**Sambrook, Katie (2021)** ***Beyond the reef: the influence of seascape structure on the composition and function of tropical fish communities.*** **PhD Thesis, James Cook University.**



https://doi.org/10.25903/zm62%2Dz440

# Beyond the reef: the influence of seascape structure on the composition and function of tropical fish communities

Thesis submitted by

Katie Sambrook (BSc, MSc)

in June 2021

For the degree of Doctor of Philosophy in Marine Ecology

in the ARC Centre of Excellence for Coral Reef Studies,

James Cook University, Australia

ARC CENTRE OF EXCELLENCE

Coral Reef Studies

This thesis is dedicated to

*Dr Eilir Hedd Morgan, Dr Giulia Cambiè*, and *Kate Downes*

Marine scientists, educators, mentors, and friends. I am forever indebted to each of you for your friendship, kindness, humour, and wisdom along this journey.

You will never be forgotten.

*Those who dwell, as scientists or laymen, among the beauties or mysteries of the earth are never alone or weary of life…Those who contemplate the beauty of the earth find reserves of strength that will endure as long as life lasts.*

- Rachel Carson, The Sense of Wonder (1965)

*The first law of ecology is that everything is connected to everything else*

- Barry Commoner (1971)

# Acknowledgements

I feel very fortunate to have been advised by a team of experts during the course of my PhD who have each made a unique contribution. Without their input, I would not be where I am today. Professor Andrew Hoey has been incredibly supportive, consistently providing prompt insightful feedback and engaging discussions that helped refine my ideas, as well as patiently helping me improve my fish ID skills during many hours of watching video footage. Dr Mary Bonin has been a source of wisdom and encouragement throughout, and her clarity and ability to see the bigger picture has been invaluable. Professor Serge Andréfouët shared his wealth of experience in habitat mapping. Dr Stephanie Duce generously provided mentoring, training and mapping advice, and Professor Graeme Cumming provided valuable direction and insight thanks to his extensive background in landscape ecology.

I am greatly indebted to the people of the Tigak Islands where I conducted my fieldwork for so generously sharing their local knowledge, granting me permission to survey around their islands, and allowing me and my team the chance to enjoy an occasional lunch break in some of the most spectacular locations on the planet – *giro*. The staff and other researchers from the Nago Island Mariculture & Research Facility and the team at Nusa Island Retreat never failed to help me overcome the challenges associated with working in such a remote location. Jeff Kinch, Peter Minimulu, Eric Casper, Thane Militz, Nittya Simard, Cathy Hair, Warren Pingo, Esther Leini, Esau and Bradley Saesaria from Nago, and Shannon, Shaun, Jono, Eva, big Simon, little Simon and Exley from Nusa – *tenkyu tru*. My skipper, Peksi Essau, deserves a special mention. I have been fortunate enough to work with and learn from Peksi since my Masters and it has been one of the greatest privileges of my life. As a Tigak Islander, Peksi's connection with the local seascape, love of the ocean and his knowledge of the environment are unsurpassable, as was his ability to beat my GPS in re-locating survey sites. His good humour, problem-solving skills and tolerance of miserable wet weather conditions meant we rarely missed a day in the field which made all the difference – *giro* Peksi. I am also grateful to my field volunteers: Eoghan Aston, Michael Bradley, Jess Hoey and Ryan Marshall - so many good times and enough stories to fill several books.

Back in Townsville at James Cook University, I would like to thank the behind the scenes team at the ARC Centre of Excellence for Coral Reef Studies. These incredible women keep everything running smoothly with patience and good humour and are always there cheering us students on: Janet Swanson, Vivian Doherty, Olga Bazaka, Jennifer Lappin and last, but most definitely not least, Associate Professor Alana Grech. Jodie Wilson from the Graduate Research School also deserves a special mention for her kindness, reassurance and understanding during some challenging times. Thank you to the JCU Boating & Diving team for logistical support and last minute gear fixing.

In addition, getting to Townsville in the first place would not have been possible without the support and opportunities given to me during my time at Falmouth Marine School and Bangor University. In particular, I would like to thank Professor Stuart Jenkins for his belief in my abilities.

I have made some incredible friends along the way who have each made a significant contribution to this journey. Particular thanks go to Ale, César, Debs, Eoghan, Hannah, Karmen, Laura, Maria, Motson, Natalia, Saul, Sivee, Sunny, Tess, and Thea, some of the brightest minds and kindest souls I have ever met – how lucky I am to call each of you a friend. I am also thankful for the friends who have been around so long they have become family – Hayley, Dee, Maxine and Sara, thank you for always being there.

To my godchildren, Evie and George, watching you grow up during the course of this PhD has been a joy and your support, through the drawings you've sent and the questions you've asked, has been lovely. I hope you see this PhD and my path in life as proof that there is always time to try out different options. Take the time to dream a little and explore a lot. The world is big and there are many paths.

A brief turn away from thanking humans to thank my oversized puppy, Tyto. From the day I found you at Tyto Wetlands early on in my PhD, you have enriched my life in so many ways. Unfortunately, your skills do not extend to the ability to read this thesis, but rest assured, you will be getting a delicious reward for being such a good support doggo.

Finally, I want to thank my sister Lorna (the 'wind beneath my wings'), and my uncle and aunt, Martin and Jan. You have championed and cheered me on every step of the way which has meant the world to me – thank you.

# Statement of the contribution of others

This research is the result of collaborations with my Advisors Professor Andrew S Hoey, Dr Mary C Bonin, Professor Graeme Cumming, Dr Stephanie Duce and Professor Serge Andréfouët. Throughout the thesis, I was responsible for the project concept and design, data collection and analysis, interpretation and all written work. My Advisors provided editorial and intellectual input (all), financial support (ASH), equipment (ASH, MCB, and SD), and the benthic habitat map (SA).

