitat.

Figure 4.5. Average parrotfish density of all individuals observed on visual census surveys within each habitat type.



4.5 DISCUSSION

This study demonstrated considerable use of non-reef habitats by juvenile parrotfishes, with ontogenetic shifts representing prevalent and important life-history transitions for many species. Moreover, for some of these species collected as juveniles, adults were observed only on the reef, suggesting that ontogenetic habitat shifts occur. From visual surveys, I observed substantially more small parrotfishes in non-reef habitats compared to coral reefs, further providing evidence that macroalgal, lagoon, and seagrass habitats on Siquijor potentially act as nursery habitats for some parrotfish species. To my knowledge, this is one of the few studies that used DNA analysis to verify species identifications of juvenile parrotfish to explore habitat use patterns across a diverse seascape (Weigt et al. 2012).

Parrotfishes across all life stages, particularly juveniles, can be extremely difficult to identify correctly to the species level. Although time consuming and expensive compared to visual surveys, DNA results can allow for direct links to be made between juvenile and adult stages and can even reveal the presence of species that may not be observed in visual surveys. For example, *Scarus psittacus* was the most abundant species (n = 107, 46%) from juvenile collections in non-reef habitats but was not observed on surveys in any habitat. *S. psittacus* has previously been observed in the

Philippines on coral reefs (Stockwell et al. 2009; Russ et al. 2015b) and on coral reefs in the same area as these surveys (McClure et al. 2020b). Furthermore, *S. psittacus* is a species frequently observed in fish markets in the local area (personal observations). The ecology of *S. psittacus* can explain the lack of observations on surveys, as they mainly occupy areas of the reef with larger sand patches (G.R.R. personal observation), often within a back reef system characterized by sand and rubble, or lagoon areas of the middle and outer coral shelves of the Great Barrier Reef (GBR) (Russ 1984b, 1984a; Russ et al. 2015b). These back-reef areas were not targeted in UVC for this study. The reef flat and back-reef areas are important habitats in tropical seascapes (Bellwood et al. 2018), and we may be missing key features of fish communities by not including them in surveys. These results highlight the need to expand surveys to areas surrounding coral reefs (e.g., sandy habitat adjacent to coral reefs and immediate back-reef habitats). *S. psittacus* are also known to school, and perhaps this attribute skewed the results of the juvenile collections by collecting entire schooling groups. The other species not identified in adult surveys but collected as juveniles in non-reef habitat were *Chlorurus japanensis/capistratoides*, *Scarus rubroviolaceus*, and *Scarus spinus*. These species are relatively rare on Philippine coral reefs in this region (Russ et al. 2015b) and thus are unlikely to be observed with any regularity. Capturing rare species in an ecosystem can be critical, as they can often be the most vulnerable to disturbance and exploitation impacts (Dulvy et al. 2003; Lavergne et al. 2005).

It is important to acknowledge that collections of juvenile parrotfishes did not capture all species observed on visual surveys. For example, the most abundant adult parrotfish on coral reefs (*Scarus niger*) was not found in the juvenile non-reef collections. *S. niger* is one the few species that can be confidently identified as a juvenile, and while most *S. niger* juveniles were observed in UVC plot surveys on coral reefs, two observations were made in lagoon habitat (Table 4.4). Six of the nine species observed as adults but not as juveniles were classified as exclusive users of coral reefs. Perhaps, these juveniles recruit directly to coral reefs, and as my collections were focused on non-reef habitats, species that settle directly on reefs would have been missed during my juvenile collections. To advance our knowledge, further research should collect parrotfish juveniles from coral reef habitats as well as non-reef habitats.

I also acknowledge that I cannot provide 100% certainty for all the species identifications derived from DNA analysis. Some hits on GenBank and/or BOLD selected other species not listed here; however, these hits were unreliable, were of poor quality, were incorrect, and/or were unverifiable, and thus were removed from consideration. This highlights the importance of improved vetting of GenBank additions and of providing supplemental information when uploading sequences, particularly for species groups that are difficult to identify such as parrotfishes. I suggest that DNA sequences should be calibrated to a sequence for which the species identification has been verified. I endeavoured to scrupulously check all species hits but acknowledge that DNA analysis brings its own caveats. Furthermore, using only one gene fragment (COI) rather than a multilocus approach limits our ability to identify samples to the species level. However, the COI gene has been used widely (Hubert et al. 2012; Weigt et al. 2012) and is an appropriate method for identifying species (Hubert and Hanner 2015).

In Siquijor, lagoon and macroalgal habitats had the greatest number of parrotfish juveniles. In contrast with other studies, there were zero visual observations of parrotfishes in mangrove habitats. Strong relationships between parrotfishes and mangrove habitats have been shown in the Caribbean (Nagelkerken et al. 2000c; Cocheret de la Morinière et al. 2003; Mumby 2006), Australia (Olds et al. 2012b, 2012a, 2013; Martin et al. 2015), and the Indian Ocean (Dorenbosch et al. 2005; Lugendo et al. 2006). The use of mangroves by fish is likely tidally influenced, such that areas with high tidal flux have reduced reliance of fish on mangrove habitat (Lugendo et al. 2007; Igulu et al. 2014). In Siquijor, mangroves are mostly only accessible to fish at high tides and are also quite muddy and silty due to the planting of *Rhizophora* stands. Seagrass beds are also often exposed at low tide, which may further support my evidence that seagrass beds were not as important as a nursery area for juvenile parrotfishes. The lagoon habitat is well recorded as a juvenile nursery habitat for fish across a wide range of locations (Nagelkerken et al. 2000b; Adams and Ebersole 2002; Cocheret De La Morinière et al. 2002; Mellin et al. 2007). Care should be taken with the results here, as the variability in juvenile parrotfish observations in lagoons was extremely high on Siquijor. This variability is likely due to the tendency for small juveniles of parrotfish to school, combined with the patchiness of structured habitat in the lagoon, which consists predominately of sand scattered with seagrass and isolated coral patches. Therefore, I suspect that observations of large schools of juvenile parrotfishes were possibly chance encounters. Recently, macroalgal habitat has become a major focus of research in tropical systems, and research has shown that macroalgal beds can be more important than seagrass beds as a nursery area for juvenile fishes (Tano et al. 2016; Fulton et al. 2019, 2020). Macroalgal beds have high levels of epiphytes and invertebrate epifauna (Tano et al. 2016; Fong et al. 2018), which are often the target prey for juvenile parrotfishes (Bellwood 1988; Chen 2002; Feitosa and Ferreira 2014). Considering the potential importance of macroalgal beds for coral reef fishes, there has been relatively little research conducted in these habitats under the framework of understanding how macroalgal beds may contribute to abundance patterns of coral reef fishes (Fulton et al. 2019, 2020; Sambrook et al. 2019). I conclude that juvenile parrotfish utilised a diversity of non-reef habitats as nurseries in Siquijor, and juvenile densities were typically highest in lagoon and macroalgal habtiats.

Parrotfishes have long been documented as multi-habitat users (Nagelkerken et al. 2000b; Dorenbosch et al. 2005; Igulu et al. 2014; Bradley et al. 2019; Fulton et al. 2019; Sambrook et al. 2019).

Of the species collected in non-reef habitats as juveniles, 93% of those could be classified as multi-habitat users. This starkly contrasts the results from the adult survey data, where only 42% of species would be classified as multi-habitat users. This discrepancy between the two data sets implies that visual surveys alone may not be capturing the full extent to which parrotfish species use a seascape and that we may be underestimating the degree to which fishes utilize multiple habitats. While I acknowledge that the majority of parrotfish individuals are on coral reefs, their presence in non-reef habitats implies connections between different habitats in a seascape. Two of the three most abundant species collected as juveniles and observed as adults on UVC were classified as coral reef exclusive habitat users (*Scarus rivulatus* and *Scarus quoyi*). Relatively little is known about the habitat use patterns or life stages of *S. quoyi*. However, *S. rivulatus* has been well studied but mainly focused on coral reefs. On the GBR, *S. rivulatus* is a species characteristic of mid-shelf reefs, often being present in lagoons and back reef habitats (Russ 1984b, 1984a; Johnson et al. 2019), and has been shown to have limited home range movements as adults (Welsh and Bellwood 2012b).

Non-reef habitat use as juveniles might be contingent on whether these habitats are near coral reefs, as I see here in Siquijor, Philippines. The seminal work on juvenile parrotfishes by Bellwood and Choat (Bellwood and Choat 1989) shows distinct differentiation in habitat use across coral reefs. This study was focused on the reef slope, reef flat, and back reef on the GBR. Many of the species identified in the present study in non-reef habitats were also recorded across multiple coral reef locations(Bellwood and Choat 1989). I argue that occurrences are possible both in reef and non-reef habitats and that these species are opportunistically using non-reef habitats such as macroalgal beds when they are available and in close spatial proximity to their adult habitat. The links between non-reef habitats and coral reefs are therefore likely a function of habitat availability and the spatial connectivity of a seascape. Moreover, it is necessary to recognize that, if juveniles are present in non-reef habitats, they are likely settling there as recruits. Recruitment and settlement dynamics are complex, but individuals do have the ability to settle to specific microhabitats (Williams 1980; Tolimieri 1998; Sale et al. 2005). Habitat availability, food availability, density dependence, and predation are all pressures driving settlement and post-settlement survival. Most certainly, these are all influencing the presence and abundance of juvenile fishes I explored here. Furthermore, island-scale variability in available habitat can be the main driver of parrotfish diversity, as shown in Micronesia (Taylor et al. 2015). It is not unreasonable to hypothesize that nursery habitat is acting as a recruitment bottleneck for adult parrotfish diversity here in Siquijor, especially considering the relatively high larval connectivity in this region (Abesamis et al. 2017). However, nursery habitat bottlenecks will not be relevant to all species (e.g., species recruiting directly to coral reefs) and will be more important for species that lack the flexibility to recruit to multiple habitats. Importantly, Siquijor was specifically selected because of its diverse seascape, with high spatial proximity of multiple habitats to coral reefs. The conclusions I draw here must be considered through the lens of a highly connected seascape and may not be applicable to another coral reef system where habitats are much more spatially segregated (e.g., the GBR). Further research should incorporate the spatial dynamics of the seascape when exploring fish-habitat patterns and critically evaluate whether flexibility in habitat use is driven by the spatial availability and connectivity of habitats.

The underlying assumption behind ontogenetic habitat shifts is that the benefit of using an alternative habitat must outweigh the risk of predation (Dorenbosch et al. 2009; Grol et al. 2011; Kimirei et al. 2013b). Here, following the nursery trade-off hypothesis, the presumed benefit for parrotfishes to use non-reef habitats as juveniles would be reduced predation, and also reduced competition with other herbivores and invertivores. But the trade-off is then reduced growth rates. Although research on parrotfish growth demonstrates that the earlier life phases have the fastest growth, the lower size limit for species evaluated is usually 10-cm TL (Taylor and Choat 2014). One of the few papers that explores growth rates of small juvenile parrotfish does demonstrate slower growth when individuals are under 10-cm TL (for *S. rivulatus* and *S. schlegeli*) (Lou 1992), which would confirm the nursery trade-off hypothesis of slow growth for small juveniles. Furthermore, at very early life stages, parrotfishes have been shown to be herbivorous (Feitosa and Ferreira 2014) or carnivorous (Bellwood 1988; Chen 2002), before switching to a protein-rich diet of autotrophic cyanobacteria present in sand, in the epilithic algal matrix (EAM), and/or imbedded in calcareous reef substrate (Clements et al. 2017; Nicholson and Clements 2020). This dietary switch, which has been observed at around 10-cm TL (Feitosa and Ferreira 2014)(Feitosa and Ferreira 2014), would further support the change in diet that mirrors the growth relationships observed in Lou (Lou 1992), where the fastest growth would occur once individuals switch to a cyanobacteria diet. Furthermore, juvenile parrotfishes have the jaw morphology to accommodate herbivory and carnivory before development of the beak-like fused teeth which characterize this group as scrapers and excavators in their adult stages (Chen 2002). Although Bonaldo and Bellwood (Bonaldo and Bellwood 2008) showed that *S. rivulatus* targeted EAM regardless of size class, they performed feeding observations of *S. rivulatus* on coral reef habitat only. Potentially, these species may exhibit greater flexibility in diet in their juvenile stage when non-reef habitats are available and used, emphasizing that non-reef habitat use may be opportunistic rather than obligatory. To fully understand ontogenetic dietary changes, feeding observations, gut content analysis, and biomarkers of targeted nutrients should be studied. Furthermore, such research should be conducted across multiple habitats and life stages to explore how ontogenetic shifts may be mediated by the spatial characteristics of the seascape.

Dietary changes may also coincide with increased movement (Welsh et al. 2013; Bradley et al. 2019), leading to ontogenetic migrations to coral reefs to acquire their target food source as adults. Bradley et al. (Bradley et al. 2019) observed early juvenile parrotfishes in two habitat types (vegetated habitat and coral reef), but late juvenile phase parrotfishes occupied three habitats (vegetated habitats, rocky reefs, and coral reefs). Streit and Bellwood (Streit and Bellwood 2017) also correlated parrotfish size with willingness to return to their home reef when experimentally moved, where larger fishes moved greater distances. Welsh et al. (Welsh et al. 2013) identified the greatest change in relative home range size of parrotfishes occurring when species were less than 10-cm TL. Plasticity in movement based on available habitat has been evaluated for some parrotfish species, where variation in movement differed substantially based on resource availability (Welsh et al. 2013) and spatiotemporal scale (Davis et al. 2017b), but such evaluations have focused on adults on coral reefs. The potential for ontogenetic shifts to coincide with habitat migrations are clearly present, yet these movements are mediated by habitat availability, spatial connectivity, and resource availability and should be explored further.

In a diverse seascape in the Philippines, I found that lagoon, macroalgal beds, and seagrass beds are habitats for juvenile parrotfishes. Of the juveniles collected in non-reef habitats, 93% of those species should be classified as multi-habitat users. Furthermore, the species composition of adults and juveniles was quite distinct in the same habitats, indicating potential ontogenetic habitat shifts. Finally, I suggest it would be important to consider whether ontogenetic movements are shifts or switches. Shifts are unidirectional flows, and switches are interchanges between locations. The underlying ecological processes driving shifts and switches could vary considerably. For example, shifts may be driven by competition, whereas switches might be driven by inter-specific competition. Considering the ecological and economic importance of parrotfishes, there exists a significant knowledge gap about their habitat use patterns as juveniles, especially when framed in the context of potential ontogenetic habitat shifts across a seascape. My research provides yet more evidence of the connectivity between different benthic habitats of a seascape. The strength of the link between nursery habitat and coral reefs can have strong consequences on adult populations (Huijbers et al. 2013) and can lead to synergistic effects of effective protection with marine reserves (Olds et al. 2012b). This is particularly relevant for locations like the Philippines, where reserves rarely include these habitats. Incorporating knowledge of ontogenetic movement into marine reserve design and population dynamics can provide better estimations of reserve impact on populations (Moffitt et al. 2009; Grüss et al. 2011; Nagelkerken et al. 2015; Weeks 2017). To appropriately protect species, we must first understand how species use the wider seascape and identify what habitats might be important for populations.

CHAPTER 5. AVAILABILITY OF NON-REEF HABITAT DRIVES VARIATION IN CORAL REEF FISH ISOTOPIC DIETARY SIGNATURES

5.1 ABSTRACT

Characterizing habitat-use patterns of species across diverse seascapes improves our understanding of population dynamics and our ability to prioritize conservation zones more effectively. I used stable isotope analysis to explore the diet and habitat-use patterns of species from two important coral reef fish groups: Parrotfishes (Scarinae;,*Scarus dimidiatus, S. flavipectoralis, S. psittacus*) and rabbitfishes (Siganidae; *Siganus virgatus, S. fuscecens, S. guttatus*). My aims were to understand how fish species might be using coral reef and different non-reef habitats at a relatively small spatial extent (16 km of coastline) within a highly connected seascape. Specifically, I investigated if there existed a relationship between habitat use and availability of adjacent non-reef habitats. By comparing stable isotope signatures of fish and potential food sources in different habitats, I identified a clear trend in diet for parrotfishes relating to the degree of reliance of particular species or life stages on non-reef habitats. The proportion of dietary contribution switched from non-reef macroalgal sources (*Sargassum*) to coral reef sources (algal turf) as parrotfish species and life stages shifted from non-reef habitats to coral reefs. Parrotfish juveniles are not consuming *Sargassum* directly, but instead are likely targeting epiphytes and invertebrates that feed on *Sargassum*. In this instance, *Sargassum* and turf isotope signatures were used as indicators of habitats use, and not diet. For species reliant on coral reefs (*Siganus virgatus* and adult *Scarus dimidiatus*) there was significant similarity in isotopic signatures between fish from reef areas that differed in the extent of adjacent non-reef habitat. Comparatively, species and life stages (parrotfish juveniles and subadults) with greater reliance on non-reef habitats showed considerable differences in isotopic signatures between reef sections with varying amounts of non-reef habitats. Fish collected from locations with multiple non-reef habitats showed isotopic signatures reflective of mixed diets. Whereas, fish collected in locations with very little diversity and area of non-reef habitats showed stronger signatures of just one habitat type. This suggests that their habitat use and/or diet may be influenced by available habitats. For the parrotfish *Scarus dimidiatus* there were clear transitions in isotopic dietary signatures from juvenile to initial phase (IP) sub-adults, and from IP sub-adults to terminal phase (TP) adults, suggesting dietary and habitat changes with ontogeny. Finally, there was greater overlap in isotopic signatures between the rabbitfishes compared to the parrotfishes, indicating that habitat use and/or dietary preferences of rabbitfish are not as greatly influenced by habitat availability. Stable isotope analysis allowed for the examination of subtle patterns that may not be revealed by visual surveys, feeding observations, or

gut content analysis. I demonstrated that the amount of available non-reef habitat can affect diet and habitat use patterns in coral reef fish. My findings suggest the need to incorporate spatial data of the entire seascape when exploring species patterns and designing spatial conservation measures.

5.2 INTRODUCTION

Characterizing how species use habitats across complex seascapes improves our understanding of population dynamics and our ability to manage and conserve marine resources (McCook et al. 2009; Edwards et al. 2010; Olds et al. 2012b). Coral reef fishes use a diverse range of benthic habitats to feed, spawn, evade predation, and reduce competition. The ecological connectivity of multiple habitats in a reef seascape can therefore influence nutrient fluxes (Hyndes et al. 2014), migratory patterns (Nagelkerken et al. 2000c, 2008), and species processes (Mumby and Hastings 2008; Eggertsen et al. 2020). This can have cascading effects on community composition, habitat structure, and ecosystem resilience (Downie et al. 2013; Nagelkerken et al. 2015). The ability of fishes to use multiple habitats is dictated by access to these habitats, the availability of the habitats themselves, and the resource requirements of each species. The spatial arrangement of habitats in a seascape can therefore modify habitat-use patterns of species by facilitating or inhibiting movement among habitats (Turgeon et al. 2010; Hitt et al. 2011), which alter relative abundances of species within and among habitats (Dorenbosch et al. 2005; Olds et al. 2012a), and can affect entire communities (van Lier et al. 2018). However, there is still much to learn when it comes to how species use different habitats, which habitats are more connected than others, and which habitats are most important for particular life stages. In tropical systems, there is a growing effort to understand how non-reef habitats surrounding coral reefs contribute to coral reef populations. Through this effort, more species are now being reclassified as multi-habitat users, with many of these species previously thought to be coral reef specific (Sambrook et al. 2019; Sievers et al. 2020a, Chapter 4).

The availability and spatial arrangement of benthic habitats can alter species habitat-use patterns across a seascape. For example, mangroves are a common nursery habitat for many marine species (Lee et al. 2014), but in highly tidal systems, the importance of mangroves is reduced because mangroves are inaccessible at low tide (Igulu et al. 2014). When habitats are far away from each other, access is also reduced, and there may be a threshold distance beyond which habitats are no longer connected (Berkström et al. 2020). In an island system in the Red Sea, juvenile snappers (*Lutjanus ehrenbergii*) were found to use seagrass habitats when coral reefs were close to seagrass. However, for coral reefs on far offshore islands, juveniles were using coral reef habitats of the offshore islands (McMahon et al. 2012). Juvenile habitat use was therefore dictated by the seascape configuration itself. In the Caribbean, French grunts (*Haemulon flavolineatum)* from coral reefs showed similar isotope signatures as *H. flavolineatum* from seagrass beds, but only when seagrass beds were accessible from coral reefs, inferring that these fish travel to seagrass beds to forage. However, *H. flavolineatum* from coral reefs adjacent to seagrass beds that were inaccessible (i.e., were in restricted bays) had isotopic signatures that differed from seagrass signatures (Nagelkerken et al. 2008). Foraging migrations were thus altered based on the spatial configuration and accessibility of habitats in a seascape. Fragmentation of habitats, creating barriers such as sand channels, can alter fish movement patterns and limit migrations (Turgeon et al. 2010). Species can also alter their habitat-use patterns based on predator levels and perceived risk of predation (Catano et al. 2016; Rooker et al. 2018). Clearly, there is evidence that the spatial configuration, availability, and accessibility of habitats can alter how species are using the seascape. But few studies have evaluated how the spatial configuration of habitat can alter fish movement, habitat use, and diet, and most have done so for a limited group of species (e.g., Lutjanids and Haemulids) (Nagelkerken et al. 2008; Nakamura et al. 2008; McMahon et al. 2012; Kimirei et al. 2013a; Huijbers et al. 2015).

Juveniles and sub-adults of many coral reef fish species use non-reef habitats (Nagelkerken et al. 2000c; Beck et al. 2001; Sheaves 2009), and ontogenetic shifts are one of the strongest links connecting habitats in a seascape (Adams and Ebersole 2002; Sheaves et al. 2015). Seagrass beds, mangroves, and macroalgal beds often support greater densities of juvenile fishes (Kimirei et al. 2013b; Tano et al. 2016; Fulton et al. 2019; Sievers et al. 2020a, Chapter 4), and can affect patterns of abundance and richness of species on coral reefs. When nursery habitats are near coral reefs, the density and biomass of fishes on coral reefs can sometimes increase (Dorenbosch et al. 2005; Berkström et al. 2013b; Olds et al. 2016), and can even improve marine reserve performance (Olds et al. 2012c). Ontogenetic changes can manifest as both dietary and habitat changes. The underlying forces driving ontogenetic changes are complex and diverse and include physiological and morphological changes that coincide with changes in behavior and species interactions (Adams et al. 2006; Kimirei et al. 2013b). However, tracking the movement of individuals across seascapes, especially movement of small juvenile fish, can be extremely labor-intensive and challenging to quantify using conventional methods such as in-field observations or tagging. Few studies have linked ontogenetic shifts and resource requirements of reef fish across a seascape with varying levels of connectivity to adjacent non-reef habitat (Cocheret de la Morinière et al. 2003; Shibuno et al. 2008; McMahon et al. 2012; Berkström et al. 2013a; Davis et al. 2015).

Stable isotopes (SI) are an excellent tool to explore resource use patterns that can describe diet, habitat use and trophic level (Peterson and Fry 1987; Bearhop et al. 2004; Fry 2006; Newsome et al. 2007). SI of consumers are linked to their diet, and SI are integrated across varying temporal scales depending on the tissue or body part analyzed (McMahon et al. 2013, 2015; Matley et al. 2016). The technique generally integrates over a longer time period (e.g., 10-150 days for muscle tissue) compared to snapshot-in-time methods such as gut content analysis, resulting in lower dietary resolution. However, SI allows for the exploration of ecological processes such as differentiation in habitat use (Lugendo et al. 2006), habitat migrations (Nagelkerken et al. 2008; McMahon et al. 2012), dietary selectivity or redundancy (Plass-Johnson et al. 2013), and resource partitioning (Eurich et al. 2019) (Fig. 5.1).

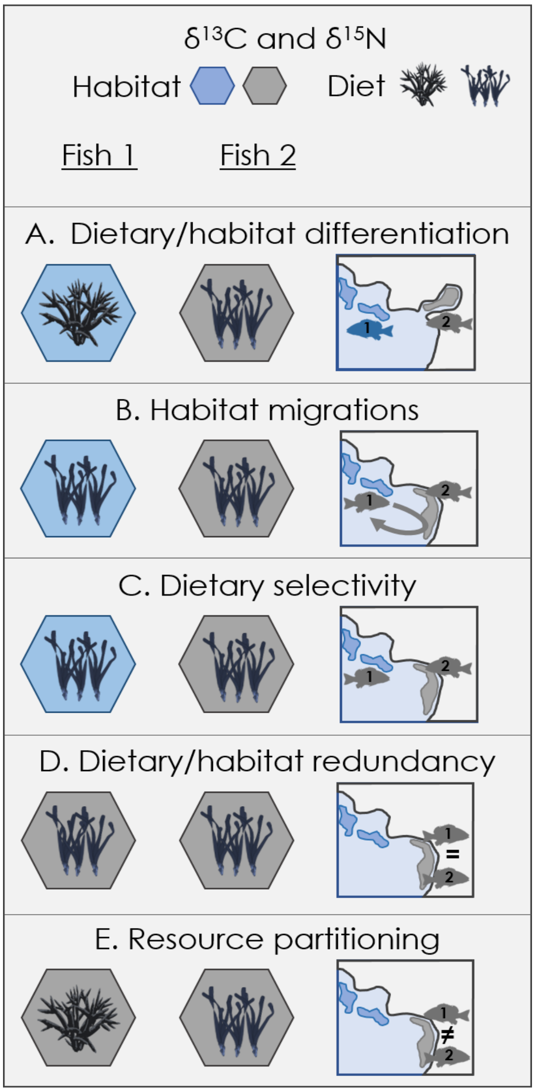
Generally, carbon isotope (δC^{13}) and nitrogen isotope (δN^{15}) ratios describe diet and trophic level, respectively (Fry 2006; Layman et al. 2012). These isotopes can be related to dietary sources because there are significant and consistent differences in primary food sources which are then reflected in an animal's diet (Bouillon et al. 2012, Peterson and Fry 1987), providing an isotopic signature for consumers (Parnell et al. 2010). These dietary signatures can then be related back to coarse habitat signatures when diet is representative of a dominant habitat (e.g. *Sargassum*), and can therefore be used as a proxy for habitat use and movement patterns (Hobson et al. 2010).

Here, I explore the habitat relationships of coral reef fish species across a diverse seascape off Siquijor Island in the Philippines. My study site has a continuum of coral reef and adjacent non-reef habitats that change substantially in area and distribution across a relatively small distance (<20km). This provides a unique opportunity to explore how fish classified as coral reef species may use different habitats during their post-settlement life stages, as well as explore the relationship between habitat use and habitat availability. I use parrotfishes (Sub-Family: Scarinae) and rabbitfishes (Family: Siganidae) as my study species. Parrotfishes are a diverse taxon of herbivores that graze, scrape, excavate, and browse on reef substrate to target epilithic and endolithic cyanobacteria and nitrogen rich microorganisms as adults (Clements et al. 2017; Nicholson and Clements 2020). Parrotfishes play an important role in reef erosion and coral reef dynamics (Bonaldo et al. 2014; Morgan and Kench 2016) but are also shown to be multiple habitat users across life stages (Eggertsen et al. 2020; Sievers et al. 2020a, Chapter 4). Isotopes are particularly useful for parrotfishes because gut content analysis is extremely difficult with this group, as they grind their food using their pharyngeal mill, making gut content analysis problematic (Choat et al. 2002). Rabbitfish are an excellent group to compare with parrotfishes as they are more 'traditional' herbivores, cropping and grazing on fleshy macroalgae (Hoey et al. 2013). Rabbitfishes are also found in a diverse range of habitat types, and present an opportunity to evaluate potential variation in habitat use patterns across a heterogeneous tropical seascape (Hoey et al. 2013).

I approached my questions in a confirmatory and then exploratory analysis framework. Because diet and habitat can often be confounded with stable isotope data, I followed a series of theoretical scenarios (Fig. 5.1). Firstly, I sought to confirm whether stable isotopes can be used to identify habitat use (Fig. 5.1, Scenario A). In my study seascape, habitats are within relatively close proximity, on a continuous submerged reef area, with a narrow daily tidal range (<1-2m), and no strong estuarine influence. Generally, stable isotopes are used to track movement and habitat use across larger spatial scales (McMahon et al. 2012; Currey et al. 2014), or with an environmental gradient such as along a river or estuary (Lugendo et al. 2006; Connolly and Waltham 2015; Davis et al. 2015) which provides strong spatial variation in isotopic signatures, known as an isoscape. Here, I explore the potential for stable isotopes to detect habitat patterns in fishes where the isoscape is more subtle. Secondly, I aim to confirm ontogenetic shifts across different habitats. I hypothesize that parrotfish species will exhibit ontogenetic habitat shifts from non-reef habitats as juveniles to coral reef habitats as adults, and that stable isotope data will reflect this shift. Finally, my exploratory analysis seeks to understand how habitat availability may alter fish-habitat use patterns (Fig. 5.1, Scenario A and B). Specifically, does the availability (total area) and accessibility (proximity) of non-reef habitats to coral reefs alter whether fish use these habitats? And, can this be identified by using stable isotopes that track diet and movement patterns? The availability of non-reef habitats varies substantially along the coastline of my study location, allowing for a comparison between two reef sections with different amounts of non-reef habitats available. I hypothesize that for species and or life stages (e.g., adult fish) not reliant on non-reef habitats, no isotopic differences between the two reef sections will be apparent. On the other hand, species that might be more reliant on non-reef habitats would show variation in isotopic signatures between these reef sections, especially during their juvenile life stages.

My general aim is to understand how habitat use differs among species in two coral reef fish groups, parrotfish and rabbitfish. I used stable isotopes to investigate whether ontogenetic and habitat-use patterns in the study species may be influenced by the available habitat in a seascape. Specifically, I asked: 1. Do different fish species exhibit different stable isotopic signatures that I can relate back to habitat use? 2. How useful are stable isotopic signatures in detecting ontogenetic shifts? 3. Do individuals of the same species show changes in isotopic signatures based on available habitat?

Figure 5.1. Scenarios which differentiate between diet and habitat use when using stable isotopes of fishes. The colored hexagons represent different habitats, and the diet icons are dietary signatures identified using $\delta^{13}C$ and $\delta^{15}N$ isotopes. In Scenario A, two fish are collected from different habitats, and have different diet signatures. These two fish have dietary and habitat differentiation and likely do not interact at all with one another. In Scenario B, fish are collected from two different habitats, but have similar diets. This is indicative of a habitat migration occurring, where Fish 1 is travelling to Fish 2's habitat, eating, and then migrating back to their original habitat. This scenario could also reflect nutrient transport by waves, tides, and currents. Therefore, the oceanography and physical environment of the study system must be closely examined. Scenario A and B represent two outcomes dependent on habitat availability. In Scenario A, the grey habitat is in a closed bay, and therefore not accessible to Fish 1. In Scenario B, the grey habitat is in an open bay, and is accessible to Fish 1. Scenario C represents dietary selectivity, where species are selectively feeding on resources that occur in both habitat types. Disentangling Scenarios B and C require careful examination of fish ecology, and dietary signatures. Scenario D demonstrates dietary and habitat redundancy, where two fish are collected from the same habitat, and have the same diet, and thus likely have strong niche overlap. In Scenario E, fish are collected in the same habitat but have different diets. This is an example of resource partitioning, where fish have different diets within the same habitat.

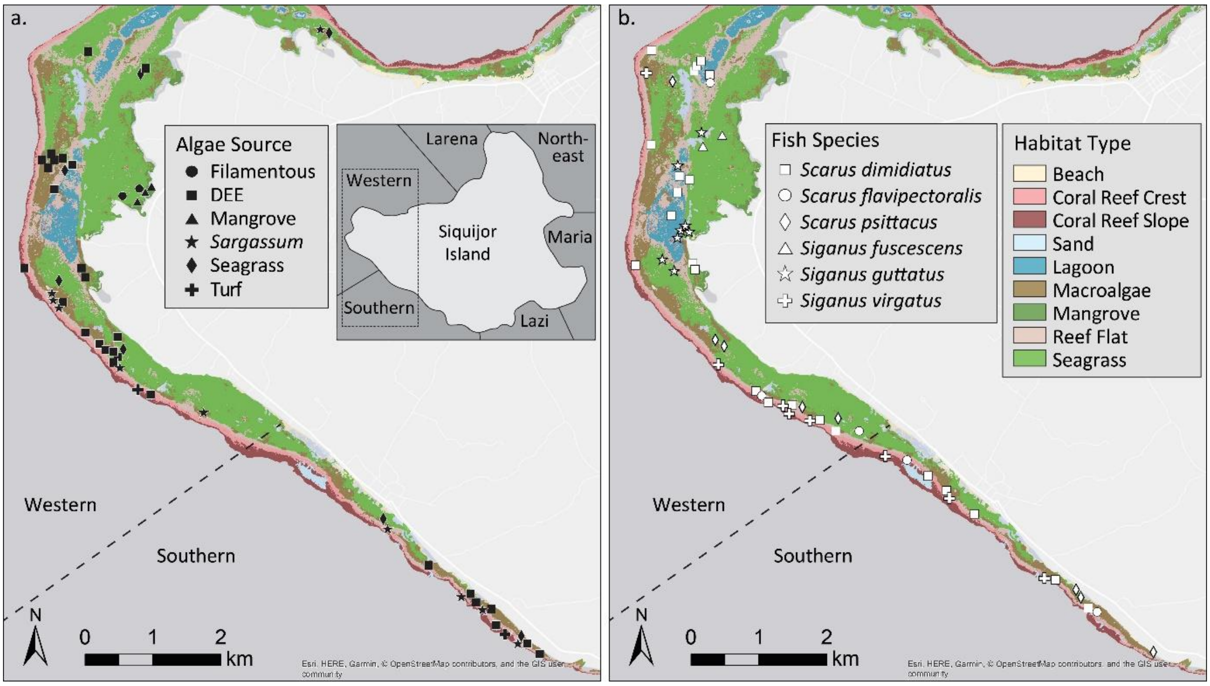


5.3 METHODS

5.3.1 Study Site

The western and south-western side of Siquijor Island are characterized by fringing coral reef with a range of adjacent non-reef habitats such as seagrass beds, macroalgal beds, mangrove stands, and lagoons, spanning approximately 16 km (Fig. 5.2). The western tip of the island has non-reef habitats that extend up to 1.5km from shore, with decreasing areas of non-reef habitat towards the south. I separated the coastline into two 'sections': western and southern (Fig. 5.2). Non-reef habitats within the western section consist of large expanses of lagoon, macroalgal, seagrass, and mangrove habitats; while those in the southern section only had a narrow band of seagrass and macroalgal beds.

Figure 5.2. Habitat map and collection locations of fish and potential food sources from Siquijor Island Philippines. Habitat map shows classified habitat derived from satellite imagery. Collection locations are shown for potential food sources (a) and fish species (b). DEE source is the category for detritus, epilithic algal matrix, and epiphytes. The western and southern division delineates two coastal sections of the island typified by differing amounts of non-reef habitats where the Western section has greater diversity and greater total area of non-reef habitats, and the Southern section has a much smaller amount of non-reef habitats.



5.3.2 Field Collections

Fish

Fish tissue was collected in 2017 and 2018 to analyse stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$). Generally, carbon signatures are indicative of diet, and nitrogen signatures are used to evaluate trophic level in the food web (Fry 2006; Layman et al. 2012). Turnover rates of these isotopes in muscle tissue ranges between 50-120 days (Vander Zanden et al. 2015; Matley et al. 2016) depending on the age and metabolism of a fish. Adult fish collections were conducted in collaboration with local fishers, and every attempt was made to sample evenly across the study area. Fishers were notified of my interest in collecting particular species, and if individuals of these species were caught, the location of capture was noted, and scientists were contacted. Fishers were paid for their time, and fish were purchased at market price. Upon receipt, fish were either frozen or dissected immediately. Muscle tissue was taken from the dorsal portion of the body of each fish specimen for stable isotope analysis.

In June 2017, *Scarus dimidiatus* (Yellowbarred parrotfish) Terminal Phase (TP) and *Siganus virgatus* (Barhead rabbitfish) adults were collected from the fishery in coral reef habitat. From May – June 2018, *Scarus dimidiatus* (Yellowbarred Parrotfish)*, Scarus flavipectoralis* (Yellowfin Parrotfish), *Siganus guttatus* (Orange-spotted Rabbitfish), and *Siganus fuscescens* (Black Rabbitfish) were collected from the fishery in coral reef, reef flat, lagoon, and seagrass habitats (Table 5.1). Only sub-adult initial phase (IP) individuals of parrotfish species were collected in 2018 because many fishers had shifted from fishing to a tourism livelihood, and specimens from the fishery were much fewer compared to the year prior. In 2018, juvenile parrotfishes were also collected from non-reef habitats (seagrass, macroalgal beds, lagoons). It is important to acknowledge the imperfect sampling design in fish species collections, where not all species were collected in all locations. Collections were strongly limited to fishery catch, and fishermen availability (Table 5.1)Due to the difficulty in identifying juvenile parrotfishes *in-situ,* all juvenile parrotfishes collected were later identified to the species level using DNA analysis (Sievers et al. 2020a, Chapter 4). The results from DNA analysis identified *Scarus dimidiatus* and *Scarus psittacus* as the two juvenile parrotfish species most commonly collected from non-reef habitats. *Scarus dimidiatus* juveniles were mainly collected in lagoons, and *Scarus psittacus* were collected from macroalgal beds and seagrass habitat (Fig. 5.2, Table 5.1). Species and life stages were classified by their general reliance on non-reef habitat, where high reliance means they were common on, or abundant in, non-reef habitats and were rarely or occasionally observed on coral reefs. Low reliance means that the species or life stage were observed predominately on coral reefs, and were rarely observed in non-reef habitats. These classifications were informed by external references, expert knowledge, surveys of the island sections, and external resources such as FishBase (Froese and

Pauly 2020) (Table 5.1). *Scarus dimidiatus* is abundant on coral reefs as adults (Russ et al. 2015b), and utilises non-reef habitat as juveniles in Siquijor (Sievers et al. 2020a, Chapter 4). *Scarus flavipectoralis* is a relatively common species, and often occupies sandy, sheltered habitats as adults. *Scarus psittacus* is also a common parrotfish species seen in sandy and rubble habitat adjacent to coral reefs as adults and is extremely abundant as juveniles in non-reef habitats, specifically macroalgal beds (Sievers et al. 2020a, Chapter 4). The three rabbitfish species (*S. virgatus, S. guttatus, S. fuscescens)* represent a wide variety of habitat-use patterns within the same family. *Siganus guttatus* is occasionally seen on coral reef as adults, but is common in turbid nearshore waters, and its juveniles reside in mangrove habitat (Froese and Pauly 2020). *Siganus fuscescens* is found in macroalgal and seagrass habitat, and *Siganus virgatus* is a relatively abundant coral reef species. I was not able to collect samples of juvenile rabbitfishes despite best efforts.

Table 5.1. Sample sizes for fish, with additional information on degree of reliance on non-reef habitat and probable primary habitat based on literature and previous surveys in the study site. Average size and size range are in total length (TL, mm). IP is for initial phase, and TP is terminal phase. Refs are reference key: 1. Sievers *et al.* 2020a (Chapter 4), 2. Russ *et al.* 2015, 3. Nicholson *et al.* 2020, 4. Russ 1984, 5. Johnson *et al.* 2019, 6. Mellin *et al.* 2007 , 7. Olds *et al.* 2012a, 8. Olds *et al.* 2012b, 9. Fox *et al.* 2009, 10. Fox and Bellwood 2007.

Species	Phase	Reliance	Primary Habitat	West 2017	South 2017	West 2018	South 2018	Ave Size (mm)	Size Range (mm)	Refs
Scarus dimidiatus	Juvenile	Low	Macroalgae, Lagoon	0	0	31	3	73	32-98	1
	IP	Medium	Reef Flat	7	2	4	0	147	100-253	1
	TP	High	Coral Reef	15	11	0	0	200	147-310	2, 3
Scarus flavipectoralis	IP	Medium	Reef Flat	0	0	5	12	160	102-195	4, 5
Scarus psittacus	Juvenile	Low	Macroalgae	0	0	21	26	36	25-51	1
Siganus fuscesens	Adult	Low	Macroalgae	0	0	35	0	151	123-208	6, 7
Siganus guttatus	Adult	Medium	Coral Reef, Mangrove	0	0	52	0	185	118-281	8, 9
Siganus virgatus	Adult	High	Coral Reef	23	15	0	0	166	142-196	8, 9

Dietary/Habitat Sources

A range of food and habitat source samples were collected in 2017 and 2018. Source collections were informed by gut contents from current samples, behavioural observations, and surveys of the fish study species conducted previously (McClure 2019), and also briefly prior to sample collections. A minimum of three replicate samples of sources of potential food were collected from each habitat spanning my fish collections area (Fig. 5.2). Samples of potential food sources were: algal turf, detritus, seagrass, *Sargassum*, epiphytes from seagrass, epiphytes from *Sargassum*, epilithic algal matrix (EAM), mangrove leaves, and filamentous algae (*Enteromorpha*) (Table 5.2). These sources were collected to represent a combination of potential diet and habitat. Algal turf samples were collected from caged limestone tiles that were deployed (together with uncaged tiles) on reef crests for six weeks, and thus represented the coral reef signature. The tiles were deployed in May of 2017 in two locations spanning the areas where fish were caught (Fig. 5.2). After tiles were retrieved, they were gently rinsed with seawater and any material sloughing off was collected and labelled as detritus. Tiles were cleaned of crustaceans, molluscs, and encrusting organisms, and scraped for one minute using a paint scraper. The material scraped off was sieved through a 64 µm plankton net and labelled as turf. Algal material growing on tiles consisted of a wide range of filamentous algae, turf, and small red and green algae. Uncaged tiles exhibited clear signs of grazing, presumably by fish, and characteristic scraping marks from parrotfishes, confirming the importance of algal turf as a potential dietary source. The signature used for macroalgal habitat was *Sargassum spp*. Whole *Sargassum* plants were collected from macroalgal habitat during May – July in both 2017 and 2018 when plants still had reproductive parts. *Sargassum* leaves were cleaned in fresh water and epiphytes were gently removed from *Sargassum* parts. Leaves and stems across the whole plant were selected randomly. Epiphytes were filtered through a 64 µm plankton net and collected. Seagrass blades (*Cymodocea* spp*., Halodule* spp*., Thalassia* spp*.)* and seagrass epiphytes were collected, representing the signatures for seagrass beds. Similar to *Sargassum*, seagrasses were cleaned of epiphytes and stored in ziplock bags. EAM samples were collected by observing feeding of *Scarus dimidiatus* and *S. flavipectoralis* individuals. In a location where feeding bouts took place, dead coral and rocks with clear signs of scraping marks were collected, generally occurring in the reef flat area (Fig. 5.2). These specimens were gently scraped to not flake off any calcium carbonate skeleton, and the scraped material was rinsed through a 64 µm plankton net and placed in vials. Recently fallen mangrove leaves were collected from mangrove habitat, scraped of any epiphytes, and stored in ziplock bags. Filamentous algae (*Enteromorpha*) were collected near mangrove habitats in the deeper lagoon area as *Siganus guttatus* individuals were observed feeding on this, and filamentous algae was also present in their foreguts. All source samples were immediately frozen after processing. Frozen fish muscle tissue and all source samples were dried in a 60°C oven for 48 hours until completely dehydrated before milling into a fine powder.

Table 5.2. Sample sizes for each potential food source between years and reef section on Siquijor Island. The Source Group column details the final grouping for analysis displayed in Fig. 5.3. EAM is epilithic algal matrix, DEE is the grouping for detritus, EAM, and epiphytes.

Algal Class	**Source Group**	**West 2017**	**South 2017**	**West 2018**	**South 2018**
Detritus	DEE	3	5		
EAM	DEE			6	2
Epiphytes - *Sargassum*	DEE			11	10
Epiphytes – Seagrass	DEE			10	2
Filamentous Algae	Filamentous			3	
Mangrove	Mangrove			3	
Sargassum	*Sargassum*	9	6	3	3
Seagrass	Seagrass	6	6	6	
Turf	Turf	5	3		

5.3.3 Stable Isotopes

Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes were sampled at the Advanced Analytical Centre at James Cook University, Australia using a ThermoFisher GasBench III coupled to a Delta V^{plus} isotope ratio mass spectrometer via a Conflo IV. Isotopic ratios are expressed relative to repeat reference standards to account for drift and measurement precision. Carbon isotope ratios are reported relative to Vienna Pee-Dee Belemnite (VPDB) and nitrogen isotope ratios are reported relative to atmospheric nitrogen. Both are expressed in delta (δ) notation relative to their standard and reported in parts per thousand (‰). Tissue samples were run for $\delta^{13}C$ and $\delta^{15}N$ simultaneously. Source samples of diet were subsamples and run for $\delta^{15}N$, with another subsample acidified with HCl, dried, and run for $\delta^{13}C$.

5.3.4 Statistical Analysis

Isotope data were evaluated for any potential outliers or anomalies (such has high C:N ratios). C:N ratios were assessed to ensure no values were >4. Isotopic biplots of $\delta^{13}C$ and $\delta^{15}N$ were made to evaluate the isotopic signatures of potential food sources and fish tissues. Biplots revealed any trends between and among potential food sources, years, and island sections (western, southern). Some food sources were aggregated, as their signatures overlapped substantially with each other, representing similar dietary sources in isospace (C:N biplots). Epiphytes from *Sargassum* and seagrass, EAM, and detritus occurred in overlapping isospace, and were *a-priori* aggregated into one potential food source category for further analyses (DEE) (Table 5.2). Although these sources are all unique and important when evaluating micro-selectivity of diet, they overlapped so much in isospace that they were included as one metric (Dromard et al. 2017). Ecologically, these four sources often consist of similar material, providing further justification for their aggregation (Wilson et al. 2003).

To estimate the proportion of each habitat source in describing fish tissue signatures, Stable Isotope Mixing Models in R (simmr) analysis was used (Parnell et al. 2013). Simmr uses Bayesian mixing model techniques utilizing the JAGS program to assign proportions of an end member (fish) to a potential dietary source (algae, turf, detritus etc). I used vague uninformative priors, and the simmr default parameters for JAGS (iterations = 10,000, burn-in = 1000, thin = 10, chains = 4). Trophic discrimination factors (TDF) (or fractionation values) were set at 1.63 ‰ $\delta^{13}C$ and 3.54 ‰ $\delta^{15}N$ with a standard deviation of 0.63 ‰ $\delta^{13}C$ and 0.74 ‰ $\delta^{15}N$ ‰. TDFs can be highly variable and are species and life stage dependent (Caut et al. 2009, Post 2002, Hussey et al. 2014). However, to my knowledge, there are no laboratory studies evaluating TDFs for parrotfishes or rabbitfishes, and I therefore used TDFs from other coral reef fish species (*Fundulus heteroclitus, Plectropomus leopardus, Pomacentrus spp.*) as a proxy (Elsdon et al. 2010; McMahon et al. 2010; Matley et al. 2016; Eurich et al. 2019). Until controlled experimental studies of fractionation effects are conducted on parrotfish and rabbitfish across life stages, I feel these fractionation values capture the potential range of TDF within an ecologically relevant range. Two simmr models were run, one for each year. For each model, six potential food sources (source group) were used (Table 5.2) so that models between years were comparable to each other. Fish were separated by species and species life stage (juvenile, sub-adult initial phase (IP) parrotfish, adult terminal phase (TP) parrotfish, and adult). Separation by life stage was done specifically to evaluate how diet and/or habitat use may change with ontogeny. Then, to understand how fish diets were different between species and life stages, dietary proportions were compared for each food source.