**Funding**

An Australia Postgraduate Award (APA) was awarded to Katie Sambrook to cover tuition fees at James Cook University, and 3.5 years of stipend. A grant from the Digital Globe Foundation provided satellite imagery to produce the benthic habitat. The Australian Society for Fish Biology (ASFB) Michael Hall Innovation Award granted to Katie Sambrook provided partial funding for Chapter 3. The David Yellowlees Excellence in Research Award partially funded Chapter 4. A grant from the ARC Centre of Excellence for Coral Reef Studies Higher Degree by Research Enhancement Scheme provided partial funding for Chapter 5.

**Collaborators and volunteers**

The Papua New Guinea (PNG) National Fisheries Authority through both the PNG National Fisheries College and the Nago Island Mariculture and Research Facility provided logistical support for fieldwork. Ryan Marshall and Jessica Hoey assisted in the field. Michael Bradley assisted in the field, provided guidance on camera design and deployments, and helped with fish identification for Chapter 3. Eoghan Aston assisted in the field with benthic data collection, and provided statistical advice for Chapter 4. Katie Sievers provided statistical and mapping advice for Chapter 4.

# Ethics and copyright

This research has been conducted under the James Cook University Animal Research Ethics Committee approval numbers A2455 and A2526.

Every reasonable effort has been made to gain permission and acknowledge the owners of copyright material. I would be pleased to hear from any copyright owner who has been omitted or incorrectly acknowledged.

..............................

Katie Sambrook

June 2021

# List of publications arising from this thesis

**Sambrook K**, Hoey AS, Andréfouët S, Cumming GS, Duce S, Bonin MC (2019) Beyond the reef: The widespread use of non-reef habitats by coral reef fishes. ***Fish & Fisheries*** 20: 903-920 (**Chapter 2**).

**Sambrook K**, Bonin MC, Bradley M, Cumming GS, Duce S, Andréfouët S, Hoey AS (2020) Broadening our horizons: seascape use by coral reef-associated fishes in Kavieng, Papua New Guinea, is common and diverse. ***Coral Reefs*** 39: 1187-1197 (**Chapter 3**).

**Sambrook K**, Andréfouët S, Aston EA, Bonin MC, Cumming GS, Duce S, Sievers KT, Hoey AS (in revision) Relative importance of seascape versus within-habitat variables on the distribution of fishes in tropical seagrass beds. ***Estuarine, Coastal and Shelf Science*** (**Chapter 4**).

**Sambrook K**, Bonin MC, Cumming GS, Duce S, Andréfouët S, Hoey AS (in prep) Influence of seascape and within-reef variables on a key ecosystem process, macroalgal browsing, on coral reefs in Papua New Guinea. ***Oecologia*** (**Chapter 5**).

# Other outputs during candidature

Torda G*, **Sambrook K***, Cross P, Sato Y, Bourne DG, Lukoschek V, Hill T, Torras Jorda G, Moya A, Willis BL (2018) Decadal erosion of coral assemblages by multiple disturbances in the Palm Islands, central Great Barrier Reef. ***Nature Scientific Reports*** 8: 11885 ****Shared first authorship***

Jones GP, Barone G, **Sambrook K**, Bonin MC (2020) Isolation promotes abundance and species richness of fishes recruiting to coral reef patches. ***Marine Biology*** 167: 1-13

# Abstract

Tropical shallow-water seascapes are heterogeneous environments composed of a mosaic of different habitat patches (e.g., coral reef, mangroves, macroalgal and seagrass beds) that occur in varying shapes, sizes and spatial configurations. These habitat patches are ecologically linked through the flow of materials, nutrients and organisms yet are often studied as discrete entities. While some species of coral reef fishes are known to use multiple habitat types during their lifecycle, we still know very little about the extent of non-reef habitat use among reef fishes, or how the spatial patterning of seascapes might influence fish-habitat relationships or ecological processes associated with coral reef seascapes. Thus, my overarching aim was to examine the influence of seascape structure on the composition and function of tropical fish communities, primarily those associated with coral reef habitats. Specifically, my objectives were to: (1) determine the extent of non-reef habitat use by coral reef fishes at a global scale; (2) examine fish-habitat relationships in tropical seascapes in Papua New Guinea; (3) investigate the relative influence of seascape structure and within-habitat variables on fish distribution and abundance patterns in tropical seagrass beds; and (4) examine the influence of seascape structure and within-reef benthic variables on macroalgae browsing activity on coral reefs.

**Chapter 2** systematically reviews and synthesizes the evidence for non-reef habitat use by coral reef fishes across biogeographic regions, life stages and feeding guilds. Non-reef habitat use was found to be extensive, with at least 670 species of coral reef fish observed away from the reef in a wide range of habitats and study locations. Three-quarters of the fish species for which adult and juvenile data were available occurred in non-reef habitats at both life stages, which suggests that fish interactions with non-reef habitats are complex and multifaceted. In addition, over half of the species recorded from non-reef habitats are potential fisheries targets. In the Caribbean, a similar number of fish species used mangroves and seagrass beds. In contrast, in the Indo-Pacific, seagrass beds emerged as the dominant non-reef habitat used by reef fishes. These differences between biogeographic regions may reflect environmental variation (e.g., tidal regimes) or be a result of unbalanced survey effort across habitats in the Indo-Pacific. Based on the synthesis, I estimate approximately one-fifth of' ‘coral reef’ fishes could be non-reef habitat users, but suggest numbers could be higher given the paucity of data for much of the Indo-Pacific region.

**Chapter 3** builds on some of the research gaps identified in the global synthesis and examines fish-habitat relationships in the remote Tigak Islands, New Ireland Province, Papua New Guinea in the Indo-Pacific. Using remote video cameras, fish communities were surveyed in five habitat types (coral reef slope, coral reef flat, macroalgal beds, mangroves and seagrass meadows). Of the 282 shallow-water reef-associated fish species observed across 360 videos, 99 species (35%) were recorded in non-reef habitats, the majority of which (78 species) were seen on multiple occasions. This suggests that non-reef habitat use by coral reef fishes could be even more extensive than suggested by my synthesis (**Chapter 2)** and reinforces the need to incorporate a range of habitats into study designs in the Indo-Pacific. Of the three non-reef habitats, species richness and relative abundances were highest in macroalgae beds. Fish communities in mangroves and seagrass beds were distinct from each other but contained a similar number of species. Supporting the findings of **Chapter 2**, many of the fish families commonly found in non-reef habitats in this location, particularly from seagrass beds, are targeted by local fishers and are critical for sustaining local livelihoods.

The seagrass meadows around the Tigak Islands cover large areas of shallow water, harbour diverse fish communities, support coastal fisheries and are found in close proximity to a range of other habitat types. In **Chapter 4**, I use a multi-scale approach to examine the relative influence of within-habitat variables and seascape structure on the distribution patterns of 17 fish taxa (i.e., families and species), and life stages (adults and juveniles) for two taxa, in 32 seagrass patches around the Tigak Islands. Of the 21 fish groups examined, two-thirds were influenced more by seascape than within-habitat variables. Site-attached taxa were generally more influenced by within-habitat variables, while taxa with larger home ranges (e.g., rabbitfishes, snappers) and ontogenetic habitat-shifters (e.g., emperors) were generally more influenced by the surrounding seascape. Despite the majority of taxa being reef-associated, proximity to or area of adjacent coral reefs appeared to have limited influence on local abundances. Instead, proximity and area of hardground, macroalgae and mangroves emerged as more influential. My findings show that seagrass patches are not functionally equivalent to each other and that the surrounding seascape can be more important in shaping tropical fish assemblages in seagrass beds than within-habitat variables.

Given the evidence that the surrounding seascape can influence fish distribution patterns, **Chapter 5** explores whether features of the seascape can also impact a key ecological process on coral reefs, specifically macroalgae browsing by reef fishes. I investigated whether seascape and within-reef benthic variables influenced the rates and agents of macroalgal removal using experimental macroalgae assays and remote video cameras at 24 shallow coral reef sites around the Tigak islands. I predicted that the presence of potential alternative sources of food near to reefs (e.g., neighbouring macroalgal beds), would affect macroalgae removal rates, community composition and/or browsing behaviour of fishes. Contrary to expectations, macroalgae at the seascape or within-reef scale was not a good predictor of macroalgal removal rates. Instead, both rates and agents of browsing were most strongly influenced by distance to oceanic environment, and exhibited differential responses to other seascape (e.g., area of seagrass within 250 m) and benthic variables. My findings provide support for the notion that the surrounding seascape can influence ecological processes on reefs.

Overall, my research highlights that non-reef habitat use among fish typically classified as reef-associated is more common and widespread than has previously been recognised, yet we still know very little about reasons underpinning multi-habitat use. This thesis contributes to the emerging field of seascape ecology by demonstrating that the wider seascape can influence both fish-habitat relationships and ecological processes. Importantly it provides strong support for the need to transition from a habitat- or patch-centric approach to encompass the surrounding seascape. It shows that the spatial context of a habitat patch may affect who uses the patch, from species to life stages, and this information has the potential to be particularly important in terms of identifying and managing critical shallow-water nursery habitats. The adoption of a multi-scale approach to examine fish-habitat relationships and ecological processes in coastal ecosystems can provide a more nuanced perspective, enabling the development of more refined spatial management strategies. Given the widespread loss and degradation of many coastal habitats in the tropics, combined with the importance of coastal fisheries for developing island nations, this thesis highlights the need to scale up research to incorporate the broader seascape if we are to manage and study shallow-water coastal ecosystems effectively in the future.

# Table of contents

## List of figures

# List of tables

# Chapter 1

## General Introduction

How animals perceive, select and interact with their environment have been longstanding research themes in ecology. Such information can provide valuable insight into how populations and communities are assembled (Hairston et al. 1960; Paine 1966; Estes & Palmisano 1974; Lubchenco & Gaines 1981; Paine & Levin 1981), how species support the functioning of ecosystems (e.g., herbivory, nutrient cycling, Naeem et al. 1994; Tilman et al. 1997; Walker et al. 1999; Burkepile & Hay 2008), maintain ecosystem integrity (e.g., prevention of tipping points, Tilman & Downing 1994; Laurance et al. 2011; Newbold et al. 2016), and sustain ecosystem services (e.g., agriculture, fisheries, coastal protection) that promote human well-being (Scheffer et al. 2001; Elmqvist et al. 2003; Cadotte et al. 2011; Oliver 2016). However, unravelling species-environment relationships is inherently complicated given that such relationships are the product of a complex interplay between numerous abiotic (e.g., light, temperature, precipitation) and biotic (e.g., predation, competition, mutualism) variables operating across a range of spatial and temporal scales (Hutchinson 1957; Connell 1961; Whittaker 1965; Connell 1983; Menge & Olson 1990; Levin 1992; Menge 2000; Harborne et al. 2011).

The spatial distributions of species are shaped by their tolerance to abiotic and biotic conditions (i.e., fundamental niche), as well as a range of intrinsic (e.g., need to find food, find a mate) and extrinsic (e.g., predation, competition) factors that determine the environment where an individual actually occurs (i.e., realised niche; Hutchinson 1957). Several theories have been proposed to explain how individuals are distributed across space (e.g., ideal free distribution, Fretwell & Lucas 1970), and how they make decisions around habitat or patch selection (e.g., optimal foraging theory, Emlen 1966; MacArthur & Pianka 1966; central place foraging, Orians & Pearson 1979; coexistence theory, Chesson 2000; and the landscape of fear, Laundré et al. 2001). For example, optimal foraging theory predicts that individuals seek to maximise fitness by adopting a strategy that maximises energy acquisition, while minimising the costs associated with foraging (e.g., energy acquisition vs. search times, handling of prey, Schoener et al. 1971; Pyke 1984). In contrast, the landscape of fear model predicts that predation risk motivates patch choice and behaviour, for instance by influencing foraging decisions for prey that must select patches across a gradient from risky but profitable, to safe but less profitable

(Brown et al. 1999, Laundré et al. 2010). While these theories have been useful in predicting and understanding spatial distributions within a habitat, they have rarely been applied among habitats, especially in the marine environment.