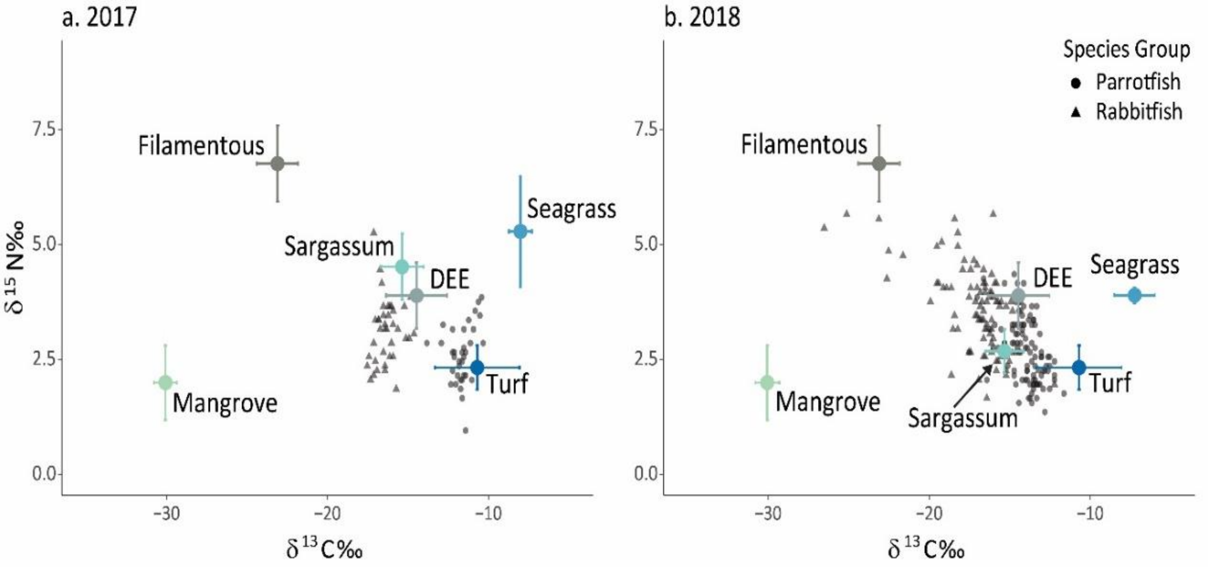
The second series of models used were Stable Isotope Bayesian Ellipses in R (SIBER) (Jackson et al. 2011). These models fit ellipses onto groups of data in isospace and calculate the Bayesian standard ellipse area (SEA_b) from the posterior distributions. Again, I used vague priors and the default setting in SIBER for the JAGS parameters (iterations = 10,000, burn-in = 1000, thin = 10, chains = 2). I can then compare SEA_b among and between species or groups, by comparing the distributions of the SEA_b

posterior draws between groups. Comparisons between SEA_b (total ellipse areas) were considered significant if 90% of posterior draw measures of the SEA_b estimates for one species (or species and stage combination) was greater than another. This approach aims to describe the total variety in diet, or how diverse a species diet may be, based on the area of the isotopic ellipse. To quantify how similar species resources may be, I calculated isotopic overlap. The proportion of overlap was calculated between two ellipses measured at the 95% probability ellipse area, where 95% of observations are included in the ellipses. Percent overlap was calculated as the area of overlap divided by the sum of the area of the two ellipses minus the area of overlap. Overlap values greater than 50% were considered to be indicative of similar resource use requirements (Brandl and Bellwood 2014). I ran two SIBER models. The first model compared species between island reef sections (western vs. southern) for species that were collected in both sections. This excluded *S. guttatus* and *S. fuscescens* as they were only collected in the western section. The second SIBER model evaluated the differences between species and life stages. This model also evaluated the differences between life stages of *Scarus dimidiatus*, as this species had the largest sample size. Specifically, I compared *S. dimidiatus* for juvenile, initial phase immature sub-adults (IP), and terminal phase reproductive adults (TP).

5.4 RESULTS

A total of 261 fish, and 111 potential food source samples were collected for stable isotope analysis across the southwestern side of Siquijor Island (Fig. 5.2, Table 5.1, Table 5.2). There were no C:N tissue values >4, and thus all tissue data were kept for analysis. Food sources and fish species were analysed separately by year (2017, 2018), as there were differences in *Sargassum* and seagrass signatures between years (Fig. 5.3). For each year, algal turf, mangrove, filamentous algae, and DEE were included in dietary analysis, and only the seagrass and *Sargassum* signatures changed by year (Fig. 5.3). Dietary sources were also compared between reef locations (Appendix D, Fig. S5.1). Some sources had different signatures between locations, but only for one isotope. The relative location of each source in the isotopic biplot did not change, allowing for a comparison of dietary proportions between different sources.

Figure 5.3. Isotope ($\delta^{13}C$ and $\delta^{15}N$) biplots of source material for 2017 (a) and 2018 (b) with fish signatures overlaid in black points. Colored points with error bars are the mean and standard deviation of algal isotope groups. Black points are individual fish isotope values. DEE is the group for detritus, epilithic algal matrix, and epiphytes.



Simmr analysis revealed differences in the dietary proportion of potential food sources between families, species, and life stages of fish (Fig. 5.4). For parrotfishes, there was a clear relationship between *Sargassum* and algal turf dietary proportions, where, as the amount of algal turf in the diet decreased, the proportion of *Sargassum* in the diet increased. This relationship reflected the probable degree of reliance on non-reef habitat (Table 5.1). Correlation matrices were evaluated to understand any correlation between opposing diets in isospace (Appendix D, Fig. S5.2). Species and life stages that were more reliant on non-reef habitats (Table 5.1) compared to coral reef habitat had a higher proportion of *Sargassum* and a lower proportion of turf in their diet. *Scarus psittacus* juveniles, which occur predominately in macroalgal habitat, had almost twice the amount of *Sargassum* in their diet compared to turf (48% and 27%, respectively) (Table 5.3). Comparatively, *Scarus dimidiatus* adults, an abundant fish on coral reefs, had proportions of turf in their diet 24 times higher than that of *Sargassum*, with turf representing 85% of their diet (Table 5.3). *Scarus flavipectoralis* IP dietary proportions had a mixture of coral reef (turf) and non-reef habitat (*Sargassum*) signatures. In comparison, rabbitfish showed variable trends with their dietary proportions that reflected their habitat preferences. *Siganus virgatus*, collected from coral reef habitat, had the highest proportion of turf in their diet among the rabbitfishes, with an average of 49.5%. *Siganus fuscescens*, which are usually found in the macroalgal and seagrass habitat, had the highest levels of *Sargassum* in their diet, with some influence of turf. *Siganus guttatus* had an even dietary mixture across all potential food sources, with a notable increase in mangrove signature in their diet compared to all other species.

Figure 5.4. Dietary proportions from algal sources for (a) *Scarus* spp., and (b) *Siganus* spp. estimated by simmr analysis. Colors are dietary sources, and each boxplot grouping is a different fish species and/or life phase. Species are ordered according to increasing reliance on non-reef habitat, indicated by the arrow.

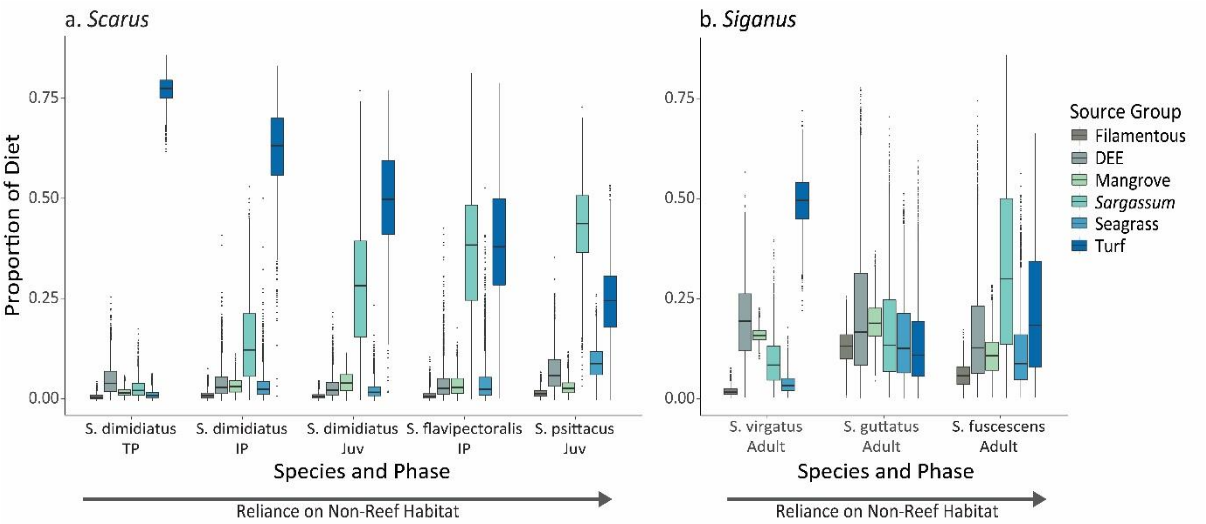
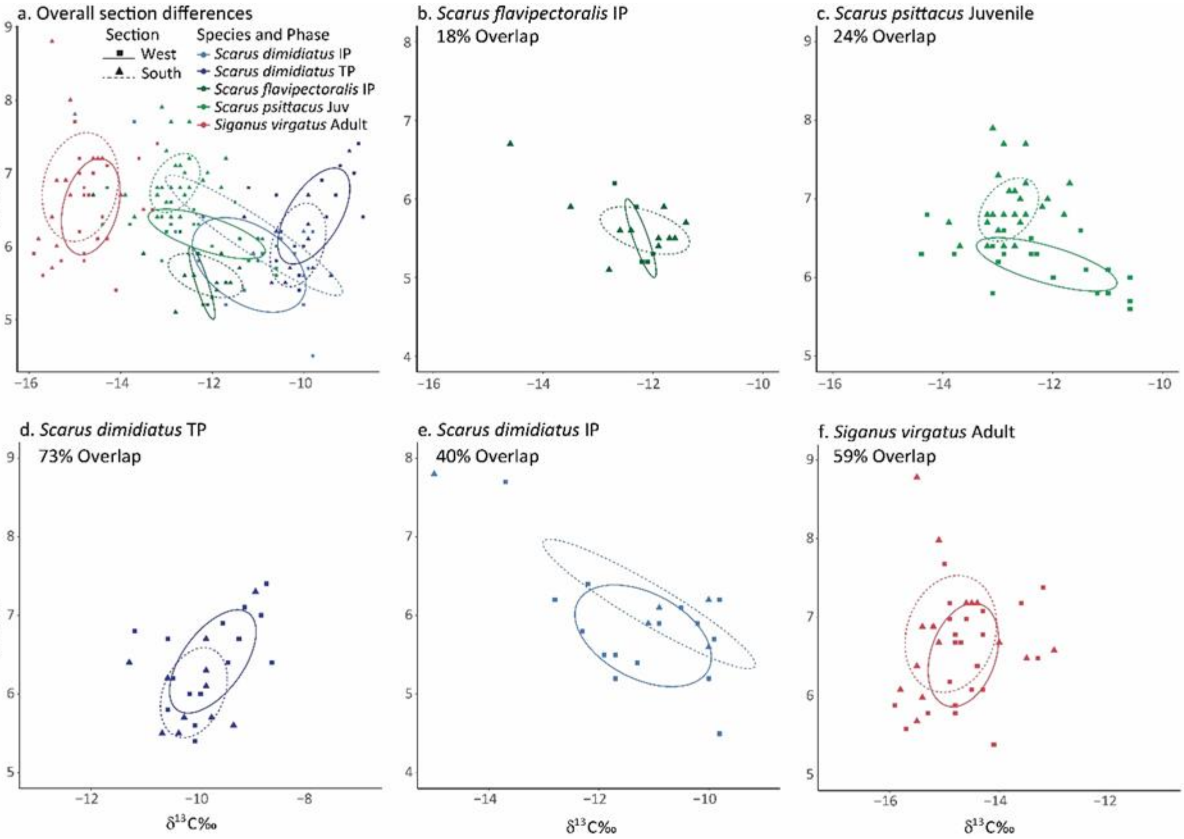


Table 5.3. The magnitude of differences between the proportions of *Sargassum* versus turf in the diet of each species group. *Sargassum* and turf values represent the mean dietary proportion. Difference is the ratio of turf to *Sargassum* (Turf/*Sargassum*).

Species and Life Phase	*Sargassum*	Turf	Difference
Scarus dimidiatus Adult (TP)	0.035	0.854	24
Scarus dimidiatus Sub-adult (IP)	0.161	0.690	4.3
Scarus dimidiatus Juvenile	0.313	0.554	1.8
Scarus flavipectoralis Sub-adult (IP)	0.401	0.436	1.1
Scarus psittacus Juvenile	0.481	0.270	0.56
Siganus fuscescens Adult	0.331	0.217	0.66
Siganus guttatus Adult	0.173	0.139	0.8
Siganus virgatus Adult	0.095	0.493	5.2

Variability in dietary isotopic signatures was strongest among species, and then within species there was evidence of a distinction between the western and southern reef sections based on Bayesian standard ellipses areas (SEA_b), (Fig. 5.5). The greatest overlap in isospace between island sections occurred for *Scarus dimidiatus* TP and adult *Siganus virgatus* which have the lowest reliance on non-reef habitats, and show 73% and 59% overlap between island sections, respectively (Fig. 5.5d,f; Table 5.4). Comparatively, *Scarus flavipectoralis* IP, *Scarus psittacus* juvenile, and *Scarus dimidiatus* IP, had weaker overlaps between reef sections (Fig 5.5b,c,e; Table 5.4). When comparing *S. dimidiatus* TPs and IPs between sections, TPs and IPs had marginally higher overlap in the southern (24%) compared to the western (20%) sections of the island.

Figure 5.5. Reef section differences in the Bayesian Standard ellipse areas (SEA_b) of stable isotope values with 50% ellipses (includes 50% of raw data) presenting isotopic overlap between the Western section (solid line) and Southern section (dashed line). Points are individual fish. Only species collected in both sections are presented here. Plot a. shows ellipses for all species, and plots b-f highlight the comparison for each species individually. Overlap values for each species (b-f) are the Bayesian fitted values calculating the overlap between reef sections estimated from the 95% ellipses.

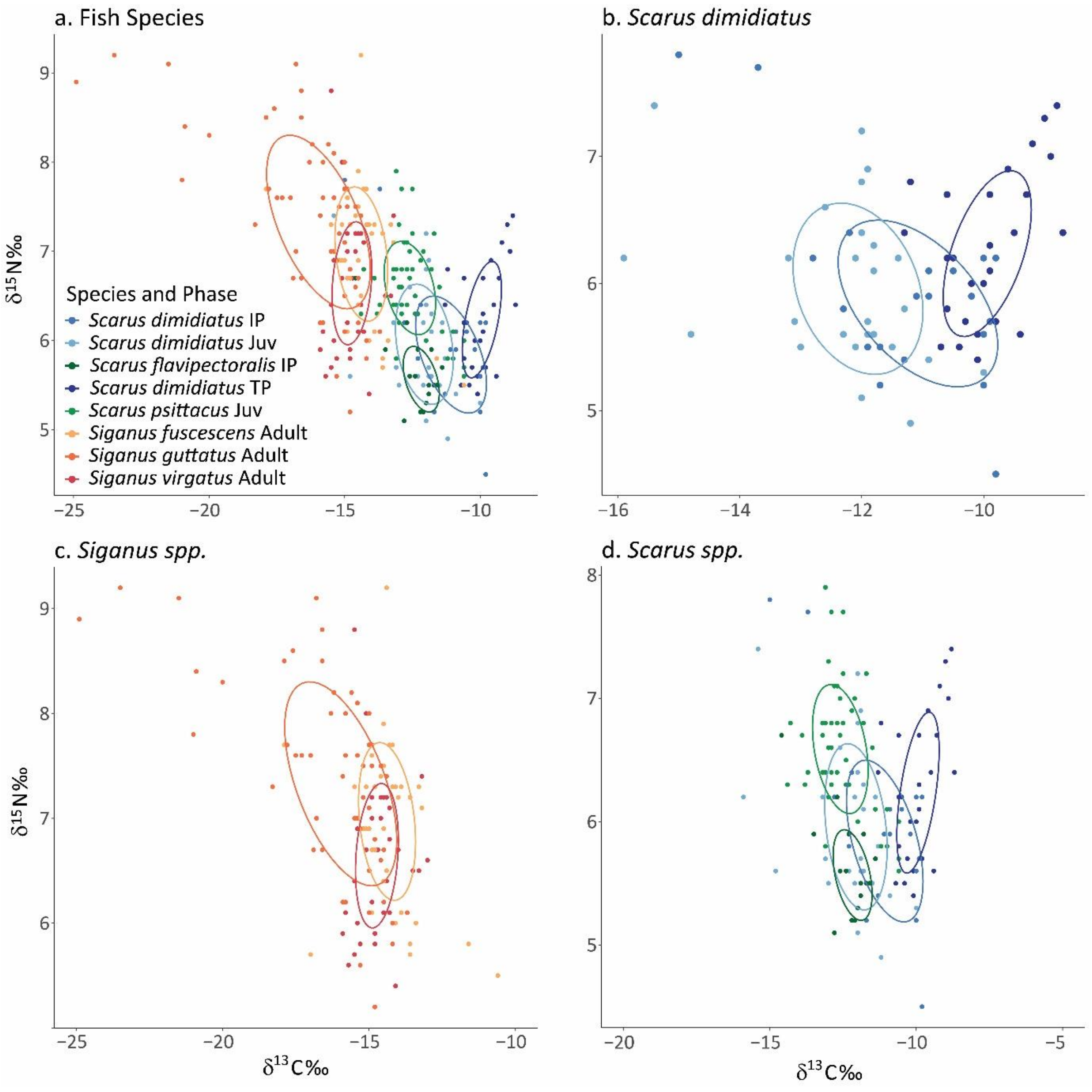


There were also clear distinctions between species and life stages within each family. For parrotfishes, the greatest overlap in SEA_b was for *S. dimidiatus* IP and *S. dimidiatus* juvenile with a 62% overlap, followed by the comparison between the juveniles of *S. dimidiatus* and *S. psittacus* with 50% overlap. All other parrotfishes had unique isospace signatures, with low proportional overlap (0.18-0.40) (Table 5.4). When exploring SEA_b for life stages within *S. dimidiatus* (Fig. 5.6b), there was a clear shift in signatures from juvenile to IP, and from IP to adult TP, where carbon values become less negative as fish mature. This result is corroborated by the dietary proportion signatures (Fig. 5.3), where the more negative carbon signatures represent *Sargassum*, and the less negative carbon signatures associated with adult TPs represent algal turf from coral reefs. For rabbitfishes, there was 50% overlap of SEA_b between *S. virgatus* compared to *S. fuscescens*, and also between *S. fuscescens* and *S. guttatus* (Fig. 5.6). This indicated that even with location and habitat differences, rabbitfish diet is likely more consistent across species compared with the parrotfish examples.

Table 5.4. Comparisons calculating the proportion of overlap area of isotopic space calculated from 95% standard ellipse areas. Type column is the comparison evaluating differences between reef sections, species, or life phases. Grouping is the overarching group which the comparison is evaluating. The Comparison column details the specific ellipses compared. Bolded rows are overlap proportions 50% or greater, indicating similar isotopic space between comparisons. TP = terminal phase adults, IP = initial phase sub-adults, Juv = juvenile.

Species Group	Type	Grouping	Comparison	Overlap
Parrotfish	Sections	*S. dimidiatus* IP	Western vs Southern	0.40
Parrotfish	**Sections**	***S. dimidiatus* TP**	**Western vs Southern**	**0.73**
Parrotfish	Sections	*S. flavipectoralis* IP	Western vs Southern	0.18
Parrotfish	Sections	*S. psittacus* Juv	Western vs Southern	0.24
Parrotfish	Sections	Western	*S. dimidiatus* TP vs *S. dimidiatus* IP	0.24
Parrotfish	Sections	Southern	*S. dimidiatus* TP vs *S. dimidiatus* IP	0.20
Rabbitfish	**Sections**	***S. virgatus* Adult**	**Western vs Southern**	**0.59**
Parrotfish	Phase	*S. dimidiatus*	IP vs TP	0.25
Parrotfish	Phase	*S. dimidiatus*	TP vs Juv	0.23
Parrotfish	**Phase**	***S. dimidiatus***	**Juv vs IP**	**0.62**
Parrotfish	**Species**	**Juveniles**	***S. dimidiatus* Juv vs *S. psittacus* Juv**	**0.50**
Parrotfish	Species	Initial Phase	*S. dimidiatus* IP vs *S. flavipectoralis* IP	0.28
Parrotfish	Phase	Off reef species	*S. flavipectoralis* IP vs *S. psittacus* Juv	0.29
Rabbitfish	Species	Siganids	*S. virgatus* adult vs *S. guttatus* adult	0.27
Rabbitfish	Species	Siganids	*S. virgatus* adult vs *S. fuscescens* adult	0.49
Rabbitfish	Species	Siganids	*S. fuscescens* adult vs *S. guttatus* adult	0.49

Figure 5.6. Species and life phase differences between Bayesian Standard ellipse areas (SEA_b) of stable isotope values with 50% ellipses (includes 50% raw data) to evaluate isotopic overlap. (a) All species and life stages on one plot for broader comparisons. (b). Comparison of the isotopic overlap for *Scarus dimidiatus* between three life phases (Juvenile, Sub-adult IP, Adult TP) (c) *Siganus* (Rabbitfish) species only, (d) Comparison of *Scarus* (Parrotfish) species including different life phases.



5.5 DISCUSSION

Stable isotope data showed clear evidence of habitat and dietary shifts that coincided with a fish's estimated degree of reliance to non-reef habitat. I was able to confirm habitat use with dietary proportion data, where dietary signatures reflected the habitat and location where species were collected. Therefore, I could relate stable isotopic signatures back to habitat use (Fig. 5.4). Informed by this first result, I could then identify ontogenetic habitat shifts for *Scarus dimidiatus,* which showed transitions in isotopic space with life stage (Fig. 5.6). Finally, by comparing isotopic space of species between two reef sections that varied in the amount of non-reef habitat available, I demonstrated that there is a potential for flexibility in habitat use for fishes that use non-reef habitats (Fig 5.5) due to the greater diversity in non-reef food sources when they are available in the surrounding seascape.

I observed a clear trend in diet which reflected habitat use patterns in species, where diet of algal turf (coral reef signature) changed to *Sargassum* (macroalgal signature) for species that used non-reef habitats. This trend held for both parrotfish and rabbitfish. For example, species collected on coral reef habitat, *Scarus dimidiatus* adult and *Signanus virgatus* adult, had high amounts of algal turf in their diet. Whereas *Scarus psittacus* juvenile, collected in macroalgal beds, had greater amounts of *Sargassum* in their diet. These dietary proportions mirror the ecology of the species, where species more reliant on non-reef habitats had dietary signatures that reflected their habitat-use patterns (e.g., increased amounts of *Sargassum* for species occupying macroalgal habitat). It is important to note that although algal turf and *Sargassum* are used in this study to signify dietary proportions, it does not necessarily mean that those individual fish are specifically consuming algal turf or *Sargassum*. I used these dietary signatures as coarse habitat signatures for coral reef (turf) and macroalgal beds (*Sargassum*) because isotopic signatures differ between habitats and can be used as a proxy for habitat use (Peterson and Fry 1987; Hemminga and Mateo 1996; Fry 2006; Bouillon et al. 2012; Davis et al. 2014).

Adult Rabbitfishes, *Siganus virgauts, S. fuscescens,* and *S. guttatus* had distinctly different dietary proportions, which indicate differences in habitat use for the study system. Interestingly, *S. guttatus* had the highest amount of mangrove in their signature, even though they were collected in deep water lagoon areas with high seagrass cover. This result alludes to the potential for movement of *S. guttatus* across habitat boundaries. But we cannot preclude the possibility of passive movement of organic matter from mangroves to deep water where it might be consumed by resident *S. guttatus*. Further research on nutrient transport would be needed to disentangle these hypotheses.On the Great Barrier Reef (GBR), *S. guttatus'* conspecific *S. lineatus* (Woodland 1990), targeted filamentous algae, and was also found to be less dependent on coral reef habitat (Fox et al. 2009). On Siquijor, mangrove habitat is less influential compared to other non-reef habitats in structuring species distributions (Sievers et al. 2020b, Chapter 2), due to the tidal flux which leaves mangroves exposed at low tide. Nevertheless, for adult *Siganus guttatus*, mangrove habitat seemed to be of notable importance. Furthermore, *S. guttatus* is occasionally observed on coral reef habitats on Siquijor (McClure et al. 2020a). Using the combination of observations and stable isotope results, I can infer that *S. guttatus* is travelling among habitat types, which would in turn, generate physical and trophic linkages in a seascape. Migrations among habitat types can create strong trophic linkages (Krumme 2009), but these linkages are often dependent on the spatial configuration of the seascape, which can alter migration patterns and trophic transfers (Davis et al. 2014; Hyndes et al. 2014). Siquijor's spatially connected seascape may be facilitating movements for species like *S. guttatus*, and thereby generating a functionally connected seascape. Highly connected seascapes can lead to improved reserve performance and reef resilience (Olds et al. 2012c), and perhaps *S. guttatus* is one example of connectivity in the Siquijor seascape.

The rabbitfish examples demonstrate interesting patterns in the selectivity of diet and habitat use. Although *Siganus guttatus* and *S. fuscescens* were collected in relatively close proximity to each other, the two species showed nuanced differences in their dietary proportions. *S. fuscescens* had greater proportions of *Sargassum* and algal turf signatures compared to *S. guttatus*. Often found in macroalgal,mangrove, and seagrass habitats, *Siganus fuscescens* is a common browser (Nakamura et al. 2003; Mellin et al. 2007; Hoey et al. 2013; Davis et al. 2014), but has been observed on coral reef habitats, and thus are sometimes nominally considered a coral reef species (Yabsley et al. 2016). Yet, the differences in *S. fuscescens* and *S. guttatus* highlight that while species are in close spatial proximity to each other, their overall habitat use patterns may differ. Seascapes are probably acting on species movement and habitat-use at scales larger than what we can infer from visual observations alone. Here, stable isotopes paired with spatial habitat maps allowed us to extrapolate habitat-use patterns across broader spatial scales. *Siganus virgatus* was the only rabbitfish collected in both reef sections, and showed a strong coral reef signature with little differentiation in isotopic dietary signatures between island sections. This is consistent with other findings which show *Siganus doliatus,* a species closely related to *S. virgatus* (Woodland 1990), is a coral reef fish highly attached to the reef, feeding mainly on EAM and filamentous turf algae (Hoey et al. 2013). However, in other study locations in the tropical Pacific, *S. virgatus* was recorded to feed heavily on *Sargassum*, but these examples were in degraded reef habitats or inshore reefs where *Sargassum* was plentiful (Plass-Johnson et al. 2015; Bauman et al. 2017). Although rabbitfish had overlapping isotopic signatures (Fig. 5.6), the nuanced differences among rabbitfish dietary proportions indicate selectivity in diet, which in turn, represent diverse and distinct habitat-use patterns. This has been observed in other regions, where there was significant partitioning of feeding behavior between rabbitfish species on the GBR (Fox et al. 2009). For example, Hoey et al. (2013), showed consistency in diet within a species regardless of continental shelf location, suggesting their selectivity in diet. This result would be most similar to my results observed here for *Siganus virgatus,* which did not show variation in isotopic signatures between reef sections. Here, I build upon work highlighting the differences in diet and habitat use between species within the same genus (Hoey et al. 2013; Nanami 2018) and demonstrate the nuanced differences between diet and habitat use patterns for an important herbivorous species group.

Using parrotfishes, I was able to confirm ontogenetic habitat shifts with stable isotopic signatures. I observed a switch between *Sargassum* and algal turf that illustrated a parrotfishes' reliance to non-reef habitat as juveniles. The switch also coincided with life stage, where the transition from *Sargassum* to algal turf reflected the transition from macroalgal beds as juveniles to algal turf for adults. For juvenile parrotfishes (*Scarus psittacus, Scarus dimidiatus*), the dominant dietary signature was *Sargassum*, signifying macroalgal beds are important habitat for parrotfish juveniles. Macroalgal beds are increasingly recognized as important juvenile habitat, especially for parrotfishes (Evans et al. 2014; Tano et al. 2017; Fulton et al. 2020; Sievers et al. 2020a, Chapter 4). Furthermore, the shift in macroalgal dietary sources towards coral reef sources indicates that these habitats are linked through ontogenetic migrations of fish. Linkages between habitats by ontogenetic migrations can have considerable population level consequences for coral reef fishes (Wilson et al. 2010; Harborne et al. 2016), but further research must be conducted to confirm whether macroalgal habitats are true nursery locations in this system. This ontogenetic shift was most evident with *Scarus dimidiatus,* with clear differences in isotopic space between life stages**.** Juvenile *Scarus dimidiatus* had more negative $\delta^{13}C$ values, which shifted towards less negative $\delta^{13}C$ values as adults. This shift follows the change from macroalgal beds (*Sargassum*) to coral reef (turf). Enriched (less negative) $\delta^{13}C$ values can also be evidence of cyanobacteria in the dietary signal (Shahraki et al. 2014), which is a dominant food source for adult parrotfishes (Clements et al. 2017; Nicholson and Clements 2020). However, to isolate and evaluate specific dietary sources (e.g., cyanobacteria) and nutritional uptake, compound-specific amino acid isotope analysis is superior to bulk stable isotope analysis (McMahon et al. 2011), as used here. Nevertheless, the ontogenetic shift in *Scarus dimidiatus* was clear, suggesting their use of other habitats and their use of a range of food resources for younger life stages compared to adults. Other parrotfish species exhibit ontogenetic changes in home range (Welsh et al. 2013), willingness to move (Streit and Bellwood 2017), and diet (Feitosa and Ferreira 2014). Yet we know relatively little about how parrotfish use habitat in their early life stages, especially across a diverse seascape. Given the ecological and economic importance of adult parrotfish across tropical oceans globally, it is important to fill this knowledge gap regarding habitat use and resource requirements for early life stages of parrotfish.

For parrotfishes, isotopic dietary signatures seem to be highly specific within a life stage, but diverse across life stages. Parrotfishes can be highly selective in their targeted diet (Clements et al. 2017; Nicholson and Clements 2020), and show unique isotopic signatures (Plass-Johnson et al. 2013). But research has focused predominately on adult TPs and coral reef habitat, whereas in the present study, IP and juvenile parrotfish contributed to a broader dietary area in the isotope biplot. For example, *Scarus dimidiatus* juveniles were collected in lagoon habitats, whereas *Scarus psittacus* juveniles were collected in *Sargassum* dominated macroalgal habitat, yet these species had 50% overlap in isospace. This suggests that regardless of habitat, juvenile parrotfishes are likely targeting similar food sources in different habitats. It is important to note that I evaluated diet and habitat use by using stable isotopes, whereas other dietary and niche space research for these taxa predominately used behavioral observations, gut content analysis, and morphology (Adams et al. 2006; Fox and Bellwood 2013; Brandl and Bellwood 2014). Further research on isotopic niche space should explore the interaction between niche space, diet, and seascape connectivity in more detail.

I also explored whether the availability of non-reef habitats altered habitat-use patterns. *Scarus dimidiatus* TP and *Siganus virgatus* adults, which are rarely observed in other non-reef habitats, had a coral reef (algal turf) signature which showed weak differentiation in their isotopic dietary space between the western and southern sections of the reef. This indicates high fidelity to coral reef habitat, regardless of the diversity or amount of adjacent non-reef habitats available. In contrast, the isotopic dietary signatures of juvenile and sub-adult parrotfishes between reef sections were more differentiated, suggesting that these life stages can utilize more of the different types of adjacent non-reef habitat when they are available. Accessibility and availability of habitats has been shown to affect movement patterns of fishes across many spatial scales (Nagelkerken et al. 2008; Turgeon et al. 2010; Hitt et al. 2011; Kimirei et al. 2011), which alter community composition between reefs of varying levels of spatial connectivity (Kimirei et al. 2013b; Nagelkerken et al. 2015; Davis et al. 2017a). For example, juvenile *Scarus psittacus* was collected in non-reef habitats only, and showed the strongest differences in isotopic signatures between reef sections. I suggest that variation in non-reef habitat use was the most likely driver in the different isotopic signatures between reef sections for this species. When exploring alternate explanations, one might argue that these differences are due to natural environmental gradients in the seascape. However, the analysis of dietary source signatures allowed me to rule out this effect as the differences in fish tissue did not match the natural variation in food sources. Thus, the results probably reflect dietary and habitat effects. I acknowledge the imperfect sampling design in this study because not all species or diet sources were collected in all habitats, limiting my inference of these results. However, collections were very much limited by what fishers caught, and was hindered by the availability of fish and the fishing effort during that time. Stable isotope analysis comes with many caveats which limit interpretations. Again, improved field sampling techniques would have alleviated some of the issues inherent to this method. Nevertheless, I am still measuring differences which I feel are ecologically relevant and invite further research to corroborate these results.

These results highlight the nuanced attributes that may affect the resource requirements, diet, and habitat use of fishes. My findings show that species more reliant on non-reef habitats may be more flexible in their habitat-use patterns based on the availability of adjacent non-reef habitats. Accounting for the seascape connectivity when developing population models and spatial conservation practices is necessary for successful management of marine resources (Olds et al. 2013, 2016). If the spatial configuration of a seascape has the potential to alter how species utilize habitats, then is it essential to account for the spatial configuration of habitat when exploring species patterns. Here, stable isotopes illustrated linkages between habitats created by fishes, revealed diverse habitat-use patterns, and highlighted selectivity in diet among species. Further expansion of the concept of flexibility in habitat use within the context of spatial connectivity of a seascape will allow for a more comprehensive understanding of obligatory and opportunistic habitat use. Given our expanding understanding of the importance of non-reef habitats for coral reef fishes, seascape level analysis of fish-habitat patterns is more important than ever.

CHAPTER 6. GENERAL DISCUSSION

6.1 OVERVIEW

Ecological connectivity in marine systems is a central concept of ecosystem studies, conservation strategies, and spatial management design (Jones et al. 2009). However, seascape connectivity, which incorporates movement of post-settlement fishes across multiple habitats in a seascape, is understudied and often underrepresented in scientific studies of tropical systems, particularly studies of spatial management design (Sheaves 2009; Berkström et al. 2012a). One reason for this deficiency is the significant gap in our understanding of how species utilize multiple habitats, and the relative influence of different non-focal habitats compared to the focal habitat (in this case, coral reefs) on species distribution, abundance, and assemblage structure. This is especially true for tropical marine systems in the Indo-Pacific, and the Coral Triangle region, where research on this topic is noticeably lacking. My thesis addressed some of these deficiencies by exploring seascape ecology on the island of Siquijor in the Philippines, providing an important reference to compare and contrast results from other locations.

The research presented in this thesis broadens our understanding of how the surrounding seascape influences patterns of abundance of fish species observed on coral reefs (**Chapter 2 and 3**). Furthermore, these chapters include macroalgal beds, a habitat only recently being included and acknowledged in studies on ecological connectivity within tropical seascapes. In **Chapter 2,** I explored the relative influence of local scale coral reef and large scale seascape metrics in driving density and biomass of fishes on coral reefs. Wrasses, parrotfishes, and especially juveniles of these fish were more strongly influenced by the amount of other benthic habitats in the surrounding seascape. Specifically, the area of macroalgae within 500-m of a coral reef had positive effects on these species groups on coral reefs. The 500-m spatial scale was the most significant scale when relating seascape metrics to species density and biomass in my study system on Siquijor Island. I then examined how fish assemblages and diversity may vary, depending on the characteristics of the surrounding seascape (**Chapter 3**). I found that even on a small island like Siquijor, there were significant differences in coral reef fish assemblages and diversity, driven by the amount of non-reef habitats within 500-m of coral reef survey sites. I also identified that the density and presence of unique fish species was attributed to adjacent non-reef habitats even when observed on coral reefs (e.g., *Cheilio inermis* and *Scarus psittacus*). In **Chapter 4,** I sought to identify which coral reef fish species were using non-reef habitats as juveniles, and focused this chapter on the common and important taxon, parrotfishes. Using DNA analysis to confirm species identifications, I observed different species assemblages between adults and juveniles within the same habitat type, inferring ontogenetic habitat shifts. I also confirmed that many more parrotfish species are using multiple habitat types than previously identified, and highlighted the importance of macroalgal beds as potential nursery habitat in my study system. Finally, in **Chapter 5,** I used stable isotopes to explore habitat use, ontogenetic shifts, and whether habitat use was altered by habitat availability for two important coral reef taxa, parrotfishes, and rabbitfishes. Although Siquijor has a relatively subtle isoscape, I was able to demonstrate that isotopic signatures can be effective proxies of habitat use for fish. This validation then confirmed ontogenetic habitat shifts in the species *Scarus dimidiatus*. I also compared isotopic signatures of fishes between two reef sections that varied in the amount of available non-reef habitat nearby. Fish species and life stages using non-reef habitats showed variation in isotopic signatures, which suggested differences in habitat use between reef sections. These results allude to a potential in flexibility of habitat use based on habitat availability.

Combining the results from these four data chapters demonstrates a substantial impact of non-reef benthic habitats on structuring coral reef fish distribution, abundance, and species assemblages. My research further expands our knowledge of evaluating distribution patterns of fish species within a coastal ecosystem mosaic in the tropics, particularly within the data deficient location of the Coral Triangle region. In this concluding chapter I synthesize the results presented in my preceding data chapters and discuss the results in the context of the relevant literature.

6.2 RELATIVE INFLUENCE OF WITHIN REEF VS. SEASCAPE

Both the composition and configuration of habitats have the ability to alter species assemblages, distributions, and population dynamics (Grober-Dunsmore et al. 2008; Olds et al. 2012a). Fish relationships to habitat composition (i.e. coral cover, shoot density) generally manifests at small spatial scales (centimetres to meters), whereas habitat configuration (i.e. fragmentation, habitat area, spatial proximity) acts at larger spatial scales (10-1000s of meters). Inherent in studies that include both composition and configuration of habitats is the effect of spatial scale. Therefore, when assessing the relative influence of these two habitat categories, one must take a multi-scale approach. It is also necessary to be cautious of interpretations of these habitat categories, as differing responses of species related to spatial scale are usually the consequences of different ecological processes. For example, fish relationships to within-habitat composition (e.g. coral cover) is probably a fish's response to shelter or food. Whereas, habitat configuration across a seascape likely influences processes like migrations, and ontogenetic habitat shifts. In my analyses, overall, I found that fish density, biomass, and assemblage structure were responding to coral reef (within-habitat) variables first, and then secondarily, to seascape variables (Chapter 2 and 3).

There are two simple, yet major considerations when discussing the results of my thesis. Because my work focused on the relative effects of coral reef and non-reef habitats on fishes, we must presume that: 1. Coral reef habitat is present, and 2. Non-reef habitats (seagrass, mangrove, and macroalgal beds) are present. First, there is a hierarchical control, where the presence of the fish evaluated in this thesis are dictated primarily by the presence of coral reef habitat, and then the nuanced results of populations and assemblages observed here are in response to the characteristics of the other non-reef habitats in the seascape. In short, coral reefs must be present for coral reef fish. As seen in both Chapters 2 and 3, the primary driver of fish patterns was benthic characteristics of coral reef at the transect scale. In Chapter 2, coral reef variables were chosen more often than seascape variables in top models. In Chapter 3, species assemblages were first split by coral reef characteristics (coral vs rubble) and then, within those groupings, seascape metrics contributed to the variability observed in fish patterns. The relative importance of within habitat and surrounding seascape metrics is often dictated by the seascape structure (habitat composition and spatial configuration). Other results have observed this hierarchical effect, where species distributions and habitat functions were first controlled by habitat configuration. For example, environmental controls (salinity) defined species distributions in a tropical estuary, where snapper presence was first determined by estuarine or marine waters, and then within those groupings, by within-habitat structural complexity (Baker et al. 2019). Configuration can also change a habitats function, whereby nursery function was altered for the same habitat type (mangroves) depending on its location (estuarine vs marine) (Bradley et al. 2019), or whether there was strong tidal flux (Igulu et al. 2014). While seascape configuration can be the primary driver structuring species assemblages (Grober-Dunsmore et al. 2008; Pittman and Brown 2011; Olds et al. 2012a), the context of the seascape must be taken into consideration when interpreting results. Spatial, tidal, temporal, and environmental factors can determine the order of control between the broader seascape and the local within habitat characteristics. In my study system, there were no strong environmental effects, and I found that coral reef habitat was the first determining factor driving my results.

Secondly, the thesis operated under the premise that seagrass, macroalgal and mangrove habitats are near coral reefs. The reef system on Siquijor Island is a highly connected seascape, where multiple habitats are in very close proximity to each other. This provided me with the greatest potential to observe non-reef habitat effects on coral reef fish. Clearly, this is not the case for all coral reefs globally, some of which are nowhere near these types of non-reef habitats (e.g., outer reefs of the Great Barrier Reef, GBR, Australia). However, all coral reefs are surrounded by some other type of benthic habitat, such as inter-reefal soft substrata, deep rubble beds, and sand. While these habitats are not directly comparable, they could be analogues to the non-reef benthic habitats I observed on

Siquijor. For example, deep water soft substrata habitat in the GBR could be spawning sites, juvenile habitat, and essential habitat for important fishery species, such as Lutjanids and Lethrinids (Williams and Russ 1994; Cappo et al. 2004; Currey et al. 2009). Across the GBR seascape, seascape connectivity is operating at much larger spatial scales (inter-reefal and inter-island), and would require an altered approach to the study of fish-habitat relationships that was adopted in this thesis. Deep water reefs, often dominated by rubble and deep water sponges, have gained increasing attention as potential refuges for shallow water fish species from storm damage and climactic threats (Abesamis et al. 2018), but also harbor unique assemblages distinctly separate from shallow water systems (Rocha et al. 2018). While direct comparisons cannot necessarily be extrapolated from my thesis to other habitat types, generalizations about coral reefs interacting with other adjacent habitats in a seascape can be made.

6.3 IMPORTANT BENTHIC HABITATS

I found macroalgal beds to be the most important non-reef habitat for coral reef fishes on Siquijor Island. Macroalgal beds are increasingly recognised as important habitat in tropical seascapes, and as potential nursery habitats for many coral reef fishes (Fulton et al. 2019, 2020). While there has been an increase in publications concerning tropical macroalgae (Fulton et al. 2020), when considering their nursery value, research on macroalgal beds lags significantly behind studies of other non-reef habitats (Lefcheck et al. 2019). In my system, I hypothesize that macroalgal beds are the influential non-reef benthic habitat for two reasons. 1. Greater structural complexity compared to seagrass habitat, and 2. Tidal influence which renders mangrove habitat less important for fishes on Siquijor reefs. Macroalgal beds can often have greater amounts of epiphytes and epifauna on macroalgal fronds compared to seagrass beds (Tano et al. 2016). These epibionts are important food sources for many juvenile fishes (Bellwood 1988; Feitosa and Ferreira 2014). Additionally, on Siquijor, and in the Indo-Pacific generally, mangrove habitats are used less by fishes, and specifically juveniles, because of the strong tidal amplitude, leaving habitats like mangroves exposed and inaccessible to fishes during low tide (Unsworth et al. 2007; Igulu et al. 2014). Therefore, on Siquijor, macroalgal beds seems to provide the resources and accessibility needed to operate as important nursery habitat for coral reef fishes. However, quantifying true nursery function of macroalgal habitat was not conducted in this thesis, and should be the basis of future work to support the above statements. I also found that less common habitats revealed important patterns observed in coral reef fishes. In Chapter 4, the juvenile parrotfish species that was collected most in non-reef habitats was *Scarus psittacus*, a species that had zero observations as adults in any habitat (coral reef, seagrass, macroalgae). This is probably due to the affinity of this species to back reef areas that consist of patchy coral with sand and rubble. This result was corroborated by my third chapter, where *Scarus psittacus* was observed as a species uniquely attributed to locations with greater amounts of back reef habitat adjacent to coral reef. While back reefs are acknowledged as important habitat (Adams and Ebersole 2002; Bellwood et al. 2018), they can often be overlooked when examining coral reef fish-habitat relationships. Furthermore, the definition of backreef habitat is quite varied, often classified as mixed coral/seagrass areas in other studies (Berkström et al. 2013b). In the Philippines, *Scarus psittacus* is a common fishery species (Russ et al. 2015b), and by omitting less prominent habitats, like the reef flat, it can lead to missing information about important fishery species. In Chapter 2, I identified that the area of sand within 500-m of coral reefs had strong effects on fish density and biomass on reefs. I hypothesized that areas of sand created a concentration effect, which condensed and retained fishes in suitable habitat. Quite often, sand is excluded from research on tropical habitats, and is even actively avoided in such studies. Perhaps we are underrepresenting the full extent of species distributions and assemblage structures when only focusing studies on coral reef habitat (e.g. crest and slope), and omitting adjacent non-reef habitats. By incorporating multiple habitats across a seascape it allows for better examinations of species abundance patterns, and less prominent habitats such as sand habitat should at least be considered in future studies.

6.4 MARINE RESERVE AND CONNECTIVITY EFFECTS

Interestingly, I did not find any measurable no-take marine reserve (NTMR) effect on coral reef fish abundance or assemblage structure in my analyses. While NTMRs were included in both Chapter 2 and 3, no clear reserve effect was detected. In chapter 2, NTMR status was selected only once across all 32 models, for Acanthurids (surgeonfishes). This species group is moderately fished in the Philippines, and is strongly influenced by coral reef benthic variables (Chapter 2, Russ et al. 2018), rather than by the surrounding seascape. Acanthurids have been shown to have NTMR effects in the Philippines before (McClure et al. 2020a), but such effects were only detected when island type and disturbance level was accounted for (McClure et al. 2020b). Again, we observe an element of hierarchical control, where more nuanced effects, for example NTMRs, can only be identified when controlling for the upper level effects (benthic cover). Protection from fishing may also have both direct (reducing damage of fishing gear on habitat) and indirect (increase of browsers controlling macroalgal-live coral competition) on benthic cover, which is not necessarily detected when comparing overall fish abundance and biomass between sites with and without NTMRs. Recently, 31 years of data were synthesised, evaluating the relative top down (fishing) versus bottom up (benthos) effects on fish biomass at two small islands in the Philippines very near to Siquijor Island. Only two trophic groups, generalist large predators and large planktivores, displayed significant NTMR effects (Russ et al. 2021), whereas benthic cover affected the biomass of 11 of the 13 trophic groups assessed. Due to the inclusion of so many types of benthic cover variables (within coral reef and surrounding habitat), it is not surprising that I did not observe significant NTMR effects. Nonetheless, this does not negate the importance of NTMRs to coral reef fish. Both McClure et al. (2020a) and Russ et al. (2021) did find some NTMR effects, and interestingly, McClure et al. (2020a) identified that NTMRs as small as 15 hectares can enhance density and biomass of targeted reef fish. Small reserves can be effective in increasing abundance of target species (Lester et al. 2009), and the Philippines has thousands of NTMRs (Horigue et al. 2012; Cabral et al. 2014). Yet, these reserves protect only 2.7-3.4% of coral reefs in the Philippines (Weeks et al. 2010), and there is a significant effort to increase this percentage in the country. With so many small reserves, connectivity among reserves, driven by larval transport has been demonstrated in this region (Abesamis et al. 2017), which has helped strengthen stakeholder engagement in NTMR establishment and management. It is now important to consider representative area management, by additionally protecting non-reef habitats adjacent to coral reefs. Inclusion of non-reef habitats in NTMR networks accounts for movement of fish beyond coral reef boundaries (Weeks et al. 2017), incorporates seascape connectivity (Engelhard et al. 2017; Weeks 2017), and provides more effective management outcomes for target fishes (Olds et al. 2016).

6.5 REFLECTIONS AND IMPROVEMENTS

When reflecting on the four year journey of this thesis, I have had ample time to consider improvements, additions, and extensions to the research. In my opinion, Chapters 4 and 5 have the greatest potential for improvement, and could have been enhanced by a few simple alterations. Specifically, Chapter 4 could have been improved if I had also collected juvenile parrotfishes from coral reef habitat. This would have provided a more balanced comparison among the different habitat types. Secondly, conducting a more standardized sampling effort across all benthic habitats, rather than opportunistic collections for juveniles within the various non-reef habitats, would have allowed for a better quantitative analysis to compare relative densities. Had I created an even sampling effort across habitats, I believe that the chapter would have been more robust. Finally, DNA analysis and species identification was a challenge due to the inconsistencies in publicly uploaded DNA sequences which sometimes came from fish that were incorrectly identified. Fin clips of adult voucher species collected from local fish markets would have resulted in more reliable species identifications.

In Chapter 5, stable isotope analysis comes with many caveats which limit interpretations. Again, improved field sampling techniques would have alleviated some of the issues inherent to this method. If possible, I would have developed a rigorous sampling design of species across habitats and life stages. Not all species were collected in all habitats, not all life stages were collected, and such collections were not always made from both reef sections. This limited my analysis, and consequently the interpretability of the results. However, collections were very much limited by what fishers caught, and was hindered by the availability of fish and the fishing effort during that time. Furthermore, I should have collected source samples (algae etc.) from all habitats. Stable isotope analysis is quite restrictive in the number of sources that you can add as potential diet for fishes. However, it would have been beneficial to explore in greater depth the variability of dietary sources such as turf, EAM (epilithic algal matrix), detritus, and *Sargassum* across all habitats. This would have allowed for stronger interpretation of the results, providing the ability to more confidently determine whether results were responses to diet or to habitat.

6.6 FUTURE DIRECTIONS

There are many research ideas that have arisen from my thesis. I am most interested in targeted research to disentangle the relationships between context, composition, and configuration of habitats with relation to fish patterns. Listed below are project ideas that would be fruitful avenues for future research.