Primarily, multiple habitat use is thought to be driven by an inability to obtain the full complement of resources required by an individual throughout their life cycle from within a single habitat type (Werner & Gilliam 1984; Dunning et al. 1992; Pope et al. 2000). In this scenario, access to different components of a landscape or seascape may be necessary for survival, such as the need to access specific resources (e.g., shelter or food) (Holbrook et al. 1990; Mittelbach & Osenberg 1993; Dahlgren & Eggleston 2000; Hunt & Seibel 2000). For instance, access to water and suitable grazing habitat underpin the seasonal long-distance migrations of the Serengeti wildebeest (Torney et al. 2018). Atlantic salmon *(Salmo salar*) use freshwater habitats as juveniles, migrate to marine environments to feed as adults, before eventually returning to natal rivers to spawn (Klemetsen et al. 2003). As well as these examples of long-distance migrations which can take place over timescales from months to years, other taxa undertake more frequent (e.g., daily) movements among habitat types, often between feeding and refuge sites (e.g., Ogden & Buckman 1973; Ager et al. 2003; Hitt et al. 2011). Through their cross-habitat movements, multiple habitat users can be an important source of cross-habitat subsidies, for example, through pollination, nutrient transport, and by altering predator-prey interactions as they move around the landscape (Polis et al. 1997; Lundberg & Moberg 2003; Kremen et al. 2007; Heck et al. 2008). Accounting for the range of habitat types found in a landscape and their spatial arrangement can therefore be important for understanding both species distribution patterns and ecological processes.

Recognising that habitats, and therefore species-habitat relationships, rarely function in isolation, has led to a shift away from traditional and reductionist approaches that typically consider a single habitat or patch to a broader landscape perspective that considers the composition and spatial arrangement of habitat patches (Massol et al. 2011). In terrestrial ecosystems, the development of the field of landscape ecology has been gaining momentum since the 1980s (Addicott et al. 1987; Turner 1989; Taylor et al. 1993; Wiens et al. 1993; Wu & Loucks 1995; Turner 2005). Landscape ecology is based around the central tenet that the spatial context of a habitat patch is of ecological importance (Turner 2005), and commonly uses high resolution habitat, vegetation, or land-use maps to relate patterns in landscape structure to biotic patterns and processes. Landscape ecology has provided a useful framework to evaluate the influence of landscape heterogeneity on biodiversity, species distribution patterns and community structure (e.g., Wiens 1976; Dormann et al. 2007; Tscharntke et al. 2012), to understand the effects of disturbance, habitat loss and fragmentation (e.g., Saunders et al. 1991; Andrén 1994; Ricketts 2001; Fahrig 2003; Fischer & Lindenmayer 2007; Turner 2010), and to inform terrestrial conservation planning (e.g., Phua & Minowa 2005; Pressey et al. 2007; Wiens 2007; McAlpine et al. 2015).

In addition, the field of landscape ecology has also been central in demonstrating the value of considering the spatial scale across which species-habitat relationships are examined (Wiens 1989; Levin 1992; Holland et al. 2004; Wheatley & Johnson 2009). For instance, the spatial scale(s) across which a species perceives and interacts with its environment can vary depending on traits such as body size, mobility, and foraging behaviour (Holland et al. 2004; Miguet et al. 2016). Adopting a single spatial scale to study patterns and processes based on human-imposed concepts of habitat or scale, risks missing the true scale of effect (Orians & Wittenberger 1991; Jackson & Fahrig 2015). Instead, landscape ecology promotes studying species-habitat relationships across multiple spatial scales simultaneously (e.g., from mm's to km's) to determine which scale, or combination of factors operating at different scales, best explain ecological patterns and processes (Wedding et al. 2011; Miguet et al. 2016).

Despite the challenges and complexity associated with disentangling species-environment relationships, the need to collect, interpret and synthesise data on such relationships has never been greater. Globally, we are witnessing transformations of both terrestrial and aquatic environments at unprecedented rates due to anthropogenic-induced disturbances (e.g., climate change, development, pollution, overharvesting, Hughes 2000; Jackson et al. 2001; Brooks et al. 2002; Williams et al. 2003; Hoekstra et al. 2005). One of the most visible and quantifiable impacts of human activity can be seen through alterations to the physical structure and composition of habitats (e.g., land-use change, habitat loss, habitat fragmentation, shifts in foundation species, and biotic homogenisation), which can concomitantly affect the population dynamics of fauna that interact with those habitats (McKinney & Lockwood 1999; Cushman 2006; Bonin et al. 2011; Powers & Jetz 2019). For species that are highly dependent on a single habitat type, the effects of habitat change on populations can be rapid (e.g., Warren et al. 2001), and future outcomes for such taxa can be predicted with reasonable confidence. However, for taxa that use multiple habitat types throughout their lives (Pulliam et al. 1992; Schreiber &

Rudolf 2008; Jackson et al. 2019), we know far less about habitat dependencies for these species or how they might be impacted as different habitat types undergo change.

In marine systems, the conventional approach to studying species-habitat relationships has been to focus on a single habitat type in isolation to identify the within-habitat characteristics that best explain biodiversity, species distribution or abundance patterns (e.g., Jones et al. 2004; Graham & Nash 2013). Although this approach may be suitable for those species that complete their entire life cycle within that habitat type (i.e., habitat specialists), it is less suitable for understanding the distribution and abundance patterns of species that use multiple habitats, nor does it consider how external influences operating elsewhere in the seascape might influence biotic and abiotic conditions within a focal habitat patch. Instead, an approach that accounts for the spatial arrangement and composition of habitats and habitat patches within a seascape may provide a more complete picture, and enable us to make more meaningful predictions about future environmental change (Boström et al. 2011; Pittman 2018).