1. Compare results here with a less connected tropical seascape. Siquijor is a highly connected seascape, and not necessarily representative of seascapes in the Philippines or coral reefs elsewhere. Conducting similar research in other locations in the Philippines, or other less connected seascape (e.g. GBR), would allow me to understand whether the spatial relationships observed in this thesis hold true for other locations.
2. Nursery habitat. To define appropriately any of the non-reef habitats as nurseries, I would need to quantify whether the juveniles in non-reef habitats are contributing to adult populations by supplying a greater than average number of individuals to the total population on coral reefs. This would require visual surveys, population modelling, and some tracking or tagging data.
3. Larval settlement and juvenile habitat use in non-reef habitat. Relatively little is known about recruitment of fishes, and the habitat-use patterns of juvenile fishes, to non-reef habitats. This project would conduct settlement and recruitment surveys in non-reef habitats, and explore how fishes use non-reef habitats as juveniles. This would likely be a combination of surveys, benthic habitat analysis, recruitment surveys, predation experiments, and assessment of the condition of juveniles in different habitat types. Through this, one could also explore the obligatory versus opportunistic use of non-reef habitats by juveniles.
4. Spatial mismatch between larval and adult connectivity. This would inform spatial management design. Sometimes reef fish larvae can settle back on to the same reef in the same location (Jones et al. 1999; Harrison et al. 2012). This would mean that larval dispersal can, at times, occur at smaller spatial scales than adult movement. Other times, larvae are transported tens to hundreds of kilometres (Williamson et al. 2016; Abesamis et al. 2017), meaning that larval connectivity is at

a much greater spatial scale than adult connectivity. Larval population models overlaying networks of NTMRs have already been developed for this region in the Philippines, and this project could incorporate the seascape connectivity of both adult and juvenile fishes across multiple benthic habitats. This would allow for multi-scale hierarchical connectivity models to be developed.

5. No-take marine reserve (NTMR) placement. Using some of the data presented in potential projects above, this project would explore where to place NTMRs in non-reef habitats in the southern Philippines. This research would require data on fishing effort and local landings as well as fish distribution and population data, to identify priority conservation areas. Collaborations with local managers would be essential for this project to be successful.
6. Movement of fishes. The implicit assumption behind much of this research is that fishes move across habitat boundaries. However, survey data can only infer these movements. Using tags (telemetry, natural, genetic, external, or pit tags) to track movement of individuals would substantially improve our ability to confidently interpret connectivity results. Telemetry and external tags would be the most beneficial to quantify movements of adult fishes. Ontogenetic shifts would likely need to be measured by using parentage analysis and other types of genetic tags (e.g. SNPs) due to the small size of juveniles.
7. Coral reef effects on non-reef habitats. This thesis explored the non-reef habitat effects on coral reefs. Now, I think it is necessary to explore coral reef effects on non-reef habitats. The approach would be similar to this thesis, and would incorporate benthic composition (e.g., shoot density) and seascape configuration (e.g., distance to coral reef) to understand how fish populations and assemblages in non-reef habitats are altered by adjacent coral reefs.

6.7 CONCLUDING REMARKS

Finally, I want to summarise the most salient points that arose from this thesis. Firstly, coral reef fishes often use other benthic habitats. It is imperative that we begin to account for the surrounding seascape when exploring species-habitat relationships. This is now possible with remote sensing resources and spatial analysis software becoming readily available, easily accessible, and often free to researchers. Secondly, Siquijor is a highly connected seascape and results from here should be interpreted cautiously when comparing to other seascapes. Lastly, it is now more important than ever to include representative protection in spatial management practices (e.g. networks of NTMRs). Not only does it more wholly protect species, but in a changing environment with compounding environmental and anthropogenic stressors, it is essential to preserve habitats that interact and integrate with one another. Ultimately, this thesis is an argument to consider the context of the seascape, the species or species assemblages in question, and the processes being explored, to extract the most relevant results and appropriately protect our natural resources.

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SUPPLEMENTAL

APPENDIX A – SUPPORTING INFORMATION FOR CHAPTER 2

Table S.2.1 Wilcoxon rank sum tests for variables > 10% relative influence comparing the values between habitat categories (Local reef vs Adjacent Habitat) for each grouping. Bold and * indicates significant difference.

Comparison Grouping	W	p value
Overall	2306	0.248
Crest	531	0.232
Slope	613	0.743
Adult	1487	0.950
Juvenile	**78**	**0.022***
Biomass	240	0.711
Density	793	0.144
Presence	14	0.421
Surgeonfishes	**11**	**0.011***
Butterflyfishes	40	0.397
Chlorurus	68	0.628
Wrasses	**104**	**0.008***
Wrasse juvenile	9	0.377
Wrasse adult	**42**	**0.050***
Snappers	0	0.242
Damselfishes	12	1.000
Scarus	96	0.158
Groupers	7	0.860

Table S.2.2. Summary of radii selection for adjacent habitat variables. Values reported are only for influential variables with a relative importance >10% in final BRT models.

Radius	**Macroalgae**	**Mangrove**	**Seagrass**	**Reef Flat**	**Sand**	**Total**
250	0	0	0	1	1	2
500	4	8	0	1	6	19
1000	1	0	6	0	1	8
Total	5	8	6	2	8	29

Table S.2.3. Model output from bootstrapped boosted regression trees for each response variable, showing the mean relative importance for each variable in order of importance, and the 95% lower and upper confidence intervals for relative importance in parentheses. Variables with Dist_ (Distance) or with a value (250, 500, 1000) represent Adjacent Habitat variables calculated at the seascape scale. Variables with (L) are Local Reef scale variables measured on coral reef transects. Bolded values are mean relative importance values greater than 10%, representing high importance variables. MA = macroalgae, SG = seagrass, RF = reef flat, MG = mangrove, Res size = reserve size, Rub = Rubble, SC (L) = soft coral, SC = structural complexity, HC = hard coral, Rob C = robust coral, Frag C = fragile coral, EAM = epilithic algal matrix. For reef fish groups, Acanth = Acanthuridae (Surgeonfishes), Chaet = Chaetodontidae (Butterflyfishes), Serr = Serranidae (Groupers), Pom = Pomacentridae (Damselfishes), Lutj = Lutjanidae (Snapper). *Scarus* and *Chlorurus* are genera from the parrotfish family. Models were run for adults and juveniles (Juv), for density (Den), biomass (Bio), and presence (P/A).

Model	Species	Stage	Metric	Level	1	2	3	4	5	6	7	8	9	10
1	Acanth	Adult	Bio	Crest	**Depth** **16.4** (6.6, 32.1)	**Sand (L)** **15.7** (3.9, 30.9)	**Res size** **13.9** (1.8, 33.5)	**SG1000** **12.0** (3.5, 23.2)	**Dist.Shore** **10.6** (2.7, 22.9)	MA (L) 9.1 (1.2, 17.9)	Dist_MA 8.9 (1.9, 20.1)	Dist_MG 6.6 (1.5, 18.3)	MG500 4.5 (0.5, 14.6)	Status 2.3 (0.1, 5.9)
2	Acanth	Adult	Bio	Slope	**SC (L)** **16.9** (0.8, 38.1)	**Frag_C (L)** **16.1** (3.5, 38)	**MA500** **13.3** (1.3, 39.3)	**SG1000** **12.7** (2.4, 34.7)	**Dist_SG** **10.7** (1.5, 23.7)	**Rub (L)** **10.6** (0.6, 23.3)	Sand500 8.9 (1.6, 23)	Res size 6.6 (0.2, 28.9)	MG500 3.8 (0.3, 12.9)	Status 0.4 (0, 1)
3	Acanth	Adult	Abund	Crest	**Depth** **16.0** (2.8, 43.3)	**Res size** **15.6** (4.4, 34.5)	**Sand (L)** **13.0** (2.7, 32.8)	**Dist_MG** **12.3** (1.2, 36.3)	SG1000 9.6 (2.1, 24.8)	MA (L) 8.9 (3, 18.2)	MG500 8.8 (1.3, 29)	Rub (L) 7.9 (1.7, 26.2)	Dist.Shore 6.3 (1.6, 14.5)	Status 1.6 (0.4, 4.3)
4	Acanth	Adult	Abund	Slope	**Frag_C (L)** **16.3** (3.2, 36.4)	**Sand500** **15.5** (2.6, 34.9)	**SG1000** **14.9** (1.7, 36.9)	**Dist_MG** **11.0** (1.9, 29.1)	**Dist_SG** **10.6** (1.4, 25.7)	MA (L) 9.4 (0.7, 23.5)	Res size 7.8 (0.5, 37.4)	Sand (L) 7.8 (0.4, 27.3)	SC (L) 6.3 (1, 19.5)	Status 0.4 (0, 2)
5	Chaet	Adult	Bio	Crest	**MG500** **23.6** (2.1, 55.7)	**Depth** **22.1** (3.1, 54.9)	**MA500** **18.9** (2.1, 54.4)	HC (L) 7.6 (1.3, 18.8)	Sand500 7.1 (1, 24.8)	EAM (L) 6.9 (1.4, 18.1)	Sand (L) 4.7 (0.7, 10.4)	Res size 4.7 (0.2, 14)	Dist_SG 4.3 (0.5, 16.6)	Status 0.2 (0, 0.7)
6	Chaet	Adult	Bio	Slope	**Depth** **18.9** (1.1, 46.7)	**Dist_MG** **15.7** (2.2, 48.8)	**Rub (L)** **12.9** (1.7, 30.7)	Frag_C (L) 10.0 (1.1, 25)	Sand500 9.7 (0.7, 30.5)	MG500 9.4 (0.6, 36.2)	CR250 7.8 (1.2, 25.1)	Dist_SG 7.1 (0.7, 21.2)	Sand (L) 6.8 (0.9, 19.4)	Status 1.6 (0.1, 6.9)

7	Chaet	Adult	Abund	Crest	**Depth** **24.6** (3.4, 62.6)	**MG500** **23.3** (5.3, 55.9)	**MA500** **18.1** (1.3, 61.2)	Sand (L) 9.4 (1.2, 24.4)	Dist_SG 5.8 (0.5, 24.5)	HC (L) 5.8 (1.1, 17.2)	Sand500 4.9 (0.9, 20.9)	EAM (L) 4.3 (0.6, 11.7)	Res size 3.5 (0.3, 9.5)	Status 0.2 (0, 0.8)
8	Chaet	Adult	Abund	Slope	**MG500** **20.1** (1.8, 56.9)	**Sand500** **15.8** (1.6, 45.2)	**Dist_MG** **15.7** (2.6, 41.7)	**Rub (L)** **11.4** (2.3, 36.4)	**SG1000** **10.7** (1.7, 24.4)	**Depth** **10.3** (0.9, 22.7)	Frag_C (L) 6.2 (0.7, 16.8)	Sand (L) 5.0 (1.3, 11.2)	Dist_SG 3.7 (0.3, 10.1)	Status 1.3 (0.1, 3.9)
9	*Scarus*	Adult	Bio	Crest	**MA (L)** **17.0** (5.8, 28.5)	**MG500** **14.2** (2.5, 42.7)	**Depth** **13.9** (3.9, 32)	**Rub (L)** **13.5** (3, 33)	**HC (L)** **10.7** (3.8, 26.1)	Sand (L) **10.7** (3, 27.9)	SC (L) 9.2 (2.5, 18.7)	MA1000 4.6 (0.8, 16.8)	SC 3.8 (0.1, 12.7)	Status 2.4 (0.2, 8.9)
10	*Scarus*	Adult	Bio	Slope	**Rob_C (L)** **22.1** (6.3, 43.8)	**Dist_SG** **15.6** (3.6, 41.8)	**MA (L)** **13.7** (2.9, 28.6)	**Sand (L)** **11.3** (2.8, 22.9)	**Rub (L)** **11.0** (2.7, 34.9)	SG250 8.0 (1.3, 25.3)	MA250 6.6 (1.2, 18)	Dist.Shore 5.8 (0.9, 17)	RF500 4.4 (0.6, 15.5)	Status 1.6 (0.1, 8.3)
11	*Scarus*	Adult	Abund	Crest	**MA (L)** **17.1** (7.2, 33.3)	**MG500** **15.5** (2, 42.8)	**Depth** **14.6** (4.7, 30.3)	**Sand (L)** **10.6** (2.8, 21.7)	**HC (L)** **10.5** (4.6, 26.5)	MA1000 8.9 (1.1, 30.5)	Dist_SG 7.7 (1.8, 20.5)	Sand500 7.2 (1.9, 17.1)	SC 5.7 (0.2, 19.5)	Status 2.0 (0.2, 8.4)
12	*Scarus*	Adult	Abund	Slope	**EAM (L)** **15.0** (6.5, 30.9)	**Dist_SG** **13.7** (3, 33.4)	**MA (L)** **13.6** (3.1, 24.3)	**Frag_C (L)** **12.6** (5.2, 24.8)	**RF250** **11.1** (3.6, 21.8)	SC (L) 9.0 (2.3, 21.5)	Sand (L) 8.3 (3.5, 19.8)	Sand500 7.9 (2, 22)	Dist.Shore 6.9 (1.6, 16.2)	Status 1.9 (0.1, 5.6)
13	*Scarus*	Juv	Abund	Crest	**Frag_C (L)** **41.8** (11.3, 76.9)	**Dist_MG** **23.5** (1.6, 56.7)	Depth 7.6 (1.4, 24.5)	SG1000 6.2 (0.5, 29.1)	Sand (L) 5.1 (0.8, 21.1)	SC (L) 4.7 (0.9, 10.1)	Sand500 4.7 (0.5, 18.8)	MG500 3.0 (0.2, 12.3)	Dist_MA 2.6 (0.3, 7.3)	Status 0.6 (0, 2.3)
14	*Scarus*	Juv	Abund	Slope	**Frag_C (L)** **26.4** (7.8, 58.7)	**Sand500** **20.4** (5.1, 51.5)	**MA (L)** **12.4** (3.1, 26)	**Sand (L)** **10.2** (3.4, 22.8)	Dist_MG 7.9 (0.6, 27.3)	Depth 7.8 (0.5, 22.7)	EAM (L) 7.1 (1.4, 19.1)	SG1000 4.7 (1.2, 16)	MG500 1.6 (0.1, 5.6)	Status 1.5 (0.1, 7.4)
15	*Chlorurus*	Adult	Bio	Crest	**Frag_C (L)** **26.0** (10.1, 47.7)	**Dist_SG** **14.7** (1.5, 52.5)	**MA (L)** **12.7** (2.2, 28.8)	**MG500** **10.4** (1.8, 29.9)	Res size 9.5 (1, 23.9)	Sand500 8.5 (1.7, 19.3)	SC 6.6 (0.2, 22.7)	SG1000 6.5 (1.1, 19.1)	Dist_MG 4.6 (0.6, 11.5)	Status 0.5 (0, 1.7)
16	*Chlorurus*	Adult	Bio	Slope	**Rob_C (L)** **24.5** (9.1, 45.2)	**Sand (L)** **19.1** (4.5, 37.4)	**Rub (L)** **11.1** (2.6, 20.3)	**Sand500** 9.6 (2.4, 22.3)	SG1000 9.2 (2.1, 28.6)	MA (L) 8.8 (2.2, 21.5)	MG500 6.8 (1.4, 16)	SC 5.2 (0.9, 16.6)	Res size 5.1 (0.4, 18.5)	Status 0.6 (0, 2.8)

17	*Chlorurus*	Adult	Abund	Crest	**Frag_C (L)** **20.0** (4.3, 52.5)	**SG1000** **16.8** (1.9, 49.2)	**Dist_SG** **16.8** (1.7, 41.3)	**MA (L)** **13.7** (3, 27.2)	Depth **12.5** (2.1, 30.2)	MG500 5.8 (0.4, 20.3)	Res size 5.1 (0.4, 13.7)	SC 5.0 (0.1, 20.6)	Dist_MG 3.9 (0.7, 15.8)	Status 0.4 (0, 1.5)
18	*Chlorurus*	Adult	Abund	Slope	**Sand (L)** **17.1** (5, 33.5)	**Rob_C (L)** **17.0** (5.4, 32.6)	**MA (L)** **15.6** (2.5, 44.1)	**Sand500** **14.3** (2.1, 39.5)	SG500 9.7 (1.8, 27.4)	Dist_MG 8.4 (1.4, 21.9)	Dist.Shore 5.6 (1.9, 13)	SC 5.6 (0.6, 14.8)	RF250 4.9 (1.6, 12.6)	Status 1.8 (0.1, 8.7)
19	*Chlorurus*	Juv	Abund	Crest	**Sand500** **31.2** (2.6, 68.8)	**Sand (L)** **17.4** (2.9, 48.2)	**Frag_C (L)** **10.1** (1.1, 36.5)	**SC (L)** **8.5** (1.2, 22.3)	Res size 7.0 (0.4, 24.9)	SG500 6.4 (0.9, 14.8)	Dist_MA 6.1 (0.7, 21.6)	MG1000 5.3 (0.3, 23.4)	Dist_MG 4.8 (0.1, 14.8)	Status 3.2 (0.1, 14.1)
20	*Chlorurus*	Juv	Abund	Slope	**Sand1000** **22.6** (0.3, 77.7)	**Dist_SG** **22.3** (0.8, 74.2)	**Sand (L)** **19.8** (0.2, 62)	**Rub (L)** **11.3** (0.1, 39.5)	Depth 8.4 (0.3, 49)	MG1000 4.0 (0.1, 25.8)	Dist.Shore 3.9 (0.1, 18.1)	Dist_MG 3.0 (0.1, 21.6)	Dist_MA 2.9 (0.1, 17.9)	Status 1.7 (0, 12.5)
21	Labridae	Adult	Bio	Crest	**MA500** **20.8** (5.2, 44.6)	**Depth** **14.6** (4, 32.6)	**EAM (L)** **13.6** (3, 30.9)	**HC (L)** **12.1** (1.7, 34.1)	**Sand (L)** **11.9** (2, 40.5)	RF250 9.4 (1.3, 26.3)	Dist_MA 7.5 (1.2, 20)	SG1000 4.9 (0.6, 13.6)	SC 3.5 (0, 15.7)	Status 1.7 (0.1, 6.9)
22	Labridae	Adult	Bio	Slope	**Sand250** **16.2** (2.6, 39.1)	**Depth** **15.2** (3.8, 33.9)	**EAM (L)** **10.9** (2.2, 20.8)	**MA (L)** **10.7** (3.7, 21.6)	**Rob_C (L)** **10.5** (2.8, 25.5)	**Sand (L)** **10.2** (2.9, 22.1)	RF250 9.5 (2.3, 25.5)	Dist.Shore 8.2 (2.3, 19)	SC (L) 6.9 (1.4, 18.2)	Status 1.7 (0.2, 4.9)
23	Labridae	Adult	Abund	Crest	**Dist_MG** **24.4** (3.2, 56.6)	**HC (L)** **19.9** (3.1, 48.3)	**Depth** **18.7** (1.9, 39.1)	**EAM (L)** **12.4** (3.3, 29.5)	Sand (L) 10.0 (1.2, 29.9)	SG1000 4.9 (0.5, 14)	Dist_MA 3.6 (0.5, 10)	Sand250 2.9 (0.4, 10.1)	MG500 1.8 (0.1, 9)	Status 1.4 (0.1, 4.6)
24	Labridae	Adult	Abund	Slope	**HC (L)** **24.8** (7.6, 47.1)	**Sand (L)** **18.6** (6.5, 43.4)	**Depth** **13.8** (4.5, 34.6)	EAM (L) 8.9 (2.3, 16.9)	MA (L) 7.7 (1.7, 18)	SC (L) 7.4 (1.7, 12.7)	SG1000 6.5 (2, 13.3)	RF250 5.8 (1.3, 16.1)	Sand500 5.3 (0.7, 14.3)	Status 1.3 (0.1, 5.3)
25	Labridae	Juv	Abund	Crest	**Sand500** **28.1** (6.1, 55)	**Frag_C (L)** **18.4** (2, 48.7)	**SG1000** **13.8** (1.9, 36.7)	**Sand (L)** **12.8** (3.6, 30.7)	MA (L) 6.4 (1.4, 17.7)	Rub (L) 6.1 (1.4, 14.3)	Dist_SG 4.8 (1, 12.3)	SC 4.2 (0.1, 11.3)	MA500 2.7 (0.7, 6.4)	Status 2.6 (0.6, 8.5)
26	Labridae	Juv	Abund	Slope	**MA1000** **26.6** (7.5, 45.6)	**Sand (L)** **16.1** (4.6, 36)	**MA (L)** **14.0** (2.6, 37.8)	Dist_SG 9.8 (2, 29.9)	Frag_C (L) 9.4 (2.6, 18.1)	Rub (L) 8.0 (1.9, 19.2)	Dist.Shore 5.7 (0.9, 14.4)	Sand250 5.2 (1.8, 11)	SG500 4.4 (0.7, 21.6)	Status 0.7 (0.1, 2)

27	Pom	Adult	Abund	Crest	**Depth**	**Frag_C (L)**	**EAM (L)**	**Dist.Shore**	MA (L)	CR250	MA250	Sand250	Dist_MA	Status
					35.4	**14.2**	**12.0**	**10.2**	8.6	6.0	5.9	3.8	2.9	1.0
					(11.4, 61.4)	(4.2, 34.2)	(2.3, 26.2)	(2.4, 22.1)	(1.4, 22.6)	(1.1, 16.6)	(1.5, 15.3)	(0.4, 8.5)	(0.5, 8.2)	(0.1, 4.5)
28	Pom	Adult	Abund	Slope	**Dist_MG**	**Dist_SG**	**Rub (L)**	**Depth**	**Dist.Shore**	**MA (L)**	CR250	Res size	MG500	Status
					18.4	**17.7**	**14.7**	**13.8**	**13.5**	**11.5**	4.7	3.0	2.1	0.6
					(2.4, 41.9)	(1.6, 47.6)	(4.7, 32.3)	(3.4, 42.3)	(1.3, 56.1)	(1.8, 28.2)	(0.7, 16.3)	(0.2, 10.3)	(0.2, 10.1)	(0, 2.4)
29	Lutj	Adult	P/A	Crest	**Sand (L)**	**Frag_C (L)**	**Dist.Shore**	MA1000	RF250	Sand250	SC	SG500	Res size	Status
					25.0	**20.9**	**12.0**	8.1	7.8	7.4	7.2	6.7	4.7	0.3
					(4.8, 64.2)	(2.9, 55)	(1.9, 41.3)	(1.6, 19.9)	(1, 24.2)	(1.2, 22.7)	(0, 29.5)	(0.9, 17)	(1, 12.4)	(0, 1.5)
30	Lutj	Adult	P/A	Slope	**SC (L)**	**Rub (L)**	**Sand (L)**	Frag_C (L)	CR500	Depth	MA (L)	Dist.Shore	RF1000	Status
					21.4	**20.3**	**19.4**	8.4	7.7	7.2	5.9	3.9	3.8	1.9
					(4.5, 53.8)	(3.5, 44.2)	(3.5, 38.2)	(1, 31.4)	(1.3, 23.2)	(1.8, 18.5)	(1.4, 15)	(0.5, 14.6)	(0.3, 13)	(0.2, 5.9)
31	Serr	Adult	P/A	Crest	**Dist_SG**	**MG500**	**HC (L)**	Res size	SC (L)	SG250	Dist.Shore	RF500	Dist_MG	Status
					32.4	**19.7**	**11.6**	8.3	7.2	6.4	5.5	4.9	3.2	0.7
					(4.5, 64.2)	(3.1, 46.8)	(1.8, 25.7)	(0.6, 30.1)	(1.1, 16.9)	(0.8, 23.2)	(0.7, 14.2)	(0.7, 14.9)	(0.4, 9.2)	(0, 2.8)
32	Serr	Adult	P/A	Slope	**MA (L)**	**EAM (L)**	**RF500**	**MG500**	Res size	SG250	Sand250	SC	Dist_MG	Status
					22.1	**15.1**	**12.9**	**12.0**	9.5	9.4	6.6	5.9	5.4	1.2
					(7.9, 42.9)	(3.5, 35.4)	(1, 38.8)	(2.7, 29.4)	(0.9, 21.8)	(1.7, 25.4)	(1.1, 17.5)	(0.1, 18.3)	(0.9, 18.7)	(0.1, 4.1)

APPENDIX B – SUPPORTING INFORMATION FOR CHAPTER 3

Table. S.3.1. Full fish species list from survey transects on coral reef crest and slope habitat. Values are averaged per site on Siquijor Island, and represent average density, and average biomass in brackets per 1000 m^2.

Family	Genus species	Bino-ongan	Maite	Nonoc	Olang	Paliton	Sandugan	Tubod	Tulapos
Acanthuridae									
	Acanthurus mata	12(0.49)	17.7(0.74)	0(0)	28(0.99)	0(0)	5.3(0.18)	6(1.17)	6.4(0.15)
	Acanthurus nigricans	0(0)	4(0.05)	0(0)	0(0)	0(0)	0(0)	0(0)	4(0.11)
	Acanthurus nigricauda	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	4(0.32)	0(0)
	Acanthurus nigrofuscus	8(0.14)	0(0)	0(0)	5.3(0.09)	0(0)	0(0)	0(0)	5.3(0.1)
	Acanthurus pyroferus	0(0)	4(0.06)	0(0)	4(0.19)	4(0.1)	4.5(0.26)	5.3(0.1)	4(0.21)
	Acanthurus sp.	0(0)	0(0)	4(0.21)	0(0)	0(0)	0(0)	0(0)	0(0)
	Acanthurus thompsoni	0(0)	4(0.16)	0(0)	0(0)	4(0.1)	0(0)	4(0.21)	0(0)
	Acanthurus triostegus	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	4(0.08)	0(0)
	Ctenochaetus binotatus	5.4(0.1)	7.3(0.1)	8(0.13)	5.9(0.11)	4(0.07)	4.6(0.07)	7.1(0.11)	4(0.06)
	Ctenochaetus cyanocheilus	0(0)	10(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
	Ctenochaetus sp.	12(0.02)	0(0)	0(0)	0(0)	0(0)	0(0)	16.2(0.08)	0(0)
	Ctenochaetus striatus	4.9(0.17)	8.6(0.2)	4.9(0.14)	5.9(0.2)	6.2(0.17)	4.9(0.16)	9.1(0.2)	6.1(0.17)
	Ctenochaetus tominiensis	0(0)	8.1(0.06)	4(0.02)	5.5(0.07)	5.7(0.09)	4(0.03)	8(0.09)	0(0)
	Naso brevirostris	0(0)	11(0.18)	8(0.23)	0(0)	4(0.08)	0(0)	10.7(0.27)	0(0)
	Naso hexacanthus	9.3(0.23)	18.9(0.31)	0(0)	0(0)	18(0.45)	16(0.3)	12(0.59)	4(0.12)
	Naso lituratus	4(0.24)	5.8(0.15)	0(0)	4(0.34)	4(0.25)	0(0)	6.3(0.3)	4(0.21)
	Naso minor	0(0)	166(7.34)	4(0.18)	28(0.7)	14(0.56)	146.7(5.9)	0(0)	0(0)
	Naso sp.	0(0)	4(0.38)	0(0)	0(0)	0(0)	0(0)	35(7.44)	0(0)
	Naso unicornis	4(0.27)	4(0.49)	4(0.47)	4(0.44)	4(0.26)	0(0)	6(0.48)	0(0)
	Naso vlamingii	0(0)	12(0.13)	0(0)	4(0.18)	5.3(0.23)	0(0)	0(0)	0(0)
	Zebrasoma scopas	4(0.02)	9(0.13)	4(0.02)	5.6(0.1)	5.9(0.07)	5.1(0.12)	11.3(0.17)	0(0)
	Zebrasoma veliferum	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	4(0.23)	0(0)
Balistidae									

Balistoides viridescens	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	4(0.41)	0(0)
Caesionidae								
Caesio caerulaurea	0(0)	0(0)	0(0)	0(0)	40(1.51)	0(0)	0(0)	0(0)
Caesio sp.	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	4(0.2)	0(0)
Caesio teres	0(0)	0(0)	0(0)	0(0)	160(3.2)	0(0)	0(0)	0(0)
Pterocaesio pisang	80(1.81)	0(0)	0(0)	0(0)	80(1.03)	120(2.25)	0(0)	0(0)
Pterocaesio tile	0(0)	0(0)	0(0)	80(2.19)	214(6.04)	0(0)	40(0.75)	0(0)
Carangidae								
Caranx melampygus	0(0)	0(0)	0(0)	0(0)	8(1.24)	0(0)	40(2.32)	0(0)
Caranx sp.	0(0)	0(0)	0(0)	0(0)	4(0.37)	0(0)	4(0.08)	0(0)
Elagatis bipinnulata	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	24(0)	0(0)
Chaetodontidae								
Chaetodon adiergastos	0(0)	4(0.13)	0(0)	0(0)	8(0.15)	0(0)	0(0)	0(0)
Chaetodon auriga	0(0)	4(0.1)	0(0)	0(0)	0(0)	0(0)	4(0.1)	0(0)
Chaetodon baronessa	10(0)	6.7(0.07)	6.9(0.07)	6.5(0.08)	4.6(0.06)	5.8(0.08)	6(0.08)	0(0)
Chaetodon kleinii	6(0.07)	10.4(0.1)	0(0)	6.8(0.06)	7.4(0.06)	6.4(0.08)	9.3(0.13)	9.1(0.08)
Chaetodon lineolatus	0(0)	0(0)	0(0)	0(0)	0(0)	4(0.11)	4(0.29)	0(0)
Chaetodon lunula	0(0)	5.3(0.27)	5.3(0.2)	4(0.15)	0(0)	4(0.13)	4(0.08)	0(0)
Chaetodon lunulatus	10(0)	10.4(0.1)	6(0.04)	8(0.09)	7.4(0.09)	5.3(0.05)	11.3(0.1)	8(0.1)
Chaetodon melannotus	0(0)	10(0.01)	0(0)	0(0)	0(0)	0(0)	5.3(0.05)	0(0)
Chaetodon mertensii	0(0)	0(0)	15(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Chaetodon ocellicaudus	8(0.15)	0(0)	0(0)	0(0)	4(0.06)	0(0)	0(0)	0(0)
Chaetodon octofasciatus	0(0)	0(0)	10(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Chaetodon ornatissimus	4(0.21)	4(0.18)	0(0)	0(0)	6.7(0.26)	8(0.36)	8(0.41)	0(0)
Chaetodon pelewensis	0(0)	6.7(0.12)	0(0)	0(0)	0(0)	0(0)	8.7(0.11)	0(0)
Chaetodon punctatofasciatus	0(0)	12(0.15)	10(0.01)	4(0.03)	14(0.04)	0(0)	0(0)	0(0)
Chaetodon rafflesii	0(0)	8(0.19)	4(0.13)	0(0)	8(0.15)	0(0)	6.7(0.19)	0(0)
Chaetodon sp.	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	10(0)	10(0)
Chaetodon ulietensis	0(0)	0(0)	0(0)	0(0)	4(0.07)	0(0)	0(0)	0(0)
Chaetodon unimaculatus	0(0)	0(0)	0(0)	0(0)	6(0.17)	0(0)	0(0)	0(0)

Chaetodon vagabundus	0(0)	0(0)	12(0.38)	8(0.25)	4(0.09)	4(0.13)	4(0.09)	4(0.13)
Chelmon sp.	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	4(0.03)	0(0)
Coradion sp.	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	4(0.03)	0(0)
Forcipiger flavissimus	0(0)	8(0.26)	0(0)	0(0)	0(0)	0(0)	4(0.12)	0(0)
Forcipiger longirostris	0(0)	4(0.09)	0(0)	0(0)	8(0.22)	0(0)	0(0)	0(0)
Hemitaurichthys polylepis	0(0)	0(0)	0(0)	0(0)	44(1.17)	0(0)	0(0)	0(0)
Heniochus sp.	0(0)	10(0)	10(0)	0(0)	10(0)	10(0)	0(0)	0(0)
Ephippidae								
Platax sp.	0(0)	0(0)	0(0)	4(0.59)	0(0)	0(0)	10(0)	0(0)
Haemulidae								
Plectorhinchus chaetodonoides	0(0)	10(0)	4(0.43)	10(0)	10(0)	7(0.34)	15(0)	0(0)
Plectorhinchus lineatus	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	6(1.12)	4(0.13)
Plectorhinchus sp.	10(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	10(0)
Plectorhinchus vittatus	4(0.14)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Kyphosidae								
Kyphosus sp.	4(0.18)	4(0.42)	0(0)	0(0)	40(3.29)	0(0)	0(0)	0(0)
Labridae								
Anampses caeruleopunctatus	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	8(0.07)	0(0)
Anampses geographicus	0(0)	9(0.05)	0(0)	0(0)	0(0)	10(0)	0(0)	0(0)
Anampses meleagrides	7.6(0.06)	4(0.01)	0(0)	0(0)	10(0)	0(0)	4(0.01)	0(0)
Anampses sp.	9.9(0.1)	0(0)	7(0.07)	7(0.03)	7(0.14)	7(0.1)	0(0)	12.3(0.09)
Anampses twistii	0(0)	30(0)	0(0)	0(0)	4(0.04)	4(0.07)	12(0.02)	0(0)
Bodianus dictynna	4(0.05)	0(0)	0(0)	0(0)	4(0.05)	0(0)	0(0)	4(0.07)
Bodianus mesothorax	4(0.07)	4(0.09)	4(0.09)	4(0.06)	4(0.09)	0(0)	6(0.16)	4(0.09)
Bodianus sp.	0(0)	4(0.33)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Cheilinus chlorourus	4(0.1)	4(0.11)	4(0.21)	0(0)	4(0.05)	4(0.1)	4(0.07)	5.6(0.08)
Cheilinus fasciatus	4(0.09)	10(0)	0(0)	5(0.12)	7(0.09)	5(0.17)	0(0)	0(0)
Cheilinus oxycephalus	4(0.02)	4(0.04)	4(0.04)	0(0)	0(0)	0(0)	10.3(0.07)	0(0)
Cheilinus trilobatus	4(0.23)	0(0)	4(0.12)	4(0.18)	7.3(0.2)	5(0.31)	4(0.25)	4(0.17)
Cheilio inermis	0(0)	0(0)	4(0.12)	0(0)	4(0.1)	4(0.08)	4(0.05)	4(0.05)

Choerodon anchorago	0(0)	4(0.19)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Choerodon sp.	4(0.15)	0(0)	4(0.18)	0(0)	0(0)	4.4(0.16)	0(0)	0(0)
Cirrhilabrus sp.	629(0)	612(0)	194.4(0)	574.2(0)	230(0)	304.7(0)	456.3(0)	127.5(0)
Coris batuensis	4(0.06)	6(0.05)	8.7(0.06)	5.7(0.05)	0(0)	14.2(0.04)	0(0)	4(0.03)
Coris gaimard	4.8(0.15)	7(0.26)	4(0.11)	0(0)	4(0.11)	23.3(0)	7(0.02)	4(0.12)
Epibulus brevis	10(0)	4(0.11)	0(0)	0(0)	10(0)	4(0.11)	6(0.19)	0(0)
Epibulus insidiator	0(0)	4(0.08)	0(0)	0(0)	0(0)	0(0)	4(0.07)	0(0)
Gomphosus varius	6(0.09)	7.7(0.12)	0(0)	0(0)	4(0.08)	0(0)	13.6(0.08)	0(0)
Halichoeres chrysus	13.3(0)	0(0)	0(0)	0(0)	32.5(0)	10(0)	0(0)	34(0.05)
Halichoeres hortulanus	4.6(0.11)	7.8(0.11)	4(0.1)	0(0)	5.7(0.1)	9.3(0.17)	15.8(0.07)	6(0.05)
Halichoeres marginatus	0(0)	4(0.04)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Halichoeres melanurus	0(0)	11(0.03)	9.6(0.02)	10(0)	10(0)	4(0.03)	12(0.01)	0(0)
Halichoeres nigrescens	0(0)	4(0.03)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Halichoeres podostigma	0(0)	8.5(0.01)	4(0.09)	0(0)	0(0)	4(0.08)	10(0)	4(0.03)
Halichoeres prosopeion	0(0)	4(0.06)	4(0.07)	0(0)	8.5(0.05)	8(0.04)	4(0.05)	4(0.03)
Halichoeres richmondi	0(0)	10(0)	0(0)	0(0)	4(0.06)	4(0.05)	4(0.04)	0(0)
Halichoeres scapularis	4(0.14)	0(0)	12.3(0.08)	4(0.09)	0(0)	17.7(0.15)	0(0)	19.4(0.09)
Halichoeres sp.	10(0)	8.5(0.04)	0(0)	0(0)	15(0)	10(0)	8(0.04)	10(0)
Hemigymnus fasciatus	9.5(0.12)	9.4(0.08)	0(0)	9.3(0.07)	8.5(0.03)	10(0)	8.5(0.03)	0(0)
Hemigymnus melapterus	4(0.19)	6.4(0.05)	0(0)	4(0.25)	0(0)	0(0)	6.4(0.05)	4(0.2)
Hologymnosus annulatus	0(0)	0(0)	0(0)	0(0)	0(0)	4(0)	0(0)	0(0)
Hologymnosus doliatus	10(0)	0(0)	0(0)	0(0)	0(0)	10(0)	0(0)	0(0)
Hologymnosus sp.	4(0)	0(0)	6.4(0)	0(0)	0(0)	10(0)	0(0)	8(0)
Labrichthys unilineatus	7(0.07)	17.2(0.06)	10(0)	0(0)	36.7(0)	10(0.01)	10.8(0.04)	0(0)
Labrid sp.	0(0)	10(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Labroides dimidiatus	10(0)	22.5(0)	10(0)	10(0)	25(0)	13.3(0)	17.5(0)	10(0)
Labroides sp.	0(0)	0(0)	0(0)	0(0)	0(0)	10(0)	0(0)	0(0)
Labropsis manabei	0(0)	4(0.03)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Labropsis xanthonota	0(0)	0(0)	4(0.03)	0(0)	0(0)	8(0.05)	0(0)	0(0)
Macropharyngodon meleagris	12.7(0.04)	6.8(0.03)	4(0.02)	8.4(0.01)	4(0.03)	7(0.03)	8.5(0.03)	8(0.02)

Macropharyngodon negrosensis	10(0)	0(0)	10.8(0.02)	10(0)	40(0)	13.3(0)	0(0)	12(0.06)
Novaculichthys taeniourus	4(0)	0(0)	4(0)	4(0)	4(0)	0(0)	0(0)	4(0)
Oxycheilinus celebicus	0(0)	0(0)	0(0)	4(0.11)	0(0)	4(0.13)	0(0)	0(0)
Oxycheilinus digramma	6.3(0.09)	23.1(0.17)	4(0.12)	4(0.19)	6(0.15)	6.6(0.14)	11.5(0.17)	6(0.1)
Oxycheilinus sp.	10(0)	20(0)	10(0)	10(0)	0(0)	0(0)	6(0.1)	10(0)
Oxycheilinus unifasciatus	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	4(0.05)
Pseudocheilinus evanidus	10(0)	12.9(0)	0(0)	10(0)	10(0)	0(0)	22.9(0)	0(0)
Pseudocheilinus hexataenia	0(0)	12.5(0)	0(0)	0(0)	10(0)	10(0)	18.7(0)	0(0)
Pseudodax moluccanus	0(0)	0(0)	0(0)	0(0)	4(0)	0(0)	0(0)	0(0)
Stethojulis bandanensis	10(0)	4.9(0.03)	0(0)	4(0.01)	0(0)	0(0)	0(0)	4(0.01)
Stethojulis interrupta	16(0.01)	0(0)	20(0)	19.7(0.02)	26.7(0)	14.7(0.11)	0(0)	25.8(0.02)
Stethojulis strigiventer	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	4(0.04)	0(0)
Thalassoma amblycephalum	0(0)	70(0)	0(0)	80(0)	0(0)	0(0)	18(0.32)	0(0)
Thalassoma hardwicke	4(0.1)	8.1(0.14)	0(0)	10(0)	5(0.08)	0(0)	10.2(0.1)	0(0)
Thalassoma jansenii	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	4(0.07)
Thalassoma lunare	9.1(0.07)	42.8(0.15)	10.7(0.08)	16.2(0.08)	34.5(0.08)	14.2(0.07)	43.7(0.2)	9.2(0.07)
Labridae (Scarinae)								
Cetoscarus ocellatus	10(0)	0(0)	0(0)	4(0.15)	0(0)	0(0)	4(2.07)	0(0)
Chlorurus bleekeri	8.1(0.27)	9.3(0.51)	4.3(0.27)	7.2(0.31)	7.8(0.38)	5(0.33)	5.8(0.44)	0(0)
Chlorurus bowersi	4(0.41)	4(0.66)	0(0)	6(0.3)	0(0)	4(0.47)	0(0)	0(0)
Chlorurus microrhinos	0(0)	0(0)	0(0)	0(0)	7(0.38)	0(0)	0(0)	0(0)
Chlorurus sp.	26.7(0)	0(0)	10(0)	0(0)	0(0)	30(0)	0(0)	10(0)
Chlorurus spilurus	16.7(0.31)	20.8(0.24)	20(0)	13(0.08)	7.7(0.42)	4(0.46)	8(0.13)	4(0.33)
Hipposcarus longiceps	0(0)	4(0.21)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Scarus chameleon	5.2(0.32)	0(0)	0(0)	6.4(0.31)	4(0.15)	8(0.18)	0(0)	4(0.12)
Scarus dimidiatus	10(0)	40.8(0.25)	4.6(0.21)	8.5(0.19)	11.3(0.38)	8.5(0.16)	26(0.24)	0(0)
Scarus flavipectoralis	5.6(0.11)	5.9(0.18)	8(0.2)	5.3(0.2)	7.1(0.15)	4.4(0.18)	4(0.11)	4.8(0.17)
Scarus forsteni	4(0.14)	4(0.16)	0(0)	5.7(0.18)	7(0.36)	4(0.17)	0(0)	4(0.1)
Scarus ghobban	0(0)	4(0.28)	4(0.26)	4(0.33)	7(0.03)	4(0.18)	4(0.24)	4.7(0.28)
Scarus hypselopterus	5.7(0.17)	16(0.29)	27.5(0)	8.3(0.2)	5.3(0.19)	8.1(0.21)	0(0)	5.1(0.21)

Scarus niger	7.3(0.23)	14.6(0.34)	9.5(0.15)	6.7(0.2)	8(0.29)	5.9(0.21)	11.8(0.33)	9.6(0.23)
Scarus prasiognathos	0(0)	0(0)	0(0)	0(0)	4(0.86)	0(0)	0(0)	0(0)
Scarus psitticus	4(0)	0(0)	7(0)	4(0)	4(0)	4(0)	0(0)	4(0)
Scarus rivulatus	4(0.42)	4(0.27)	4(0.29)	4(0.31)	4(0.61)	5.4(0.29)	8(0.18)	4(0.17)
Scarus schlegeli	4(0.02)	0(0)	0(0)	0(0)	4(0.35)	0(0)	4(0.54)	4(0.25)
Scarus sp.	20(0)	16.9(0.24)	10(0)	15(0)	10(0)	15(0)	14.7(0.29)	10(0)
Scarus tricolor	10(0)	4(0.24)	4(0.14)	6(0.16)	6.6(0.1)	6.8(0.11)	6.3(0.37)	10(0)
Lethrinidae								
Lethrinus erythracanthus	6(0.47)	4(0.18)	0(0)	0(0)	0(0)	4(0.07)	5.5(0.1)	0(0)
Lethrinus erythropterus	0(0)	4(0.11)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Lethrinus harak	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	4(0.66)	4(0.23)
Lethrinus obsoletus	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	4(0.24)	0(0)
Lethrinus ornatus	0(0)	0(0)	0(0)	0(0)	6(0.37)	0(0)	0(0)	4(0.1)
Lethrinus sp.	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	4(0.04)	0(0)
Monotaxis grandoculis	0(0)	6(0.45)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Lutjanidae								
Aprion virescens	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	4(0.1)	0(0)
Lutjanus biguttatus	0(0)	0(0)	0(0)	0(0)	0(0)	8(0.21)	0(0)	0(0)
Lutjanus bohar	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	4(0.11)	0(0)
Lutjanus decussatus	4(0.23)	6.4(0.37)	4(0.26)	4(0.21)	4.4(0.21)	4(0.15)	6(0.5)	0(0)
Lutjanus ehrenbergii	4(0.06)	15(0.27)	4(0.08)	0(0)	0(0)	4(0.05)	4(0.07)	6(0.13)
Lutjanus fulviflamma	0(0)	4(0.08)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Lutjanus fulvus	4(0.2)	4(0.13)	0(0)	0(0)	4(0.22)	0(0)	4(0.2)	0(0)
Lutjanus monostigma	0(0)	5.3(0.34)	0(0)	6(0.27)	4(0.18)	0(0)	8(0.45)	0(0)
Macolor macularis	4.6(0.23)	7.3(0.73)	0(0)	5.3(0.26)	4.7(0.29)	8(0.22)	11.6(2.81)	8(0.33)
Mullidae								
Mulloidichthys flavolineatus	6.7(0.13)	0(0)	5(0.1)	0(0)	0(0)	0(0)	0(0)	0(0)
Parupeneus barberinoides	0(0)	4(0.06)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Parupeneus barberinus	4.4(0.19)	8(0.16)	4(0.11)	4.8(0.26)	7(0.09)	4(0.16)	4(0.15)	4.7(0.18)
Parupeneus crassilabris	4(0.12)	4(0.18)	0(0)	4(0.06)	4(0.1)	4(0.28)	4(0.07)	0(0)

Parupeneus cyclostomus	0(0)	4(0.09)	0(0)	0(0)	0(0)	0(0)	4(0.17)	0(0)
Parupeneus multifasciatus	4(0.1)	4(0.07)	0(0)	4.7(0.17)	4(0.11)	4(0.17)	4(0.04)	4(0.15)
Parupeneus sp.	0(0)	4(0.07)	0(0)	0(0)	0(0)	0(0)	5.3(0.07)	0(0)
Nemipteridae								
Scolopsis bilineatus	4.7(0.14)	6(0.19)	4.4(0.11)	5(0.1)	5(0.13)	4.6(0.13)	0(0)	4.9(0.1)
Scolopsis sp.	8(0.26)	0(0)	0(0)	0(0)	0(0)	0(0)	4(0.1)	0(0)
Plotosidae								
Plotosus lineatus	200(0)	1000(0)	0(0)	0(0)	1000(0)	0(0)	0(0)	0(0)
Pomacanthidae								
Apolemichthys trimaculatus	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	4(0.1)
Centropyge bicolor	0(0)	0(0)	0(0)	0(0)	0(0)	7.3(0.03)	0(0)	4(0.04)
Centropyge bispinosa	0(0)	7(0.02)	0(0)	0(0)	4(0.03)	0(0)	0(0)	0(0)
Centropyge nox	0(0)	9(0.06)	10(0)	20(0)	8.5(0.03)	0(0)	9.3(0.03)	0(0)
Centropyge tibicen	11.2(0.05)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	6(0.04)
Centropyge vrolikii	12.5(0)	8.5(0.03)	10.6(0.03)	15(0)	24.4(0)	10(0)	10.9(0.07)	10(0)
Chaetodontoplus mesoleucus	0(0)	4(0.1)	4(0.1)	5(0.07)	0(0)	9.5(0.03)	4(0.07)	0(0)
Genicanthus lamarck	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	4(0)
Pomacanthus navarchus	0(0)	0(0)	0(0)	0(0)	4(0.3)	0(0)	0(0)	0(0)
Pomacanthus sexstriatus	4(0.53)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Pomacanthus xanthometopon	0(0)	0(0)	0(0)	0(0)	0(0)	4(0.24)	0(0)	0(0)
Pygoplites diacanthus	4.7(0.12)	4.6(0.19)	4(0.12)	4(0.16)	5.3(0.17)	4.4(0.21)	4.7(0.19)	4(0.21)
Pomacentridae								
Amblyglyphidodon aureus	0(0)	65(0)	0(0)	0(0)	0(0)	0(0)	20.7(0.11)	0(0)
Amblyglyphidodon curacao	30(0)	33.3(0)	10(0)	0(0)	0(0)	24(0)	156.7(0)	0(0)
Amblyglyphidodon leucogaster	10(0)	60(0)	28(0)	15(0)	10(0)	14.4(0)	0(0)	0(0)
Amphiprion ocellaris	0(0)	20(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Amphiprion sp.	0(0)	20(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Chromis amboinensis	0(0)	30(0)	0(0)	25(0)	0(0)	10(0)	33.3(0)	0(0)
Chromis analis	0(0)	0(0)	0(0)	0(0)	0(0)	80(1.13)	0(0)	0(0)
Chromis atripectoralis	0(0)	200(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)