Emerging technologies are now enabling the principles of landscape ecology to be tested in marine systems (Pittman et al. 2004; Boström et al. 2011; Wedding et al. 2011). To date, a seascape ecology approach has been applied to examine how the seascape structure influences the distribution and abundance patterns of a range of taxa (e.g., invertebrates: Turner et al. 1999; Pittman et al. 2004; Carroll & Peterson 2013; fishes: Moore et al. 2011; Berkström et al. 2013a; Ricart et al. 2018), in a variety of habitat types (e.g., coral reefs, Wedding & Friedlander 2008; Kendall et al. 2011; kelp forests, Parnell 2015; Sievers et al. 2016; macroalgae beds, van Lier et al. 2018; Eggertsen et al. 2019; mangrove forests, Pittman et al. 2007; Drew & Eggleston 2008; rocky reefs, Swadling et al. 2019; saltmarshes, Green et al. 2012; and seagrass, Staveley et al. 2017; Olson et al. 2019) and across a range of temperate (e.g., Perry et al. 2018; Rees et al. 2018), subtropical (e.g., Olds et al. 2012a; Gilby et al. 2016) and tropical (e.g., Grober-Dunsmore et al. 2008; Olds et al. 2013; Berkström et al. 2020) ecosystems. Collectively these studies have shown that the seascape surrounding a focal patch can influence species distribution and abundance patterns, although the influence and relative importance of seascape versus within-habitat attributes (e.g., structural complexity) varies among taxa, and between geographic locations. In addition, similar to studies from terrestrial systems (e.g., Thornton et al. 2011), the few seascape studies that have incorporated a range of spatial scales to measure different aspects of the surrounding seascape (e.g., area of habitat within different sized radii) have found that that the spatial scales considered can influence outcomes (e.g., Kendall 2005; Grober-Dunsmore et al. 2008).

There is increasing recognition that a seascape ecology approach may be particularly beneficial for examining patterns and processes in tropical shallow-water seascapes. Tropical shallow-water seascapes often contain a complex mosaic of different habitat types (e.g., coral and rocky reefs, seagrass meadows, mangroves), in a multitude of spatial configurations, habitat combinations and patch sizes, and these habitats can be interlinked through abiotic and biotic processes (Ogden 1988; Boström et al. 2011; Pittman & Olds 2015). Many of these habitat types are vulnerable to terrestrial influences (e.g., human development, pollution, riverine outflows), and are among the habitats most threatened by climate change (Jackson et al. 2001; Hughes et al. 2003; Orth et al. 2006; Barlow et al. 2018; Halpern et al. 2019). In many locations, widespread changes have already occurred including habitat loss, fragmentation, and degradation (e.g., coral reefs, Hughes et al. 1994; De'ath et al. 2012; mangroves, Richards & Friess 2016; Goldberg et al. 2020; seagrass, Waycott et al. 2009; Rasheed et al. 2014). Alterations to, or the loss of, the foundation species that are responsible for creating the physical habitat structure can directly or indirectly affect species distribution patterns and ecosystem processes (Ellison et al. 2005; Byrnes et al. 2011; Pratchett et al. 2011; Richardson et al. 2017). However, without a more complete understanding about how the spatial arrangement and composition of tropical shallow-water seascapes can influence patterns or processes, our ability to predict future change is limited.

Tropical fishes are an important group to consider within a seascape context. Some species use completely different habitats at different life stages, or may use multiple habitat types on a regular basis for foraging, spawning or refuge (Pittman & McAlpine 2003; Nagelkerken et al. 2015). By using the wider seascape, fish can act as mobile links through nutrient transport, and can affect food web dynamics between different habitat types and habitat patches (Meyer & Shultz 1985; Parrish 1989; Polis et al. 1997; Moberg & Folke 1999; Lundberg & Moberg 2003; Sheaves 2009). Cumulatively, these multi-habitat users could be significant in the transfer of energy, and maintenance of key functions across a range of habitats. However, the prevalence of multiple habitat use among tropical fishes is largely unknown. Furthermore, although several studies have begun to relate tropical fish distribution patterns to spatial patterns of the seascape, this research has typically been restricted to a few geographic locations (e.g., Caribbean, Kendall 2005; Grober-Dunsmore et al. 2007; Pittman et al. 2007; Sekund & Pittman 2017;

Western Indian Ocean, Dorenbosch et al. 2006a; Berkström et al. 2012; Aller et al. 2014). Making generalisations about fish-habitat relationships based on a limited number of localities and without accounting for the spatial context could mean we are making poor decisions about how best to manage individual habitats or seascapes. In addition, few studies have expanded seascape research beyond ecological patterns to examine how the surrounding seascape can influence ecological processes (e.g., herbivory).

Knowledge of both fish-habitat relationships and how the spatial arrangement of habitat types and patches can influence ecological patterns and processes are prerequisites for the effective management of tropical shallow-water seascapes. Without such information, we cannot fully evaluate the effects of habitat loss, degradation, and reconfiguration under different disturbance scenarios, design ecologically meaningful reserve networks, identify and protect critical nursery habitats, or implement appropriate intervention or restoration strategies.

***Research aims and thesis structure***

The overarching aim of this thesis was to investigate the influence of seascape structure on the composition and function of tropical fish communities, primarily those considered as coral reef-associated fishes. This aim is achieved through four distinct objectives, each of which relates to a separate chapter.

The first two objectives relate to examining fish distribution patterns in multiple habitats found in tropical shallow-water seascapes, specifically to:

1) Synthesise the extent of non-reef habitat use by coral reef-associated fishes at a global scale
2) Describe fish-habitat relationships in a tropical shallow-water seascape in Papua New Guinea in the Indo-Pacific.

The second two objectives consider how the spatial configuration and composition of the seascape, and different spatial scales, can influence both fish distribution patterns and ecological processes, specifically to:

3) Investigate how within-patch and seascape variables influence fish distribution patterns in tropical seagrass beds
4) Examine how seascape and within-reef benthic variables influence rates and agents of macroalgal removal on coral reefs.