Chromis lepidolepis	10(0)	40(0)	0(0)	0(0)	0(0)	0(0)	20(0)	0(0)
Chromis margaritifer	46(0)	12.5(0)	20(0)	0(0)	22.5(0)	10(0)	22.5(0)	30(0)
Chromis reticulatus	0(0)	0(0)	85(0)	0(0)	50(0)	0(0)	0(0)	0(0)
Chromis retrofasciata	28(0)	91(0)	42(0)	61.3(0)	70(0)	117.1(0)	252.5(0)	0(0)
Chromis ternatensis	50(0)	1221(0)	35(0)	65(0)	228(0)	103.3(0)	346.8(0)	0(0)
Chromis viridis	0(0)	500(0)	183.3(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Chrysiptera rollandi	0(0)	13(0)	25(0)	10(0)	10(0)	12.9(0)	16.7(0)	0(0)
Chrysiptera springeri	0(0)	40(0)	30(0)	30(0)	0(0)	30(0)	75(0)	0(0)
Chrysiptera talboti	10(0)	20(0)	28(0)	12.2(0)	14.4(0)	20(0)	27.5(0)	10(0)
Dascyllus aruanus	0(0)	32(0)	135(0)	20(0)	0(0)	85.5(0)	30(0)	30(0)
Dascyllus reticulatus	40(0)	20(0)	30(0)	20(0)	33.3(0)	56.7(0)	45(0)	20(0)
Dascyllus trimaculatus	35(0)	0(0)	23.3(0)	0(0)	10(0)	12.5(0)	38.3(0)	15(0)
Dischistodus melanotus	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	4(0)	0(0)
Dischistodus perspicillatus	0(0)	0(0)	5.3(0.06)	0(0)	0(0)	4(0.03)	0(0)	0(0)
Hemiglyphidodon plagiometopon	0(0)	0(0)	0(0)	4(0.07)	0(0)	0(0)	0(0)	0(0)
Neoglyphidodon nigroris	10(0)	20(0)	20(0)	20(0)	10(0)	12.9(0)	12.5(0)	0(0)
Plectroglyphidodon lacrymatus	10(0.01)	10.5(0.04)	10(0.01)	10(0.01)	47.3(0.03)	0(0)	17.9(0.07)	0(0)
Pomacentrus adelus	0(0)	0(0)	10(0)	0(0)	0(0)	20(0)	20(0)	0(0)
Pomacentrus alexanderae	0(0)	45.7(0)	72.2(0)	30(0)	15(0)	37.5(0)	50(0)	0(0)
Pomacentrus amboinensis	88(0)	55.5(0)	217.3(0)	55.4(0)	74(0)	168.7(0)	49(0)	88.2(0)
Pomacentrus bankanensis	30(0)	21.7(0)	10(0)	10(0)	10(0)	24(0)	14(0)	0(0)
Pomacentrus brachialis	91.2(0)	90.4(0)	107.6(0)	59.3(0)	146.5(0)	199.7(0)	86.2(0)	66.7(0)
Pomacentrus coelestis	68.8(0)	0(0)	25(0)	10(0)	78.6(0)	88(0)	0(0)	253.3(0)
Pomacentrus lepidogenys	10(0)	10(0)	10(0)	30(0)	0(0)	0(0)	20(0)	0(0)
Pomacentrus moluccensis	64.4(0)	155.6(0)	145.2(0)	103.6(0)	117.6(0)	108.4(0)	155.9(0)	30(0)
Pomacentrus nagasakiensis	0(0)	45(0)	33.3(0)	0(0)	0(0)	22.5(0)	20(0)	0(0)
Pomacentrus sp.	0(0)	0(0)	10(0)	0(0)	0(0)	0(0)	20(0)	0(0)
Pomacentrus stigma	0(0)	0(0)	36.7(0)	0(0)	0(0)	15(0)	0(0)	0(0)
Stegastes sp.	0(0)	0(0)	0(0)	20(0.01)	0(0)	0(0)	0(0)	0(0)

Scombridae								
Rastrelliger kanagurta	0(0)	0(0)	0(0)	0(0)	0(0)	120(0)	0(0)	0(0)
Serranidae								
Cephalopholis argus	4(0.27)	4(0.51)	0(0)	0(0)	4.9(0.17)	4(0.29)	4.7(0.58)	4(0.29)
Cephalopholis cyanostigma	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	4(0.33)	0(0)
Cephalopholis microprion	4(0.17)	0(0)	0(0)	0(0)	0(0)	0(0)	4.8(0.08)	0(0)
Cephalopholis miniata	0(0)	0(0)	0(0)	0(0)	0(0)	4(0.16)	0(0)	4(0.18)
Cephalopholis urodeta	0(0)	0(0)	0(0)	4(0.06)	6.4(0.06)	0(0)	4(0.1)	0(0)
Epinephelus erythrurus	0(0)	0(0)	4(0.07)	0(0)	0(0)	0(0)	0(0)	0(0)
Epinephelus fasciatus	0(0)	0(0)	0(0)	0(0)	4(0.16)	4(0.22)	0(0)	0(0)
Epinephelus merra	4(0.06)	7.2(0.07)	0(0)	4(0.06)	6(0.05)	0(0)	4.5(0.1)	0(0)
Epinephelus ongus	0(0)	10(0)	0(0)	0(0)	0(0)	0(0)	10(0)	0(0)
Epinephelus polyphekadion	0(0)	4(0.07)	0(0)	0(0)	0(0)	0(0)	4(0.15)	0(0)
Epinephelus sp.	0(0)	0(0)	0(0)	4(0.03)	4(0.06)	0(0)	0(0)	0(0)
Plectropomus areolatus	0(0)	0(0)	0(0)	0(0)	4(0.62)	0(0)	0(0)	0(0)
Plectropomus leopardus	0(0)	10(0)	4(0.28)	0(0)	0(0)	0(0)	0(0)	0(0)
Plectropomus oligacanthus	0(0)	4(0.94)	4(0.16)	0(0)	0(0)	0(0)	0(0)	0(0)
Variola louti	0(0)	0(0)	0(0)	4(0.39)	0(0)	4(0.11)	0(0)	4(0.28)
Serranidae (Anthiinae)								
Pseudanthias huchtii	375(0)	347.3(0)	158(0)	30(0)	340(0)	301.7(0)	600(0)	332(0)
Pseudanthias pascalus	100(0)	426.3(0)	0(0)	200(0)	20(0)	0(0)	45(0)	0(0)
Pseudanthias squamipinnis	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	105(0)	0(0)
Siganidae								
Siganus doliatus	4(0.23)	4.7(0.31)	0(0)	0(0)	0(0)	0(0)	7.2(0.35)	0(0)
Siganus guttatus	0(0)	12(1.79)	6.7(0.58)	16(1.71)	0(0)	0(0)	6.7(0.55)	0(0)
Siganus puellus	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	9(0.5)	0(0)
Siganus punctatissimus	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	4(0.25)	0(0)
Siganus punctatus	0(0)	0(0)	0(0)	0(0)	5(0.19)	0(0)	4(0.17)	0(0)
Siganus sp.	0(0)	0(0)	4(0.14)	0(0)	0(0)	10(0)	0(0)	0(0)
Siganus spinus	0(0)	4(0.04)	0(0)	0(0)	0(0)	0(0)	12(0.35)	0(0)

Siganus unimaculatus	0(0)	6.5(0.19)	0(0)	4(0.11)	0(0)	0(0)	6.3(0.18)	0(0)
Siganus vermiculatus	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	4(0.04)	0(0)
Siganus virgatus	4(0.2)	0(0)	8(0.37)	0(0)	4(0.1)	4(0.2)	0(0)	4(0.12)
Siganus vulpinus	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	8(0.23)	0(0)
Sphyraenidae								
Sphyraena obtusata	0(0)	0(0)	0(0)	0(0)	0(0)	160(2.33)	0(0)	0(0)
Sphyraena sp.	0(0)	0(0)	0(0)	80(5.67)	0(0)	0(0)	0(0)	200(7.94)
Zanclidae								
Zanclus cornutus	4(0.14)	7(0.28)	7(0.18)	6(0.37)	8(0.29)	6.7(0.28)	4(0.16)	5.3(0.21)

Table S.3.2. Full output for SIMPER analysis for all species (A), parrotfish (B), and wrasse (C). For the all species analysis (A) only the top 50 records are displayed. Comparison is the comparison between different habitat clusters. A.MG/A.Sand is the cluster for area of mangrove and area of sand. Rub/EAM is the cluster describing rubble and EAM. Coral/A.MA is the cluster for coral cover and area of macroalgae. A.SG/Soft Coral describe the cluster for area of seagrass and soft coral cover. A.CR/A.RF is the cluster for area of coral reef and area of reef flat.

A. All Species SIMPER comparisons

All Species SIMPER comparisons										
Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
A.MG/A.Sand vs Rub/EAM	*Acanthurus nigricans*	0.002	0.737	0.007	0.300	0.004	0.000	209	0.022	0.174
A.MG/A.Sand vs Rub/EAM	*Acanthurus nigricauda*	0.000	0.737	0.000	NA	0.000	0.000	122	0.043	1
A.MG/A.Sand vs Rub/EAM	*Acanthurus nigrofuscus*	0.007	0.737	0.010	0.663	0.010	0.006	65	0.063	0.003
A.MG/A.Sand vs Rub/EAM	*Acanthurus pyroferus*	0.006	0.737	0.009	0.654	0.009	0.005	8	0.083	0.374
A.MG/A.Sand vs Rub/EAM	*Acanthurus sp.*	0.000	0.737	0.000	NA	0.000	0.000	115	0.101	1
A.MG/A.Sand vs Rub/EAM	*Acanthurus thompsoni*	0.000	0.737	0.000	NA	0.000	0.000	206	0.119	1
A.MG/A.Sand vs Rub/EAM	*Acanthurus triostegus*	0.000	0.737	0.000	NA	0.000	0.000	162	0.136	1
A.MG/A.Sand vs Rub/EAM	*Ctenochaetus binotatus*	0.015	0.737	0.011	1.335	0.017	0.035	164	0.153	0.002
A.MG/A.Sand vs Rub/EAM	*Ctenochaetus cyanocheilus*	0.000	0.737	0.000	NA	0.000	0.000	178	0.169	1
A.MG/A.Sand vs Rub/EAM	*Ctenochaetus sp.*	0.001	0.737	0.005	0.308	0.003	0.000	11	0.185	0.441
A.MG/A.Sand vs Rub/EAM	*Ctenochaetus striatus*	0.012	0.737	0.009	1.249	0.024	0.023	133	0.200	0.006
A.MG/A.Sand vs Rub/EAM	*Ctenochaetus tominiensis*	0.003	0.737	0.007	0.423	0.000	0.006	73	0.215	0.81
A.MG/A.Sand vs Rub/EAM	*Naso brevirostris*	0.000	0.737	0.000	NA	0.000	0.000	159	0.230	1
A.MG/A.Sand vs Rub/EAM	*Naso hexacanthus*	0.003	0.737	0.008	0.351	0.005	0.000	131	0.245	0.671
A.MG/A.Sand vs Rub/EAM	*Naso lituratus*	0.003	0.737	0.006	0.480	0.004	0.002	134	0.260	0.945
A.MG/A.Sand vs Rub/EAM	*Naso minor*	0.003	0.737	0.005	0.648	0.000	0.007	211	0.275	0.147
A.MG/A.Sand vs Rub/EAM	*Naso sp.*	0.000	0.737	0.000	NA	0.000	0.000	34	0.289	1
A.MG/A.Sand vs Rub/EAM	*Naso unicornis*	0.002	0.737	0.005	0.358	0.001	0.003	130	0.304	0.997
A.MG/A.Sand vs Rub/EAM	*Naso vlamingii*	0.001	0.737	0.004	0.288	0.000	0.002	77	0.318	0.418
A.MG/A.Sand vs Rub/EAM	*Zebrasoma scopas*	0.005	0.737	0.007	0.687	0.001	0.010	123	0.331	0.988
A.MG/A.Sand vs Rub/EAM	*Zebrasoma veliferum*	0.000	0.737	0.000	NA	0.000	0.000	91	0.345	1
A.MG/A.Sand vs Rub/EAM	*Balistoides viridescens*	0.000	0.737	0.000	NA	0.000	0.000	195	0.358	1
A.MG/A.Sand vs Rub/EAM	*Caesio caerulaurea*	0.000	0.737	0.000	NA	0.000	0.000	208	0.371	1

A.MG/A.Sand vs Rub/EAM	*Caesio sp.*	0.000	0.737	0.000	NA	0.000	0.000	205	0.384	1
A.MG/A.Sand vs Rub/EAM	*Caesio teres*	0.000	0.737	0.000	NA	0.000	0.000	84	0.397	1
A.MG/A.Sand vs Rub/EAM	*Pterocaesio pisang*	0.002	0.737	0.006	0.304	0.003	0.000	83	0.410	0.436
A.MG/A.Sand vs Rub/EAM	*Pterocaesio tile*	0.001	0.737	0.004	0.288	0.000	0.002	104	0.423	0.361
A.MG/A.Sand vs Rub/EAM	*Caranx melampygus*	0.000	0.737	0.000	NA	0.000	0.000	78	0.436	1
A.MG/A.Sand vs Rub/EAM	*Caranx sp.*	0.000	0.737	0.000	NA	0.000	0.000	129	0.448	1
A.MG/A.Sand vs Rub/EAM	*Elagatis bipinnulata*	0.000	0.737	0.000	NA	0.000	0.000	190	0.460	1
A.MG/A.Sand vs Rub/EAM	*Chaetodon adiergastos*	0.000	0.737	0.000	NA	0.000	0.000	126	0.473	1
A.MG/A.Sand vs Rub/EAM	*Chaetodon auriga*	0.000	0.737	0.000	NA	0.000	0.000	70	0.485	1
A.MG/A.Sand vs Rub/EAM	*Chaetodon baronessa*	0.007	0.737	0.011	0.664	0.002	0.013	171	0.497	0.974
A.MG/A.Sand vs Rub/EAM	*Chaetodon kleinii*	0.011	0.737	0.011	0.957	0.018	0.012	128	0.508	0.084
A.MG/A.Sand vs Rub/EAM	*Chaetodon lineolatus*	0.000	0.737	0.000	NA	0.000	0.000	140	0.519	1
A.MG/A.Sand vs Rub/EAM	*Chaetodon lunula*	0.001	0.737	0.005	0.288	0.000	0.003	37	0.529	0.767
A.MG/A.Sand vs Rub/EAM	*Chaetodon lunulatus*	0.008	0.737	0.011	0.711	0.003	0.014	59	0.539	0.673
A.MG/A.Sand vs Rub/EAM	*Chaetodon melannotus*	0.000	0.737	0.000	NA	0.000	0.000	79	0.549	1
A.MG/A.Sand vs Rub/EAM	*Chaetodon mertensii*	0.000	0.737	0.000	NA	0.000	0.000	33	0.559	1
A.MG/A.Sand vs Rub/EAM	*Chaetodon ocellicaudus*	0.003	0.737	0.007	0.358	0.002	0.003	3	0.568	0.133
A.MG/A.Sand vs Rub/EAM	*Chaetodon octofasciatus*	0.000	0.737	0.000	NA	0.000	0.000	100	0.577	1
A.MG/A.Sand vs Rub/EAM	*Chaetodon ornatissimus*	0.001	0.737	0.004	0.213	0.002	0.000	139	0.587	0.883
A.MG/A.Sand vs Rub/EAM	*Chaetodon pelewensis*	0.000	0.737	0.000	NA	0.000	0.000	97	0.596	1
A.MG/A.Sand vs Rub/EAM	*Chaetodon punctatofasciatus*	0.001	0.737	0.003	0.288	0.000	0.002	94	0.605	0.814
A.MG/A.Sand vs Rub/EAM	*Chaetodon rafflesii*	0.000	0.737	0.000	NA	0.000	0.000	232	0.614	1
A.MG/A.Sand vs Rub/EAM	*Chaetodon sp.*	0.002	0.737	0.007	0.213	0.003	0.000	227	0.623	0.191
A.MG/A.Sand vs Rub/EAM	*Chaetodon ulietensis*	0.000	0.737	0.000	NA	0.000	0.000	106	0.632	1
A.MG/A.Sand vs Rub/EAM	*Chaetodon unimaculatus*	0.000	0.737	0.000	NA	0.000	0.000	132	0.641	1
A.MG/A.Sand vs Rub/EAM	*Chaetodon vagabundus*	0.004	0.737	0.008	0.477	0.005	0.004	188	0.649	0.428
A.MG/A.Sand vs Rub/EAM	*Chelmon sp.*	0.000	0.737	0.000	NA	0.000	0.000	4	0.658	1

Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
A.MG/A.Sand vs Coral/A.MA	*Acanthurus nigricans*	0.003	0.793	0.008	0.342	0.004	0.001	209	0.021677	0.019
A.MG/A.Sand vs Coral/A.MA	*Acanthurus nigricauda*	0.001	0.793	0.003	0.179	0.000	0.001	65	0.04132	0.259
A.MG/A.Sand vs Coral/A.MA	*Acanthurus nigrofuscus*	0.005	0.793	0.010	0.512	0.010	0.000	206	0.059913	0.014

A.MG/A.Sand vs Coral/A.MA	*Acanthurus pyroferus*	0.006	0.793	0.009	0.682	0.009	0.005	115	0.075998	0.353
A.MG/A.Sand vs Coral/A.MA	*Acanthurus sp.*	0.000	0.793	0.000	NA	0.000	0.000	164	0.090321	1
A.MG/A.Sand vs Coral/A.MA	*Acanthurus thompsoni*	0.001	0.793	0.004	0.258	0.000	0.002	34	0.104509	0.476
A.MG/A.Sand vs Coral/A.MA	*Acanthurus triostegus*	0.000	0.793	0.003	0.179	0.000	0.001	37	0.118119	0.261
A.MG/A.Sand vs Coral/A.MA	*Ctenochaetus binotatus*	0.010	0.793	0.008	1.128	0.017	0.013	162	0.131584	0.643
A.MG/A.Sand vs Coral/A.MA	*Ctenochaetus cyanocheilus*	0.001	0.793	0.003	0.179	0.000	0.001	11	0.144856	0.259
A.MG/A.Sand vs Coral/A.MA	*Ctenochaetus sp.*	0.003	0.793	0.006	0.437	0.003	0.003	73	0.157649	0.017
A.MG/A.Sand vs Coral/A.MA	*Ctenochaetus striatus*	0.011	0.793	0.006	1.671	0.024	0.026	33	0.170088	0.014
A.MG/A.Sand vs Coral/A.MA	*Ctenochaetus tominiensis*	0.004	0.793	0.006	0.717	0.000	0.008	178	0.182477	0.398
A.MG/A.Sand vs Coral/A.MA	*Naso brevirostris*	0.002	0.793	0.005	0.467	0.000	0.005	20	0.194799	0.236
A.MG/A.Sand vs Coral/A.MA	*Naso hexacanthus*	0.005	0.793	0.008	0.618	0.005	0.006	122	0.206998	0.027
A.MG/A.Sand vs Coral/A.MA	*Naso lituratus*	0.007	0.793	0.007	0.921	0.004	0.012	8	0.21899	0.007
A.MG/A.Sand vs Coral/A.MA	*Naso minor*	0.002	0.793	0.004	0.393	0.000	0.003	211	0.230938	0.958
A.MG/A.Sand vs Coral/A.MA	*Naso sp.*	0.001	0.793	0.004	0.302	0.000	0.003	84	0.242839	0.128
A.MG/A.Sand vs Coral/A.MA	*Naso unicornis*	0.007	0.793	0.007	0.944	0.001	0.013	83	0.254458	0.054
A.MG/A.Sand vs Coral/A.MA	*Naso vlamingii*	0.000	0.793	0.003	0.179	0.000	0.001	159	0.265862	0.884
A.MG/A.Sand vs Coral/A.MA	*Zebrasoma scopas*	0.010	0.793	0.006	1.556	0.001	0.020	208	0.277182	0.001
A.MG/A.Sand vs Coral/A.MA	*Zebrasoma veliferum*	0.001	0.793	0.003	0.179	0.000	0.001	130	0.288412	0.25
A.MG/A.Sand vs Coral/A.MA	*Balistoides viridescens*	0.000	0.793	0.003	0.179	0.000	0.001	68	0.299075	0.274
A.MG/A.Sand vs Coral/A.MA	*Caesio caerulaurea*	0.000	0.793	0.000	NA	0.000	0.000	139	0.309672	1
A.MG/A.Sand vs Coral/A.MA	*Caesio sp.*	0.001	0.793	0.003	0.179	0.000	0.001	70	0.320267	0.252
A.MG/A.Sand vs Coral/A.MA	*Caesio teres*	0.000	0.793	0.000	NA	0.000	0.000	171	0.330445	1
A.MG/A.Sand vs Coral/A.MA	*Pterocaesio pisang*	0.002	0.793	0.006	0.304	0.003	0.000	134	0.340598	0.363
A.MG/A.Sand vs Coral/A.MA	*Pterocaesio tile*	0.000	0.793	0.001	0.179	0.000	0.001	217	0.350728	0.903
A.MG/A.Sand vs Coral/A.MA	*Caranx melampygus*	0.001	0.793	0.004	0.179	0.000	0.001	91	0.360779	0.377
A.MG/A.Sand vs Coral/A.MA	*Caranx sp.*	0.001	0.793	0.003	0.179	0.000	0.001	98	0.370562	0.484
A.MG/A.Sand vs Coral/A.MA	*Elagatis bipinnulata*	0.001	0.793	0.003	0.179	0.000	0.001	172	0.38034	0.251
A.MG/A.Sand vs Coral/A.MA	*Chaetodon adiergastos*	0.000	0.793	0.002	0.179	0.000	0.001	203	0.390096	0.639
A.MG/A.Sand vs Coral/A.MA	*Chaetodon auriga*	0.001	0.793	0.004	0.256	0.000	0.002	104	0.399643	0.176
A.MG/A.Sand vs Coral/A.MA	*Chaetodon baronessa*	0.010	0.793	0.006	1.553	0.002	0.019	118	0.409108	0.056
A.MG/A.Sand vs Coral/A.MA	*Chaetodon kleinii*	0.011	0.793	0.008	1.421	0.018	0.019	232	0.418558	0.002

A.MG/A.Sand vs Coral/A.MA	*Chaetodon lineolatus*	0.001	0.793	0.004	0.179	0.000	0.001	129	0.427999	0.476
A.MG/A.Sand vs Coral/A.MA	*Chaetodon lunula*	0.002	0.793	0.004	0.377	0.000	0.003	100	0.437251	0.83
A.MG/A.Sand vs Coral/A.MA	*Chaetodon lunulatus*	0.011	0.793	0.006	1.847	0.003	0.022	77	0.446472	0.001
A.MG/A.Sand vs Coral/A.MA	*Chaetodon melannotus*	0.002	0.793	0.005	0.365	0.000	0.004	59	0.455661	0.088
A.MG/A.Sand vs Coral/A.MA	*Chaetodon mertensii*	0.000	0.793	0.000	NA	0.000	0.000	188	0.464847	1
A.MG/A.Sand vs Coral/A.MA	*Chaetodon ocellicaudus*	0.001	0.793	0.005	0.213	0.002	0.000	79	0.473813	0.693
A.MG/A.Sand vs Coral/A.MA	*Chaetodon octofasciatus*	0.000	0.793	0.000	NA	0.000	0.000	112	0.482591	1
A.MG/A.Sand vs Coral/A.MA	*Chaetodon ornatissimus*	0.002	0.793	0.006	0.382	0.002	0.003	97	0.491191	0.661
A.MG/A.Sand vs Coral/A.MA	*Chaetodon pelewensis*	0.004	0.793	0.006	0.568	0.000	0.007	18	0.499786	0.007
A.MG/A.Sand vs Coral/A.MA	*Chaetodon punctatofasciatus*	0.001	0.793	0.004	0.316	0.000	0.003	15	0.508001	0.815
A.MG/A.Sand vs Coral/A.MA	*Chaetodon rafflesii*	0.003	0.793	0.006	0.526	0.000	0.007	190	0.516188	0.092
A.MG/A.Sand vs Coral/A.MA	*Chaetodon sp.*	0.002	0.793	0.008	0.265	0.003	0.001	152	0.524207	0.063
A.MG/A.Sand vs Coral/A.MA	*Chaetodon ulietensis*	0.000	0.793	0.000	NA	0.000	0.000	224	0.532011	1
A.MG/A.Sand vs Coral/A.MA	*Chaetodon unimaculatus*	0.000	0.793	0.000	NA	0.000	0.000	94	0.539814	1
A.MG/A.Sand vs Coral/A.MA	*Chaetodon vagabundus*	0.003	0.793	0.006	0.462	0.005	0.002	4	0.547563	0.803
A.MG/A.Sand vs Coral/A.MA	*Chelmon sp.*	0.001	0.793	0.003	0.179	0.000	0.001	93	0.554995	0.259

Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
A.MG/A.Sand vs A.SG/Soft Coral	*Acanthurus nigricans*	0.002	0.734	0.007	0.301	0.004	0.000	65	0.019969	0.119
A.MG/A.Sand vs A.SG/Soft Coral	*Acanthurus nigricauda*	0.000	0.734	0.000	NA	0.000	0.000	115	0.036773	1
A.MG/A.Sand vs A.SG/Soft Coral	*Acanthurus nigrofuscus*	0.005	0.734	0.010	0.512	0.010	0.000	209	0.053282	0.012
A.MG/A.Sand vs A.SG/Soft Coral	*Acanthurus pyroferus*	0.007	0.734	0.009	0.752	0.009	0.008	164	0.068932	0.099
A.MG/A.Sand vs A.SG/Soft Coral	*Acanthurus sp.*	0.001	0.734	0.004	0.192	0.000	0.001	196	0.08458	0.257
A.MG/A.Sand vs A.SG/Soft Coral	*Acanthurus thompsoni*	0.000	0.734	0.000	NA	0.000	0.000	11	0.100176	1
A.MG/A.Sand vs A.SG/Soft Coral	*Acanthurus triostegus*	0.000	0.734	0.000	NA	0.000	0.000	211	0.115653	1
A.MG/A.Sand vs A.SG/Soft Coral	*Ctenochaetus binotatus*	0.009	0.734	0.010	0.948	0.017	0.007	162	0.130589	0.786
A.MG/A.Sand vs A.SG/Soft Coral	*Ctenochaetus cyanocheilus*	0.000	0.734	0.000	NA	0.000	0.000	73	0.145482	1
A.MG/A.Sand vs A.SG/Soft Coral	*Ctenochaetus sp.*	0.001	0.734	0.005	0.308	0.003	0.000	205	0.160135	0.485
A.MG/A.Sand vs A.SG/Soft Coral	*Ctenochaetus striatus*	0.011	0.734	0.010	1.205	0.024	0.016	33	0.174593	0.001
A.MG/A.Sand vs A.SG/Soft Coral	*Ctenochaetus tominiensis*	0.002	0.734	0.005	0.339	0.000	0.003	78	0.188891	0.997
A.MG/A.Sand vs A.SG/Soft Coral	*Naso brevirostris*	0.001	0.734	0.004	0.192	0.000	0.002	159	0.202876	0.944
A.MG/A.Sand vs A.SG/Soft Coral	*Naso hexacanthus*	0.003	0.734	0.008	0.392	0.005	0.001	91	0.21682	0.613

A.MG/A.Sand vs A.SG/Soft Coral	*Naso lituratus*	0.002	0.734	0.005	0.386	0.004	0.000	137	0.230671	1
A.MG/A.Sand vs A.SG/Soft Coral	*Naso minor*	0.002	0.734	0.004	0.390	0.000	0.003	122	0.244366	0.904
A.MG/A.Sand vs A.SG/Soft Coral	*Naso sp.*	0.000	0.734	0.000	NA	0.000	0.000	34	0.258031	1
A.MG/A.Sand vs A.SG/Soft Coral	*Naso unicornis*	0.003	0.734	0.007	0.453	0.001	0.005	178	0.271635	0.989
A.MG/A.Sand vs A.SG/Soft Coral	*Naso vlamingii*	0.000	0.734	0.000	NA	0.000	0.000	206	0.284854	1
A.MG/A.Sand vs A.SG/Soft Coral	*Zebrasoma scopas*	0.004	0.734	0.007	0.542	0.001	0.007	84	0.298006	1
A.MG/A.Sand vs A.SG/Soft Coral	*Zebrasoma veliferum*	0.000	0.734	0.000	NA	0.000	0.000	132	0.311145	1
A.MG/A.Sand vs A.SG/Soft Coral	*Balistoides viridescens*	0.000	0.734	0.000	NA	0.000	0.000	130	0.3242	1
A.MG/A.Sand vs A.SG/Soft Coral	*Caesio caerulaurea*	0.000	0.734	0.000	NA	0.000	0.000	134	0.337055	1
A.MG/A.Sand vs A.SG/Soft Coral	*Caesio sp.*	0.000	0.734	0.000	NA	0.000	0.000	97	0.349883	1
A.MG/A.Sand vs A.SG/Soft Coral	*Caesio teres*	0.000	0.734	0.000	NA	0.000	0.000	83	0.362555	1
A.MG/A.Sand vs A.SG/Soft Coral	*Pterocaesio pisang*	0.002	0.734	0.007	0.360	0.003	0.002	8	0.37501	0.103
A.MG/A.Sand vs A.SG/Soft Coral	*Pterocaesio tile*	0.000	0.734	0.000	NA	0.000	0.000	74	0.387081	1
A.MG/A.Sand vs A.SG/Soft Coral	*Caranx melampygus*	0.000	0.734	0.000	NA	0.000	0.000	70	0.399121	1
A.MG/A.Sand vs A.SG/Soft Coral	*Caranx sp.*	0.000	0.734	0.000	NA	0.000	0.000	208	0.411042	1
A.MG/A.Sand vs A.SG/Soft Coral	*Elagatis bipinnulata*	0.000	0.734	0.000	NA	0.000	0.000	232	0.422688	1
A.MG/A.Sand vs A.SG/Soft Coral	*Chaetodon adiergastos*	0.000	0.734	0.000	NA	0.000	0.000	76	0.433967	1
A.MG/A.Sand vs A.SG/Soft Coral	*Chaetodon auriga*	0.000	0.734	0.000	NA	0.000	0.000	171	0.444941	1
A.MG/A.Sand vs A.SG/Soft Coral	*Chaetodon baronessa*	0.011	0.734	0.010	1.112	0.002	0.021	181	0.455806	0.008
A.MG/A.Sand vs A.SG/Soft Coral	*Chaetodon kleinii*	0.010	0.734	0.011	0.934	0.018	0.008	140	0.466622	0.175
A.MG/A.Sand vs A.SG/Soft Coral	*Chaetodon lineolatus*	0.001	0.734	0.003	0.192	0.000	0.001	193	0.477299	0.607
A.MG/A.Sand vs A.SG/Soft Coral	*Chaetodon lunula*	0.002	0.734	0.007	0.340	0.000	0.005	133	0.487791	0.517
A.MG/A.Sand vs A.SG/Soft Coral	*Chaetodon lunulatus*	0.004	0.734	0.007	0.550	0.003	0.005	77	0.498226	1
A.MG/A.Sand vs A.SG/Soft Coral	*Chaetodon melannotus*	0.000	0.734	0.000	NA	0.000	0.000	79	0.508658	1
A.MG/A.Sand vs A.SG/Soft Coral	*Chaetodon mertensii*	0.001	0.734	0.005	0.277	0.000	0.003	202	0.518621	0.156
A.MG/A.Sand vs A.SG/Soft Coral	*Chaetodon ocellicaudus*	0.001	0.734	0.005	0.213	0.002	0.000	59	0.52853	0.694
A.MG/A.Sand vs A.SG/Soft Coral	*Chaetodon octofasciatus*	0.001	0.734	0.005	0.192	0.000	0.002	197	0.538421	0.268
A.MG/A.Sand vs A.SG/Soft Coral	*Chaetodon ornatissimus*	0.001	0.734	0.005	0.287	0.002	0.001	172	0.548261	0.862
A.MG/A.Sand vs A.SG/Soft Coral	*Chaetodon pelewensis*	0.000	0.734	0.000	NA	0.000	0.000	4	0.557882	1
A.MG/A.Sand vs A.SG/Soft Coral	*Chaetodon punctatofasciatus*	0.001	0.734	0.006	0.192	0.000	0.002	195	0.567355	0.854
A.MG/A.Sand vs A.SG/Soft Coral	*Chaetodon rafflesii*	0.001	0.734	0.003	0.192	0.000	0.001	188	0.576403	0.985

A.MG/A.Sand vs A.SG/Soft Coral	*Chaetodon sp.*	0.002	0.734	0.007	0.213	0.003	0.000	217	0.585117	0.312
A.MG/A.Sand vs A.SG/Soft Coral	*Chaetodon ulietensis*	0.000	0.734	0.000	NA	0.000	0.000	128	0.593793	1
A.MG/A.Sand vs A.SG/Soft Coral	*Chaetodon unimaculatus*	0.000	0.734	0.000	NA	0.000	0.000	104	0.602457	1
A.MG/A.Sand vs A.SG/Soft Coral	*Chaetodon vagabundus*	0.005	0.734	0.008	0.550	0.005	0.006	136	0.61096	0.221
A.MG/A.Sand vs A.SG/Soft Coral	*Chelmon sp.*	0.000	0.734	0.000	NA	0.000	0.000	105	0.619073	1

Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
A.MG/A.Sand vs A.CR/A.RF	*Acanthurus nigricans*	0.002	0.747	0.007	0.300	0.004	0.000	65	0.019641	0.195
A.MG/A.Sand vs A.CR/A.RF	*Acanthurus nigricauda*	0.000	0.747	0.000	NA	0.000	0.000	209	0.038371	1
A.MG/A.Sand vs A.CR/A.RF	*Acanthurus nigrofuscus*	0.005	0.747	0.010	0.511	0.010	0.000	206	0.055686	0.076
A.MG/A.Sand vs A.CR/A.RF	*Acanthurus pyroferus*	0.006	0.747	0.009	0.665	0.009	0.005	115	0.072209	0.418
A.MG/A.Sand vs A.CR/A.RF	*Acanthurus sp.*	0.000	0.747	0.000	NA	0.000	0.000	164	0.087412	1
A.MG/A.Sand vs A.CR/A.RF	*Acanthurus thompsoni*	0.002	0.747	0.006	0.301	0.000	0.003	172	0.102348	0.15
A.MG/A.Sand vs A.CR/A.RF	*Acanthurus triostegus*	0.000	0.747	0.000	NA	0.000	0.000	34	0.117219	1
A.MG/A.Sand vs A.CR/A.RF	*Ctenochaetus binotatus*	0.010	0.747	0.008	1.204	0.017	0.016	73	0.131898	0.499
A.MG/A.Sand vs A.CR/A.RF	*Ctenochaetus cyanocheilus*	0.000	0.747	0.000	NA	0.000	0.000	162	0.146554	1
A.MG/A.Sand vs A.CR/A.RF	*Ctenochaetus sp.*	0.001	0.747	0.005	0.308	0.003	0.000	11	0.16112	0.458
A.MG/A.Sand vs A.CR/A.RF	*Ctenochaetus striatus*	0.011	0.747	0.008	1.385	0.024	0.022	217	0.175351	0.041
A.MG/A.Sand vs A.CR/A.RF	*Ctenochaetus tominiensis*	0.002	0.747	0.006	0.445	0.000	0.005	122	0.189481	0.885
A.MG/A.Sand vs A.CR/A.RF	*Naso brevirostris*	0.001	0.747	0.003	0.301	0.000	0.002	83	0.203214	0.852
A.MG/A.Sand vs A.CR/A.RF	*Naso hexacanthus*	0.005	0.747	0.009	0.549	0.005	0.005	211	0.216688	0.159
A.MG/A.Sand vs A.CR/A.RF	*Naso lituratus*	0.006	0.747	0.008	0.784	0.004	0.010	178	0.230081	0.188
A.MG/A.Sand vs A.CR/A.RF	*Naso minor*	0.001	0.747	0.003	0.434	0.000	0.003	8	0.24313	0.925
A.MG/A.Sand vs A.CR/A.RF	*Naso sp.*	0.000	0.747	0.000	NA	0.000	0.000	159	0.255944	1
A.MG/A.Sand vs A.CR/A.RF	*Naso unicornis*	0.003	0.747	0.007	0.493	0.001	0.006	84	0.268489	0.941
A.MG/A.Sand vs A.CR/A.RF	*Naso vlamingii*	0.003	0.747	0.006	0.446	0.000	0.005	130	0.281014	0.063
A.MG/A.Sand vs A.CR/A.RF	*Zebrasoma scopas*	0.008	0.747	0.007	1.133	0.001	0.017	128	0.293314	0.113
A.MG/A.Sand vs A.CR/A.RF	*Zebrasoma veliferum*	0.000	0.747	0.000	NA	0.000	0.000	232	0.305156	1
A.MG/A.Sand vs A.CR/A.RF	*Balistoides viridescens*	0.000	0.747	0.000	NA	0.000	0.000	70	0.316747	1
A.MG/A.Sand vs A.CR/A.RF	*Caesio caerulaurea*	0.002	0.747	0.006	0.301	0.000	0.004	151	0.328032	0.017
A.MG/A.Sand vs A.CR/A.RF	*Caesio sp.*	0.000	0.747	0.000	NA	0.000	0.000	188	0.339313	1
A.MG/A.Sand vs A.CR/A.RF	*Caesio teres*	0.001	0.747	0.005	0.301	0.000	0.003	195	0.350452	0.02

A.MG/A.Sand vs A.CR/A.RF	*Pterocaesio pisang*	0.003	0.747	0.007	0.429	0.003	0.003	20	0.361522	0.089
A.MG/A.Sand vs A.CR/A.RF	*Pterocaesio tile*	0.002	0.747	0.005	0.430	0.000	0.005	140	0.372381	0.029
A.MG/A.Sand vs A.CR/A.RF	*Caranx melampygus*	0.001	0.747	0.004	0.301	0.000	0.002	77	0.383232	0.187
A.MG/A.Sand vs A.CR/A.RF	*Caranx sp.*	0.001	0.747	0.004	0.301	0.000	0.003	171	0.394011	0.209
A.MG/A.Sand vs A.CR/A.RF	*Elagatis bipinnulata*	0.000	0.747	0.000	NA	0.000	0.000	208	0.404726	1
A.MG/A.Sand vs A.CR/A.RF	*Chaetodon adiergastos*	0.001	0.747	0.005	0.301	0.000	0.003	91	0.415371	0.071
A.MG/A.Sand vs A.CR/A.RF	*Chaetodon auriga*	0.000	0.747	0.000	NA	0.000	0.000	134	0.425941	1
A.MG/A.Sand vs A.CR/A.RF	*Chaetodon baronessa*	0.008	0.747	0.008	0.980	0.002	0.014	37	0.43644	0.933
A.MG/A.Sand vs A.CR/A.RF	*Chaetodon kleinii*	0.011	0.747	0.009	1.214	0.018	0.017	33	0.44664	0.046
A.MG/A.Sand vs A.CR/A.RF	*Chaetodon lineolatus*	0.000	0.747	0.000	NA	0.000	0.000	79	0.456781	1
A.MG/A.Sand vs A.CR/A.RF	*Chaetodon lunula*	0.000	0.747	0.000	NA	0.000	0.000	59	0.466513	1
A.MG/A.Sand vs A.CR/A.RF	*Chaetodon lunulatus*	0.008	0.747	0.008	0.988	0.003	0.015	224	0.475637	0.525
A.MG/A.Sand vs A.CR/A.RF	*Chaetodon melannotus*	0.000	0.747	0.000	NA	0.000	0.000	97	0.484745	1
A.MG/A.Sand vs A.CR/A.RF	*Chaetodon mertensii*	0.000	0.747	0.000	NA	0.000	0.000	104	0.493277	1
A.MG/A.Sand vs A.CR/A.RF	*Chaetodon ocellicaudus*	0.003	0.747	0.007	0.487	0.002	0.005	89	0.501705	0.037
A.MG/A.Sand vs A.CR/A.RF	*Chaetodon octofasciatus*	0.000	0.747	0.000	NA	0.000	0.000	126	0.510055	1
A.MG/A.Sand vs A.CR/A.RF	*Chaetodon ornatissimus*	0.006	0.747	0.009	0.608	0.002	0.010	92	0.51832	0.014
A.MG/A.Sand vs A.CR/A.RF	*Chaetodon pelewensis*	0.000	0.747	0.000	NA	0.000	0.000	93	0.526577	1
A.MG/A.Sand vs A.CR/A.RF	*Chaetodon punctatofasciatus*	0.003	0.747	0.006	0.439	0.000	0.005	190	0.534818	0.339
A.MG/A.Sand vs A.CR/A.RF	*Chaetodon rafflesii*	0.001	0.747	0.004	0.301	0.000	0.002	203	0.542988	0.896
A.MG/A.Sand vs A.CR/A.RF	*Chaetodon sp.*	0.002	0.747	0.007	0.213	0.003	0.000	4	0.551122	0.291
A.MG/A.Sand vs A.CR/A.RF	*Chaetodon ulietensis*	0.002	0.747	0.006	0.301	0.000	0.004	160	0.559199	0.015
A.MG/A.Sand vs A.CR/A.RF	*Chaetodon unimaculatus*	0.003	0.747	0.007	0.446	0.000	0.006	136	0.567263	0.005
A.MG/A.Sand vs A.CR/A.RF	*Chaetodon vagabundus*	0.005	0.747	0.007	0.685	0.005	0.006	15	0.575152	0.267
A.MG/A.Sand vs A.CR/A.RF	*Chelmon sp.*	0.000	0.747	0.000	NA	0.000	0.000	68	0.582964	1

Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
Rub/EAM vs Coral/A.MA	*Acanthurus nigricans*	0.000	0.724	0.002	0.179	0.000	0.001	8	0.019492	0.707
Rub/EAM vs Coral/A.MA	*Acanthurus nigricauda*	0.001	0.724	0.003	0.179	0.000	0.001	133	0.037097	0.144
Rub/EAM vs Coral/A.MA	*Acanthurus nigrofuscus*	0.003	0.724	0.008	0.424	0.006	0.000	130	0.05312	0.339
Rub/EAM vs Coral/A.MA	*Acanthurus pyroferus*	0.005	0.724	0.007	0.635	0.005	0.005	37	0.068709	0.833
Rub/EAM vs Coral/A.MA	*Acanthurus sp.*	0.000	0.724	0.000	NA	0.000	0.000	162	0.084112	1

Rub/EAM vs Coral/A.MA	*Acanthurus thompsoni*	0.001	0.724	0.004	0.257	0.000	0.002	164	0.099455	0.47
Rub/EAM vs Coral/A.MA	*Acanthurus triostegus*	0.000	0.724	0.003	0.179	0.000	0.001	178	0.114698	0.134
Rub/EAM vs Coral/A.MA	*Ctenochaetus binotatus*	0.014	0.724	0.010	1.375	0.035	0.013	206	0.129246	0.001
Rub/EAM vs Coral/A.MA	*Ctenochaetus cyanocheilus*	0.001	0.724	0.003	0.179	0.000	0.001	33	0.143434	0.149
Rub/EAM vs Coral/A.MA	*Ctenochaetus sp.*	0.001	0.724	0.005	0.305	0.000	0.003	131	0.157543	0.451
Rub/EAM vs Coral/A.MA	*Ctenochaetus striatus*	0.009	0.724	0.005	1.612	0.023	0.026	34	0.171039	0.685
Rub/EAM vs Coral/A.MA	*Ctenochaetus tominiensis*	0.006	0.724	0.007	0.827	0.006	0.008	123	0.184434	0.039
Rub/EAM vs Coral/A.MA	*Naso brevirostris*	0.002	0.724	0.005	0.467	0.000	0.005	139	0.197484	0.298
Rub/EAM vs Coral/A.MA	*Naso hexacanthus*	0.003	0.724	0.005	0.566	0.000	0.006	77	0.210423	0.619
Rub/EAM vs Coral/A.MA	*Naso lituratus*	0.006	0.724	0.007	0.893	0.002	0.012	122	0.223217	0.064
Rub/EAM vs Coral/A.MA	*Naso minor*	0.004	0.724	0.006	0.765	0.007	0.003	211	0.235886	0.034
Rub/EAM vs Coral/A.MA	*Naso sp.*	0.001	0.724	0.004	0.302	0.000	0.003	195	0.248553	0.182
Rub/EAM vs Coral/A.MA	*Naso unicornis*	0.007	0.724	0.007	0.963	0.003	0.013	205	0.261076	0.082
Rub/EAM vs Coral/A.MA	*Naso vlamingii*	0.002	0.724	0.005	0.339	0.002	0.001	20	0.273554	0.182
Rub/EAM vs Coral/A.MA	*Zebrasoma scopas*	0.009	0.724	0.006	1.438	0.010	0.020	11	0.285778	0.009
Rub/EAM vs Coral/A.MA	*Zebrasoma veliferum*	0.001	0.724	0.003	0.179	0.000	0.001	104	0.297745	0.134
Rub/EAM vs Coral/A.MA	*Balistoides viridescens*	0.000	0.724	0.003	0.179	0.000	0.001	68	0.309638	0.123
Rub/EAM vs Coral/A.MA	*Caesio caerulaurea*	0.000	0.724	0.000	NA	0.000	0.000	115	0.321484	1
Rub/EAM vs Coral/A.MA	*Caesio sp.*	0.001	0.724	0.003	0.179	0.000	0.001	134	0.33311	0.134
Rub/EAM vs Coral/A.MA	*Caesio teres*	0.000	0.724	0.000	NA	0.000	0.000	78	0.344634	1
Rub/EAM vs Coral/A.MA	*Pterocaesio pisang*	0.000	0.724	0.000	NA	0.000	0.000	100	0.356085	1
Rub/EAM vs Coral/A.MA	*Pterocaesio tile*	0.001	0.724	0.004	0.334	0.002	0.001	126	0.367382	0.272
Rub/EAM vs Coral/A.MA	*Caranx melampygus*	0.001	0.724	0.004	0.179	0.000	0.001	98	0.378546	0.321
Rub/EAM vs Coral/A.MA	*Caranx sp.*	0.001	0.724	0.003	0.179	0.000	0.001	118	0.389595	0.318
Rub/EAM vs Coral/A.MA	*Elagatis bipinnulata*	0.001	0.724	0.003	0.179	0.000	0.001	111	0.40034	0.128
Rub/EAM vs Coral/A.MA	*Chaetodon adiergastos*	0.000	0.724	0.002	0.179	0.000	0.001	140	0.411057	0.494
Rub/EAM vs Coral/A.MA	*Chaetodon auriga*	0.001	0.724	0.004	0.256	0.000	0.002	203	0.421553	0.237
Rub/EAM vs Coral/A.MA	*Chaetodon baronessa*	0.010	0.724	0.007	1.461	0.013	0.019	190	0.431837	0.041
Rub/EAM vs Coral/A.MA	*Chaetodon kleinii*	0.010	0.724	0.007	1.478	0.012	0.019	208	0.442117	0.296
Rub/EAM vs Coral/A.MA	*Chaetodon lineolatus*	0.001	0.724	0.004	0.179	0.000	0.001	172	0.45227	0.317
Rub/EAM vs Coral/A.MA	*Chaetodon lunula*	0.003	0.724	0.006	0.474	0.003	0.003	86	0.462304	0.358

Rub/EAM vs Coral/A.MA	*Chaetodon lunulatus*	0.011	0.724	0.006	1.825	0.014	0.022	159	0.472212	0.001
Rub/EAM vs Coral/A.MA	*Chaetodon melannotus*	0.002	0.724	0.005	0.365	0.000	0.004	18	0.481916	0.137
Rub/EAM vs Coral/A.MA	*Chaetodon mertensii*	0.000	0.724	0.000	NA	0.000	0.000	112	0.491549	1
Rub/EAM vs Coral/A.MA	*Chaetodon ocellicaudus*	0.002	0.724	0.006	0.288	0.003	0.000	193	0.501175	0.376
Rub/EAM vs Coral/A.MA	*Chaetodon octofasciatus*	0.000	0.724	0.000	NA	0.000	0.000	227	0.510265	1
Rub/EAM vs Coral/A.MA	*Chaetodon ornatissimus*	0.001	0.724	0.004	0.320	0.000	0.003	217	0.51927	0.831
Rub/EAM vs Coral/A.MA	*Chaetodon pelewensis*	0.004	0.724	0.006	0.568	0.000	0.007	94	0.528176	0.038
Rub/EAM vs Coral/A.MA	*Chaetodon punctatofasciatus*	0.002	0.724	0.005	0.428	0.002	0.003	129	0.537059	0.449
Rub/EAM vs Coral/A.MA	*Chaetodon rafflesii*	0.003	0.724	0.006	0.526	0.000	0.007	84	0.545939	0.132
Rub/EAM vs Coral/A.MA	*Chaetodon sp.*	0.001	0.724	0.003	0.179	0.000	0.001	15	0.554664	0.506
Rub/EAM vs Coral/A.MA	*Chaetodon ulietensis*	0.000	0.724	0.000	NA	0.000	0.000	242	0.563191	1
Rub/EAM vs Coral/A.MA	*Chaetodon unimaculatus*	0.000	0.724	0.000	NA	0.000	0.000	224	0.571599	1
Rub/EAM vs Coral/A.MA	*Chaetodon vagabundus*	0.003	0.724	0.007	0.370	0.004	0.002	120	0.579729	0.783
Rub/EAM vs Coral/A.MA	*Chelmon sp.*	0.001	0.724	0.003	0.179	0.000	0.001	202	0.587596	0.112

Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
Rub/EAM vs A.SG/Soft Coral	*Acanthurus nigricans*	0.000	0.690	0.000	NA	0.000	0.000	8	0.022825	1
Rub/EAM vs A.SG/Soft Coral	*Acanthurus nigricauda*	0.000	0.690	0.000	NA	0.000	0.000	178	0.039993	1
Rub/EAM vs A.SG/Soft Coral	*Acanthurus nigrofuscus*	0.003	0.690	0.008	0.424	0.006	0.000	162	0.056696	0.37
Rub/EAM vs A.SG/Soft Coral	*Acanthurus pyroferus*	0.006	0.690	0.008	0.704	0.005	0.008	206	0.073177	0.535
Rub/EAM vs A.SG/Soft Coral	*Acanthurus sp.*	0.001	0.690	0.004	0.192	0.000	0.001	33	0.08933	0.146
Rub/EAM vs A.SG/Soft Coral	*Acanthurus thompsoni*	0.000	0.690	0.000	NA	0.000	0.000	196	0.105408	1
Rub/EAM vs A.SG/Soft Coral	*Acanthurus triostegus*	0.000	0.690	0.000	NA	0.000	0.000	134	0.12121	1
Rub/EAM vs A.SG/Soft Coral	*Ctenochaetus binotatus*	0.016	0.690	0.011	1.406	0.035	0.007	211	0.136726	0.001
Rub/EAM vs A.SG/Soft Coral	*Ctenochaetus cyanocheilus*	0.000	0.690	0.000	NA	0.000	0.000	164	0.152242	1
Rub/EAM vs A.SG/Soft Coral	*Ctenochaetus sp.*	0.000	0.690	0.000	NA	0.000	0.000	122	0.16769	1
Rub/EAM vs A.SG/Soft Coral	*Ctenochaetus striatus*	0.010	0.690	0.008	1.235	0.023	0.016	131	0.183018	0.126
Rub/EAM vs A.SG/Soft Coral	*Ctenochaetus tominiensis*	0.004	0.690	0.007	0.542	0.006	0.003	133	0.198086	0.481
Rub/EAM vs A.SG/Soft Coral	*Naso brevirostris*	0.001	0.690	0.004	0.192	0.000	0.002	11	0.213034	0.88
Rub/EAM vs A.SG/Soft Coral	*Naso hexacanthus*	0.000	0.690	0.003	0.192	0.000	0.001	140	0.227365	0.998
Rub/EAM vs A.SG/Soft Coral	*Naso lituratus*	0.001	0.690	0.004	0.288	0.002	0.000	115	0.241674	0.999
Rub/EAM vs A.SG/Soft Coral	*Naso minor*	0.004	0.690	0.006	0.758	0.007	0.003	132	0.255835	0.032

Rub/EAM vs A.SG/Soft Coral	*Naso sp.*	0.000	0.690	0.000	NA	0.000	0.000	195	0.269928	1
Rub/EAM vs A.SG/Soft Coral	*Naso unicornis*	0.004	0.690	0.008	0.494	0.003	0.005	123	0.283993	0.909
Rub/EAM vs A.SG/Soft Coral	*Naso vlamingii*	0.001	0.690	0.004	0.288	0.002	0.000	78	0.297955	0.35
Rub/EAM vs A.SG/Soft Coral	*Zebrasoma scopas*	0.006	0.690	0.008	0.817	0.010	0.007	159	0.311788	0.869
Rub/EAM vs A.SG/Soft Coral	*Zebrasoma veliferum*	0.000	0.690	0.000	NA	0.000	0.000	77	0.325498	1
Rub/EAM vs A.SG/Soft Coral	*Balistoides viridescens*	0.000	0.690	0.000	NA	0.000	0.000	205	0.339057	1
Rub/EAM vs A.SG/Soft Coral	*Caesio caerulaurea*	0.000	0.690	0.000	NA	0.000	0.000	91	0.352314	1
Rub/EAM vs A.SG/Soft Coral	*Caesio sp.*	0.000	0.690	0.000	NA	0.000	0.000	208	0.365461	1
Rub/EAM vs A.SG/Soft Coral	*Caesio teres*	0.000	0.690	0.000	NA	0.000	0.000	130	0.378417	1
Rub/EAM vs A.SG/Soft Coral	*Pterocaesio pisang*	0.001	0.690	0.004	0.192	0.000	0.002	193	0.391187	0.622
Rub/EAM vs A.SG/Soft Coral	*Pterocaesio tile*	0.001	0.690	0.004	0.288	0.002	0.000	137	0.403783	0.379
Rub/EAM vs A.SG/Soft Coral	*Caranx melampygus*	0.000	0.690	0.000	NA	0.000	0.000	181	0.416284	1
Rub/EAM vs A.SG/Soft Coral	*Caranx sp.*	0.000	0.690	0.000	NA	0.000	0.000	202	0.428706	1
Rub/EAM vs A.SG/Soft Coral	*Elagatis bipinnulata*	0.000	0.690	0.000	NA	0.000	0.000	126	0.44093	1
Rub/EAM vs A.SG/Soft Coral	*Chaetodon adiergastos*	0.000	0.690	0.000	NA	0.000	0.000	209	0.453029	1
Rub/EAM vs A.SG/Soft Coral	*Chaetodon auriga*	0.000	0.690	0.000	NA	0.000	0.000	190	0.46472	1
Rub/EAM vs A.SG/Soft Coral	*Chaetodon baronessa*	0.011	0.690	0.009	1.190	0.013	0.021	37	0.476319	0.009
Rub/EAM vs A.SG/Soft Coral	*Chaetodon kleinii*	0.008	0.690	0.009	0.889	0.012	0.008	76	0.487898	0.959
Rub/EAM vs A.SG/Soft Coral	*Chaetodon lineolatus*	0.001	0.690	0.003	0.192	0.000	0.001	34	0.498969	0.465
Rub/EAM vs A.SG/Soft Coral	*Chaetodon lunula*	0.003	0.690	0.008	0.443	0.003	0.005	104	0.509818	0.16
Rub/EAM vs A.SG/Soft Coral	*Chaetodon lunulatus*	0.008	0.690	0.010	0.784	0.014	0.005	232	0.520264	0.441
Rub/EAM vs A.SG/Soft Coral	*Chaetodon melannotus*	0.000	0.690	0.000	NA	0.000	0.000	129	0.53067	1
Rub/EAM vs A.SG/Soft Coral	*Chaetodon mertensii*	0.001	0.690	0.005	0.277	0.000	0.003	73	0.541	0.232
Rub/EAM vs A.SG/Soft Coral	*Chaetodon ocellicaudus*	0.002	0.690	0.006	0.288	0.003	0.000	197	0.55079	0.397
Rub/EAM vs A.SG/Soft Coral	*Chaetodon octofasciatus*	0.001	0.690	0.005	0.192	0.000	0.002	227	0.560306	0.142
Rub/EAM vs A.SG/Soft Coral	*Chaetodon ornatissimus*	0.001	0.690	0.003	0.192	0.000	0.001	20	0.569657	0.944
Rub/EAM vs A.SG/Soft Coral	*Chaetodon pelewensis*	0.000	0.690	0.000	NA	0.000	0.000	86	0.579001	1
Rub/EAM vs A.SG/Soft Coral	*Chaetodon punctatofasciatus*	0.002	0.690	0.006	0.314	0.002	0.002	74	0.588308	0.466
Rub/EAM vs A.SG/Soft Coral	*Chaetodon rafflesii*	0.001	0.690	0.003	0.192	0.000	0.001	172	0.597553	0.928
Rub/EAM vs A.SG/Soft Coral	*Chaetodon sp.*	0.000	0.690	0.000	NA	0.000	0.000	100	0.606562	1
Rub/EAM vs A.SG/Soft Coral	*Chaetodon ulietensis*	0.000	0.690	0.000	NA	0.000	0.000	173	0.615399	1

Rub/EAM vs A.SG/Soft Coral	*Chaetodon unimaculatus*	0.000	0.690	0.000	NA	0.000	0.000	136	0.624089	1
Rub/EAM vs A.SG/Soft Coral	*Chaetodon vagabundus*	0.004	0.690	0.009	0.488	0.004	0.006	4	0.632304	0.293
Rub/EAM vs A.SG/Soft Coral	*Chelmon sp.*	0.000	0.690	0.000	NA	0.000	0.000	120	0.640258	1

Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
Rub/EAM vs A.CR/A.RF	*Acanthurus nigricans*	0.000	0.705	0.000	NA	0.000	0.000	8	0.018968	1
Rub/EAM vs A.CR/A.RF	*Acanthurus nigricauda*	0.000	0.705	0.000	NA	0.000	0.000	162	0.035385	1
Rub/EAM vs A.CR/A.RF	*Acanthurus nigrofuscus*	0.003	0.705	0.008	0.423	0.006	0.000	172	0.051788	0.388
Rub/EAM vs A.CR/A.RF	*Acanthurus pyroferus*	0.004	0.705	0.007	0.610	0.005	0.005	77	0.068019	0.781
Rub/EAM vs A.CR/A.RF	*Acanthurus sp.*	0.000	0.705	0.000	NA	0.000	0.000	178	0.083857	1
Rub/EAM vs A.CR/A.RF	*Acanthurus thompsoni*	0.002	0.705	0.006	0.301	0.000	0.003	164	0.099381	0.118
Rub/EAM vs A.CR/A.RF	*Acanthurus triostegus*	0.000	0.705	0.000	NA	0.000	0.000	133	0.114711	1
Rub/EAM vs A.CR/A.RF	*Ctenochaetus binotatus*	0.013	0.705	0.010	1.343	0.035	0.016	131	0.129989	0.009
Rub/EAM vs A.CR/A.RF	*Ctenochaetus cyanocheilus*	0.000	0.705	0.000	NA	0.000	0.000	217	0.145057	1
Rub/EAM vs A.CR/A.RF	*Ctenochaetus sp.*	0.000	0.705	0.000	NA	0.000	0.000	130	0.160074	1
Rub/EAM vs A.CR/A.RF	*Ctenochaetus striatus*	0.009	0.705	0.007	1.366	0.023	0.022	206	0.174525	0.427
Rub/EAM vs A.CR/A.RF	*Ctenochaetus tominiensis*	0.005	0.705	0.007	0.610	0.006	0.005	211	0.188599	0.289
Rub/EAM vs A.CR/A.RF	*Naso brevirostris*	0.001	0.705	0.003	0.301	0.000	0.002	37	0.202634	0.751
Rub/EAM vs A.CR/A.RF	*Naso hexacanthus*	0.003	0.705	0.006	0.430	0.000	0.005	140	0.216606	0.641
Rub/EAM vs A.CR/A.RF	*Naso lituratus*	0.006	0.705	0.007	0.748	0.002	0.010	123	0.230192	0.293
Rub/EAM vs A.CR/A.RF	*Naso minor*	0.004	0.705	0.005	0.769	0.007	0.003	34	0.243629	0.109
Rub/EAM vs A.CR/A.RF	*Naso sp.*	0.000	0.705	0.000	NA	0.000	0.000	11	0.257021	1
Rub/EAM vs A.CR/A.RF	*Naso unicornis*	0.004	0.705	0.007	0.527	0.003	0.006	33	0.270327	0.826
Rub/EAM vs A.CR/A.RF	*Naso vlamingii*	0.003	0.705	0.006	0.527	0.002	0.005	115	0.28358	0.014
Rub/EAM vs A.CR/A.RF	*Zebrasoma scopas*	0.008	0.705	0.007	1.168	0.010	0.017	205	0.296781	0.124
Rub/EAM vs A.CR/A.RF	*Zebrasoma veliferum*	0.000	0.705	0.000	NA	0.000	0.000	232	0.309042	1
Rub/EAM vs A.CR/A.RF	*Balistoides viridescens*	0.000	0.705	0.000	NA	0.000	0.000	126	0.321253	1
Rub/EAM vs A.CR/A.RF	*Caesio caerulaurea*	0.002	0.705	0.006	0.301	0.000	0.004	78	0.333179	0.009
Rub/EAM vs A.CR/A.RF	*Caesio sp.*	0.000	0.705	0.000	NA	0.000	0.000	20	0.345093	1
Rub/EAM vs A.CR/A.RF	*Caesio teres*	0.001	0.705	0.005	0.301	0.000	0.003	128	0.356865	0.003
Rub/EAM vs A.CR/A.RF	*Pterocaesio pisang*	0.002	0.705	0.005	0.301	0.000	0.003	195	0.368591	0.443
Rub/EAM vs A.CR/A.RF	*Pterocaesio tile*	0.003	0.705	0.006	0.520	0.002	0.005	227	0.380204	0.008

Rub/EAM vs A.CR/A.RF	*Caranx melampygus*	0.001	0.705	0.004	0.301	0.000	0.002	151	0.391817	0.234
Rub/EAM vs A.CR/A.RF	*Caranx sp.*	0.001	0.705	0.004	0.301	0.000	0.003	159	0.403309	0.171
Rub/EAM vs A.CR/A.RF	*Elagatis bipinnulata*	0.000	0.705	0.000	NA	0.000	0.000	134	0.414751	1
Rub/EAM vs A.CR/A.RF	*Chaetodon adiergastos*	0.001	0.705	0.005	0.301	0.000	0.003	208	0.425927	0.043
Rub/EAM vs A.CR/A.RF	*Chaetodon auriga*	0.000	0.705	0.000	NA	0.000	0.000	122	0.436689	1
Rub/EAM vs A.CR/A.RF	*Chaetodon baronessa*	0.009	0.705	0.009	1.092	0.013	0.014	129	0.447443	0.364
Rub/EAM vs A.CR/A.RF	*Chaetodon kleinii*	0.009	0.705	0.008	1.206	0.012	0.017	190	0.458064	0.431
Rub/EAM vs A.CR/A.RF	*Chaetodon lineolatus*	0.000	0.705	0.000	NA	0.000	0.000	104	0.46866	1
Rub/EAM vs A.CR/A.RF	*Chaetodon lunula*	0.001	0.705	0.005	0.288	0.003	0.000	203	0.478835	0.716
Rub/EAM vs A.CR/A.RF	*Chaetodon lunulatus*	0.010	0.705	0.009	1.097	0.014	0.015	224	0.488316	0.034
Rub/EAM vs A.CR/A.RF	*Chaetodon melannotus*	0.000	0.705	0.000	NA	0.000	0.000	68	0.496981	1
Rub/EAM vs A.CR/A.RF	*Chaetodon mertensii*	0.000	0.705	0.000	NA	0.000	0.000	73	0.50556	1
Rub/EAM vs A.CR/A.RF	*Chaetodon ocellicaudus*	0.004	0.705	0.007	0.529	0.003	0.005	160	0.514037	0.04
Rub/EAM vs A.CR/A.RF	*Chaetodon octofasciatus*	0.000	0.705	0.000	NA	0.000	0.000	89	0.522512	1
Rub/EAM vs A.CR/A.RF	*Chaetodon ornatissimus*	0.005	0.705	0.009	0.570	0.000	0.010	136	0.530792	0.056
Rub/EAM vs A.CR/A.RF	*Chaetodon pelewensis*	0.000	0.705	0.000	NA	0.000	0.000	15	0.538729	1
Rub/EAM vs A.CR/A.RF	*Chaetodon punctatofasciatus*	0.003	0.705	0.006	0.523	0.002	0.005	71	0.546658	0.226
Rub/EAM vs A.CR/A.RF	*Chaetodon rafflesii*	0.001	0.705	0.004	0.301	0.000	0.002	100	0.554525	0.845
Rub/EAM vs A.CR/A.RF	*Chaetodon sp.*	0.000	0.705	0.000	NA	0.000	0.000	209	0.56238	1
Rub/EAM vs A.CR/A.RF	*Chaetodon ulietensis*	0.002	0.705	0.006	0.301	0.000	0.004	132	0.570189	0.011
Rub/EAM vs A.CR/A.RF	*Chaetodon unimaculatus*	0.003	0.705	0.007	0.445	0.000	0.006	92	0.577978	0.003
Rub/EAM vs A.CR/A.RF	*Chaetodon vagabundus*	0.005	0.705	0.008	0.610	0.004	0.006	139	0.585666	0.284
Rub/EAM vs A.CR/A.RF	*Chelmon sp.*	0.000	0.705	0.000	NA	0.000	0.000	93	0.593322	1

Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
Coral.A.MA vs A.SG/Soft Coral	*Acanthurus nigricans*	0.000	0.734	0.002	0.180	0.001	0.000	206	0.01915	0.919
Coral.A.MA vs A.SG/Soft Coral	*Acanthurus nigricauda*	0.001	0.734	0.003	0.180	0.001	0.000	164	0.036499	0.532
Coral.A.MA vs A.SG/Soft Coral	*Acanthurus nigrofuscus*	0.000	0.734	0.000	NA	0.000	0.000	196	0.050767	1
Coral.A.MA vs A.SG/Soft Coral	*Acanthurus pyroferus*	0.006	0.734	0.008	0.733	0.005	0.008	37	0.064553	0.608
Coral.A.MA vs A.SG/Soft Coral	*Acanthurus sp.*	0.001	0.734	0.004	0.192	0.000	0.001	78	0.078242	0.108
Coral.A.MA vs A.SG/Soft Coral	*Acanthurus thompsoni*	0.001	0.734	0.004	0.258	0.002	0.000	205	0.091059	0.606
Coral.A.MA vs A.SG/Soft Coral	*Acanthurus triostegus*	0.000	0.734	0.003	0.180	0.001	0.000	20	0.103787	0.54

Coral.A.MA vs A.SG/Soft Coral	*Ctenochaetus binotatus*	0.007	0.734	0.007	1.046	0.013	0.007	130	0.116361	0.999
Coral.A.MA vs A.SG/Soft Coral	*Ctenochaetus cyanocheilus*	0.001	0.734	0.003	0.180	0.001	0.000	33	0.128916	0.518
Coral.A.MA vs A.SG/Soft Coral	*Ctenochaetus sp.*	0.001	0.734	0.005	0.305	0.003	0.000	178	0.141055	0.519
Coral.A.MA vs A.SG/Soft Coral	*Ctenochaetus striatus*	0.009	0.734	0.006	1.415	0.026	0.016	209	0.153133	0.873
Coral.A.MA vs A.SG/Soft Coral	*Ctenochaetus tominiensis*	0.005	0.734	0.006	0.789	0.008	0.003	68	0.165151	0.072
Coral.A.MA vs A.SG/Soft Coral	*Naso brevirostris*	0.003	0.734	0.006	0.499	0.005	0.002	208	0.177065	0.023
Coral.A.MA vs A.SG/Soft Coral	*Naso hexacanthus*	0.003	0.734	0.005	0.599	0.006	0.001	34	0.188887	0.618
Coral.A.MA vs A.SG/Soft Coral	*Naso lituratus*	0.006	0.734	0.007	0.854	0.012	0.000	11	0.200672	0.029
Coral.A.MA vs A.SG/Soft Coral	*Naso minor*	0.003	0.734	0.005	0.559	0.003	0.003	132	0.212334	0.342
Coral.A.MA vs A.SG/Soft Coral	*Naso sp.*	0.001	0.734	0.004	0.302	0.003	0.000	137	0.223885	0.16
Coral.A.MA vs A.SG/Soft Coral	*Naso unicornis*	0.008	0.734	0.008	0.994	0.013	0.005	193	0.235137	0.001
Coral.A.MA vs A.SG/Soft Coral	*Naso vlamingii*	0.000	0.734	0.003	0.180	0.001	0.000	202	0.246325	0.946
Coral.A.MA vs A.SG/Soft Coral	*Zebrasoma scopas*	0.009	0.734	0.006	1.468	0.020	0.007	139	0.257337	0.001
Coral.A.MA vs A.SG/Soft Coral	*Zebrasoma veliferum*	0.001	0.734	0.003	0.180	0.001	0.000	76	0.268205	0.539
Coral.A.MA vs A.SG/Soft Coral	*Balistoides viridescens*	0.000	0.734	0.003	0.180	0.001	0.000	203	0.279047	0.527
Coral.A.MA vs A.SG/Soft Coral	*Caesio caerulaurea*	0.000	0.734	0.000	NA	0.000	0.000	98	0.289624	1
Coral.A.MA vs A.SG/Soft Coral	*Caesio sp.*	0.001	0.734	0.003	0.180	0.001	0.000	181	0.30019	0.546
Coral.A.MA vs A.SG/Soft Coral	*Caesio teres*	0.000	0.734	0.000	NA	0.000	0.000	172	0.310703	1
Coral.A.MA vs A.SG/Soft Coral	*Pterocaesio pisang*	0.001	0.734	0.004	0.192	0.000	0.002	118	0.321039	0.786
Coral.A.MA vs A.SG/Soft Coral	*Pterocaesio tile*	0.000	0.734	0.001	0.180	0.001	0.000	140	0.331342	0.966
Coral.A.MA vs A.SG/Soft Coral	*Caranx melampygus*	0.001	0.734	0.004	0.180	0.001	0.000	18	0.341597	0.555
Coral.A.MA vs A.SG/Soft Coral	*Caranx sp.*	0.001	0.734	0.003	0.180	0.001	0.000	195	0.351846	0.663
Coral.A.MA vs A.SG/Soft Coral	*Elagatis bipinnulata*	0.001	0.734	0.003	0.180	0.001	0.000	91	0.362066	0.505
Coral.A.MA vs A.SG/Soft Coral	*Chaetodon adiergastos*	0.000	0.734	0.002	0.180	0.001	0.000	133	0.37214	0.812
Coral.A.MA vs A.SG/Soft Coral	*Chaetodon auriga*	0.001	0.734	0.004	0.256	0.002	0.000	217	0.382162	0.283
Coral.A.MA vs A.SG/Soft Coral	*Chaetodon baronessa*	0.009	0.734	0.007	1.387	0.019	0.021	8	0.392153	0.337
Coral.A.MA vs A.SG/Soft Coral	*Chaetodon kleinii*	0.009	0.734	0.006	1.349	0.019	0.008	112	0.40188	0.869
Coral.A.MA vs A.SG/Soft Coral	*Chaetodon lineolatus*	0.001	0.734	0.005	0.263	0.001	0.001	232	0.41133	0.234
Coral.A.MA vs A.SG/Soft Coral	*Chaetodon lunula*	0.004	0.734	0.007	0.495	0.003	0.005	134	0.420716	0.025
Coral.A.MA vs A.SG/Soft Coral	*Chaetodon lunulatus*	0.010	0.734	0.006	1.660	0.022	0.005	86	0.430054	0.001
Coral.A.MA vs A.SG/Soft Coral	*Chaetodon melannotus*	0.002	0.734	0.005	0.365	0.004	0.000	74	0.439138	0.061

Coral.A.MA vs A.SG/Soft Coral	*Chaetodon mertensii*	0.001	0.734	0.005	0.277	0.000	0.003	84	0.448161	0.031
Coral.A.MA vs A.SG/Soft Coral	*Chaetodon ocellicaudus*	0.000	0.734	0.000	NA	0.000	0.000	100	0.457162	1
Coral.A.MA vs A.SG/Soft Coral	*Chaetodon octofasciatus*	0.001	0.734	0.005	0.192	0.000	0.002	159	0.466124	0.128
Coral.A.MA vs A.SG/Soft Coral	*Chaetodon ornatissimus*	0.002	0.734	0.005	0.374	0.003	0.001	197	0.474811	0.789
Coral.A.MA vs A.SG/Soft Coral	*Chaetodon pelewensis*	0.004	0.734	0.006	0.568	0.007	0.000	162	0.483393	0.003
Coral.A.MA vs A.SG/Soft Coral	*Chaetodon punctatofasciatus*	0.002	0.734	0.007	0.346	0.003	0.002	190	0.491964	0.366
Coral.A.MA vs A.SG/Soft Coral	*Chaetodon rafflesii*	0.004	0.734	0.007	0.560	0.007	0.001	15	0.500108	0.01
Coral.A.MA vs A.SG/Soft Coral	*Chaetodon sp.*	0.001	0.734	0.003	0.180	0.001	0.000	129	0.508229	0.808
Coral.A.MA vs A.SG/Soft Coral	*Chaetodon ulietensis*	0.000	0.734	0.000	NA	0.000	0.000	211	0.515957	1
Coral.A.MA vs A.SG/Soft Coral	*Chaetodon unimaculatus*	0.000	0.734	0.000	NA	0.000	0.000	122	0.523673	1
Coral.A.MA vs A.SG/Soft Coral	*Chaetodon vagabundus*	0.003	0.734	0.007	0.462	0.002	0.006	207	0.531324	0.665
Coral.A.MA vs A.SG/Soft Coral	*Chelmon sp.*	0.001	0.734	0.003	0.180	0.001	0.000	4	0.538923	0.572

Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
Coral/A.MA vs A.CR/A.RF	*Acanthurus nigricans*	0.000	0.665	0.002	0.179	0.001	0.000	217	0.014614	0.805
Coral/A.MA vs A.CR/A.RF	*Acanthurus nigricauda*	0.001	0.665	0.003	0.179	0.001	0.000	172	0.028012	0.395
Coral/A.MA vs A.CR/A.RF	*Acanthurus nigrofuscus*	0.000	0.665	0.000	NA	0.000	0.000	203	0.04092	1
Coral/A.MA vs A.CR/A.RF	*Acanthurus pyroferus*	0.004	0.665	0.007	0.646	0.005	0.005	98	0.053591	0.849
Coral/A.MA vs A.CR/A.RF	*Acanthurus sp.*	0.000	0.665	0.000	NA	0.000	0.000	37	0.06615	1
Coral/A.MA vs A.CR/A.RF	*Acanthurus thompsoni*	0.003	0.665	0.007	0.395	0.002	0.003	178	0.078707	0.038
Coral/A.MA vs A.CR/A.RF	*Acanthurus triostegus*	0.000	0.665	0.003	0.179	0.001	0.000	68	0.090877	0.433
Coral/A.MA vs A.CR/A.RF	*Ctenochaetus binotatus*	0.008	0.665	0.007	1.177	0.013	0.016	34	0.102941	0.974
Coral/A.MA vs A.CR/A.RF	*Ctenochaetus cyanocheilus*	0.001	0.665	0.003	0.179	0.001	0.000	151	0.114966	0.406
Coral/A.MA vs A.CR/A.RF	*Ctenochaetus sp.*	0.001	0.665	0.005	0.305	0.003	0.000	139	0.126865	0.454
Coral/A.MA vs A.CR/A.RF	*Ctenochaetus striatus*	0.006	0.665	0.006	0.997	0.026	0.022	33	0.138508	1
Coral/A.MA vs A.CR/A.RF	*Ctenochaetus tominiensis*	0.005	0.665	0.006	0.835	0.008	0.005	140	0.150091	0.091
Coral/A.MA vs A.CR/A.RF	*Naso brevirostris*	0.003	0.665	0.005	0.554	0.005	0.002	20	0.161662	0.133
Coral/A.MA vs A.CR/A.RF	*Naso hexacanthus*	0.005	0.665	0.007	0.705	0.006	0.005	8	0.173218	0.153
Coral/A.MA vs A.CR/A.RF	*Naso lituratus*	0.007	0.665	0.007	1.033	0.012	0.010	232	0.184622	0.018
Coral/A.MA vs A.CR/A.RF	*Naso minor*	0.002	0.665	0.004	0.579	0.003	0.003	18	0.195877	0.57
Coral/A.MA vs A.CR/A.RF	*Naso sp.*	0.001	0.665	0.004	0.302	0.003	0.000	130	0.206967	0.248
Coral/A.MA vs A.CR/A.RF	*Naso unicornis*	0.007	0.665	0.007	1.009	0.013	0.006	15	0.217941	0.041

Coral/A.MA vs A.CR/A.RF	*Naso vlamingii*	0.003	0.665	0.006	0.480	0.001	0.005	195	0.228905	0.034
Coral/A.MA vs A.CR/A.RF	*Zebrasoma scopas*	0.008	0.665	0.006	1.272	0.020	0.017	224	0.239829	0.277
Coral/A.MA vs A.CR/A.RF	*Zebrasoma veliferum*	0.001	0.665	0.003	0.179	0.001	0.000	162	0.250676	0.427
Coral/A.MA vs A.CR/A.RF	*Balistoides viridescens*	0.000	0.665	0.003	0.179	0.001	0.000	118	0.261382	0.426
Coral/A.MA vs A.CR/A.RF	*Caesio caerulaurea*	0.002	0.665	0.006	0.301	0.000	0.004	112	0.271826	0.055
Coral/A.MA vs A.CR/A.RF	*Caesio sp.*	0.001	0.665	0.003	0.179	0.001	0.000	208	0.282211	0.4
Coral/A.MA vs A.CR/A.RF	*Caesio teres*	0.001	0.665	0.005	0.301	0.000	0.003	89	0.291982	0.053
Coral/A.MA vs A.CR/A.RF	*Pterocaesio pisang*	0.002	0.665	0.005	0.301	0.000	0.003	92	0.301645	0.409
Coral/A.MA vs A.CR/A.RF	*Pterocaesio tile*	0.002	0.665	0.005	0.461	0.001	0.005	129	0.311135	0.023
Coral/A.MA vs A.CR/A.RF	*Caranx melampygus*	0.002	0.665	0.005	0.345	0.001	0.002	100	0.320576	0.141
Coral/A.MA vs A.CR/A.RF	*Caranx sp.*	0.002	0.665	0.005	0.350	0.001	0.003	206	0.330012	0.098
Coral/A.MA vs A.CR/A.RF	*Elagatis bipinnulata*	0.001	0.665	0.003	0.179	0.001	0.000	84	0.339281	0.404
Coral/A.MA vs A.CR/A.RF	*Chaetodon adiergastos*	0.002	0.665	0.005	0.350	0.001	0.003	190	0.348216	0.043
Coral/A.MA vs A.CR/A.RF	*Chaetodon auriga*	0.001	0.665	0.004	0.256	0.002	0.000	160	0.357055	0.311
Coral/A.MA vs A.CR/A.RF	*Chaetodon baronessa*	0.008	0.665	0.006	1.243	0.019	0.014	128	0.365796	0.936
Coral/A.MA vs A.CR/A.RF	*Chaetodon kleinii*	0.008	0.665	0.006	1.280	0.019	0.017	42	0.374516	0.897
Coral/A.MA vs A.CR/A.RF	*Chaetodon lineolatus*	0.001	0.665	0.004	0.179	0.001	0.000	188	0.38323	0.486
Coral/A.MA vs A.CR/A.RF	*Chaetodon lunula*	0.002	0.665	0.004	0.377	0.003	0.000	111	0.391924	0.739
Coral/A.MA vs A.CR/A.RF	*Chaetodon lunulatus*	0.008	0.665	0.006	1.364	0.022	0.015	93	0.400591	0.256
Coral/A.MA vs A.CR/A.RF	*Chaetodon melannotus*	0.002	0.665	0.005	0.365	0.004	0.000	86	0.409143	0.175
Coral/A.MA vs A.CR/A.RF	*Chaetodon mertensii*	0.000	0.665	0.000	NA	0.000	0.000	11	0.417692	1
Coral/A.MA vs A.CR/A.RF	*Chaetodon ocellicaudus*	0.003	0.665	0.006	0.447	0.000	0.005	193	0.426161	0.125
Coral/A.MA vs A.CR/A.RF	*Chaetodon octofasciatus*	0.000	0.665	0.000	NA	0.000	0.000	155	0.434346	1
Coral/A.MA vs A.CR/A.RF	*Chaetodon ornatissimus*	0.006	0.665	0.009	0.653	0.003	0.010	170	0.442443	0.01
Coral/A.MA vs A.CR/A.RF	*Chaetodon pelewensis*	0.004	0.665	0.006	0.568	0.007	0.000	164	0.450518	0.053
Coral/A.MA vs A.CR/A.RF	*Chaetodon punctatofasciatus*	0.003	0.665	0.006	0.542	0.003	0.005	55	0.45857	0.118
Coral/A.MA vs A.CR/A.RF	*Chaetodon rafflesii*	0.004	0.665	0.007	0.603	0.007	0.002	108	0.466458	0.08
Coral/A.MA vs A.CR/A.RF	*Chaetodon sp.*	0.001	0.665	0.003	0.179	0.001	0.000	12	0.474244	0.65
Coral/A.MA vs A.CR/A.RF	*Chaetodon ulietensis*	0.002	0.665	0.006	0.301	0.000	0.004	209	0.482026	0.052
Coral/A.MA vs A.CR/A.RF	*Chaetodon unimaculatus*	0.003	0.665	0.007	0.446	0.000	0.006	191	0.4897	0.007
Coral/A.MA vs A.CR/A.RF	*Chaetodon vagabundus*	0.004	0.665	0.006	0.623	0.002	0.006	104	0.497341	0.534

Coral/A.MA vs A.CR/A.RF	*Chelmon sp.*	0.001	0.665	0.003	0.179	0.001	0.000	77	0.504917	0.426

Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
A.SG/Soft Coral vs A.CR/A.RF	*Acanthurus nigricans*	0.000	0.705	0.000	NA	0.000	0.000	206	0.01665	1
A.SG/Soft Coral vs A.CR/A.RF	*Acanthurus nigricauda*	0.000	0.705	0.000	NA	0.000	0.000	196	0.032825	1
A.SG/Soft Coral vs A.CR/A.RF	*Acanthurus nigrofuscus*	0.000	0.705	0.000	NA	0.000	0.000	164	0.048793	1
A.SG/Soft Coral vs A.CR/A.RF	*Acanthurus pyroferus*	0.006	0.705	0.008	0.714	0.008	0.005	172	0.063776	0.579
A.SG/Soft Coral vs A.CR/A.RF	*Acanthurus sp.*	0.001	0.705	0.004	0.192	0.001	0.000	78	0.078361	0.331
A.SG/Soft Coral vs A.CR/A.RF	*Acanthurus thompsoni*	0.002	0.705	0.006	0.301	0.000	0.003	217	0.092883	0.21
A.SG/Soft Coral vs A.CR/A.RF	*Acanthurus triostegus*	0.000	0.705	0.000	NA	0.000	0.000	205	0.107123	1
A.SG/Soft Coral vs A.CR/A.RF	*Ctenochaetus binotatus*	0.008	0.705	0.007	1.157	0.007	0.016	33	0.120841	0.918
A.SG/Soft Coral vs A.CR/A.RF	*Ctenochaetus cyanocheilus*	0.000	0.705	0.000	NA	0.000	0.000	178	0.134058	1
A.SG/Soft Coral vs A.CR/A.RF	*Ctenochaetus sp.*	0.000	0.705	0.000	NA	0.000	0.000	130	0.146824	1
A.SG/Soft Coral vs A.CR/A.RF	*Ctenochaetus striatus*	0.009	0.705	0.007	1.278	0.016	0.022	140	0.159475	0.696
A.SG/Soft Coral vs A.CR/A.RF	*Ctenochaetus tominiensis*	0.004	0.705	0.006	0.560	0.003	0.005	11	0.171915	0.594
A.SG/Soft Coral vs A.CR/A.RF	*Naso brevirostris*	0.002	0.705	0.005	0.336	0.002	0.002	132	0.184108	0.605
A.SG/Soft Coral vs A.CR/A.RF	*Naso hexacanthus*	0.003	0.705	0.006	0.472	0.001	0.005	195	0.196135	0.601
A.SG/Soft Coral vs A.CR/A.RF	*Naso lituratus*	0.005	0.705	0.007	0.703	0.000	0.010	34	0.208145	0.398
A.SG/Soft Coral vs A.CR/A.RF	*Naso minor*	0.003	0.705	0.005	0.573	0.003	0.003	137	0.220144	0.477
A.SG/Soft Coral vs A.CR/A.RF	*Naso sp.*	0.000	0.705	0.000	NA	0.000	0.000	20	0.232107	1
A.SG/Soft Coral vs A.CR/A.RF	*Naso unicornis*	0.005	0.705	0.008	0.599	0.005	0.006	162	0.243925	0.681
A.SG/Soft Coral vs A.CR/A.RF	*Naso vlamingii*	0.002	0.705	0.006	0.446	0.000	0.005	8	0.255428	0.062
A.SG/Soft Coral vs A.CR/A.RF	*Zebrasoma scopas*	0.008	0.705	0.007	1.163	0.007	0.017	151	0.266893	0.066
A.SG/Soft Coral vs A.CR/A.RF	*Zebrasoma veliferum*	0.000	0.705	0.000	NA	0.000	0.000	193	0.278316	1
A.SG/Soft Coral vs A.CR/A.RF	*Balistoides viridescens*	0.000	0.705	0.000	NA	0.000	0.000	76	0.289601	1
A.SG/Soft Coral vs A.CR/A.RF	*Caesio caerulaurea*	0.002	0.705	0.006	0.301	0.000	0.004	37	0.300873	0.109
A.SG/Soft Coral vs A.CR/A.RF	*Caesio sp.*	0.000	0.705	0.000	NA	0.000	0.000	181	0.311718	1
A.SG/Soft Coral vs A.CR/A.RF	*Caesio teres*	0.001	0.705	0.005	0.301	0.000	0.003	74	0.322538	0.105
A.SG/Soft Coral vs A.CR/A.RF	*Pterocaesio pisang*	0.002	0.705	0.006	0.356	0.002	0.003	202	0.333187	0.239
A.SG/Soft Coral vs A.CR/A.RF	*Pterocaesio tile*	0.002	0.705	0.005	0.430	0.000	0.005	159	0.343815	0.032
A.SG/Soft Coral vs A.CR/A.RF	*Caranx melampygus*	0.001	0.705	0.004	0.301	0.000	0.002	91	0.354428	0.268
A.SG/Soft Coral vs A.CR/A.RF	*Caranx sp.*	0.001	0.705	0.004	0.301	0.000	0.003	133	0.364937	0.235

A.SG/Soft Coral vs A.CR/A.RF	*Elagatis bipinnulata*	0.000	0.705	0.000	NA	0.000	0.000	197	0.375365	1
A.SG/Soft Coral vs A.CR/A.RF	*Chaetodon adiergastos*	0.001	0.705	0.005	0.301	0.000	0.003	209	0.385337	0.135
A.SG/Soft Coral vs A.CR/A.RF	*Chaetodon auriga*	0.000	0.705	0.000	NA	0.000	0.000	134	0.395273	1
A.SG/Soft Coral vs A.CR/A.RF	*Chaetodon baronessa*	0.010	0.705	0.008	1.236	0.021	0.014	73	0.405134	0.192
A.SG/Soft Coral vs A.CR/A.RF	*Chaetodon kleinii*	0.008	0.705	0.007	1.154	0.008	0.017	136	0.414995	0.751
A.SG/Soft Coral vs A.CR/A.RF	*Chaetodon lineolatus*	0.001	0.705	0.003	0.192	0.001	0.000	89	0.424709	0.623
A.SG/Soft Coral vs A.CR/A.RF	*Chaetodon lunula*	0.002	0.705	0.007	0.340	0.005	0.000	232	0.43442	0.475
A.SG/Soft Coral vs A.CR/A.RF	*Chaetodon lunulatus*	0.008	0.705	0.008	1.037	0.005	0.015	211	0.444009	0.444
A.SG/Soft Coral vs A.CR/A.RF	*Chaetodon melannotus*	0.000	0.705	0.000	NA	0.000	0.000	160	0.452997	1
A.SG/Soft Coral vs A.CR/A.RF	*Chaetodon mertensii*	0.001	0.705	0.005	0.277	0.003	0.000	128	0.461815	0.265
A.SG/Soft Coral vs A.CR/A.RF	*Chaetodon ocellicaudus*	0.003	0.705	0.006	0.447	0.000	0.005	203	0.470622	0.132
A.SG/Soft Coral vs A.CR/A.RF	*Chaetodon octofasciatus*	0.001	0.705	0.005	0.192	0.002	0.000	224	0.479338	0.386
A.SG/Soft Coral vs A.CR/A.RF	*Chaetodon ornatissimus*	0.005	0.705	0.009	0.602	0.001	0.010	190	0.48803	0.02
A.SG/Soft Coral vs A.CR/A.RF	*Chaetodon pelewensis*	0.000	0.705	0.000	NA	0.000	0.000	92	0.49664	1
A.SG/Soft Coral vs A.CR/A.RF	*Chaetodon punctatofasciatus*	0.003	0.705	0.008	0.461	0.002	0.005	122	0.505026	0.121
A.SG/Soft Coral vs A.CR/A.RF	*Chaetodon rafflesii*	0.002	0.705	0.005	0.357	0.001	0.002	115	0.513392	0.723
A.SG/Soft Coral vs A.CR/A.RF	*Chaetodon sp.*	0.000	0.705	0.000	NA	0.000	0.000	55	0.521684	1
A.SG/Soft Coral vs A.CR/A.RF	*Chaetodon ulietensis*	0.002	0.705	0.006	0.301	0.000	0.004	77	0.529918	0.097
A.SG/Soft Coral vs A.CR/A.RF	*Chaetodon unimaculatus*	0.003	0.705	0.007	0.446	0.000	0.006	68	0.538072	0.015
A.SG/Soft Coral vs A.CR/A.RF	*Chaetodon vagabundus*	0.005	0.705	0.008	0.677	0.006	0.006	4	0.54591	0.163
A.SG/Soft Coral vs A.CR/A.RF	*Chelmon sp.*	0.000	0.705	0.000	NA	0.000	0.000	93	0.553726	1

B. Parrotfish SIMPER comparisons

Parrotfish SIMPER comparisons

Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
A.MG/A.Sand vs Rub/EAM	*Chlorurus bleekeri*	0.070	0.697	0.047	1.473	0.079	0.188	9	0.109	0.006
A.MG/A.Sand vs Rub/EAM	*Chlorurus bowersi*	0.052	0.697	0.055	0.947	0.020	0.098	1	0.209	0.001
A.MG/A.Sand vs Rub/EAM	*Chlorurus microrhinos*	0.000	0.697	0.000	NA	0.000	0.000	12	0.305	1
A.MG/A.Sand vs Rub/EAM	*Chlorurus sp.*	0.014	0.697	0.034	0.401	0.027	0.000	13	0.398	0.36
A.MG/A.Sand vs Rub/EAM	*Chlorurus spilurus*	0.040	0.697	0.042	0.959	0.055	0.057	2	0.472	0.207
A.MG/A.Sand vs Rub/EAM	*Hipposcarus longiceps*	0.000	0.697	0.000	NA	0.000	0.000	7	0.542	1
A.MG/A.Sand vs Rub/EAM	*Scarus chameleon*	0.049	0.697	0.107	0.459	0.086	0.022	11	0.612	0.132
A.MG/A.Sand vs Rub/EAM	*Scarus dimidiatus*	0.041	0.697	0.030	1.341	0.005	0.082	10	0.673	0.831
A.MG/A.Sand vs Rub/EAM	*Scarus flavipectoralis*	0.076	0.697	0.091	0.834	0.148	0.131	8	0.731	0.242
A.MG/A.Sand vs Rub/EAM	*Scarus forsteni*	0.043	0.697	0.058	0.729	0.032	0.065	5	0.789	0.058
A.MG/A.Sand vs Rub/EAM	*Scarus ghobban*	0.048	0.697	0.115	0.420	0.083	0.020	18	0.845	0.438
A.MG/A.Sand vs Rub/EAM	*Scarus hypselopterus*	0.067	0.697	0.091	0.736	0.094	0.107	16	0.897	0.112
A.MG/A.Sand vs Rub/EAM	*Scarus niger*	0.065	0.697	0.049	1.321	0.154	0.151	19	0.938	0.451
A.MG/A.Sand vs Rub/EAM	*Scarus prasiognathos*	0.000	0.697	0.000	NA	0.000	0.000	15	0.964	1
A.MG/A.Sand vs Rub/EAM	*Scarus psitticus*	0.018	0.697	0.036	0.491	0.029	0.009	4	0.983	0.771
A.MG/A.Sand vs Rub/EAM	*Scarus rivulatus*	0.036	0.697	0.080	0.458	0.067	0.010	17	1.000	0.695
A.MG/A.Sand vs Rub/EAM	*Scarus schlegeli*	0.012	0.697	0.036	0.323	0.023	0.000	3	1.000	0.474
A.MG/A.Sand vs Rub/EAM	*Scarus sp.*	0.039	0.697	0.060	0.656	0.069	0.021	6	1.000	0.884
A.MG/A.Sand vs Rub/EAM	*Scarus tricolor*	0.029	0.697	0.039	0.728	0.028	0.040	14	1.000	0.93
Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
A.MG/A.Sand vs Coral/A.MA	*Chlorurus bleekeri*	0.077	0.698	0.048	1.583	0.079	0.213	1	0.110	0.001
A.MG/A.Sand vs Coral/A.MA	*Chlorurus bowersi*	0.016	0.698	0.038	0.431	0.020	0.016	9	0.217	0.848
A.MG/A.Sand vs Coral/A.MA	*Chlorurus microrhinos*	0.000	0.698	0.000	NA	0.000	0.000	18	0.319	1
A.MG/A.Sand vs Coral/A.MA	*Chlorurus sp.*	0.014	0.698	0.034	0.401	0.027	0.000	8	0.419	0.334
A.MG/A.Sand vs Coral/A.MA	*Chlorurus spilurus*	0.037	0.698	0.049	0.759	0.055	0.038	13	0.517	0.275
A.MG/A.Sand vs Coral/A.MA	*Hipposcarus longiceps*	0.007	0.698	0.026	0.258	0.000	0.013	11	0.589	0.249
A.MG/A.Sand vs Coral/A.MA	*Scarus chameleon*	0.043	0.698	0.110	0.392	0.086	0.000	12	0.660	0.091

A.MG/A.Sand vs Coral/A.MA	*Scarus dimidiatus*	0.070	0.698	0.048	1.456	0.005	0.143	7	0.722	0.001
A.MG/A.Sand vs Coral/A.MA	*Scarus flavipectoralis*	0.075	0.698	0.100	0.750	0.148	0.071	16	0.783	0.223
A.MG/A.Sand vs Coral/A.MA	*Scarus forsteni*	0.020	0.698	0.056	0.353	0.032	0.010	5	0.837	0.787
A.MG/A.Sand vs Coral/A.MA	*Scarus ghobban*	0.050	0.698	0.116	0.430	0.083	0.024	19	0.874	0.406
A.MG/A.Sand vs Coral/A.MA	*Scarus hypselopterus*	0.049	0.698	0.107	0.462	0.094	0.011	10	0.902	0.444
A.MG/A.Sand vs Coral/A.MA	*Scarus niger*	0.068	0.698	0.052	1.317	0.154	0.250	17	0.927	0.132
A.MG/A.Sand vs Coral/A.MA	*Scarus prasiognathos*	0.000	0.698	0.000	NA	0.000	0.000	2	0.950	1
A.MG/A.Sand vs Coral/A.MA	*Scarus psitticus*	0.014	0.698	0.035	0.406	0.029	0.000	15	0.971	0.957
A.MG/A.Sand vs Coral/A.MA	*Scarus rivulatus*	0.043	0.698	0.081	0.529	0.067	0.027	4	0.990	0.503
A.MG/A.Sand vs Coral/A.MA	*Scarus schlegeli*	0.017	0.698	0.046	0.364	0.023	0.012	6	1.000	0.158
A.MG/A.Sand vs Coral/A.MA	*Scarus sp.*	0.071	0.698	0.058	1.239	0.069	0.141	3	1.000	0.003
A.MG/A.Sand vs Coral/A.MA	*Scarus tricolor*	0.026	0.698	0.044	0.597	0.028	0.032	14	1.000	0.998

Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
A.MG/A.Sand vs A.SG/Soft Coral	*Chlorurus bleekeri*	0.056	0.723	0.042	1.330	0.079	0.125	9	0.111	0.431
A.MG/A.Sand vs A.SG/Soft Coral	*Chlorurus bowersi*	0.016	0.723	0.037	0.441	0.020	0.015	11	0.221	0.834
A.MG/A.Sand vs A.SG/Soft Coral	*Chlorurus microrhinos*	0.000	0.723	0.000	NA	0.000	0.000	16	0.311	1
A.MG/A.Sand vs A.SG/Soft Coral	*Chlorurus sp.*	0.023	0.723	0.046	0.505	0.027	0.024	13	0.400	0.01
A.MG/A.Sand vs A.SG/Soft Coral	*Chlorurus spilurus*	0.035	0.723	0.045	0.778	0.055	0.032	12	0.487	0.453
A.MG/A.Sand vs A.SG/Soft Coral	*Hipposcarus longiceps*	0.000	0.723	0.000	NA	0.000	0.000	1	0.565	1
A.MG/A.Sand vs A.SG/Soft Coral	*Scarus chameleon*	0.049	0.723	0.112	0.434	0.086	0.015	19	0.634	0.024
A.MG/A.Sand vs A.SG/Soft Coral	*Scarus dimidiatus*	0.028	0.723	0.032	0.887	0.005	0.056	7	0.701	1
A.MG/A.Sand vs A.SG/Soft Coral	*Scarus flavipectoralis*	0.081	0.723	0.091	0.889	0.148	0.150	18	0.758	0.044
A.MG/A.Sand vs A.SG/Soft Coral	*Scarus forsteni*	0.029	0.723	0.063	0.459	0.032	0.031	5	0.806	0.327
A.MG/A.Sand vs A.SG/Soft Coral	*Scarus ghobban*	0.079	0.723	0.108	0.734	0.083	0.104	15	0.850	0.002
A.MG/A.Sand vs A.SG/Soft Coral	*Scarus hypselopterus*	0.063	0.723	0.098	0.646	0.094	0.078	10	0.890	0.04
A.MG/A.Sand vs A.SG/Soft Coral	*Scarus niger*	0.064	0.723	0.050	1.297	0.154	0.116	8	0.929	0.462
A.MG/A.Sand vs A.SG/Soft Coral	*Scarus prasiognathos*	0.000	0.723	0.000	NA	0.000	0.000	4	0.961	1
A.MG/A.Sand vs A.SG/Soft Coral	*Scarus psitticus*	0.032	0.723	0.046	0.687	0.029	0.046	2	0.984	0.072
A.MG/A.Sand vs A.SG/Soft Coral	*Scarus rivulatus*	0.065	0.723	0.076	0.852	0.067	0.093	17	1.000	0.003
A.MG/A.Sand vs A.SG/Soft Coral	*Scarus schlegeli*	0.012	0.723	0.036	0.323	0.023	0.000	3	1.000	0.479
A.MG/A.Sand vs A.SG/Soft Coral	*Scarus sp.*	0.041	0.723	0.065	0.631	0.069	0.022	6	1.000	0.92