**Chapter 2** presents the first global systematic review to quantify the extent of non-reef habitat use among fish species typically recognised as reef-associated and identifies key knowledge gaps. These knowledge gaps inform the direction and focus of the subsequent field-based chapters conducted in the shallow water tropical seascape of the Tigak Islands, New Ireland, Papua New Guinea. **Chapter 3** describes the habitat use patterns of coral reef fish taxa in Papua New Guinea, a relatively unexplored region of the Indo-Pacific. Using remote video cameras, I quantify the occurrence of reef fish taxa across five reef and non-reef habitat types. **Chapter 4** examines fish-habitat relationships across a hierarchy of spatial scales. Specifically, I determine the relative importance of within-patch versus seascape variables as drivers of fish distribution and abundance patterns in tropical seagrass beds, and evaluate the influence of seascape structure at multiple spatial scales. In the final data chapter (**Chapter 5**), I progress from exploring patterns to examining a critical ecological process, macroalgal browsing, within a seascape context. Here, I examine the influence of seascape and within-reef benthic variables on macroalgal removal rates and agents of browsing on coral reefs. Finally the General Discussion (**Chapter 6**) considers how the findings of this thesis can direct future efforts to understand the role of the seascape in driving species distribution patterns and ecological processes.

# Chapter 2

Beyond the reef: the widespread use of non-reef habitats by coral reef fishes [1]

## 2.1 Abstract

Marine ecology seeks to understand the factors that shape biological communities. Progress towards this goal has been hampered by habitat-centric approaches that ignore the influence of the wider seascape. Coral reef fishes may use non-reef habitats (e.g., mangrove, seagrass) extensively, yet most studies have focused on within-reef attributes or connectivity between reefs to explain trends in their distribution and abundance. We systematically review the evidence for multi-habitat use by coral reef fishes across life stages, feeding guilds, and conservation status. At least 670 species of 'coral reef fish' have been observed in non-reef habitats, with almost half (293 species) being recorded in two or more non-reef habitats. Of the 170 fish species for which both adult and juvenile data were available, almost 76% were recorded in non-reef habitats in both life stages. Importantly, over half of the coral reef fish species recorded in non-reef habitats (397 spp.) were potential fisheries targets. The use of non-reef habitats by 'coral reef' fishes appears to be widespread, suggesting in turn that attempts to manage anthropogenic impacts on fisheries and coral reefs may need to consider broader scales and different forms of connectivity than traditional approaches recommend. Faced with the deteriorating condition of many coastal habitats, there is a pressing need to better understand how the wider seascape can influence reef fish populations, community dynamics, food-webs and other key ecological processes on reefs.

## 2.2 Introduction

The problem of pattern and scale has been widely acknowledged in ecology for decades (Levin 1992) but progress in unravelling the causes and consequences of spatial variance and their relevance for many ecological communities has been slow. Marine environments have been particularly challenging to study (Pittman & Olds 2015), because of the depth, inaccessibility,

---

[1] This chapter is published as: **Sambrook K,** Hoey AS, Andréfouët S, Cumming GS, Duce S, Bonin MC (2019) Beyond the reef: The widespread use of non-reef habitats by coral reef fishes. *Fish & Fisheries* 20: 903-920

and three-dimensional complexity of the ocean; high-resolution, large-extent maps and biological surveys of underwater systems are difficult to obtain (Sbrocco & Barber 2013). Whilst the development of seascape ecology has lagged behind that of landscape ecology because of these issues, the situation has improved over the last two decades. The growing availability of broad-scale datasets (e.g., Sbrocco & Barber 2013) and remote sensing technologies now allow us to apply landscape ecology principles (Pittman & Olds 2015; Grober-Dunsmore et al. 2009) to address questions about the influence of spatial variation in structuring marine communities.

Coastal seascapes are spatially heterogeneous environments (Parrish 1989; Nagelkerken 2009). In the tropics, shallow-water seascapes can include a range of coral reef, mangrove, seagrass, macroalgae and soft sediment habitats. Although these habitats often occur in close proximity to each other (Ogden 1976; Parrish 1989; Grober-Dunsmore et al. 2008), the traditional approach to understanding species distribution and abundance patterns in coastal seascapes has often been confined to observations within a single habitat type (e.g., coral reef, seagrass or mangroves) (Birkeland 1985; Beets et al. 2003; Nagelkerken 2009; Pittman & Olds 2015). Yet it is increasingly acknowledged that habitats rarely function in isolation and that interactions between habitats may be important for productivity and ecosystem functioning (Randall 1965; Ogden 1976; Birkeland 1985; Mumby & Hastings 2008). Marine habitats are linked through the transfer or movement of nutrients, materials and organisms (Nyström & Folke 2001; Lundberg & Moberg 2003; Hyndes et al. 2014; Shantz et al. 2015). As a result, ecological patterns and processes observed within one habitat may, in part, be driven by patterns and processes occurring in another habitat.

Fish are recognised as important mobile links between marine habitats (Nyström & Folke 2001; Lundberg & Moberg 2003; Berkström et al. 2012). For example, the movement of fishes can facilitate trophic subsidies and nutrient transfer between habitats (Meyer & Schultz 1985; Polis et al. 1997; Heck et al. 2008; Shantz et al. 2015). In tropical seascapes, some fishes settle directly to coral reef habitat following their pelagic larval stage and become permanent residents, while others use non-reef habitats (e.g., seagrass, mangrove) throughout their lives. One of the most frequently cited explanations for the use of non-reef habitats by coral reef fishes is that non-reef habitats, such as seagrass beds and mangroves, can be used as nursery habitat for juvenile coral reef fishes (Beck et al. 2001; Nagelkerken et al. 2002; Dahlgren et al. 2006; Nagelkerken 2009; Sheaves et al. 2015). In addition, some coral reef fishes undertake tidal, diel, monthly, seasonal, and/or yearly movements between coral reef and non-reef habitats to forage, shelter from predators, and/or spawn (Unsworth et al. 2007a; Appeldoorn et al. 2009; Hitt et al. 2011; Taylor & Mills 2013; Honda et al. 2016). Availability of, or access to, non-reef habitats may therefore be important for many coral reef fish species.