A.MG/A.Sand vs A.SG/Soft Coral	*Scarus tricolor*	0.050	0.723	0.058	0.862	0.028	0.092	14	1.000	0.064

Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
A.MG/A.Sand vs A.CR/A.RF	*Chlorurus bleekeri*	0.065	0.697	0.040	1.625	0.079	0.181	9	0.109	0.053
A.MG/A.Sand vs A.CR/A.RF	*Chlorurus bowersi*	0.010	0.697	0.034	0.294	0.020	0.000	1	0.203	0.937
A.MG/A.Sand vs A.CR/A.RF	*Chlorurus microrhinos*	0.020	0.697	0.047	0.424	0.000	0.040	12	0.290	0.013
A.MG/A.Sand vs A.CR/A.RF	*Chlorurus sp.*	0.014	0.697	0.034	0.401	0.027	0.000	13	0.373	0.381
A.MG/A.Sand vs A.CR/A.RF	*Chlorurus spilurus*	0.037	0.697	0.041	0.908	0.055	0.044	7	0.455	0.356
A.MG/A.Sand vs A.CR/A.RF	*Hipposcarus longiceps*	0.000	0.697	0.000	NA	0.000	0.000	11	0.528	1
A.MG/A.Sand vs A.CR/A.RF	*Scarus chameleon*	0.057	0.697	0.103	0.560	0.086	0.052	19	0.592	0.057
A.MG/A.Sand vs A.CR/A.RF	*Scarus dimidiatus*	0.024	0.697	0.030	0.809	0.005	0.048	16	0.653	1
A.MG/A.Sand vs A.CR/A.RF	*Scarus flavipectoralis*	0.076	0.697	0.098	0.779	0.148	0.085	18	0.713	0.225
A.MG/A.Sand vs A.CR/A.RF	*Scarus forsteni*	0.027	0.697	0.057	0.470	0.032	0.027	15	0.767	0.409
A.MG/A.Sand vs A.CR/A.RF	*Scarus ghobban*	0.051	0.697	0.115	0.440	0.083	0.025	5	0.820	0.373
A.MG/A.Sand vs A.CR/A.RF	*Scarus hypselopterus*	0.061	0.697	0.100	0.609	0.094	0.065	10	0.859	0.212
A.MG/A.Sand vs A.CR/A.RF	*Scarus niger*	0.058	0.697	0.042	1.390	0.154	0.189	8	0.894	0.819
A.MG/A.Sand vs A.CR/A.RF	*Scarus prasiognathos*	0.008	0.697	0.025	0.301	0.000	0.015	17	0.927	0.116
A.MG/A.Sand vs A.CR/A.RF	*Scarus psitticus*	0.038	0.697	0.049	0.762	0.029	0.061	3	0.955	0.043
A.MG/A.Sand vs A.CR/A.RF	*Scarus rivulatus*	0.042	0.697	0.083	0.509	0.067	0.025	4	0.975	0.509
A.MG/A.Sand vs A.CR/A.RF	*Scarus schlegeli*	0.023	0.697	0.042	0.547	0.023	0.028	2	0.989	0.077
A.MG/A.Sand vs A.CR/A.RF	*Scarus sp.*	0.042	0.697	0.061	0.683	0.069	0.030	14	1.000	0.846
A.MG/A.Sand vs A.CR/A.RF	*Scarus tricolor*	0.045	0.697	0.046	0.986	0.028	0.082	6	1.000	0.365

Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
Rub/EAM vs Coral/A.MA	*Chlorurus bleekeri*	0.046	0.561	0.035	1.313	0.188	0.213	13	0.123	0.954
Rub/EAM vs Coral/A.MA	*Chlorurus bowersi*	0.050	0.561	0.053	0.943	0.098	0.016	18	0.243	0.001
Rub/EAM vs Coral/A.MA	*Chlorurus microrhinos*	0.000	0.561	0.000	NA	0.000	0.000	9	0.347	1
Rub/EAM vs Coral/A.MA	*Chlorurus sp.*	0.000	0.561	0.000	NA	0.000	0.000	12	0.442	1
Rub/EAM vs Coral/A.MA	*Chlorurus spilurus*	0.037	0.561	0.043	0.866	0.057	0.038	8	0.536	0.317
Rub/EAM vs Coral/A.MA	*Hipposcarus longiceps*	0.007	0.561	0.026	0.258	0.000	0.013	2	0.625	0.31
Rub/EAM vs Coral/A.MA	*Scarus chameleon*	0.011	0.561	0.026	0.426	0.022	0.000	1	0.706	0.917
Rub/EAM vs Coral/A.MA	*Scarus dimidiatus*	0.053	0.561	0.038	1.401	0.082	0.143	5	0.773	0.095
Rub/EAM vs Coral/A.MA	*Scarus flavipectoralis*	0.059	0.561	0.043	1.375	0.131	0.071	10	0.833	0.714

Rub/EAM vs Coral/A.MA	*Scarus forsteni*	0.034	0.561	0.043	0.789	0.065	0.010	19	0.885	0.189
Rub/EAM vs Coral/A.MA	*Scarus ghobban*	0.019	0.561	0.034	0.558	0.020	0.024	11	0.919	0.997
Rub/EAM vs Coral/A.MA	*Scarus hypselopterus*	0.053	0.561	0.033	1.588	0.107	0.011	16	0.950	0.258
Rub/EAM vs Coral/A.MA	*Scarus niger*	0.069	0.561	0.050	1.377	0.151	0.250	7	0.969	0.188
Rub/EAM vs Coral/A.MA	*Scarus prasiognathos*	0.000	0.561	0.000	NA	0.000	0.000	6	0.981	1
Rub/EAM vs Coral/A.MA	*Scarus psitticus*	0.005	0.561	0.016	0.288	0.009	0.000	17	0.992	0.996
Rub/EAM vs Coral/A.MA	*Scarus rivulatus*	0.017	0.561	0.039	0.448	0.010	0.027	15	1.000	0.996
Rub/EAM vs Coral/A.MA	*Scarus schlegeli*	0.006	0.561	0.033	0.179	0.000	0.012	3	1.000	0.782
Rub/EAM vs Coral/A.MA	*Scarus sp.*	0.067	0.561	0.054	1.254	0.021	0.141	4	1.000	0.03
Rub/EAM vs Coral/A.MA	*Scarus tricolor*	0.029	0.561	0.037	0.783	0.040	0.032	14	1.000	0.963
Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
Rub/EAM vs A.SG/Soft Coral	*Chlorurus bleekeri*	0.053	0.604	0.044	1.217	0.188	0.125	13	0.104	0.622
Rub/EAM vs A.SG/Soft Coral	*Chlorurus bowersi*	0.050	0.604	0.052	0.952	0.098	0.015	9	0.199	0.001
Rub/EAM vs A.SG/Soft Coral	*Chlorurus microrhinos*	0.000	0.604	0.000	NA	0.000	0.000	1	0.288	1
Rub/EAM vs A.SG/Soft Coral	*Chlorurus sp.*	0.012	0.604	0.039	0.309	0.000	0.024	11	0.375	0.43
Rub/EAM vs A.SG/Soft Coral	*Chlorurus spilurus*	0.034	0.604	0.039	0.890	0.057	0.032	2	0.457	0.493
Rub/EAM vs A.SG/Soft Coral	*Hipposcarus longiceps*	0.000	0.604	0.000	NA	0.000	0.000	19	0.539	1
Rub/EAM vs A.SG/Soft Coral	*Scarus chameleon*	0.018	0.604	0.043	0.409	0.022	0.015	16	0.617	0.712
Rub/EAM vs A.SG/Soft Coral	*Scarus dimidiatus*	0.037	0.604	0.028	1.320	0.082	0.056	12	0.693	0.969
Rub/EAM vs A.SG/Soft Coral	*Scarus flavipectoralis*	0.058	0.604	0.043	1.345	0.131	0.150	10	0.758	0.759
Rub/EAM vs A.SG/Soft Coral	*Scarus forsteni*	0.040	0.604	0.048	0.825	0.065	0.031	8	0.819	0.08
Rub/EAM vs A.SG/Soft Coral	*Scarus ghobban*	0.053	0.604	0.058	0.909	0.020	0.104	5	0.876	0.349
Rub/EAM vs A.SG/Soft Coral	*Scarus hypselopterus*	0.046	0.604	0.033	1.376	0.107	0.078	15	0.919	0.405
Rub/EAM vs A.SG/Soft Coral	*Scarus niger*	0.063	0.604	0.048	1.311	0.151	0.116	18	0.951	0.551
Rub/EAM vs A.SG/Soft Coral	*Scarus prasiognathos*	0.000	0.604	0.000	NA	0.000	0.000	7	0.980	1
Rub/EAM vs A.SG/Soft Coral	*Scarus psitticus*	0.025	0.604	0.041	0.615	0.009	0.046	4	1.000	0.365
Rub/EAM vs A.SG/Soft Coral	*Scarus rivulatus*	0.047	0.604	0.056	0.846	0.010	0.093	3	1.000	0.337
Rub/EAM vs A.SG/Soft Coral	*Scarus schlegeli*	0.000	0.604	0.000	NA	0.000	0.000	6	1.000	1
Rub/EAM vs A.SG/Soft Coral	*Scarus sp.*	0.019	0.604	0.040	0.479	0.021	0.022	14	1.000	1
Rub/EAM vs A.SG/Soft Coral	*Scarus tricolor*	0.050	0.604	0.052	0.953	0.040	0.092	17	1.000	0.161
Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p

Rub/EAM vs A.CR/A.RF	*Chlorurus bleekeri*	0.040	0.562	0.033	1.199	0.188	0.181	9	0.103	0.983
Rub/EAM vs A.CR/A.RF	*Chlorurus bowersi*	0.049	0.562	0.055	0.895	0.098	0.000	13	0.202	0.001
Rub/EAM vs A.CR/A.RF	*Chlorurus microrhinos*	0.020	0.562	0.047	0.424	0.000	0.040	2	0.289	0.013
Rub/EAM vs A.CR/A.RF	*Chlorurus sp.*	0.000	0.562	0.000	NA	0.000	0.000	12	0.373	1
Rub/EAM vs A.CR/A.RF	*Chlorurus spilurus*	0.035	0.562	0.035	0.985	0.057	0.044	19	0.449	0.494
Rub/EAM vs A.CR/A.RF	*Hipposcarus longiceps*	0.000	0.562	0.000	NA	0.000	0.000	1	0.519	1
Rub/EAM vs A.CR/A.RF	*Scarus chameleon*	0.030	0.562	0.037	0.800	0.022	0.052	8	0.586	0.337
Rub/EAM vs A.CR/A.RF	*Scarus dimidiatus*	0.037	0.562	0.028	1.332	0.082	0.048	10	0.651	0.906
Rub/EAM vs A.CR/A.RF	*Scarus flavipectoralis*	0.058	0.562	0.044	1.323	0.131	0.085	5	0.712	0.685
Rub/EAM vs A.CR/A.RF	*Scarus forsteni*	0.037	0.562	0.043	0.856	0.065	0.027	15	0.770	0.186
Rub/EAM vs A.CR/A.RF	*Scarus ghobban*	0.019	0.562	0.032	0.607	0.020	0.025	7	0.823	0.976
Rub/EAM vs A.CR/A.RF	*Scarus hypselopterus*	0.047	0.562	0.033	1.445	0.107	0.065	18	0.862	0.305
Rub/EAM vs A.CR/A.RF	*Scarus niger*	0.056	0.562	0.041	1.348	0.151	0.189	3	0.897	0.843
Rub/EAM vs A.CR/A.RF	*Scarus prasiognathos*	0.008	0.562	0.025	0.301	0.000	0.015	11	0.932	0.116
Rub/EAM vs A.CR/A.RF	*Scarus psitticus*	0.032	0.562	0.047	0.682	0.009	0.061	16	0.961	0.167
Rub/EAM vs A.CR/A.RF	*Scarus rivulatus*	0.017	0.562	0.043	0.388	0.010	0.025	17	0.986	0.961
Rub/EAM vs A.CR/A.RF	*Scarus schlegeli*	0.014	0.562	0.032	0.445	0.000	0.028	14	1.000	0.38
Rub/EAM vs A.CR/A.RF	*Scarus sp.*	0.022	0.562	0.036	0.600	0.021	0.030	4	1.000	0.994
Rub/EAM vs A.CR/A.RF	*Scarus tricolor*	0.042	0.562	0.040	1.060	0.040	0.082	6	1.000	0.502

Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
Coral.A.MA vs A.SG/Soft Coral	*Chlorurus bleekeri*	0.059	0.644	0.043	1.368	0.213	0.125	13	0.120	0.12
Coral.A.MA vs A.SG/Soft Coral	*Chlorurus bowersi*	0.014	0.644	0.030	0.471	0.016	0.015	18	0.230	0.961
Coral.A.MA vs A.SG/Soft Coral	*Chlorurus microrhinos*	0.000	0.644	0.000	NA	0.000	0.000	9	0.331	1
Coral.A.MA vs A.SG/Soft Coral	*Chlorurus sp.*	0.012	0.644	0.039	0.310	0.000	0.024	1	0.423	0.454
Coral.A.MA vs A.SG/Soft Coral	*Chlorurus spilurus*	0.029	0.644	0.046	0.647	0.038	0.032	8	0.514	0.856
Coral.A.MA vs A.SG/Soft Coral	*Hipposcarus longiceps*	0.007	0.644	0.026	0.258	0.013	0.000	11	0.598	0.328
Coral.A.MA vs A.SG/Soft Coral	*Scarus chameleon*	0.007	0.644	0.039	0.192	0.000	0.015	16	0.676	0.993
Coral.A.MA vs A.SG/Soft Coral	*Scarus dimidiatus*	0.059	0.644	0.043	1.375	0.143	0.056	19	0.754	0.001
Coral.A.MA vs A.SG/Soft Coral	*Scarus flavipectoralis*	0.065	0.644	0.050	1.319	0.071	0.150	12	0.817	0.59
Coral.A.MA vs A.SG/Soft Coral	*Scarus forsteni*	0.019	0.644	0.043	0.444	0.010	0.031	5	0.862	0.869
Coral.A.MA vs A.SG/Soft Coral	*Scarus ghobban*	0.054	0.644	0.059	0.905	0.024	0.104	15	0.898	0.32

Coral.A.MA vs A.SG/Soft Coral	*Scarus hypselopterus*	0.041	0.644	0.043	0.933	0.011	0.078	10	0.928	0.685
Coral.A.MA vs A.SG/Soft Coral	*Scarus niger*	0.077	0.644	0.054	1.430	0.250	0.116	2	0.950	0.001
Coral.A.MA vs A.SG/Soft Coral	*Scarus prasiognathos*	0.000	0.644	0.000	NA	0.000	0.000	4	0.969	1
Coral.A.MA vs A.SG/Soft Coral	*Scarus psitticus*	0.023	0.644	0.042	0.552	0.000	0.046	7	0.980	0.495
Coral.A.MA vs A.SG/Soft Coral	*Scarus rivulatus*	0.051	0.644	0.057	0.888	0.027	0.093	6	0.991	0.147
Coral.A.MA vs A.SG/Soft Coral	*Scarus schlegeli*	0.006	0.644	0.033	0.180	0.012	0.000	17	1.000	0.881
Coral.A.MA vs A.SG/Soft Coral	*Scarus sp.*	0.071	0.644	0.056	1.264	0.141	0.022	3	1.000	0.001
Coral.A.MA vs A.SG/Soft Coral	*Scarus tricolor*	0.050	0.644	0.056	0.888	0.032	0.092	14	1.000	0.037

Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
Coral/A.MA vs A.CR/A.RF	*Chlorurus bleekeri*	0.040	0.561	0.030	1.340	0.213	0.181	18	0.120	0.994
Coral/A.MA vs A.CR/A.RF	*Chlorurus bowersi*	0.008	0.561	0.024	0.320	0.016	0.000	8	0.227	0.976
Coral/A.MA vs A.CR/A.RF	*Chlorurus microrhinos*	0.020	0.561	0.047	0.424	0.000	0.040	9	0.319	0.013
Coral/A.MA vs A.CR/A.RF	*Chlorurus sp.*	0.000	0.561	0.000	NA	0.000	0.000	13	0.407	1
Coral/A.MA vs A.CR/A.RF	*Chlorurus spilurus*	0.033	0.561	0.042	0.791	0.038	0.044	19	0.486	0.548
Coral/A.MA vs A.CR/A.RF	*Hipposcarus longiceps*	0.007	0.561	0.026	0.258	0.013	0.000	1	0.558	0.31
Coral/A.MA vs A.CR/A.RF	*Scarus chameleon*	0.026	0.561	0.037	0.704	0.000	0.052	12	0.619	0.474
Coral/A.MA vs A.CR/A.RF	*Scarus dimidiatus*	0.060	0.561	0.044	1.367	0.143	0.048	5	0.678	0.015
Coral/A.MA vs A.CR/A.RF	*Scarus flavipectoralis*	0.051	0.561	0.047	1.089	0.071	0.085	15	0.733	0.967
Coral/A.MA vs A.CR/A.RF	*Scarus forsteni*	0.017	0.561	0.033	0.514	0.010	0.027	7	0.780	0.798
Coral/A.MA vs A.CR/A.RF	*Scarus ghobban*	0.021	0.561	0.037	0.575	0.024	0.025	16	0.823	0.979
Coral/A.MA vs A.CR/A.RF	*Scarus hypselopterus*	0.035	0.561	0.043	0.811	0.011	0.065	11	0.861	0.866
Coral/A.MA vs A.CR/A.RF	*Scarus niger*	0.050	0.561	0.037	1.343	0.250	0.189	3	0.896	0.987
Coral/A.MA vs A.CR/A.RF	*Scarus prasiognathos*	0.008	0.561	0.025	0.301	0.000	0.015	17	0.931	0.116
Coral/A.MA vs A.CR/A.RF	*Scarus psitticus*	0.031	0.561	0.048	0.637	0.000	0.061	10	0.961	0.157
Coral/A.MA vs A.CR/A.RF	*Scarus rivulatus*	0.024	0.561	0.051	0.470	0.027	0.025	2	0.974	0.96
Coral/A.MA vs A.CR/A.RF	*Scarus schlegeli*	0.019	0.561	0.043	0.451	0.012	0.028	14	0.988	0.121
Coral/A.MA vs A.CR/A.RF	*Scarus sp.*	0.067	0.561	0.054	1.238	0.141	0.030	6	1.000	0.032
Coral/A.MA vs A.CR/A.RF	*Scarus tricolor*	0.044	0.561	0.044	1.008	0.032	0.082	4	1.000	0.374

Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
A.SG/Soft Coral vs A.CR/A.RF	*Chlorurus bleekeri*	0.048	0.625	0.037	1.292	0.125	0.181	9	0.103	0.885
A.SG/Soft Coral vs A.CR/A.RF	*Chlorurus bowersi*	0.008	0.625	0.022	0.345	0.015	0.000	13	0.200	0.979

A.SG/Soft Coral vs A.CR/A.RF	*Chlorurus microrhinos*	0.020	0.625	0.047	0.424	0.000	0.040	19	0.289	0.013
A.SG/Soft Coral vs A.CR/A.RF	*Chlorurus sp.*	0.012	0.625	0.039	0.309	0.024	0.000	11	0.374	0.431
A.SG/Soft Coral vs A.CR/A.RF	*Chlorurus spilurus*	0.030	0.625	0.036	0.820	0.032	0.044	16	0.457	0.721
A.SG/Soft Coral vs A.CR/A.RF	*Hipposcarus longiceps*	0.000	0.625	0.000	NA	0.000	0.000	1	0.534	1
A.SG/Soft Coral vs A.CR/A.RF	*Scarus chameleon*	0.032	0.625	0.047	0.673	0.015	0.052	12	0.606	0.341
A.SG/Soft Coral vs A.CR/A.RF	*Scarus dimidiatus*	0.033	0.625	0.030	1.096	0.056	0.048	15	0.673	0.995
A.SG/Soft Coral vs A.CR/A.RF	*Scarus flavipectoralis*	0.064	0.625	0.049	1.309	0.150	0.085	8	0.725	0.433
A.SG/Soft Coral vs A.CR/A.RF	*Scarus forsteni*	0.026	0.625	0.045	0.569	0.031	0.027	7	0.776	0.475
A.SG/Soft Coral vs A.CR/A.RF	*Scarus ghobban*	0.053	0.625	0.058	0.920	0.104	0.025	5	0.824	0.317
A.SG/Soft Coral vs A.CR/A.RF	*Scarus hypselopterus*	0.046	0.625	0.041	1.122	0.078	0.065	10	0.864	0.425
A.SG/Soft Coral vs A.CR/A.RF	*Scarus niger*	0.061	0.625	0.042	1.443	0.116	0.189	18	0.902	0.678
A.SG/Soft Coral vs A.CR/A.RF	*Scarus prasiognathos*	0.008	0.625	0.025	0.301	0.000	0.015	3	0.934	0.116
A.SG/Soft Coral vs A.CR/A.RF	*Scarus psitticus*	0.041	0.625	0.049	0.839	0.046	0.061	17	0.956	0.012
A.SG/Soft Coral vs A.CR/A.RF	*Scarus rivulatus*	0.052	0.625	0.059	0.877	0.093	0.025	4	0.975	0.225
A.SG/Soft Coral vs A.CR/A.RF	*Scarus schlegeli*	0.014	0.625	0.032	0.445	0.000	0.028	2	0.988	0.307
A.SG/Soft Coral vs A.CR/A.RF	*Scarus sp.*	0.023	0.625	0.045	0.517	0.022	0.030	14	1.000	0.999
A.SG/Soft Coral vs A.CR/A.RF	*Scarus tricolor*	0.056	0.625	0.049	1.130	0.092	0.082	6	1.000	0.037

C. Wrasse SIMPER comparisons

Wrasse SIMPER comparisons										
Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
A.MG/A.Sand vs Rub/EAM	*Anampses caeruleopunctatus*	0.000	0.851	0.000	NA	0.000	0.000	41	0.078	1
A.MG/A.Sand vs Rub/EAM	*Anampses meleagrides*	0.000	0.851	0.000	NA	0.000	0.000	52	0.148	1
A.MG/A.Sand vs Rub/EAM	*Anampses sp.*	0.012	0.851	0.031	0.398	0.015	0.010	50	0.209	0.952
A.MG/A.Sand vs Rub/EAM	*Anampses twistii*	0.018	0.851	0.050	0.353	0.014	0.023	14	0.268	0.324
A.MG/A.Sand vs Rub/EAM	*Bodianus dictynna*	0.037	0.851	0.086	0.426	0.000	0.074	12	0.326	0.016
A.MG/A.Sand vs Rub/EAM	*Bodianus mesothorax*	0.045	0.851	0.067	0.678	0.016	0.084	16	0.382	0.29
A.MG/A.Sand vs Rub/EAM	*Bodianus sp.*	0.000	0.851	0.000	NA	0.000	0.000	21	0.437	1
A.MG/A.Sand vs Rub/EAM	*Cheilinus chlorourus*	0.026	0.851	0.057	0.449	0.026	0.030	6	0.490	0.474
A.MG/A.Sand vs Rub/EAM	*Cheilinus fasciatus*	0.033	0.851	0.079	0.421	0.025	0.046	11	0.540	0.094
A.MG/A.Sand vs Rub/EAM	*Cheilinus oxycephalus*	0.002	0.851	0.012	0.192	0.004	0.000	15	0.587	0.969
A.MG/A.Sand vs Rub/EAM	*Cheilinus trilobatus*	0.042	0.851	0.064	0.658	0.079	0.012	5	0.631	0.349
A.MG/A.Sand vs Rub/EAM	*Cheilio inermis*	0.049	0.851	0.074	0.663	0.075	0.035	9	0.670	0.026
A.MG/A.Sand vs Rub/EAM	*Choerodon anchorago*	0.000	0.851	0.000	NA	0.000	0.000	28	0.701	1
A.MG/A.Sand vs Rub/EAM	*Choerodon sp.*	0.050	0.851	0.064	0.784	0.100	0.000	45	0.732	0.01
A.MG/A.Sand vs Rub/EAM	*Coris batuensis*	0.041	0.851	0.057	0.711	0.081	0.000	8	0.762	0.368
A.MG/A.Sand vs Rub/EAM	*Coris gaimard*	0.048	0.851	0.074	0.653	0.007	0.094	19	0.789	0.021
A.MG/A.Sand vs Rub/EAM	*Epibulus brevis*	0.012	0.851	0.043	0.272	0.023	0.000	37	0.813	0.463
A.MG/A.Sand vs Rub/EAM	*Epibulus insidiator*	0.000	0.851	0.000	NA	0.000	0.000	27	0.836	1
A.MG/A.Sand vs Rub/EAM	*Gomphosus varius*	0.023	0.851	0.055	0.419	0.000	0.046	26	0.857	0.102
A.MG/A.Sand vs Rub/EAM	*Halichoeres chrysus*	0.000	0.851	0.000	NA	0.000	0.000	4	0.878	1
A.MG/A.Sand vs Rub/EAM	*Halichoeres hortulanus*	0.046	0.851	0.064	0.723	0.031	0.078	39	0.896	0.111
A.MG/A.Sand vs Rub/EAM	*Halichoeres marginatus*	0.000	0.851	0.000	NA	0.000	0.000	25	0.911	1
A.MG/A.Sand vs Rub/EAM	*Halichoeres melanurus*	0.008	0.851	0.023	0.338	0.016	0.000	3	0.926	0.534
A.MG/A.Sand vs Rub/EAM	*Halichoeres nigrescens*	0.000	0.851	0.000	NA	0.000	0.000	17	0.939	1
A.MG/A.Sand vs Rub/EAM	*Halichoeres podostigma*	0.013	0.851	0.033	0.399	0.027	0.000	47	0.950	0.362
A.MG/A.Sand vs Rub/EAM	*Halichoeres prosopeion*	0.018	0.851	0.040	0.450	0.024	0.015	23	0.959	0.402
A.MG/A.Sand vs Rub/EAM	*Halichoeres richmondi*	0.020	0.851	0.048	0.407	0.021	0.022	36	0.967	0.143

A.MG/A.Sand vs Rub/EAM	*Halichoeres scapularis*	0.027	0.851	0.049	0.552	0.054	0.000	40	0.976	0.653
A.MG/A.Sand vs Rub/EAM	*Halichoeres sp.*	0.000	0.851	0.000	NA	0.000	0.000	30	0.983	1
A.MG/A.Sand vs Rub/EAM	*Hemigymnus fasciatus*	0.006	0.851	0.020	0.301	0.000	0.012	38	0.987	0.945
A.MG/A.Sand vs Rub/EAM	*Hemigymnus melapterus*	0.000	0.851	0.000	NA	0.000	0.000	34	0.991	1
A.MG/A.Sand vs Rub/EAM	*Hologymnosus annulatus*	0.003	0.851	0.016	0.192	0.006	0.000	32	0.995	0.37
A.MG/A.Sand vs Rub/EAM	*Hologymnosus sp.*	0.002	0.851	0.012	0.192	0.005	0.000	33	0.997	0.774
A.MG/A.Sand vs Rub/EAM	*Labrichthys unilineatus*	0.003	0.851	0.018	0.192	0.007	0.000	10	1.000	0.998
A.MG/A.Sand vs Rub/EAM	*Labropsis manabei*	0.000	0.851	0.000	NA	0.000	0.000	1	1.000	1
A.MG/A.Sand vs Rub/EAM	*Labropsis xanthonota*	0.007	0.851	0.026	0.276	0.014	0.000	2	1.000	0.283
A.MG/A.Sand vs Rub/EAM	*Macropharyngodon meleagris*	0.020	0.851	0.052	0.393	0.013	0.030	7	1.000	0.798
A.MG/A.Sand vs Rub/EAM	*Macropharyngodon negrosensis*	0.004	0.851	0.019	0.192	0.007	0.000	13	1.000	0.469
A.MG/A.Sand vs Rub/EAM	*Novaculichthys taeniourus*	0.015	0.851	0.034	0.446	0.020	0.012	18	1.000	0.474
A.MG/A.Sand vs Rub/EAM	*Oxycheilinus celebicus*	0.007	0.851	0.025	0.277	0.014	0.000	20	1.000	0.549
A.MG/A.Sand vs Rub/EAM	*Oxycheilinus digramma*	0.066	0.851	0.065	1.023	0.116	0.047	22	1.000	0.308
A.MG/A.Sand vs Rub/EAM	*Oxycheilinus sp.*	0.000	0.851	0.000	NA	0.000	0.000	24	1.000	1
A.MG/A.Sand vs Rub/EAM	*Oxycheilinus unifasciatus*	0.000	0.851	0.000	NA	0.000	0.000	29	1.000	1
A.MG/A.Sand vs Rub/EAM	*Pseudocheilinus hexataenia*	0.000	0.851	0.000	NA	0.000	0.000	31	1.000	1
A.MG/A.Sand vs Rub/EAM	*Pseudodax moluccanus*	0.026	0.851	0.085	0.301	0.000	0.051	35	1.000	0.11
A.MG/A.Sand vs Rub/EAM	*Stethojulis bandanensis*	0.000	0.851	0.000	NA	0.000	0.000	42	1.000	1
A.MG/A.Sand vs Rub/EAM	*Stethojulis interrupta*	0.009	0.851	0.032	0.277	0.018	0.000	43	1.000	0.818
A.MG/A.Sand vs Rub/EAM	*Stethojulis strigiventer*	0.000	0.851	0.000	NA	0.000	0.000	44	1.000	1
A.MG/A.Sand vs Rub/EAM	*Thalassoma amblycephalum*	0.000	0.851	0.000	NA	0.000	0.000	46	1.000	1
A.MG/A.Sand vs Rub/EAM	*Thalassoma hardwicke*	0.052	0.851	0.093	0.567	0.000	0.105	48	1.000	0.059
A.MG/A.Sand vs Rub/EAM	*Thalassoma jansenii*	0.000	0.851	0.000	NA	0.000	0.000	49	1.000	1
A.MG/A.Sand vs Rub/EAM	*Thalassoma lunare*	0.059	0.851	0.039	1.512	0.141	0.173	51	1.000	0.019

Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
A.MG/A.Sand vs Coral/A.MA	*Anampses caeruleopunctatus*	0.002	0.821	0.011	0.179	0.000	0.004	41	0.076	0.52
A.MG/A.Sand vs Coral/A.MA	*Anampses meleagrides*	0.009	0.821	0.028	0.342	0.015	0.005	6	0.138	0.035
A.MG/A.Sand vs Coral/A.MA	*Anampses sp.*	0.043	0.821	0.042	1.047	0.087	0.000	50	0.194	0.001
A.MG/A.Sand vs Coral/A.MA	*Anampses twistii*	0.012	0.821	0.043	0.280	0.000	0.024	3	0.247	0.562
A.MG/A.Sand vs Coral/A.MA	*Bodianus dictynna*	0.010	0.821	0.027	0.371	0.020	0.000	21	0.297	0.628

A.MG/A.Sand vs Coral/A.MA	*Bodianus mesothorax*	0.051	0.821	0.041	1.235	0.014	0.106	11	0.344	0.031
A.MG/A.Sand vs Coral/A.MA	*Bodianus sp.*	0.002	0.821	0.013	0.179	0.000	0.005	16	0.389	0.52
A.MG/A.Sand vs Coral/A.MA	*Cheilinus chlorourus*	0.034	0.821	0.053	0.648	0.062	0.013	34	0.434	0.097
A.MG/A.Sand vs Coral/A.MA	*Cheilinus fasciatus*	0.005	0.821	0.025	0.213	0.011	0.000	28	0.478	0.984
A.MG/A.Sand vs Coral/A.MA	*Cheilinus oxycephalus*	0.017	0.821	0.031	0.543	0.008	0.029	52	0.522	0.039
A.MG/A.Sand vs Coral/A.MA	*Cheilinus trilobatus*	0.039	0.821	0.046	0.841	0.077	0.007	8	0.563	0.496
A.MG/A.Sand vs Coral/A.MA	*Cheilio inermis*	0.014	0.821	0.034	0.421	0.022	0.008	37	0.600	0.965
A.MG/A.Sand vs Coral/A.MA	*Choerodon anchorago*	0.003	0.821	0.014	0.179	0.000	0.005	31	0.636	0.503
A.MG/A.Sand vs Coral/A.MA	*Choerodon sp.*	0.004	0.821	0.014	0.308	0.008	0.000	15	0.667	1
A.MG/A.Sand vs Coral/A.MA	*Coris batuensis*	0.026	0.821	0.039	0.673	0.045	0.014	30	0.692	0.975
A.MG/A.Sand vs Coral/A.MA	*Coris gaimard*	0.037	0.821	0.048	0.768	0.071	0.010	26	0.713	0.089
A.MG/A.Sand vs Coral/A.MA	*Epibulus brevis*	0.009	0.821	0.024	0.377	0.000	0.018	46	0.734	0.63
A.MG/A.Sand vs Coral/A.MA	*Epibulus insidiator*	0.005	0.821	0.020	0.257	0.000	0.010	10	0.755	0.276
A.MG/A.Sand vs Coral/A.MA	*Gomphosus varius*	0.016	0.821	0.031	0.521	0.012	0.024	47	0.774	0.336
A.MG/A.Sand vs Coral/A.MA	*Halichoeres chrysus*	0.005	0.821	0.024	0.213	0.010	0.000	19	0.794	0.196
A.MG/A.Sand vs Coral/A.MA	*Halichoeres hortulanus*	0.041	0.821	0.043	0.946	0.064	0.048	12	0.811	0.264
A.MG/A.Sand vs Coral/A.MA	*Halichoeres marginatus*	0.007	0.821	0.027	0.256	0.000	0.014	4	0.826	0.247
A.MG/A.Sand vs Coral/A.MA	*Halichoeres melanurus*	0.008	0.821	0.024	0.317	0.000	0.015	33	0.840	0.563
A.MG/A.Sand vs Coral/A.MA	*Halichoeres nigrescens*	0.003	0.821	0.015	0.179	0.000	0.005	5	0.852	0.52
A.MG/A.Sand vs Coral/A.MA	*Halichoeres podostigma*	0.009	0.821	0.023	0.382	0.005	0.013	2	0.863	0.74
A.MG/A.Sand vs Coral/A.MA	*Halichoeres prosopeion*	0.017	0.821	0.042	0.408	0.015	0.022	17	0.874	0.448
A.MG/A.Sand vs Coral/A.MA	*Halichoeres richmondi*	0.006	0.821	0.026	0.254	0.000	0.013	25	0.885	0.824
A.MG/A.Sand vs Coral/A.MA	*Halichoeres scapularis*	0.036	0.821	0.062	0.583	0.072	0.000	39	0.895	0.232
A.MG/A.Sand vs Coral/A.MA	*Halichoeres sp.*	0.005	0.821	0.021	0.258	0.000	0.011	23	0.905	0.248
A.MG/A.Sand vs Coral/A.MA	*Hemigymnus fasciatus*	0.021	0.821	0.038	0.550	0.017	0.029	22	0.913	0.151
A.MG/A.Sand vs Coral/A.MA	*Hemigymnus melapterus*	0.029	0.821	0.044	0.665	0.044	0.025	27	0.921	0.212
A.MG/A.Sand vs Coral/A.MA	*Hologymnosus annulatus*	0.000	0.821	0.000	NA	0.000	0.000	29	0.928	1
A.MG/A.Sand vs Coral/A.MA	*Hologymnosus sp.*	0.011	0.821	0.031	0.369	0.023	0.000	9	0.934	0.036
A.MG/A.Sand vs Coral/A.MA	*Labrichthys unilineatus*	0.037	0.821	0.041	0.899	0.004	0.074	44	0.941	0.001
A.MG/A.Sand vs Coral/A.MA	*Labropsis manabei*	0.003	0.821	0.016	0.179	0.000	0.006	20	0.947	0.495
A.MG/A.Sand vs Coral/A.MA	*Labropsis xanthonota*	0.000	0.821	0.000	NA	0.000	0.000	18	0.953	1

A.MG/A.Sand vs Coral/A.MA	*Macropharyngodon meleagris*	0.030	0.821	0.039	0.755	0.032	0.042	42	0.958	0.361
A.MG/A.Sand vs Coral/A.MA	*Macropharyngodon negrosensis*	0.004	0.821	0.020	0.213	0.009	0.000	51	0.964	0.496
A.MG/A.Sand vs Coral/A.MA	*Novaculichthys taeniourus*	0.009	0.821	0.022	0.386	0.017	0.000	38	0.969	0.885
A.MG/A.Sand vs Coral/A.MA	*Oxycheilinus celebicus*	0.000	0.821	0.000	NA	0.000	0.000	14	0.974	1
A.MG/A.Sand vs Coral/A.MA	*Oxycheilinus digramma*	0.063	0.821	0.045	1.383	0.060	0.138	48	0.979	0.562
A.MG/A.Sand vs Coral/A.MA	*Oxycheilinus sp.*	0.004	0.821	0.017	0.257	0.000	0.009	43	0.983	0.257
A.MG/A.Sand vs Coral/A.MA	*Oxycheilinus unifasciatus*	0.003	0.821	0.016	0.213	0.007	0.000	35	0.986	0.217
A.MG/A.Sand vs Coral/A.MA	*Pseudocheilinus hexataenia*	0.005	0.821	0.021	0.256	0.000	0.011	24	0.989	0.244
A.MG/A.Sand vs Coral/A.MA	*Pseudodax moluccanus*	0.000	0.821	0.000	NA	0.000	0.000	13	0.992	1
A.MG/A.Sand vs Coral/A.MA	*Stethojulis bandanensis*	0.017	0.821	0.036	0.465	0.007	0.029	7	0.995	0.165
A.MG/A.Sand vs Coral/A.MA	*Stethojulis interrupta*	0.016	0.821	0.036	0.446	0.032	0.000	1	0.998	0.565
A.MG/A.Sand vs Coral/A.MA	*Stethojulis strigiventer*	0.004	0.821	0.021	0.179	0.000	0.007	49	1.000	0.492
A.MG/A.Sand vs Coral/A.MA	*Thalassoma amblycephalum*	0.002	0.821	0.010	0.179	0.000	0.004	32	1.000	0.507
A.MG/A.Sand vs Coral/A.MA	*Thalassoma hardwicke*	0.046	0.821	0.041	1.108	0.005	0.093	36	1.000	0.029
A.MG/A.Sand vs Coral/A.MA	*Thalassoma jansenii*	0.004	0.821	0.020	0.213	0.009	0.000	40	1.000	0.251
A.MG/A.Sand vs Coral/A.MA	*Thalassoma lunare*	0.036	0.821	0.035	1.014	0.115	0.113	45	1.000	0.966

Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
A.MG/A.Sand vs A.SG/Soft Coral	*Anampses caeruleopunctatus*	0.000	0.785	0.000	NA	0.000	0.000	41	0.077	1
A.MG/A.Sand vs A.SG/Soft Coral	*Anampses meleagrides*	0.008	0.785	0.026	0.292	0.015	0.000	11	0.149	0.159
A.MG/A.Sand vs A.SG/Soft Coral	*Anampses sp.*	0.045	0.785	0.042	1.076	0.087	0.015	14	0.214	0.001
A.MG/A.Sand vs A.SG/Soft Coral	*Anampses twistii*	0.007	0.785	0.037	0.192	0.000	0.014	15	0.276	0.807
A.MG/A.Sand vs A.SG/Soft Coral	*Bodianus dictynna*	0.010	0.785	0.027	0.370	0.020	0.000	28	0.337	0.6
A.MG/A.Sand vs A.SG/Soft Coral	*Bodianus mesothorax*	0.014	0.785	0.032	0.448	0.014	0.016	3	0.394	1
A.MG/A.Sand vs A.SG/Soft Coral	*Bodianus sp.*	0.000	0.785	0.000	NA	0.000	0.000	12	0.448	1
A.MG/A.Sand vs A.SG/Soft Coral	*Cheilinus chlorourus*	0.038	0.785	0.055	0.696	0.062	0.026	21	0.497	0.023
A.MG/A.Sand vs A.SG/Soft Coral	*Cheilinus fasciatus*	0.017	0.785	0.042	0.396	0.011	0.025	8	0.546	0.638
A.MG/A.Sand vs A.SG/Soft Coral	*Cheilinus oxycephalus*	0.006	0.785	0.017	0.361	0.008	0.004	16	0.593	0.905
A.MG/A.Sand vs A.SG/Soft Coral	*Cheilinus trilobatus*	0.057	0.785	0.058	0.974	0.077	0.079	52	0.638	0.007
A.MG/A.Sand vs A.SG/Soft Coral	*Cheilio inermis*	0.042	0.785	0.061	0.692	0.022	0.075	47	0.667	0.022
A.MG/A.Sand vs A.SG/Soft Coral	*Choerodon anchorago*	0.000	0.785	0.000	NA	0.000	0.000	31	0.695	1
A.MG/A.Sand vs A.SG/Soft Coral	*Choerodon sp.*	0.051	0.785	0.062	0.823	0.008	0.100	37	0.722	0.001

A.MG/A.Sand vs A.SG/Soft Coral	*Coris batuensis*	0.048	0.785	0.052	0.923	0.045	0.081	26	0.745	0.058
A.MG/A.Sand vs A.SG/Soft Coral	*Coris gaimard*	0.037	0.785	0.049	0.754	0.071	0.007	39	0.767	0.089
A.MG/A.Sand vs A.SG/Soft Coral	*Epibulus brevis*	0.012	0.785	0.043	0.273	0.000	0.023	9	0.788	0.449
A.MG/A.Sand vs A.SG/Soft Coral	*Epibulus insidiator*	0.000	0.785	0.000	NA	0.000	0.000	25	0.807	1
A.MG/A.Sand vs A.SG/Soft Coral	*Gomphosus varius*	0.006	0.785	0.019	0.303	0.012	0.000	6	0.826	0.949
A.MG/A.Sand vs A.SG/Soft Coral	*Halichoeres chrysus*	0.005	0.785	0.024	0.213	0.010	0.000	33	0.842	0.196
A.MG/A.Sand vs A.SG/Soft Coral	*Halichoeres hortulanus*	0.039	0.785	0.046	0.843	0.064	0.031	17	0.857	0.377
A.MG/A.Sand vs A.SG/Soft Coral	*Halichoeres marginatus*	0.000	0.785	0.000	NA	0.000	0.000	27	0.870	1
A.MG/A.Sand vs A.SG/Soft Coral	*Halichoeres melanurus*	0.008	0.785	0.023	0.338	0.000	0.016	5	0.883	0.556
A.MG/A.Sand vs A.SG/Soft Coral	*Halichoeres nigrescens*	0.000	0.785	0.000	NA	0.000	0.000	30	0.894	1
A.MG/A.Sand vs A.SG/Soft Coral	*Halichoeres podostigma*	0.015	0.785	0.034	0.450	0.005	0.027	23	0.904	0.178
A.MG/A.Sand vs A.SG/Soft Coral	*Halichoeres prosopeion*	0.018	0.785	0.046	0.397	0.015	0.024	38	0.914	0.378
A.MG/A.Sand vs A.SG/Soft Coral	*Halichoeres richmondi*	0.010	0.785	0.038	0.273	0.000	0.021	2	0.923	0.575
A.MG/A.Sand vs A.SG/Soft Coral	*Halichoeres scapularis*	0.048	0.785	0.063	0.762	0.072	0.054	36	0.933	0.006
A.MG/A.Sand vs A.SG/Soft Coral	*Halichoeres sp.*	0.000	0.785	0.000	NA	0.000	0.000	4	0.942	1
A.MG/A.Sand vs A.SG/Soft Coral	*Hemigymnus fasciatus*	0.009	0.785	0.028	0.308	0.017	0.000	40	0.950	0.937
A.MG/A.Sand vs A.SG/Soft Coral	*Hemigymnus melapterus*	0.022	0.785	0.043	0.516	0.044	0.000	10	0.958	0.553
A.MG/A.Sand vs A.SG/Soft Coral	*Hologymnosus annulatus*	0.003	0.785	0.016	0.192	0.000	0.006	19	0.966	0.438
A.MG/A.Sand vs A.SG/Soft Coral	*Hologymnosus sp.*	0.013	0.785	0.032	0.415	0.023	0.005	20	0.972	0.006
A.MG/A.Sand vs A.SG/Soft Coral	*Labrichthys unilineatus*	0.005	0.785	0.019	0.269	0.004	0.007	34	0.979	1
A.MG/A.Sand vs A.SG/Soft Coral	*Labropsis manabei*	0.000	0.785	0.000	NA	0.000	0.000	51	0.984	1
A.MG/A.Sand vs A.SG/Soft Coral	*Labropsis xanthonota*	0.007	0.785	0.026	0.277	0.000	0.014	46	0.989	0.216
A.MG/A.Sand vs A.SG/Soft Coral	*Macropharyngodon meleagris*	0.021	0.785	0.036	0.579	0.032	0.013	43	0.993	0.849
A.MG/A.Sand vs A.SG/Soft Coral	*Macropharyngodon negrosensis*	0.008	0.785	0.027	0.287	0.009	0.007	32	0.997	0.166
A.MG/A.Sand vs A.SG/Soft Coral	*Novaculichthys taeniourus*	0.017	0.785	0.034	0.503	0.017	0.020	50	1.000	0.438
A.MG/A.Sand vs A.SG/Soft Coral	*Oxycheilinus celebicus*	0.007	0.785	0.025	0.277	0.000	0.014	1	1.000	0.595
A.MG/A.Sand vs A.SG/Soft Coral	*Oxycheilinus digramma*	0.061	0.785	0.055	1.101	0.060	0.116	7	1.000	0.707
A.MG/A.Sand vs A.SG/Soft Coral	*Oxycheilinus sp.*	0.000	0.785	0.000	NA	0.000	0.000	13	1.000	1
A.MG/A.Sand vs A.SG/Soft Coral	*Oxycheilinus unifasciatus*	0.003	0.785	0.016	0.213	0.007	0.000	18	1.000	0.217
A.MG/A.Sand vs A.SG/Soft Coral	*Pseudocheilinus hexataenia*	0.000	0.785	0.000	NA	0.000	0.000	22	1.000	1
A.MG/A.Sand vs A.SG/Soft Coral	*Pseudodax moluccanus*	0.000	0.785	0.000	NA	0.000	0.000	24	1.000	1

A.MG/A.Sand vs A.SG/Soft Coral	*Stethojulis bandanensis*	0.003	0.785	0.016	0.213	0.007	0.000	29	1.000	0.966
A.MG/A.Sand vs A.SG/Soft Coral	*Stethojulis interrupta*	0.023	0.785	0.043	0.525	0.032	0.018	35	1.000	0.225
A.MG/A.Sand vs A.SG/Soft Coral	*Stethojulis strigiventer*	0.000	0.785	0.000	NA	0.000	0.000	42	1.000	1
A.MG/A.Sand vs A.SG/Soft Coral	*Thalassoma amblycephalum*	0.000	0.785	0.000	NA	0.000	0.000	44	1.000	1
A.MG/A.Sand vs A.SG/Soft Coral	*Thalassoma hardwicke*	0.003	0.785	0.012	0.213	0.005	0.000	45	1.000	1
A.MG/A.Sand vs A.SG/Soft Coral	*Thalassoma jansenii*	0.004	0.785	0.020	0.213	0.009	0.000	48	1.000	0.251
A.MG/A.Sand vs A.SG/Soft Coral	*Thalassoma lunare*	0.035	0.785	0.032	1.088	0.115	0.141	49	1.000	0.978

Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
A.MG/A.Sand vs A.CR/A.RF	*Anampses caeruleopunctatus*	0.000	0.839	0.000	NA	0.000	0.000	52	0.081	1
A.MG/A.Sand vs A.CR/A.RF	*Anampses meleagrides*	0.008	0.839	0.026	0.292	0.015	0.000	16	0.154	0.255
A.MG/A.Sand vs A.CR/A.RF	*Anampses sp.*	0.043	0.839	0.040	1.067	0.087	0.010	50	0.217	0.001
A.MG/A.Sand vs A.CR/A.RF	*Anampses twistii*	0.011	0.839	0.038	0.301	0.000	0.023	21	0.279	0.546
A.MG/A.Sand vs A.CR/A.RF	*Bodianus dictynna*	0.043	0.839	0.084	0.519	0.020	0.074	41	0.333	0.004
A.MG/A.Sand vs A.CR/A.RF	*Bodianus mesothorax*	0.044	0.839	0.064	0.691	0.014	0.084	6	0.386	0.357
A.MG/A.Sand vs A.CR/A.RF	*Bodianus sp.*	0.000	0.839	0.000	NA	0.000	0.000	5	0.438	1
A.MG/A.Sand vs A.CR/A.RF	*Cheilinus chlorourus*	0.041	0.839	0.061	0.670	0.062	0.030	3	0.489	0.07
A.MG/A.Sand vs A.CR/A.RF	*Cheilinus fasciatus*	0.028	0.839	0.078	0.354	0.011	0.046	8	0.537	0.201
A.MG/A.Sand vs A.CR/A.RF	*Cheilinus oxycephalus*	0.004	0.839	0.013	0.307	0.008	0.000	11	0.584	0.894
A.MG/A.Sand vs A.CR/A.RF	*Cheilinus trilobatus*	0.040	0.839	0.046	0.853	0.077	0.012	28	0.627	0.501
A.MG/A.Sand vs A.CR/A.RF	*Cheilio inermis*	0.027	0.839	0.060	0.449	0.022	0.035	37	0.661	0.482
A.MG/A.Sand vs A.CR/A.RF	*Choerodon anchorago*	0.000	0.839	0.000	NA	0.000	0.000	9	0.694	1
A.MG/A.Sand vs A.CR/A.RF	*Choerodon sp.*	0.004	0.839	0.014	0.307	0.008	0.000	19	0.726	0.991
A.MG/A.Sand vs A.CR/A.RF	*Coris batuensis*	0.023	0.839	0.038	0.593	0.045	0.000	12	0.759	0.937
A.MG/A.Sand vs A.CR/A.RF	*Coris gaimard*	0.061	0.839	0.066	0.928	0.071	0.094	45	0.789	0.002
A.MG/A.Sand vs A.CR/A.RF	*Epibulus brevis*	0.000	0.839	0.000	NA	0.000	0.000	15	0.816	1
A.MG/A.Sand vs A.CR/A.RF	*Epibulus insidiator*	0.000	0.839	0.000	NA	0.000	0.000	31	0.842	1
A.MG/A.Sand vs A.CR/A.RF	*Gomphosus varius*	0.027	0.839	0.055	0.494	0.012	0.046	47	0.862	0.041
A.MG/A.Sand vs A.CR/A.RF	*Halichoeres chrysus*	0.005	0.839	0.024	0.213	0.010	0.000	26	0.879	0.303
A.MG/A.Sand vs A.CR/A.RF	*Halichoeres hortulanus*	0.052	0.839	0.057	0.903	0.064	0.078	30	0.895	0.037
A.MG/A.Sand vs A.CR/A.RF	*Halichoeres marginatus*	0.000	0.839	0.000	NA	0.000	0.000	39	0.911	1
A.MG/A.Sand vs A.CR/A.RF	*Halichoeres melanurus*	0.000	0.839	0.000	NA	0.000	0.000	4	0.925	1

A.MG/A.Sand vs A.CR/A.RF	*Halichoeres nigrescens*	0.000	0.839	0.000	NA	0.000	0.000	33	0.938	1
A.MG/A.Sand vs A.CR/A.RF	*Halichoeres podostigma*	0.003	0.839	0.013	0.213	0.005	0.000	27	0.951	0.954
A.MG/A.Sand vs A.CR/A.RF	*Halichoeres prosopeion*	0.014	0.839	0.040	0.355	0.015	0.015	2	0.960	0.598
A.MG/A.Sand vs A.CR/A.RF	*Halichoeres richmondi*	0.011	0.839	0.036	0.301	0.000	0.022	20	0.966	0.501
A.MG/A.Sand vs A.CR/A.RF	*Halichoeres scapularis*	0.036	0.839	0.062	0.583	0.072	0.000	51	0.971	0.313
A.MG/A.Sand vs A.CR/A.RF	*Halichoeres sp.*	0.000	0.839	0.000	NA	0.000	0.000	38	0.977	1
A.MG/A.Sand vs A.CR/A.RF	*Hemigymnus fasciatus*	0.014	0.839	0.032	0.429	0.017	0.012	14	0.982	0.619
A.MG/A.Sand vs A.CR/A.RF	*Hemigymnus melapterus*	0.022	0.839	0.043	0.515	0.044	0.000	10	0.986	0.516
A.MG/A.Sand vs A.CR/A.RF	*Hologymnosus annulatus*	0.000	0.839	0.000	NA	0.000	0.000	46	0.990	1
A.MG/A.Sand vs A.CR/A.RF	*Hologymnosus sp.*	0.011	0.839	0.031	0.369	0.023	0.000	43	0.995	0.139
A.MG/A.Sand vs A.CR/A.RF	*Labrichthys unilineatus*	0.002	0.839	0.009	0.213	0.004	0.000	25	0.998	0.998
A.MG/A.Sand vs A.CR/A.RF	*Labropsis manabei*	0.000	0.839	0.000	NA	0.000	0.000	34	1.000	1
A.MG/A.Sand vs A.CR/A.RF	*Labropsis xanthonota*	0.000	0.839	0.000	NA	0.000	0.000	1	1.000	1
A.MG/A.Sand vs A.CR/A.RF	*Macropharyngodon meleagris*	0.028	0.839	0.051	0.553	0.032	0.030	7	1.000	0.458
A.MG/A.Sand vs A.CR/A.RF	*Macropharyngodon negrosensis*	0.004	0.839	0.020	0.213	0.009	0.000	13	1.000	0.574
A.MG/A.Sand vs A.CR/A.RF	*Novaculichthys taeniourus*	0.013	0.839	0.027	0.489	0.017	0.012	17	1.000	0.568
A.MG/A.Sand vs A.CR/A.RF	*Oxycheilinus celebicus*	0.000	0.839	0.000	NA	0.000	0.000	18	1.000	1
A.MG/A.Sand vs A.CR/A.RF	*Oxycheilinus digramma*	0.045	0.839	0.065	0.697	0.060	0.047	22	1.000	0.992
A.MG/A.Sand vs A.CR/A.RF	*Oxycheilinus sp.*	0.000	0.839	0.000	NA	0.000	0.000	23	1.000	1
A.MG/A.Sand vs A.CR/A.RF	*Oxycheilinus unifasciatus*	0.003	0.839	0.016	0.213	0.007	0.000	24	1.000	0.328
A.MG/A.Sand vs A.CR/A.RF	*Pseudocheilinus hexataenia*	0.000	0.839	0.000	NA	0.000	0.000	29	1.000	1
A.MG/A.Sand vs A.CR/A.RF	*Pseudodax moluccanus*	0.026	0.839	0.085	0.301	0.000	0.051	32	1.000	0.11
A.MG/A.Sand vs A.CR/A.RF	*Stethojulis bandanensis*	0.003	0.839	0.016	0.213	0.007	0.000	35	1.000	0.901
A.MG/A.Sand vs A.CR/A.RF	*Stethojulis interrupta*	0.016	0.839	0.036	0.446	0.032	0.000	36	1.000	0.516
A.MG/A.Sand vs A.CR/A.RF	*Stethojulis strigiventer*	0.000	0.839	0.000	NA	0.000	0.000	40	1.000	1
A.MG/A.Sand vs A.CR/A.RF	*Thalassoma amblycephalum*	0.000	0.839	0.000	NA	0.000	0.000	42	1.000	1
A.MG/A.Sand vs A.CR/A.RF	*Thalassoma hardwicke*	0.053	0.839	0.091	0.584	0.005	0.105	44	1.000	0.05
A.MG/A.Sand vs A.CR/A.RF	*Thalassoma jansenii*	0.004	0.839	0.020	0.213	0.009	0.000	48	1.000	0.357
A.MG/A.Sand vs A.CR/A.RF	*Thalassoma lunare*	0.068	0.839	0.047	1.428	0.115	0.173	49	1.000	0.001
Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
Rub/EAM vs Coral/A.MA	*Anampses caeruleopunctatus*	0.002	0.793	0.011	0.179	0.000	0.004	41	0.089	0.42

Rub/EAM vs Coral/A.MA	*Anampses meleagrides*	0.002	0.793	0.013	0.179	0.000	0.005	6	0.162	0.708
Rub/EAM vs Coral/A.MA	*Anampses sp.*	0.011	0.793	0.027	0.422	0.023	0.000	52	0.234	0.97
Rub/EAM vs Coral/A.MA	*Anampses twistii*	0.012	0.793	0.043	0.280	0.000	0.024	15	0.297	0.512
Rub/EAM vs Coral/A.MA	*Bodianus dictynna*	0.000	0.793	0.000	NA	0.000	0.000	50	0.355	1
Rub/EAM vs Coral/A.MA	*Bodianus mesothorax*	0.058	0.793	0.046	1.263	0.041	0.106	31	0.413	0.023
Rub/EAM vs Coral/A.MA	*Bodianus sp.*	0.002	0.793	0.013	0.179	0.000	0.005	37	0.460	0.413
Rub/EAM vs Coral/A.MA	*Cheilinus chlorourus*	0.011	0.793	0.029	0.360	0.010	0.013	34	0.507	0.966
Rub/EAM vs Coral/A.MA	*Cheilinus fasciatus*	0.026	0.793	0.048	0.542	0.052	0.000	47	0.541	0.22
Rub/EAM vs Coral/A.MA	*Cheilinus oxycephalus*	0.014	0.793	0.031	0.460	0.000	0.029	39	0.575	0.2
Rub/EAM vs Coral/A.MA	*Cheilinus trilobatus*	0.023	0.793	0.055	0.423	0.041	0.007	9	0.608	0.938
Rub/EAM vs Coral/A.MA	*Cheilio inermis*	0.004	0.793	0.022	0.179	0.000	0.008	21	0.641	0.997
Rub/EAM vs Coral/A.MA	*Choerodon anchorago*	0.003	0.793	0.014	0.179	0.000	0.005	28	0.673	0.391
Rub/EAM vs Coral/A.MA	*Choerodon sp.*	0.000	0.793	0.000	NA	0.000	0.000	30	0.705	1
Rub/EAM vs Coral/A.MA	*Coris batuensis*	0.050	0.793	0.066	0.751	0.096	0.014	40	0.736	0.095
Rub/EAM vs Coral/A.MA	*Coris gaimard*	0.010	0.793	0.026	0.386	0.012	0.010	46	0.767	0.989
Rub/EAM vs Coral/A.MA	*Epibulus brevis*	0.009	0.793	0.024	0.377	0.000	0.018	11	0.796	0.562
Rub/EAM vs Coral/A.MA	*Epibulus insidiator*	0.005	0.793	0.020	0.257	0.000	0.010	10	0.814	0.318
Rub/EAM vs Coral/A.MA	*Gomphosus varius*	0.012	0.793	0.028	0.422	0.000	0.024	4	0.830	0.586
Rub/EAM vs Coral/A.MA	*Halichoeres chrysus*	0.000	0.793	0.000	NA	0.000	0.000	19	0.845	1
Rub/EAM vs Coral/A.MA	*Halichoeres hortulanus*	0.026	0.793	0.040	0.654	0.010	0.048	3	0.859	0.935
Rub/EAM vs Coral/A.MA	*Halichoeres marginatus*	0.007	0.793	0.027	0.256	0.000	0.014	26	0.872	0.331
Rub/EAM vs Coral/A.MA	*Halichoeres melanurus*	0.008	0.793	0.024	0.317	0.000	0.015	8	0.886	0.542
Rub/EAM vs Coral/A.MA	*Halichoeres nigrescens*	0.003	0.793	0.015	0.179	0.000	0.005	16	0.898	0.43
Rub/EAM vs Coral/A.MA	*Halichoeres podostigma*	0.006	0.793	0.020	0.317	0.000	0.013	17	0.910	0.795
Rub/EAM vs Coral/A.MA	*Halichoeres prosopeion*	0.011	0.793	0.029	0.365	0.000	0.022	23	0.919	0.768
Rub/EAM vs Coral/A.MA	*Halichoeres richmondi*	0.006	0.793	0.026	0.254	0.000	0.013	22	0.928	0.771
Rub/EAM vs Coral/A.MA	*Halichoeres scapularis*	0.025	0.793	0.048	0.526	0.051	0.000	27	0.936	0.665
Rub/EAM vs Coral/A.MA	*Halichoeres sp.*	0.005	0.793	0.021	0.258	0.000	0.011	25	0.944	0.324
Rub/EAM vs Coral/A.MA	*Hemigymnus fasciatus*	0.025	0.793	0.040	0.624	0.030	0.029	29	0.951	0.058
Rub/EAM vs Coral/A.MA	*Hemigymnus melapterus*	0.046	0.793	0.081	0.568	0.078	0.025	44	0.958	0.024
Rub/EAM vs Coral/A.MA	*Hologymnosus annulatus*	0.000	0.793	0.000	NA	0.000	0.000	18	0.964	1

Rub/EAM vs Coral/A.MA	*Hologymnosus sp.*	0.000	0.793	0.000	NA	0.000	0.000	42	0.970	1
Rub/EAM vs Coral/A.MA	*Labrichthys unilineatus*	0.037	0.793	0.042	0.879	0.000	0.074	12	0.975	0.01
Rub/EAM vs Coral/A.MA	*Labropsis manabei*	0.003	0.793	0.016	0.179	0.000	0.006	48	0.979	0.403
Rub/EAM vs Coral/A.MA	*Labropsis xanthonota*	0.000	0.793	0.000	NA	0.000	0.000	35	0.983	1
Rub/EAM vs Coral/A.MA	*Macropharyngodon meleagris*	0.037	0.793	0.057	0.661	0.046	0.042	24	0.986	0.129
Rub/EAM vs Coral/A.MA	*Macropharyngodon negrosensis*	0.000	0.793	0.000	NA	0.000	0.000	13	0.989	1
Rub/EAM vs Coral/A.MA	*Novaculichthys taeniourus*	0.027	0.793	0.066	0.407	0.054	0.000	2	0.992	0.088
Rub/EAM vs Coral/A.MA	*Oxycheilinus celebicus*	0.025	0.793	0.087	0.288	0.050	0.000	7	0.995	0.112
Rub/EAM vs Coral/A.MA	*Oxycheilinus digramma*	0.070	0.793	0.050	1.411	0.135	0.138	1	0.998	0.131
Rub/EAM vs Coral/A.MA	*Oxycheilinus sp.*	0.004	0.793	0.017	0.257	0.000	0.009	49	1.000	0.315
Rub/EAM vs Coral/A.MA	*Oxycheilinus unifasciatus*	0.000	0.793	0.000	NA	0.000	0.000	5	1.000	1
Rub/EAM vs Coral/A.MA	*Pseudocheilinus hexataenia*	0.005	0.793	0.021	0.255	0.000	0.011	14	1.000	0.306
Rub/EAM vs Coral/A.MA	*Pseudodax moluccanus*	0.000	0.793	0.000	NA	0.000	0.000	20	1.000	1
Rub/EAM vs Coral/A.MA	*Stethojulis bandanensis*	0.024	0.793	0.049	0.498	0.024	0.029	32	1.000	0.042
Rub/EAM vs Coral/A.MA	*Stethojulis interrupta*	0.027	0.793	0.068	0.404	0.055	0.000	33	1.000	0.106
Rub/EAM vs Coral/A.MA	*Stethojulis strigiventer*	0.004	0.793	0.021	0.179	0.000	0.007	36	1.000	0.416
Rub/EAM vs Coral/A.MA	*Thalassoma amblycephalum*	0.002	0.793	0.010	0.179	0.000	0.004	38	1.000	0.411
Rub/EAM vs Coral/A.MA	*Thalassoma hardwicke*	0.046	0.793	0.042	1.101	0.000	0.093	43	1.000	0.106
Rub/EAM vs Coral/A.MA	*Thalassoma jansenii*	0.000	0.793	0.000	NA	0.000	0.000	45	1.000	1
Rub/EAM vs Coral/A.MA	*Thalassoma lunare*	0.057	0.793	0.044	1.302	0.193	0.113	51	1.000	0.016

Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
Rub/EAM vs A.SG/Soft Coral	*Anampses caeruleopunctatus*	0.000	0.764	0.000	NA	0.000	0.000	41	0.096	1
Rub/EAM vs A.SG/Soft Coral	*Anampses meleagrides*	0.000	0.764	0.000	NA	0.000	0.000	15	0.177	1
Rub/EAM vs A.SG/Soft Coral	*Anampses sp.*	0.017	0.764	0.035	0.501	0.023	0.015	11	0.245	0.787
Rub/EAM vs A.SG/Soft Coral	*Anampses twistii*	0.007	0.764	0.037	0.192	0.000	0.014	14	0.310	0.756
Rub/EAM vs A.SG/Soft Coral	*Bodianus dictynna*	0.000	0.764	0.000	NA	0.000	0.000	52	0.375	1
Rub/EAM vs A.SG/Soft Coral	*Bodianus mesothorax*	0.026	0.764	0.054	0.493	0.041	0.016	28	0.430	0.976
Rub/EAM vs A.SG/Soft Coral	*Bodianus sp.*	0.000	0.764	0.000	NA	0.000	0.000	31	0.481	1
Rub/EAM vs A.SG/Soft Coral	*Cheilinus chlorourus*	0.017	0.764	0.040	0.425	0.010	0.026	12	0.530	0.82
Rub/EAM vs A.SG/Soft Coral	*Cheilinus fasciatus*	0.034	0.764	0.053	0.638	0.052	0.025	39	0.574	0.088
Rub/EAM vs A.SG/Soft Coral	*Cheilinus oxycephalus*	0.002	0.764	0.012	0.192	0.000	0.004	9	0.618	0.975

Rub/EAM vs A.SG/Soft Coral	*Cheilinus trilobatus*	0.051	0.764	0.072	0.714	0.041	0.079	47	0.662	0.096
Rub/EAM vs A.SG/Soft Coral	*Cheilio inermis*	0.037	0.764	0.063	0.592	0.000	0.075	40	0.703	0.18
Rub/EAM vs A.SG/Soft Coral	*Choerodon anchorago*	0.000	0.764	0.000	NA	0.000	0.000	37	0.738	1
Rub/EAM vs A.SG/Soft Coral	*Choerodon sp.*	0.050	0.764	0.064	0.784	0.000	0.100	6	0.773	0.004
Rub/EAM vs A.SG/Soft Coral	*Coris batuensis*	0.062	0.764	0.064	0.977	0.096	0.081	21	0.798	0.007
Rub/EAM vs A.SG/Soft Coral	*Coris gaimard*	0.009	0.764	0.026	0.345	0.012	0.007	3	0.821	0.987
Rub/EAM vs A.SG/Soft Coral	*Epibulus brevis*	0.012	0.764	0.043	0.272	0.000	0.023	8	0.843	0.482
Rub/EAM vs A.SG/Soft Coral	*Epibulus insidiator*	0.000	0.764	0.000	NA	0.000	0.000	30	0.862	1
Rub/EAM vs A.SG/Soft Coral	*Gomphosus varius*	0.000	0.764	0.000	NA	0.000	0.000	25	0.880	1
Rub/EAM vs A.SG/Soft Coral	*Halichoeres chrysus*	0.000	0.764	0.000	NA	0.000	0.000	26	0.896	1
Rub/EAM vs A.SG/Soft Coral	*Halichoeres hortulanus*	0.019	0.764	0.040	0.480	0.010	0.031	46	0.911	0.982
Rub/EAM vs A.SG/Soft Coral	*Halichoeres marginatus*	0.000	0.764	0.000	NA	0.000	0.000	17	0.927	1
Rub/EAM vs A.SG/Soft Coral	*Halichoeres melanurus*	0.008	0.764	0.023	0.338	0.000	0.016	27	0.940	0.534
Rub/EAM vs A.SG/Soft Coral	*Halichoeres nigrescens*	0.000	0.764	0.000	NA	0.000	0.000	16	0.952	1
Rub/EAM vs A.SG/Soft Coral	*Halichoeres podostigma*	0.013	0.764	0.033	0.399	0.000	0.027	23	0.962	0.339
Rub/EAM vs A.SG/Soft Coral	*Halichoeres prosopeion*	0.012	0.764	0.036	0.338	0.000	0.024	36	0.971	0.707
Rub/EAM vs A.SG/Soft Coral	*Halichoeres richmondi*	0.010	0.764	0.038	0.272	0.000	0.021	4	0.981	0.561
Rub/EAM vs A.SG/Soft Coral	*Halichoeres scapularis*	0.042	0.764	0.054	0.767	0.051	0.054	38	0.986	0.148
Rub/EAM vs A.SG/Soft Coral	*Halichoeres sp.*	0.000	0.764	0.000	NA	0.000	0.000	34	0.990	1
Rub/EAM vs A.SG/Soft Coral	*Hemigymnus fasciatus*	0.015	0.764	0.035	0.424	0.030	0.000	32	0.994	0.533
Rub/EAM vs A.SG/Soft Coral	*Hemigymnus melapterus*	0.039	0.764	0.084	0.465	0.078	0.000	33	0.997	0.083
Rub/EAM vs A.SG/Soft Coral	*Hologymnosus annulatus*	0.003	0.764	0.016	0.192	0.000	0.006	10	1.000	0.371
Rub/EAM vs A.SG/Soft Coral	*Hologymnosus sp.*	0.002	0.764	0.012	0.192	0.000	0.005	1	1.000	0.782
Rub/EAM vs A.SG/Soft Coral	*Labrichthys unilineatus*	0.003	0.764	0.018	0.192	0.000	0.007	2	1.000	0.998
Rub/EAM vs A.SG/Soft Coral	*Labropsis manabei*	0.000	0.764	0.000	NA	0.000	0.000	5	1.000	1
Rub/EAM vs A.SG/Soft Coral	*Labropsis xanthonota*	0.007	0.764	0.026	0.276	0.000	0.014	7	1.000	0.303
Rub/EAM vs A.SG/Soft Coral	*Macropharyngodon meleagris*	0.027	0.764	0.057	0.479	0.046	0.013	13	1.000	0.51
Rub/EAM vs A.SG/Soft Coral	*Macropharyngodon negrosensis*	0.004	0.764	0.019	0.192	0.000	0.007	18	1.000	0.462
Rub/EAM vs A.SG/Soft Coral	*Novaculichthys taeniourus*	0.034	0.764	0.066	0.511	0.054	0.020	19	1.000	0.026
Rub/EAM vs A.SG/Soft Coral	*Oxycheilinus celebicus*	0.031	0.764	0.087	0.356	0.050	0.014	20	1.000	0.036
Rub/EAM vs A.SG/Soft Coral	*Oxycheilinus digramma*	0.073	0.764	0.060	1.210	0.135	0.116	22	1.000	0.075

Rub/EAM vs A.SG/Soft Coral	*Oxycheilinus sp.*	0.000	0.764	0.000	NA	0.000	0.000	24	1.000	1
Rub/EAM vs A.SG/Soft Coral	*Oxycheilinus unifasciatus*	0.000	0.764	0.000	NA	0.000	0.000	29	1.000	1
Rub/EAM vs A.SG/Soft Coral	*Pseudocheilinus hexataenia*	0.000	0.764	0.000	NA	0.000	0.000	35	1.000	1
Rub/EAM vs A.SG/Soft Coral	*Pseudodax moluccanus*	0.000	0.764	0.000	NA	0.000	0.000	42	1.000	1
Rub/EAM vs A.SG/Soft Coral	*Stethojulis bandanensis*	0.012	0.764	0.041	0.288	0.024	0.000	43	1.000	0.504
Rub/EAM vs A.SG/Soft Coral	*Stethojulis interrupta*	0.034	0.764	0.070	0.482	0.055	0.018	44	1.000	0.031
Rub/EAM vs A.SG/Soft Coral	*Stethojulis strigiventer*	0.000	0.764	0.000	NA	0.000	0.000	45	1.000	1
Rub/EAM vs A.SG/Soft Coral	*Thalassoma amblycephalum*	0.000	0.764	0.000	NA	0.000	0.000	48	1.000	1
Rub/EAM vs A.SG/Soft Coral	*Thalassoma hardwicke*	0.000	0.764	0.000	NA	0.000	0.000	49	1.000	1
Rub/EAM vs A.SG/Soft Coral	*Thalassoma jansenii*	0.000	0.764	0.000	NA	0.000	0.000	50	1.000	1
Rub/EAM vs A.SG/Soft Coral	*Thalassoma lunare*	0.049	0.764	0.038	1.297	0.193	0.141	51	1.000	0.235

Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
Rub/EAM vs A.CR/A.RF	*Anampses caeruleopunctatus*	0.000	0.836	0.000	NA	0.000	0.000	41	0.089	1
Rub/EAM vs A.CR/A.RF	*Anampses meleagrides*	0.000	0.836	0.000	NA	0.000	0.000	52	0.171	1
Rub/EAM vs A.CR/A.RF	*Anampses sp.*	0.015	0.836	0.029	0.516	0.023	0.010	50	0.234	0.823
Rub/EAM vs A.CR/A.RF	*Anampses twistii*	0.011	0.836	0.038	0.301	0.000	0.023	6	0.296	0.561
Rub/EAM vs A.CR/A.RF	*Bodianus dictynna*	0.037	0.836	0.087	0.425	0.000	0.074	16	0.355	0.035
Rub/EAM vs A.CR/A.RF	*Bodianus mesothorax*	0.052	0.836	0.070	0.749	0.041	0.084	15	0.412	0.147
Rub/EAM vs A.CR/A.RF	*Bodianus sp.*	0.000	0.836	0.000	NA	0.000	0.000	9	0.466	1
Rub/EAM vs A.CR/A.RF	*Cheilinus chlorourus*	0.019	0.836	0.050	0.381	0.010	0.030	21	0.515	0.689
Rub/EAM vs A.CR/A.RF	*Cheilinus fasciatus*	0.045	0.836	0.079	0.569	0.052	0.046	31	0.562	0.035
Rub/EAM vs A.CR/A.RF	*Cheilinus oxycephalus*	0.000	0.836	0.000	NA	0.000	0.000	5	0.606	1
Rub/EAM vs A.CR/A.RF	*Cheilinus trilobatus*	0.025	0.836	0.055	0.450	0.041	0.012	37	0.647	0.844
Rub/EAM vs A.CR/A.RF	*Cheilio inermis*	0.018	0.836	0.059	0.301	0.000	0.035	39	0.684	0.781
Rub/EAM vs A.CR/A.RF	*Choerodon anchorago*	0.000	0.836	0.000	NA	0.000	0.000	47	0.717	1
Rub/EAM vs A.CR/A.RF	*Choerodon sp.*	0.000	0.836	0.000	NA	0.000	0.000	45	0.747	1
Rub/EAM vs A.CR/A.RF	*Coris batuensis*	0.048	0.836	0.068	0.699	0.096	0.000	28	0.778	0.178
Rub/EAM vs A.CR/A.RF	*Coris gaimard*	0.049	0.836	0.073	0.672	0.012	0.094	40	0.808	0.033
Rub/EAM vs A.CR/A.RF	*Epibulus brevis*	0.000	0.836	0.000	NA	0.000	0.000	11	0.838	1
Rub/EAM vs A.CR/A.RF	*Epibulus insidiator*	0.000	0.836	0.000	NA	0.000	0.000	19	0.865	1
Rub/EAM vs A.CR/A.RF	*Gomphosus varius*	0.023	0.836	0.055	0.418	0.000	0.046	30	0.888	0.133

Rub/EAM vs A.CR/A.RF	*Halichoeres chrysus*	0.000	0.836	0.000	NA	0.000	0.000	8	0.911	1
Rub/EAM vs A.CR/A.RF	*Halichoeres hortulanus*	0.041	0.836	0.063	0.649	0.010	0.078	12	0.932	0.35
Rub/EAM vs A.CR/A.RF	*Halichoeres marginatus*	0.000	0.836	0.000	NA	0.000	0.000	3	0.950	1
Rub/EAM vs A.CR/A.RF	*Halichoeres melanurus*	0.000	0.836	0.000	NA	0.000	0.000	46	0.964	1
Rub/EAM vs A.CR/A.RF	*Halichoeres nigrescens*	0.000	0.836	0.000	NA	0.000	0.000	4	0.978	1
Rub/EAM vs A.CR/A.RF	*Halichoeres podostigma*	0.000	0.836	0.000	NA	0.000	0.000	27	0.991	1
Rub/EAM vs A.CR/A.RF	*Halichoeres prosopeion*	0.008	0.836	0.026	0.301	0.000	0.015	26	1.000	0.777
Rub/EAM vs A.CR/A.RF	*Halichoeres richmondi*	0.011	0.836	0.036	0.301	0.000	0.022	1	1.000	0.438
Rub/EAM vs A.CR/A.RF	*Halichoeres scapularis*	0.025	0.836	0.049	0.525	0.051	0.000	2	1.000	0.625
Rub/EAM vs A.CR/A.RF	*Halichoeres sp.*	0.000	0.836	0.000	NA	0.000	0.000	7	1.000	1
Rub/EAM vs A.CR/A.RF	*Hemigymnus fasciatus*	0.019	0.836	0.037	0.519	0.030	0.012	10	1.000	0.333
Rub/EAM vs A.CR/A.RF	*Hemigymnus melapterus*	0.039	0.836	0.084	0.465	0.078	0.000	13	1.000	0.154
Rub/EAM vs A.CR/A.RF	*Hologymnosus annulatus*	0.000	0.836	0.000	NA	0.000	0.000	14	1.000	1
Rub/EAM vs A.CR/A.RF	*Hologymnosus sp.*	0.000	0.836	0.000	NA	0.000	0.000	17	1.000	1
Rub/EAM vs A.CR/A.RF	*Labrichthys unilineatus*	0.000	0.836	0.000	NA	0.000	0.000	18	1.000	1
Rub/EAM vs A.CR/A.RF	*Labropsis manabei*	0.000	0.836	0.000	NA	0.000	0.000	20	1.000	1
Rub/EAM vs A.CR/A.RF	*Labropsis xanthonota*	0.000	0.836	0.000	NA	0.000	0.000	22	1.000	1
Rub/EAM vs A.CR/A.RF	*Macropharyngodon meleagris*	0.034	0.836	0.067	0.506	0.046	0.030	23	1.000	0.298
Rub/EAM vs A.CR/A.RF	*Macropharyngodon negrosensis*	0.000	0.836	0.000	NA	0.000	0.000	24	1.000	1
Rub/EAM vs A.CR/A.RF	*Novaculichthys taeniourus*	0.031	0.836	0.065	0.477	0.054	0.012	25	1.000	0.099
Rub/EAM vs A.CR/A.RF	*Oxycheilinus celebicus*	0.025	0.836	0.087	0.288	0.050	0.000	29	1.000	0.216
Rub/EAM vs A.CR/A.RF	*Oxycheilinus digramma*	0.074	0.836	0.075	0.995	0.135	0.047	32	1.000	0.091
Rub/EAM vs A.CR/A.RF	*Oxycheilinus sp.*	0.000	0.836	0.000	NA	0.000	0.000	33	1.000	1
Rub/EAM vs A.CR/A.RF	*Oxycheilinus unifasciatus*	0.000	0.836	0.000	NA	0.000	0.000	34	1.000	1
Rub/EAM vs A.CR/A.RF	*Pseudocheilinus hexataenia*	0.000	0.836	0.000	NA	0.000	0.000	35	1.000	1
Rub/EAM vs A.CR/A.RF	*Pseudodax moluccanus*	0.026	0.836	0.086	0.301	0.000	0.051	36	1.000	0.11
Rub/EAM vs A.CR/A.RF	*Stethojulis bandanensis*	0.012	0.836	0.042	0.288	0.024	0.000	38	1.000	0.532
Rub/EAM vs A.CR/A.RF	*Stethojulis interrupta*	0.027	0.836	0.068	0.404	0.055	0.000	42	1.000	0.17
Rub/EAM vs A.CR/A.RF	*Stethojulis strigiventer*	0.000	0.836	0.000	NA	0.000	0.000	43	1.000	1
Rub/EAM vs A.CR/A.RF	*Thalassoma amblycephalum*	0.000	0.836	0.000	NA	0.000	0.000	44	1.000	1
Rub/EAM vs A.CR/A.RF	*Thalassoma hardwicke*	0.052	0.836	0.093	0.567	0.000	0.105	48	1.000	0.091

Rub/EAM vs A.CR/A.RF	*Thalassoma jansenii*	0.000	0.836	0.000	NA	0.000	0.000	49	1.000	1
Rub/EAM vs A.CR/A.RF	*Thalassoma lunare*	0.069	0.836	0.050	1.361	0.193	0.173	51	1.000	0.002

Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
Coral.A.MA vs A.SG/Soft Coral	*Anampses caeruleopunctatus*	0.002	0.800	0.011	0.180	0.004	0.000	41	0.077	0.55
Coral.A.MA vs A.SG/Soft Coral	*Anampses meleagrides*	0.002	0.800	0.013	0.180	0.005	0.000	6	0.144	0.797
Coral.A.MA vs A.SG/Soft Coral	*Anampses sp.*	0.008	0.800	0.028	0.277	0.000	0.015	14	0.207	1
Coral.A.MA vs A.SG/Soft Coral	*Anampses twistii*	0.018	0.800	0.054	0.340	0.024	0.014	50	0.265	0.16
Coral.A.MA vs A.SG/Soft Coral	*Bodianus dictynna*	0.000	0.800	0.000	NA	0.000	0.000	15	0.319	1
Coral.A.MA vs A.SG/Soft Coral	*Bodianus mesothorax*	0.054	0.800	0.043	1.253	0.106	0.016	11	0.370	0.001
Coral.A.MA vs A.SG/Soft Coral	*Bodianus sp.*	0.002	0.800	0.013	0.180	0.005	0.000	12	0.419	0.526
Coral.A.MA vs A.SG/Soft Coral	*Cheilinus chlorourus*	0.018	0.800	0.044	0.414	0.013	0.026	34	0.466	0.902
Coral.A.MA vs A.SG/Soft Coral	*Cheilinus fasciatus*	0.012	0.800	0.037	0.331	0.000	0.025	21	0.507	0.854
Coral.A.MA vs A.SG/Soft Coral	*Cheilinus oxycephalus*	0.016	0.800	0.032	0.497	0.029	0.004	52	0.546	0.043
Coral.A.MA vs A.SG/Soft Coral	*Cheilinus trilobatus*	0.041	0.800	0.065	0.639	0.007	0.079	28	0.580	0.311
Coral.A.MA vs A.SG/Soft Coral	*Cheilio inermis*	0.039	0.800	0.063	0.618	0.008	0.075	37	0.611	0.032
Coral.A.MA vs A.SG/Soft Coral	*Choerodon anchorago*	0.003	0.800	0.014	0.180	0.005	0.000	26	0.637	0.547
Coral.A.MA vs A.SG/Soft Coral	*Choerodon sp.*	0.050	0.800	0.064	0.785	0.000	0.100	17	0.661	0.001
Coral.A.MA vs A.SG/Soft Coral	*Coris batuensis*	0.043	0.800	0.055	0.772	0.014	0.081	4	0.684	0.244
Coral.A.MA vs A.SG/Soft Coral	*Coris gaimard*	0.008	0.800	0.025	0.321	0.010	0.007	8	0.706	0.999
Coral.A.MA vs A.SG/Soft Coral	*Epibulus brevis*	0.019	0.800	0.045	0.429	0.018	0.023	25	0.729	0.01
Coral.A.MA vs A.SG/Soft Coral	*Epibulus insidiator*	0.005	0.800	0.020	0.257	0.010	0.000	27	0.749	0.295
Coral.A.MA vs A.SG/Soft Coral	*Gomphosus varius*	0.012	0.800	0.028	0.422	0.024	0.000	10	0.769	0.684
Coral.A.MA vs A.SG/Soft Coral	*Halichoeres chrysus*	0.000	0.800	0.000	NA	0.000	0.000	30	0.787	1
Coral.A.MA vs A.SG/Soft Coral	*Halichoeres hortulanus*	0.033	0.800	0.046	0.716	0.048	0.031	46	0.805	0.795
Coral.A.MA vs A.SG/Soft Coral	*Halichoeres marginatus*	0.007	0.800	0.027	0.257	0.014	0.000	23	0.822	0.306
Coral.A.MA vs A.SG/Soft Coral	*Halichoeres melanurus*	0.014	0.800	0.030	0.465	0.015	0.016	31	0.838	0.014
Coral.A.MA vs A.SG/Soft Coral	*Halichoeres nigrescens*	0.003	0.800	0.015	0.180	0.005	0.000	9	0.854	0.566
Coral.A.MA vs A.SG/Soft Coral	*Halichoeres podostigma*	0.018	0.800	0.035	0.509	0.013	0.027	19	0.869	0.008
Coral.A.MA vs A.SG/Soft Coral	*Halichoeres prosopeion*	0.021	0.800	0.042	0.498	0.022	0.024	39	0.881	0.205
Coral.A.MA vs A.SG/Soft Coral	*Halichoeres richmondi*	0.016	0.800	0.043	0.370	0.013	0.021	47	0.892	0.156
Coral.A.MA vs A.SG/Soft Coral	*Halichoeres scapularis*	0.027	0.800	0.049	0.552	0.000	0.054	16	0.902	0.743

Coral.A.MA vs A.SG/Soft Coral	*Halichoeres sp.*	0.005	0.800	0.021	0.258	0.011	0.000	3	0.912	0.302
Coral.A.MA vs A.SG/Soft Coral	*Hemigymnus fasciatus*	0.015	0.800	0.033	0.449	0.029	0.000	36	0.921	0.629
Coral.A.MA vs A.SG/Soft Coral	*Hemigymnus melapterus*	0.013	0.800	0.030	0.424	0.025	0.000	40	0.930	0.967
Coral.A.MA vs A.SG/Soft Coral	*Hologymnosus annulatus*	0.003	0.800	0.016	0.192	0.000	0.006	22	0.938	0.251
Coral.A.MA vs A.SG/Soft Coral	*Hologymnosus sp.*	0.002	0.800	0.012	0.192	0.000	0.005	29	0.945	0.894
Coral.A.MA vs A.SG/Soft Coral	*Labrichthys unilineatus*	0.038	0.800	0.042	0.900	0.074	0.007	44	0.952	0.001
Coral.A.MA vs A.SG/Soft Coral	*Labropsis manabei*	0.003	0.800	0.016	0.180	0.006	0.000	18	0.958	0.533
Coral.A.MA vs A.SG/Soft Coral	*Labropsis xanthonota*	0.007	0.800	0.026	0.277	0.000	0.014	42	0.963	0.059
Coral.A.MA vs A.SG/Soft Coral	*Macropharyngodon meleagris*	0.025	0.800	0.040	0.621	0.042	0.013	48	0.968	0.695
Coral.A.MA vs A.SG/Soft Coral	*Macropharyngodon negrosensis*	0.004	0.800	0.019	0.192	0.000	0.007	38	0.973	0.425
Coral.A.MA vs A.SG/Soft Coral	*Novaculichthys taeniourus*	0.010	0.800	0.030	0.335	0.000	0.020	32	0.977	0.873
Coral.A.MA vs A.SG/Soft Coral	*Oxycheilinus celebicus*	0.007	0.800	0.025	0.277	0.000	0.014	35	0.980	0.589
Coral.A.MA vs A.SG/Soft Coral	*Oxycheilinus digramma*	0.062	0.800	0.045	1.368	0.138	0.116	24	0.983	0.629
Coral.A.MA vs A.SG/Soft Coral	*Oxycheilinus sp.*	0.004	0.800	0.017	0.257	0.009	0.000	13	0.986	0.314
Coral.A.MA vs A.SG/Soft Coral	*Oxycheilinus unifasciatus*	0.000	0.800	0.000	NA	0.000	0.000	33	0.989	1
Coral.A.MA vs A.SG/Soft Coral	*Pseudocheilinus hexataenia*	0.005	0.800	0.021	0.256	0.011	0.000	2	0.992	0.305
Coral.A.MA vs A.SG/Soft Coral	*Pseudodax moluccanus*	0.000	0.800	0.000	NA	0.000	0.000	7	0.995	1
Coral.A.MA vs A.SG/Soft Coral	*Stethojulis bandanensis*	0.015	0.800	0.035	0.414	0.029	0.000	1	0.998	0.297
Coral.A.MA vs A.SG/Soft Coral	*Stethojulis interrupta*	0.009	0.800	0.032	0.277	0.000	0.018	49	1.000	0.918
Coral.A.MA vs A.SG/Soft Coral	*Stethojulis strigiventer*	0.004	0.800	0.021	0.180	0.007	0.000	5	1.000	0.547
Coral.A.MA vs A.SG/Soft Coral	*Thalassoma amblycephalum*	0.002	0.800	0.010	0.180	0.004	0.000	20	1.000	0.559
Coral.A.MA vs A.SG/Soft Coral	*Thalassoma hardwicke*	0.046	0.800	0.042	1.102	0.093	0.000	43	1.000	0.008
Coral.A.MA vs A.SG/Soft Coral	*Thalassoma jansenii*	0.000	0.800	0.000	NA	0.000	0.000	45	1.000	1
Coral.A.MA vs A.SG/Soft Coral	*Thalassoma lunare*	0.031	0.800	0.025	1.266	0.113	0.141	51	1.000	1

Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
Coral/A.MA vs A.CR/A.RF	*Anampses caeruleopunctatus*	0.002	0.807	0.011	0.179	0.004	0.000	41	0.091	0.416
Coral/A.MA vs A.CR/A.RF	*Anampses meleagrides*	0.002	0.807	0.013	0.179	0.005	0.000	50	0.178	0.686
Coral/A.MA vs A.CR/A.RF	*Anampses sp.*	0.005	0.807	0.017	0.301	0.000	0.010	52	0.258	0.997
Coral/A.MA vs A.CR/A.RF	*Anampses twistii*	0.022	0.807	0.053	0.413	0.024	0.023	6	0.334	0.165
Coral/A.MA vs A.CR/A.RF	*Bodianus dictynna*	0.037	0.807	0.086	0.426	0.000	0.074	16	0.395	0.014
Coral/A.MA vs A.CR/A.RF	*Bodianus mesothorax*	0.062	0.807	0.052	1.200	0.106	0.084	21	0.455	0.006

Coral/A.MA vs A.CR/A.RF	*Bodianus sp.*	0.002	0.807	0.013	0.179	0.005	0.000	5	0.501	0.384
Coral/A.MA vs A.CR/A.RF	*Cheilinus chlorourus*	0.020	0.807	0.053	0.381	0.013	0.030	34	0.546	0.715
Coral/A.MA vs A.CR/A.RF	*Cheilinus fasciatus*	0.023	0.807	0.077	0.301	0.000	0.046	37	0.586	0.295
Coral/A.MA vs A.CR/A.RF	*Cheilinus oxycephalus*	0.014	0.807	0.031	0.460	0.029	0.000	19	0.625	0.223
Coral/A.MA vs A.CR/A.RF	*Cheilinus trilobatus*	0.009	0.807	0.023	0.395	0.007	0.012	45	0.657	0.997
Coral/A.MA vs A.CR/A.RF	*Cheilio inermis*	0.021	0.807	0.060	0.346	0.008	0.035	9	0.685	0.736
Coral/A.MA vs A.CR/A.RF	*Choerodon anchorago*	0.003	0.807	0.014	0.179	0.005	0.000	4	0.712	0.414
Coral/A.MA vs A.CR/A.RF	*Choerodon sp.*	0.000	0.807	0.000	NA	0.000	0.000	12	0.738	1
Coral/A.MA vs A.CR/A.RF	*Coris batuensis*	0.007	0.807	0.022	0.315	0.014	0.000	8	0.763	1
Coral/A.MA vs A.CR/A.RF	*Coris gaimard*	0.049	0.807	0.073	0.666	0.010	0.094	30	0.786	0.017
Coral/A.MA vs A.CR/A.RF	*Epibulus brevis*	0.009	0.807	0.024	0.377	0.018	0.000	26	0.807	0.557
Coral/A.MA vs A.CR/A.RF	*Epibulus insidiator*	0.005	0.807	0.020	0.257	0.010	0.000	27	0.827	0.294
Coral/A.MA vs A.CR/A.RF	*Gomphosus varius*	0.031	0.807	0.055	0.567	0.024	0.046	46	0.845	0.018
Coral/A.MA vs A.CR/A.RF	*Halichoeres chrysus*	0.000	0.807	0.000	NA	0.000	0.000	10	0.863	1
Coral/A.MA vs A.CR/A.RF	*Halichoeres hortulanus*	0.048	0.807	0.060	0.810	0.048	0.078	31	0.879	0.074
Coral/A.MA vs A.CR/A.RF	*Halichoeres marginatus*	0.007	0.807	0.027	0.256	0.014	0.000	11	0.890	0.302
Coral/A.MA vs A.CR/A.RF	*Halichoeres melanurus*	0.008	0.807	0.024	0.317	0.015	0.000	17	0.901	0.527
Coral/A.MA vs A.CR/A.RF	*Halichoeres nigrescens*	0.003	0.807	0.015	0.179	0.005	0.000	23	0.911	0.411
Coral/A.MA vs A.CR/A.RF	*Halichoeres podostigma*	0.006	0.807	0.020	0.317	0.013	0.000	15	0.919	0.796
Coral/A.MA vs A.CR/A.RF	*Halichoeres prosopeion*	0.017	0.807	0.035	0.475	0.022	0.015	22	0.928	0.46
Coral/A.MA vs A.CR/A.RF	*Halichoeres richmondi*	0.016	0.807	0.041	0.394	0.013	0.022	25	0.936	0.238
Coral/A.MA vs A.CR/A.RF	*Halichoeres scapularis*	0.000	0.807	0.000	NA	0.000	0.000	39	0.943	1
Coral/A.MA vs A.CR/A.RF	*Halichoeres sp.*	0.005	0.807	0.021	0.258	0.011	0.000	29	0.950	0.316
Coral/A.MA vs A.CR/A.RF	*Hemigymnus fasciatus*	0.019	0.807	0.035	0.540	0.029	0.012	44	0.957	0.33
Coral/A.MA vs A.CR/A.RF	*Hemigymnus melapterus*	0.013	0.807	0.030	0.423	0.025	0.000	3	0.963	0.884
Coral/A.MA vs A.CR/A.RF	*Hologymnosus annulatus*	0.000	0.807	0.000	NA	0.000	0.000	18	0.970	1
Coral/A.MA vs A.CR/A.RF	*Hologymnosus sp.*	0.000	0.807	0.000	NA	0.000	0.000	42	0.975	1
Coral/A.MA vs A.CR/A.RF	*Labrichthys unilineatus*	0.037	0.807	0.042	0.879	0.074	0.000	48	0.980	0.017
Coral/A.MA vs A.CR/A.RF	*Labropsis manabei*	0.003	0.807	0.016	0.179	0.006	0.000	35	0.983	0.412
Coral/A.MA vs A.CR/A.RF	*Labropsis xanthonota*	0.000	0.807	0.000	NA	0.000	0.000	24	0.986	1
Coral/A.MA vs A.CR/A.RF	*Macropharyngodon meleagris*	0.032	0.807	0.053	0.607	0.042	0.030	13	0.990	0.293

Coral/A.MA vs A.CR/A.RF	*Macropharyngodon negrosensis*	0.000	0.807	0.000	NA	0.000	0.000	2	0.992	1
Coral/A.MA vs A.CR/A.RF	*Novaculichthys taeniourus*	0.006	0.807	0.021	0.301	0.000	0.012	7	0.995	0.902
Coral/A.MA vs A.CR/A.RF	*Oxycheilinus celebicus*	0.000	0.807	0.000	NA	0.000	0.000	1	0.998	1
Coral/A.MA vs A.CR/A.RF	*Oxycheilinus digramma*	0.073	0.807	0.052	1.418	0.138	0.047	49	1.000	0.071
Coral/A.MA vs A.CR/A.RF	*Oxycheilinus sp.*	0.004	0.807	0.017	0.257	0.009	0.000	14	1.000	0.314
Coral/A.MA vs A.CR/A.RF	*Oxycheilinus unifasciatus*	0.000	0.807	0.000	NA	0.000	0.000	20	1.000	1
Coral/A.MA vs A.CR/A.RF	*Pseudocheilinus hexataenia*	0.005	0.807	0.021	0.255	0.011	0.000	28	1.000	0.302
Coral/A.MA vs A.CR/A.RF	*Pseudodax moluccanus*	0.026	0.807	0.085	0.301	0.000	0.051	32	1.000	0.11
Coral/A.MA vs A.CR/A.RF	*Stethojulis bandanensis*	0.015	0.807	0.035	0.414	0.029	0.000	33	1.000	0.334
Coral/A.MA vs A.CR/A.RF	*Stethojulis interrupta*	0.000	0.807	0.000	NA	0.000	0.000	36	1.000	1
Coral/A.MA vs A.CR/A.RF	*Stethojulis strigiventer*	0.004	0.807	0.021	0.179	0.007	0.000	38	1.000	0.388
Coral/A.MA vs A.CR/A.RF	*Thalassoma amblycephalum*	0.002	0.807	0.010	0.179	0.004	0.000	40	1.000	0.423
Coral/A.MA vs A.CR/A.RF	*Thalassoma hardwicke*	0.071	0.807	0.073	0.966	0.093	0.105	43	1.000	0.001
Coral/A.MA vs A.CR/A.RF	*Thalassoma jansenii*	0.000	0.807	0.000	NA	0.000	0.000	47	1.000	1
Coral/A.MA vs A.CR/A.RF	*Thalassoma lunare*	0.064	0.807	0.045	1.418	0.113	0.173	51	1.000	0.001