Over the last two decades, research into the use of non-reef habitats by fishes in tropical seascapes has expanded considerably, largely because many of the species that use multiple habitat types are ecologically or economically important (see reviews by Adams et al. 2006; Nagelkerken et al. 2008; Appeldoorn et al. 2009; Igulu et al. 2014). However, this growing body of research has not yet been synthesised to determine the number of coral reef fish species that have been observed in non-reef habitats, nor which non-reef habitats are commonly used. Fuelled by growing concerns about global habitat loss and increasing recognition that the wider seascape may influence species distribution and abundance patterns, such a review is both timely and important. Here, a systematic review of the occurrence of coral reef fishes in non-reef habitats is conducted. The findings are separated into two biogeographic regions, the tropical Atlantic and the Indo-Pacific, because they have distinct reef fish assemblages and benthic communities. Specifically, the following themes were examined: 1) how many coral reef fish species have been observed in non-reef habitats; 2) which habitats are used by coral reef fishes in addition to reefs; 3) differences and similarities between the two biogeographic regions; whether habitat use differs depending on 4) life stage or 5) feeding ecology; 6) which multi-habitat fish species are of interest to fisheries; and 7) whether any multi-habitat coral reef fish species are currently endangered, threatened or vulnerable.

## 2.3 Methods

The literature was systematically searched for original research articles published between 1967 and November 2018 using ISI Web of Science and Scopus. To identify publications that had investigated the use of non-reef habitats by fishes that are generally considered coral reef-associated, the search terms “coral reef*” and “fish*” were used in combination with a range of different habitat types namely “seagrass*”, “grass*”, “mangrove*”, “macroalga*”, “alga*”, “vegetat*”, “unvegetat*”, “mud*”, “rock*”, “estuar*”, “sand*”, and “soft sediment*”. Papers were searched for that specifically included these terms in the Title, Keywords and/or Abstract. Outputs from these searches resulted in 2,992 potential papers from the ISI Web of Science database, and 1,419 papers from Scopus. To be included in subsequent analyses, the following selection criteria were applied to each paper: 1) data were collected from a coral reef and also in at least one other habitat type; 2) non-reef habitats were clearly defined as discrete patches within the study region, rather than as microhabitats within a coral reef; and 3) the paper or supplementary material contained species-specific information. Citations within all papers matching the selection criteria were also examined to identify any additional literature not captured within the literature search. Although many studies will have recorded the presence of coral reef fishes in non-reef habitats (e.g., Unsworth et al. 2009; Chaves et al. 2013; Bradley et al. 2017), only those studies that had surveyed both reef and non-reef habitat were included because this provided unequivocal evidence of the use of both reef and non-reef habitats by a given species within the same study area. In addition, the selection criteria excluded papers that correlated presence or abundance of fishes on the reef with proximity to a non-reef habitat without surveying the non-reef habitat (e.g., Grober-Dunsmore et al. 2007; Olds et al. 2012b).

For each study, fish species were included in the analysis if they were observed both on the reef and in at least one other habitat type, and were classified as 'reef-associated' in *FishBase* (Froese & Pauly 2018), hereafter termed 'coral reef fishes'. Observations of coral reef fish species were recorded as presence/absence data and separated into life history stages (i.e., adults and juveniles) if the data were available. Presence/absence rather than abundance or biomass data was recorded to capture the widest possible range of species that have been observed in non-reef habitats as well as on coral reefs. This decision was driven by the diverse range of reporting variables contained within the literature (e.g., density, presence/absence, proportional abundance, biomass), the different methodologies (e.g., tagging, visual censuses, timed surveys, fishing), as well as the variety of life stages examined by studies (e.g., larvae, early stage juveniles, juveniles, sub-adults and adults). The combination of these factors makes it challenging to present and interpret abundance or biomass data in a meaningful way. Parrotfishes (subfamily Scarinae) were recognised as distinct from the wrasses (Labridae) because of the functional importance of parrotfishes for coral reef ecosystems (e.g., Hoey & Bonaldo 2018).

Each presence/absence observation was assigned to one of seven habitat classes: coral reef, seagrass bed, mangrove, macroalgal bed, sand, estuary or other. Although the benthic composition of seagrass, macroalgae, mangrove and coral reef habitats will differ between regions and studies and could influence coral reef fish use of these habitats, this review does not distinguish between different taxonomic composition in a particular habitat type (e.g., types of seagrass) as this information was not consistently available from the literature. Mangrove habitat refers only to non-estuarine mangroves. Estuary includes a range of habitats found within the estuary, including mangroves and rocky substrates. The habitat category “other” includes a range of additional non-reef habitats such as channels not dominated by coral communities, rocky boulders and notches, mudflats, gorgonian plains and submerged vegetation. To explore potential biogeographic differences in habitat use by reef fishes, data were separated into two distinct regions: 1) the tropical Atlantic, which includes the Caribbean, Florida Keys, and tropical reefs in Brazil; and 2) the Indo-Pacific, which includes the Indian and Pacific Oceans, as well as the Red Sea.

To examine whether feeding ecology influences the use of multiple habitat types by coral reef fishes, each species was assigned to one of six feeding guilds (i.e., carnivores, corallivores, herbivores, omnivores, piscivores and planktivores) primarily derived from the ‘Diet’ and ‘Food item” categories in *FishBase* (Froese & Pauly 2018). Here carnivores were defined as species that predominantly consume macro-invertebrates (e.g., crustaceans, molluscs, polychaetes) and/or fish. Fish that consume both animal and plant material were classed as omnivores, and herbivores included species that feed on macroalgae, turf algae, seagrass, microscopic phototrophs and detritus. To explore whether body size might be a factor influencing which taxa were observed in non-reef habitats, and as a proxy for mobility, the maximum total length (cm) recorded for each species was also extracted from *FishBase* (Froese & Pauly 2018). Species were also evaluated based on their importance to fisheries using the five categories reported by *FishBase* (i.e., commercial, minor commercial, subsistence, recreational and, of no interest to fisheries) (Froese & Pauly 2018). Species could be assigned to more than one fisheries category (e.g., commercial and recreational). In addition, multiple habitat-using coral reef fish species were classified as endangered, near threatened or vulnerable or “other” according to the IUCN Red List (IUCN 2018).