Comparison	species	average	overall	sd	ratio	ava	avb	ord	cusum	p
A.SG/Soft Coral vs A.CR/A.RF	*Anampses caeruleopunctatus*	0.000	0.851	0.000	NA	0.000	0.000	41	0.078	1
A.SG/Soft Coral vs A.CR/A.RF	*Anampses meleagrides*	0.000	0.851	0.000	NA	0.000	0.000	52	0.148	1
A.SG/Soft Coral vs A.CR/A.RF	*Anampses sp.*	0.012	0.851	0.031	0.398	0.015	0.010	50	0.209	0.952
A.SG/Soft Coral vs A.CR/A.RF	*Anampses twistii*	0.018	0.851	0.050	0.353	0.014	0.023	14	0.268	0.324
A.SG/Soft Coral vs A.CR/A.RF	*Bodianus dictynna*	0.037	0.851	0.086	0.426	0.000	0.074	12	0.326	0.016
A.SG/Soft Coral vs A.CR/A.RF	*Bodianus mesothorax*	0.045	0.851	0.067	0.678	0.016	0.084	16	0.382	0.29
A.SG/Soft Coral vs A.CR/A.RF	*Bodianus sp.*	0.000	0.851	0.000	NA	0.000	0.000	21	0.437	1
A.SG/Soft Coral vs A.CR/A.RF	*Cheilinus chlorourus*	0.026	0.851	0.057	0.449	0.026	0.030	6	0.490	0.474
A.SG/Soft Coral vs A.CR/A.RF	*Cheilinus fasciatus*	0.033	0.851	0.079	0.421	0.025	0.046	11	0.540	0.094
A.SG/Soft Coral vs A.CR/A.RF	*Cheilinus oxycephalus*	0.002	0.851	0.012	0.192	0.004	0.000	15	0.587	0.969
A.SG/Soft Coral vs A.CR/A.RF	*Cheilinus trilobatus*	0.042	0.851	0.064	0.658	0.079	0.012	5	0.631	0.349
A.SG/Soft Coral vs A.CR/A.RF	*Cheilio inermis*	0.049	0.851	0.074	0.663	0.075	0.035	9	0.670	0.026
A.SG/Soft Coral vs A.CR/A.RF	*Choerodon anchorago*	0.000	0.851	0.000	NA	0.000	0.000	28	0.701	1
A.SG/Soft Coral vs A.CR/A.RF	*Choerodon sp.*	0.050	0.851	0.064	0.784	0.100	0.000	45	0.732	0.01
A.SG/Soft Coral vs A.CR/A.RF	*Coris batuensis*	0.041	0.851	0.057	0.711	0.081	0.000	8	0.762	0.368

A.SG/Soft Coral vs A.CR/A.RF	*Coris gaimard*	0.048	0.851	0.074	0.653	0.007	0.094	19	0.789	0.021
A.SG/Soft Coral vs A.CR/A.RF	*Epibulus brevis*	0.012	0.851	0.043	0.272	0.023	0.000	37	0.813	0.463
A.SG/Soft Coral vs A.CR/A.RF	*Epibulus insidiator*	0.000	0.851	0.000	NA	0.000	0.000	27	0.836	1
A.SG/Soft Coral vs A.CR/A.RF	*Gomphosus varius*	0.023	0.851	0.055	0.419	0.000	0.046	26	0.857	0.102
A.SG/Soft Coral vs A.CR/A.RF	*Halichoeres chrysus*	0.000	0.851	0.000	NA	0.000	0.000	4	0.878	1
A.SG/Soft Coral vs A.CR/A.RF	*Halichoeres hortulanus*	0.046	0.851	0.064	0.723	0.031	0.078	39	0.896	0.111
A.SG/Soft Coral vs A.CR/A.RF	*Halichoeres marginatus*	0.000	0.851	0.000	NA	0.000	0.000	25	0.911	1
A.SG/Soft Coral vs A.CR/A.RF	*Halichoeres melanurus*	0.008	0.851	0.023	0.338	0.016	0.000	3	0.926	0.534
A.SG/Soft Coral vs A.CR/A.RF	*Halichoeres nigrescens*	0.000	0.851	0.000	NA	0.000	0.000	17	0.939	1
A.SG/Soft Coral vs A.CR/A.RF	*Halichoeres podostigma*	0.013	0.851	0.033	0.399	0.027	0.000	47	0.950	0.362
A.SG/Soft Coral vs A.CR/A.RF	*Halichoeres prosopeion*	0.018	0.851	0.040	0.450	0.024	0.015	23	0.959	0.402
A.SG/Soft Coral vs A.CR/A.RF	*Halichoeres richmondi*	0.020	0.851	0.048	0.407	0.021	0.022	36	0.967	0.143
A.SG/Soft Coral vs A.CR/A.RF	*Halichoeres scapularis*	0.027	0.851	0.049	0.552	0.054	0.000	40	0.976	0.653
A.SG/Soft Coral vs A.CR/A.RF	*Halichoeres sp.*	0.000	0.851	0.000	NA	0.000	0.000	30	0.983	1
A.SG/Soft Coral vs A.CR/A.RF	*Hemigymnus fasciatus*	0.006	0.851	0.020	0.301	0.000	0.012	38	0.987	0.945
A.SG/Soft Coral vs A.CR/A.RF	*Hemigymnus melapterus*	0.000	0.851	0.000	NA	0.000	0.000	34	0.991	1
A.SG/Soft Coral vs A.CR/A.RF	*Hologymnosus annulatus*	0.003	0.851	0.016	0.192	0.006	0.000	32	0.995	0.37
A.SG/Soft Coral vs A.CR/A.RF	*Hologymnosus sp.*	0.002	0.851	0.012	0.192	0.005	0.000	33	0.997	0.774
A.SG/Soft Coral vs A.CR/A.RF	*Labrichthys unilineatus*	0.003	0.851	0.018	0.192	0.007	0.000	10	1.000	0.998
A.SG/Soft Coral vs A.CR/A.RF	*Labropsis manabei*	0.000	0.851	0.000	NA	0.000	0.000	1	1.000	1
A.SG/Soft Coral vs A.CR/A.RF	*Labropsis xanthonota*	0.007	0.851	0.026	0.276	0.014	0.000	2	1.000	0.283
A.SG/Soft Coral vs A.CR/A.RF	*Macropharyngodon meleagris*	0.020	0.851	0.052	0.393	0.013	0.030	7	1.000	0.798
A.SG/Soft Coral vs A.CR/A.RF	*Macropharyngodon negrosensis*	0.004	0.851	0.019	0.192	0.007	0.000	13	1.000	0.469
A.SG/Soft Coral vs A.CR/A.RF	*Novaculichthys taeniourus*	0.015	0.851	0.034	0.446	0.020	0.012	18	1.000	0.474
A.SG/Soft Coral vs A.CR/A.RF	*Oxycheilinus celebicus*	0.007	0.851	0.025	0.277	0.014	0.000	20	1.000	0.549
A.SG/Soft Coral vs A.CR/A.RF	*Oxycheilinus digramma*	0.066	0.851	0.065	1.023	0.116	0.047	22	1.000	0.308
A.SG/Soft Coral vs A.CR/A.RF	*Oxycheilinus sp.*	0.000	0.851	0.000	NA	0.000	0.000	24	1.000	1
A.SG/Soft Coral vs A.CR/A.RF	*Oxycheilinus unifasciatus*	0.000	0.851	0.000	NA	0.000	0.000	29	1.000	1
A.SG/Soft Coral vs A.CR/A.RF	*Pseudocheilinus hexataenia*	0.000	0.851	0.000	NA	0.000	0.000	31	1.000	1
A.SG/Soft Coral vs A.CR/A.RF	*Pseudodax moluccanus*	0.026	0.851	0.085	0.301	0.000	0.051	35	1.000	0.11
A.SG/Soft Coral vs A.CR/A.RF	*Stethojulis bandanensis*	0.000	0.851	0.000	NA	0.000	0.000	42	1.000	1

A.SG/Soft Coral vs A.CR/A.RF	*Stethojulis interrupta*	0.009	0.851	0.032	0.277	0.018	0.000	43	1.000	0.818
A.SG/Soft Coral vs A.CR/A.RF	*Stethojulis strigiventer*	0.000	0.851	0.000	NA	0.000	0.000	44	1.000	1
A.SG/Soft Coral vs A.CR/A.RF	*Thalassoma amblycephalum*	0.000	0.851	0.000	NA	0.000	0.000	46	1.000	1
A.SG/Soft Coral vs A.CR/A.RF	*Thalassoma hardwicke*	0.052	0.851	0.093	0.567	0.000	0.105	48	1.000	0.059
A.SG/Soft Coral vs A.CR/A.RF	*Thalassoma jansenii*	0.000	0.851	0.000	NA	0.000	0.000	49	1.000	1
A.SG/Soft Coral vs A.CR/A.RF	*Thalassoma lunare*	0.059	0.851	0.039	1.512	0.141	0.173	51	1.000	0.019

APPENDIX C – SUPPORTING INFORMATION FOR CHAPTER 4

Table S.4.1. Parrotfish species richness data from publications in the Negros Oriental region with a comparison to Chapter 4 of this thesis.

Publication	Location(s)	Habitat	Life Stage	Richness
Russ et al., 2015	Apo, Sumilon	Coral Reef	Adult	20
McClure et al., 2020	Apo, Sumilon, Negros, Bohol, Siquijor	Coral Reef	Adult	22
McClure et al., 2020	Siquijor	Coral Reef	Adult	18
Stockwell et al., 2009	Negros, Mindanao	Coral Reef	Adult	21
Sievers et al., 2020b	Siquijor	Coral Reef	Adult	18
Sievers et al. 2020a	Siquijor	Coral Reef + Non-Reef	Adult	19
Sievers et al. 2020a	Siquijor	Non-Reef	Adult	11
Sievers et al. 2020a	Siquijor	Non-Reef	Juvenile	15

Table S.4.2. Results from sequence cleaning and blast data: F HQ and R HQ are the percentages of high-quality base pairs for the forward (F) and reverse (R) sequences. %GC is the percent of base pairs C and G. Alignment score is percent alignment between forward and reverse sequences. Ambiguities are for the consensus sequence. BLAST confidence was assigned based on criteria detailed in the main text. Accession numbers are for GenBank.

ID	F HQ (%)	R HQ (%)	GC (%)	Align Score (%)	Sequence Used	Ambiguities	Sequence Length	BLAST Confidence	Species ID	Acession Number
1	98	99	49.2	98.8	align	0	664	High	*Scarus quoyi*	MW014070
2	98	96	48.6	97.7	align	0	666	High	*Scarus rivulatus*	MW014071
3	98	67	48.9	98.8	align	0	660	High	*Scarus quoyi*	MW014072
4	97	96	48.7	96.4	align	1	675	Low	*Scarus rivulatus*	MW014073
5	98	96	48.8	97.6	align	0	676	Med	*Scarus rivulatus*	MW014074
6	96	97	48.7	97.5	align	0	674	Low	*Scarus rivulatus*	MW014075
7	99	95	48.9	98.4	align	0	669	Low	*Scarus rivulatus*	MW014076
8	98	97	48.7	98.2	align	0	673	Med	*Scarus rivulatus*	MW014077
9	8	25	47.3	11.9	reverse	130	976	High	*Scarus psittacus*	
10	99	95	48.7	98.2	align	0	669	Low	*Scarus rivulatus*	MW014078
11	95	93	48.9	97.3	align	0	671	Low	*Scarus rivulatus*	MW014080
12	98	96	49.0	98.8	align	0	672	High	*Scarus quoyi*	MW014081
13	97	96	48.8	96.2	align	0	680	Med	*Scarus rivulatus*	MW014082
14	98	98	48.7	98.5	align	0	675	Med	*Scarus rivulatus*	MW014083
15	99	97	48.6	97.3	align	0	677	Med	*Scarus rivulatus*	MW014084
16	98	98	48.7	97.6	align	0	672	Med	*Scarus rivulatus*	MW014085
17	98	96	48.7	98.1	align	1	674	Med	*Scarus rivulatus*	MW014086
18	99	96	48.2	98.8	align	0	674	High	*Scarus ghobban*	MW014087
19	99	97	48.6	97.6	align	0	675	Med	*Scarus rivulatus*	MW014088
20	97	97	48.9	98.2	align	0	675	High	*Scarus quoyi*	MW014089
21	98	98	48.4	97.9	align	1	674	High	*Chlorurus spilurus*	MW014090
22	64	53	47.4	78.9	align	33	681	High	*Scarus psittacus*	
23	85	87	47.4	98.1	align	1	684	High	*Scarus psittacus*	MW014091
24	47	49	47.9	79.9	align	19	688	High	*Scarus psittacus*	MW014092
25	94	94	47.7	99.0	align	0	684	High	*Scarus psittacus*	MW014093
26	81	85	47.7	97.1	align	1	681	High	*Scarus psittacus*	MW014094
27	99	98	48.7	97.9	align	0	676	Med	*Scarus rivulatus*	MW014095
28	99	99	48.5	98.5	align	0	674	Med	*Scarus rivulatus*	MW014096

29	62	66	47.7	92.5	align	2	684	High	*Scarus psittacus*	MW014097
30	99	99	48.6	98.7	align	0	675	Med	*Scarus rivulatus*	MW014098
31	71	74	47.4	94.6	align	3	699	High	*Scarus psittacus*	MW014099
32	98	97	48.3	94.9	align	1	693	Med	*Scarus rivulatus*	MW014100
33	10	68	46.3	64.3	reverse	na	697	High	*Scarus psittacus*	MW014101
34	69	75	47.5	94.7	align	2	682	High	*Scarus psittacus*	MW014102
35	98	99	47.4	99.0	align	0	680	High	*Scarus psittacus*	MW014103
36	30	26	46.3	35.1	align	42	681	High	*Scarus psittacus*	MW014104
37	81	84	47.2	95.7	align	2	704	High	*Scarus psittacus*	MW014105
38	92	96	47.5	97.8	align	1	682	Med	*Chlorurus bowersi/bleekeri*	MW014106
39	98	97	48.0	96.5	align	0	689	High	*Scarus flavipectoralis*	MW014107
40	91	92	46.9	96.0	align	0	699	High	*Scarus psittacus*	MW014108
41	98	94	48.1	93.9	align	0	709	Med	*Scarus rivulatus*	MW014109
42	83	75	47.1	95.9	align	0	684	High	*Scarus psittacus*	MW014110
43	64	69	47.8	81.5	align	14	698	High	*Scarus psittacus*	MW014111
44	75	98	47.6	96.2	align	1	633	High	*Scarus schlegeli*	MW014112
45	73	71	47.6	87.7	align	5	684	High	*Scarus psittacus*	MW014113
46	70	35	48.0	72.9	align	14	680	High	*Scarus psittacus*	MW014114
47	97	97	48.7	97.7	align	0	682	High	*Scarus quoyi*	MW014116
48	91	90	47.0	95.1	align	1	709	High	*Scarus psittacus*	MW014117
49	99	97	48.5	96.3	align	0	697	Med	*Scarus rivulatus*	MW014118
50	90	91	47.3	96.4	align	0	687	High	*Scarus psittacus*	MW014119
51	84	78	47.4	97.1	align	1	685	High	*Scarus psittacus*	MW014120
52	79	93	48.9	92.4	align	6	687	High	*Scarus quoyi*	MW014121
53	98	99	48.4	97.7	align	0	682	Med	*Scarus rivulatus*	MW014122
54	90	91	49.4	96.0	align	0	700	High	*Scarus spinus*	MW014123
55	98	13	44.4	na	forward	na	640	Low	*Scarus rivulatus*	MW014124
56	99	98	48.5	97.7	align	0	686	Med	*Scarus rivulatus*	MW014125
57	99	97	46.7	97.0	align	2	689	Med	*Chlorurus bleekeri*	MW014126
58	97	95	48.5	97.3	align	1	692	High	*Scarus quoyi*	MW014127
59	98	98	48.7	96.1	align	0	684	High	*Scarus quoyi*	MW014128
60	98	99	48.5	97.8	align	0	683	Low	*Scarus rivulatus*	MW014129
61	97	95	48.7	96.0	align	0	679	High	*Scarus quoyi*	MW014130
62	70	60	47.8	91.8	align	10	684	High	*Scarus psittacus*	
63	87	83	47.4	93.7	align	2	683	High	*Scarus psittacus*	MW014131
64	98	98	47.0	98.2	align	0	685	Med	*Chlorurus bleekeri*	MW014132

65	89	91	47.9	97.2	align	0	682	Low	*Chlorurus bowersi/bleekeri*	MW014133
66	99	95	48.5	97.5	align	1	680	Med	*Scarus rivulatus*	MW014134
67	95	95	47.2	98.7	align	0	682	High	*Scarus psittacus*	MW014135
68	98	97	48.0	96.2	align	0	687	Med	*Scarus rivulatus*	MW014136
69	98	96	47.3	96.2	align	1	684	Med	*Chlorurus japanensis/capistratoides*	MW014137
70	86	83	47.3	96.5	align	1	683	High	*Scarus psittacus*	MW014138
71	91	44	47.6	96.9	align	0	680	High	*Scarus psittacus*	MW014139
72	97	97	47.6	96.8	align	0	685	Low	*Chlorurus bowersi/bleekeri*	MW014140
73	97	98	47.9	95.6	align	0	681	Med	*Scarus rubroviolaceus*	MW014141
74	81	60	46.1	84.8	align	3	777	High	*Scarus psittacus*	MW014142
75	51	3	47.6	46.3	forward	na	681	High	*Scarus psittacus*	MW014143
76	97	94	48.5	94.4	align	0	684	Med	*Scarus rivulatus*	MW014144
77	85	76	47.1	88.6	align	1	712	High	*Scarus psittacus*	MW014145
78	96	96	48.5	94.7	align	0	683	Med	*Scarus rivulatus*	MW014146
79	51	50	47.7	80.3	reverse	na	710	zero	*couldn't ID*	MW014147
80	94	97	48.4	96.9	align	0	686	Med	*Scarus rivulatus*	MW014148
81	95	94	48.4	96.4	align	1	701	High	*Scarus quoyi*	MW014149
82	93	90	47.6	90.9	align	2	705	High	*Scarus psittacus*	MW014150
83	86	73	47.4	84.3	align	1	686	High	*Scarus psittacus*	MW014151
84	33	13	48.5	33.9	forward	na	694	High	*Scarus psittacus*	
85	98	97	47.5	96.0	align	1	692	Med	*Scarus rubroviolaceus*	MW014153
86	48	59	47.5	81.4	align	11	698	High	*Scarus psittacus*	MW014154
87	87	85	47.0	94.4	align	1	712	High	*Scarus psittacus*	MW014155
88	0	46	46.4	40.8	reverse	na	711	High	*Scarus psittacus*	MW014156
89	71	67	47.1	94.5	align	2	696	High	*Scarus psittacus*	MW014157
90	97	94	48.3	96.1	align	0	700	Med	*Scarus rivulatus*	MW014158
91	0	0	44.5	0.1	not possible	na	2002	zero	*couldn't ID*	
92	74	76	47.0	92.5	align	0	708	High	*Scarus psittacus*	
93	60	61	48.9	95.7	align	0	698	High	*Calotomus spinidens*	MW014160
94	90	94	48.4	96.0	align	0	696	Med	*Scarus rivulatus*	MW014161
95	65	70	47.0	89.9	align	0	711	High	*Scarus psittacus*	MW014162
96	83	87	46.7	94.9	align	0	711	High	*Scarus psittacus*	MW014163
97	98	98	48.8	97.1	align	0	687	Med	*Scarus rivulatus*	MW014164
98	90	94	44.9	95.1	align	1	712	High	*Anampses geographicus*	MW014165
99	93	94	46.8	96.2	align	2	690	Med	*Scarus chameleon*	MW014166
100	86	93	48.3	92.4	align	1	693	Med	*Scarus rivulatus*	MW014167

101	35	32	47.5	38.6	forward	na	679	Med	*Scarus quoyi*	MW014168
102	90	89	48.3	93.0	align	0	696	Med	*Scarus rivulatus*	MW014169
103	97	97	48.3	96.6	align	1	686	Med	*Scarus rivulatus*	MW014170
104	21	24	48.1	39.8	forward	na	713	Med	*Scarus quoyi*	
105	89	91	47.0	92.9	align	0	709	High	*Scarus psittacus*	MW014171
106	93	95	48.2	93.1	align	1	707	Med	*Scarus rivulatus*	MW014172
107	98	95	48.5	95.9	align	1	690	Med	*Scarus rivulatus*	MW014173
108	80	80	47.0	90.4	align	1	711	High	*Scarus psittacus*	MW014174
109	98	94	48.5	96.4	align	1	692	Med	*Scarus rivulatus*	MW014175
110	61	57	47.6	82.6	align	8	696	High	*Scarus psittacus*	MW014176
111	58	26	48.1	67.6	forward	na	686	Med	*Scarus quoyi*	MW014177
112	1	98	48.1	84.4	reverse	0	724	Med	*Chlorurus bowersi/bleekeri*	MW014178
113	98	92	47.9	96.1	align	1	698	Med	*Scarus rivulatus*	MW014179
114	56	56	46.9	78.1	align	10	685	High	*Scarus psittacus*	MW014180
115	61	3	46.7	60.1	forward	34	716	High	*Scarus psittacus*	MW014181
116	98	5	48.7	na	forward	na	634	Low	*Scarus rivulatus*	MW014182
117	92	92	48.4	95.9	align	0	701	High	*Scarus quoyi*	MW014183
118	95	96	48.1	94.5	align	3	693	High	*Chlorurus spilurus*	MW014184
119	73	49	47.0	87.4	align	15	691	High	*Scarus psittacus*	MW014185
120	35	37	47.6	53.8	forward	na	702	High	*Scarus psittacus*	MW014186
121	30	34	47.6	47.1	forward	na	711	zero	*couldn't ID*	MW014187
122	89	89	46.7	94.9	align	0	711	High	*Scarus psittacus*	MW014188
123	99	95	47.3	94.7	align	2	696	Med	*Chlorurus bowersi/bleekeri*	MW014189
124	99	97	48.5	98.3	align	1	687	Med	*Scarus rivulatus*	MW014190
125	66	53	47.5	87.9	align	15	695	Med	*Scarus rubroviolaceus*	MW014191
126	19	0	47.9	na	forward	0	645	High	*Scarus psittacus*	
127	97	96	47.3	94.7	align	2	695	Med	*Scarus rubroviolaceus*	MW014192
128	96	13	48.0	na	forward	na	639	Med	*Scarus rubroviolaceus*	MW014193
129	96	93	47.8	92.8	align	1	685	Med	*Scarus rubroviolaceus*	MW014194
130	98	93	47.5	95.3	align	1	687	Med	*Scarus rubroviolaceus*	MW014195
131	94	93	48.2	93.0	align	1	710	High	*Calotomus spinidens*	MW014196
132	82	79	47.2	97.7	align	0	695	High	*Scarus psittacus*	MW014197
133	93	89	47.2	95.3	align	2	700	High	*Scarus psittacus*	MW014198
134	98	95	48.0	96.2	align	2	692	Med	*Scarus rivulatus*	MW014199
135	57	64	47.6	86.9	align	10	697	High	*Scarus psittacus*	MW014200
136	94	90	46.8	94.8	align	0	697	Med	*Scarus chameleon*	MW014201

137	96	92	48.6	89.9	align	1	685	High	*Scarus quoyi*	MW014202
138	98	94	48.0	92.0	align	2	697	Med	*Scarus rivulatus*	MW014203
139	21	26	47.6	52.0	reverse	na	710	High	*Scarus psittacus*	
140	81	85	47.0	95.1	align	2	697	High	*Scarus psittacus*	MW014204
141	94	91	47.0	93.7	align	2	703	High	*Scarus psittacus*	MW014205
142	80	70	48.5	92.5	align	7	697	High	*Scarus quoyi*	
143	72	71	46.9	85.2	align	5	698	High	*Scarus psittacus*	MW014206
144	65	14	48.8	66.2	forward	43	681	High	*Scarus quoyi*	
145	74	72	47.5	89.6	align	7	695	High	*Scarus psittacus*	MW014207
146	17	24	47.5	42.2	reverse	na	702	High	*Scarus psittacus*	
147	95	88	47.3	93.4	align	1	696	Med	*Chlorurus bowersi/bleekeri*	MW014208
148	71	68	47.6	88.9	align	9	696	High	*Scarus psittacus*	MW014209
149	98	94	46.4	94.7	align	0	698	High	*Chlorurus bleekeri*	MW014210
150	96	94	47.6	93.0	align	0	700	High	*Chlorurus spilurus*	MW014211
151	97	93	47.6	94.3	align	0	701	High	*Chlorurus spilurus*	MW014212
152	95	94	48.2	93.0	align	2	682	High	*Scarus ghobban*	MW014213
153	74	75	48.9	86.5	align	14	680	Med	*Scarus ghobban*	MW014214
154	97	94	48.1	95.1	align	0	695	High	*Scarus quoyi*	MW014215
155	90	88	47.0	94.7	align	3	694	High	*Scarus psittacus*	MW014216
156	83	86	48.6	98.4	align	0	695	High	*Scarus quoyi*	MW014217
157	95	93	48.2	95.7	align	1	697	High	*Calotomus spinidens*	MW014218
158	96	94	48.3	96.7	align	0	698	High	*Calotomus spinidens*	MW014219
159	96	94	47.9	94.4	align	2	695	Med	*Scarus rivulatus*	MW014220
160	62	39	47.9	69.4	forward	na	697	zero	*couldn't ID*	MW014221
161	56	48	47.8	79.8	forward	na	698	High	*Scarus psittacus*	MW014222
162	81	81	47.0	94.8	align	1	695	High	*Scarus psittacus*	MW014223
163	62	37	48.7	72.2	forward	na	695	High	*Scarus quoyi*	MW014224
164	27	58	47.1	73.1	reverse	na	709	High	*Scarus psittacus*	MW014225
165	36	41	48.3	59.6	reverse	na	706	Med	*scarus quoyi*	
166	81	77	47.0	94.8	align	1	693	High	*Scarus psittacus*	MW014226
167	35	39	47.5	48.6	forward	34	703	High	*Scarus psittacus*	
168	88	86	46.9	95.8	align	2	696	High	*Scarus psittacus*	MW014227
169	88	82	47.3	94.3	align	0	685	High	*Scarus psittacus*	MW014228
170	94	1	50.8	na	forward	na	649	High	*Scarus psittacus*	MW014229
171	94	93	46.7	94.4	align	1	698	High	*Scarus psittacus*	MW014230
172	89	84	46.9	95.4	align	0	697	High	*Scarus psittacus*	MW014231

173	92	90	46.8	94.7	align	0	696	High	*Scarus psittacus*	MW014232
174	88	91	47.0	95.8	align	1	697	High	*Scarus psittacus*	MW014233
175	81	73	47.6	83.6	align	2	683	High	*Scarus psittacus*	MW014234
176	77	63	48.1	79.2	align	9	678	High	*Scarus psittacus*	MW014235
177	97	85	46.8	89.9	align	2	696	High	*Scarus psittacus*	MW014236
178	94	94	47.0	94.0	align	1	689	High	*Scarus psittacus*	MW014237
179	91	86	47.0	93.3	align	3	697	High	*Scarus psittacus*	MW014238
180	25	34	46.8	44.8	reverse	39	689	High	*Scarus psittacus*	
181	94	86	46.8	95.8	align	1	697	High	*Scarus psittacus*	MW014239
182	95	93	46.8	94.6	align	1	699	High	*Scarus psittacus*	MW014240
183	15	18	46.9	37.0	align	38	703	High	*Scarus psittacus*	
184	74	67	47.2	85.5	align	8	698	High	*Scarus psittacus*	MW014241
185	86	73	46.4	90.3	align	1	701	High	*Scarus psittacus*	MW014242
186	0	0	48.3	2.7	align	64	731	High	*Scarus psittacus*	
187	57	62	47.7	88.7	reverse	na	697	High	*Scarus psittacus*	MW014243
188	70	32	48.7	69.6	forward	na	685	High	*Scarus quoyi*	MW014244
189	83	79	47.0	94.9	align	6	708	High	*Scarus psittacus*	MW014245
190	89	75	47.2	94.8	align	0	695	High	*Scarus psittacus*	MW014246
191	79	56	47.0	93.2	align	0	636	High	*Scarus psittacus*	MW014247
192	28	35	47.9	51.2	forward	na	687	zero	*couldn’t ID*	
193	91	89	47.0	97.8	align	0	696	High	*Scarus psittacus*	MW014248
194	87	79	46.9	94.7	align	1	695	High	*Scarus psittacus*	MW014249
195	88	84	47.0	98.3	align	2	695	High	*Scarus psittacus*	MW014250
196	11	4	48.1	18.6	align	30	689	Med	*Scarus psittacus*	
197	57	19	47.9	62.4	forward	na	697	High	*Scarus quoyi*	MW014251
198	84	79	47.0	87.7	align	3	700	High	*Scarus psittacus*	MW014252
199	50	12	47.5	47.0	forward	na	685	High	*Scarus psittacus*	MW014253
200	86	82	46.9	94.7	align	2	698	High	*Scarus psittacus*	MW014254
201	92	88	46.8	93.0	align	1	698	High	*Scarus psittacus*	MW014255
202	13	7	47.5	21.4	forward	na	695	High	*Scarus psittacus*	
203	93	95	47.0	94.4	align	0	698	High	*Scarus psittacus*	MW014256
204	71	69	48.0	80.4	align	6	693	High	*Scarus psittacus*	MW014257
205	96	97	47.3	93.9	align	1	686	High	*Scarus psittacus*	MW014258
206	96	96	46.9	94.1	align	1	696	High	*Scarus psittacus*	MW014259
207	98	94	47.1	95.5	align	1	693	High	*Scarus psittacus*	
208	97	97	47.1	95.2	align	0	683	High	*Scarus psittacus*	MW014260

209	89	85	47.0	95.3	align	2	695	High	*Scarus psittacus*	MW014261
210	96	97	47.2	94.8	align	0	705	High	*Scarus psittacus*	MW014262
211	96	97	47.1	93.4	align	1	700	High	*Scarus psittacus*	MW014263
212	97	98	47.3	96.5	align	0	687	High	*Scarus psittacus*	MW014264
213	97	96	47.0	95.9	align	0	700	High	*Scarus psittacus*	MW014265
214	95	92	49.0	94.0	align	1	682	High	*Scarus flavipectoralis*	MW014266

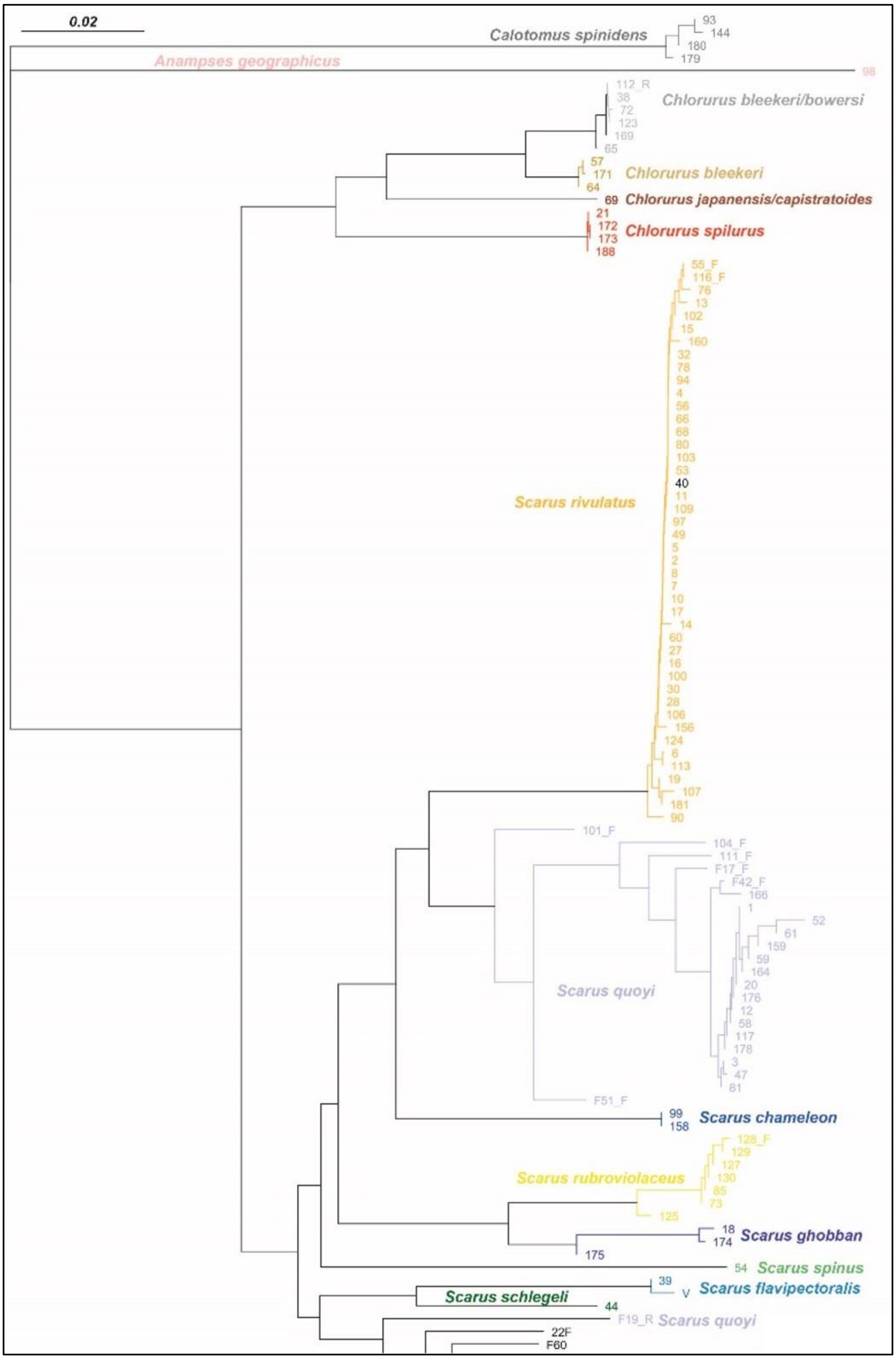
Table S.4.3. Average density per 1000-m^2 of adult parrotfish species observed on visual transects, separated by habitat type.

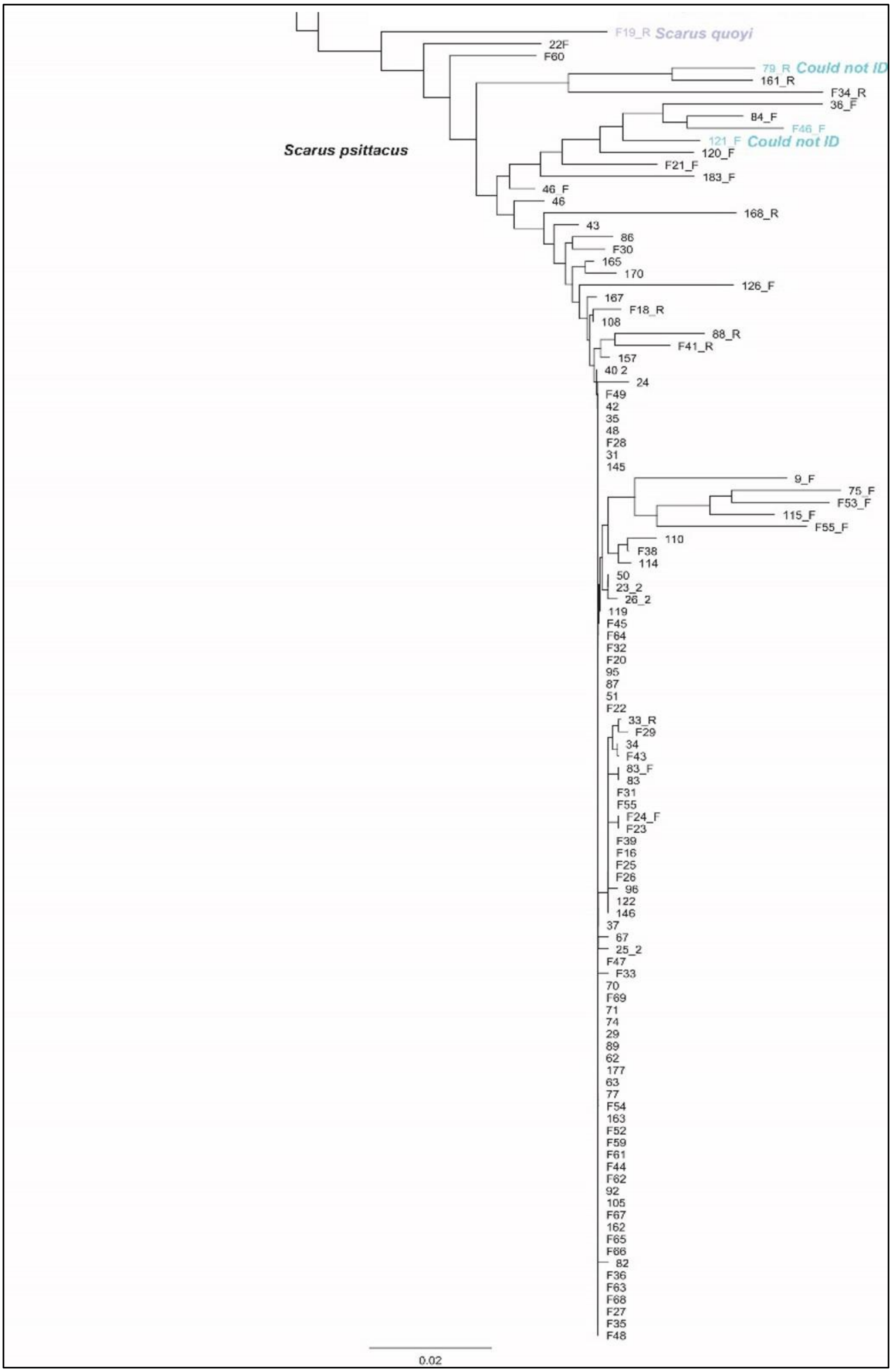
Species	Coral Reef	Algal Bed	Lagoon	Seagrass
Calotomus spinidens	0.0	5.9	0.0	11.9
Chlorurus bleekeri	15.0	5.3	3.2	0.0
Chlorurus spilurus	1.6	0.6	8.0	0.0
Scarus chameleon	0.5	0.2	5.6	1.4
Scarus dimidiatus	3.5	0.0	3.2	0.0
Scarus flavipectoralis	6.6	0.2	10.4	0.0
Scarus ghobban	0.3	0.0	0.8	0.0
Scarus quoyi	0.7	0.0	0.0	0.0
Scarus rivulatus	0.9	0.0	0.0	0.0
Scarus schlegeli	0.9	4.7	0.0	0.0
Calotomus carolinus	0.0	0.0	0.0	0.6
Cetoscarus ocellatus	0.1	0.0	0.0	0.0
Hipposcarus longiceps	1.2	0.0	0.0	0.0
Leptoscarus vaigiensis	0.0	0.2	0.0	0.0
Scarus altipinnis	3.8	0.0	0.0	0.0
Scarus forsteni	0.7	0.0	0.0	0.0
Scarus hypselopterus	4.1	12.1	3.2	0.3
Scarus niger	17.4	0.0	0.0	0.0
Scarus tricolor	2.0	0.0	0.0	0.0
Sum Total	59.3	29.3	34.2	14.2
% total DNA vs. sums total	50.6%	58.0%	90.7%	93.9%

Table. S.4.4. Mean and standard deviation (in parenthesis) of parrotfish density (individuals per 1000-m^2) across habitat types, grouped by size (centimetres) bins of total length estimates (TL) from visual surveys.

	<6 cm	6–10 cm	11–15 cm	16–20 cm	>20 cm
Algal Bed	80.5 (167.6)	31.6 (81.3)	18 (58)	0.3 (2.1)	0 (0)
Coral Reef	0.7 (5.4)	13.5 (63.6)	20.2 (42.2)	11.6 (16.6)	15.2 (21.1)
Lagoon	196 (706.6)	102.9 (140.9)	11.8 (32.7)	0 (0)	0 (0)
Seagrass	31.1 (76.9)	39 (77.1)	9.6 (18.9)	0 (0)	0 (0)

Fig. S.4.1. Phylogenetic tree generated in Geneious software for DNA sequences: The Geneious tree building method used neighbour joining tree and the Tamura–Nei genetic distance model, and no outgroup with 65% similarity.




F19_R Scarus quoyi
22F
F60
79_R Could not ID
161_R
F34_R
36_F
84_F
F46_F
121_F Could not ID
Scarus psittacus
120_F
F21_F
183_F
46_F
46
168_R
43
86
F30
165
170
126_F
167
F18_R
108
88_R
F41_R
157
40 2
24
F49
42
35
48
F28
31
145
9_F
75_F
F53_F
115_F
F55_F
110
F38
114
50
23_2
26_2
119
F45
F64
F32
F20
95
87
51
F22
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F29
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F43
83_F
83
F31
F55
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F39
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F25
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67
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89
62
177
63
77
F54
163
F52
F59
F61
F44
F62
92
105
F67
162
F65
F66
82
F36
F63
F68
F27
F35
F48
0.02

APPENDIX D – SUPPORTING INFORMATION FOR CHAPTER 5

Figure S.51. Stable isotope differences in algae sources between collections years 2017 on left, 2018 on right. Colors are different dietary sources, and shapes are reef secions.

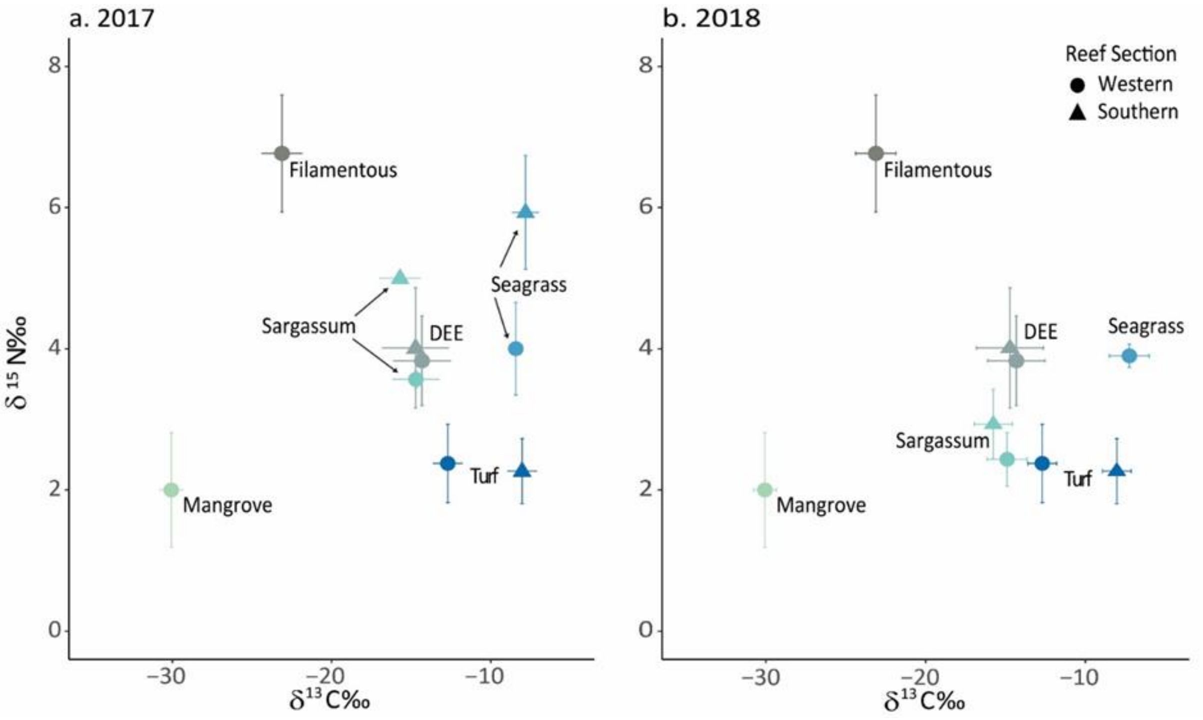
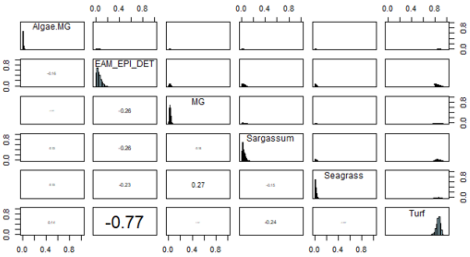
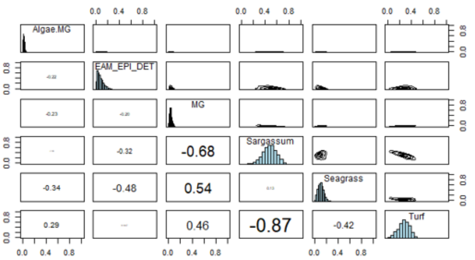


Figure S.5.1. Matrix correlation values from simmr analysis for diet source values analysed for each fish species. TP is for terminal phase adult parrotfish, IP is for initial phase parrotfish. Algae MG = filamentous algae collected in mangrove habitats, EAM_EPI_DET = the category for epilithic algal matrix (EAM), epiphytes, and detritus (referred to as DEE in manuscript). MG = Mangrove. The matrix shows histograms on the diagonal of proportion diet for each food source. The upper right section shows the contour plots. The bottom diagonal reports correlation values between sources.

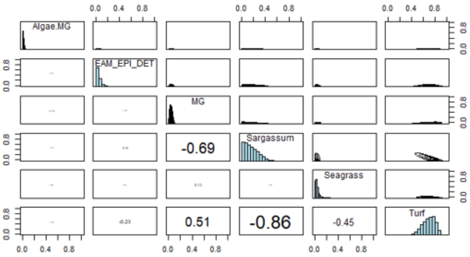
Scarus dimidiatus TP



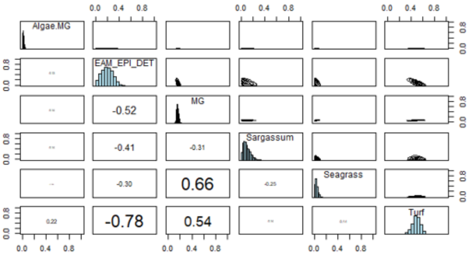
Scarus psittacus juvenile



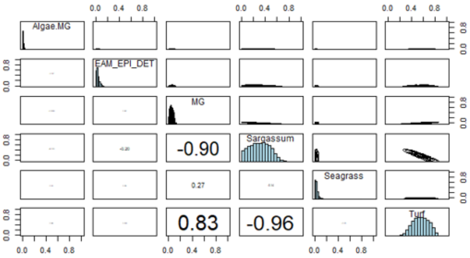
Scarus dimidiatus IP



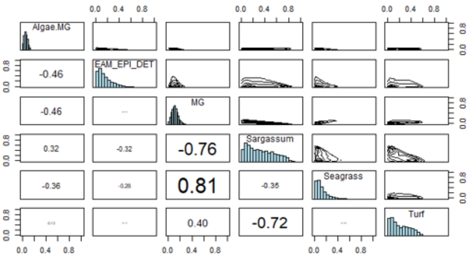
Siganus virgatus adult



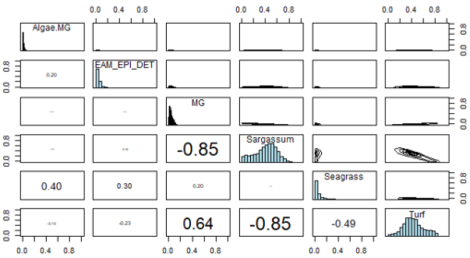
Scarus dimidiatus juvenile



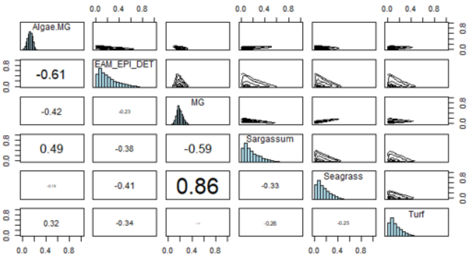
Siganus fuscescens TP



Scarus flavipectoralis IP



Siganus guttatus adult



Scarus flavipectoralis TP