## 2.4 Results

There were 107 studies that matched all of the selection criteria. Of these, 56 were based in the tropical Atlantic, 50 were in the Indo-Pacific, and one examined two species, one from each biogeographic region (i.e., Dorenbosch et al. 2006b). The foci of different studies ranged from fish communities (39 out of 107 studies) to specific groups or families (40 studies) down to a single focal species (28 studies). In the tropical Atlantic, 37% of studies (n=21) examined only one non-reef habitat type compared to 59% (n=30) in the Indo-Pacific. Three or more non-reef habitats were examined by 16 studies in the tropical Atlantic, in strong contrast to the Indo-

Pacific where there was only a single study (i.e., Kimirei et al. 2011) (Figure A2.1). Seagrass was the most frequently surveyed habitat in both regions, examined in 74% of the 57 studies in the tropical Atlantic, and 63% of the 51 studies in the Indo-Pacific. Mangrove habitats were studied almost twice as much in the tropical Atlantic (70% of the 57 studies) compared to the Indo-Pacific (37% of the 51 studies) (Figure A2.2). The remaining non-reef habitat types (macroalgae, soft sediment, estuary and "other") were surveyed on far fewer occasions (≤11 studies for each habitat) in both regions.

### *2.4.1 Coral reef fish species and families*

Species observed in multiple habitat types came from a diverse range of reef fish taxa and were recorded in a wide range of non-reef habitats. From these 107 studies, a total of 670 coral reef fish species were observed in non-reef habitats, 160 species from the tropical Atlantic, and 514 species from the Indo-Pacific region (Figure 2.1; Table A2.1). Four species of multi-habitat users (black triggerfish (*Melichthys niger*, Balistidae); spot-fin porcupinefish (*Diodon hystrix*, Diodontidae); red lionfish (*Pterois volitans*, Scorpaenidae) and; great barracuda (*Sphyraena barracuda*, Sphyraenidae)) were common to both regions. In the tropical Atlantic, the highest number of species observed in non-reef habitats were in the Serranidae (groupers) and Scarinae (parrotfishes), with 20 and 16 species respectively (Figure 2.2). In contrast, in the Indo-Pacific, the dominant taxa documented in non-reef habitats were the Labridae and Pomacentridae, with 74 and 65 species respectively (Figure 2.2).

Across both regions, 44% of species (293 of 670) were present in two or more non-reef habitats (Table A2.1). In the tropical Atlantic, 69% of species (111 of 160 species) were noted in two or more non-reef habitats (Figure 2.3), and of these 37% (41 of 111 species) were recorded in every habitat surveyed (e.g., if five non-reef habitats were surveyed, they were found in those five habitats). In particular, 100% of Acanthuridae species (3 out of 3) were observed in five or more non-reef habitats, 73% of Haemulidae species (8 out of 11 species) and 78% of Lutjanidae species (7 out of 9 species) were observed in three or more non-reef habitats in the tropical Atlantic. For example, French grunts (*Haemulon flavolineatum*, Haemulidae) has been recorded in seagrass, mangrove, macroalgae, soft sediment and other non-reef habitats including rocky boulders and mudflats (e.g., Nagelkerken et al. 2000a; Adams & Ebersole 2002; Nagelkerken & van der Velde 2002; Harborne et al. 2008; Burke et al. 2009).

In the Indo-Pacific, 36% of species (186 of 514) were observed in two or more non-reef habitat types (Figure 2.3). Of these, 62% (116 of 186) were recorded in every habitat where their presence or absence was evaluated. In this region, 100% of Mullidae (9 out of 9) and Nemipteridae (5 out of 5) species, 83% of Sphyraenidae (5 out of 6), 70% of Lethrinidae (14 out of 20), 69% of Siganidae (9 out of 13), and 57% of Lutjanidae species (8 out of 14) were recorded in two or more non-reef habitats. For example, the thumbprint emperor (*Lethrinus harak*, Lethrinidae) has been observed in seagrass, mangrove, macroalgae, soft sediment, mudflat and rocky habitats (e.g., Thollot et al. 1990; Ashworth et al. 2006; Barnes et al. 2012; Berkström et al. 2012; Kruse et al. 2016; Wilson et al. 2017).

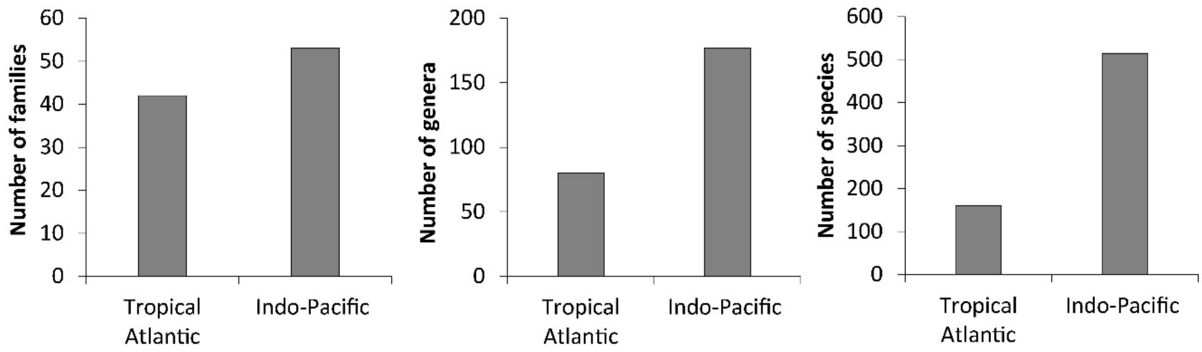


**Figure 2.1.** Number of coral reef fish a) families, b) genera and, c) species observed using both reef and non-reef habitats in the tropical Atlantic and Indo-Pacific regions. Data extracted from 107 publications.

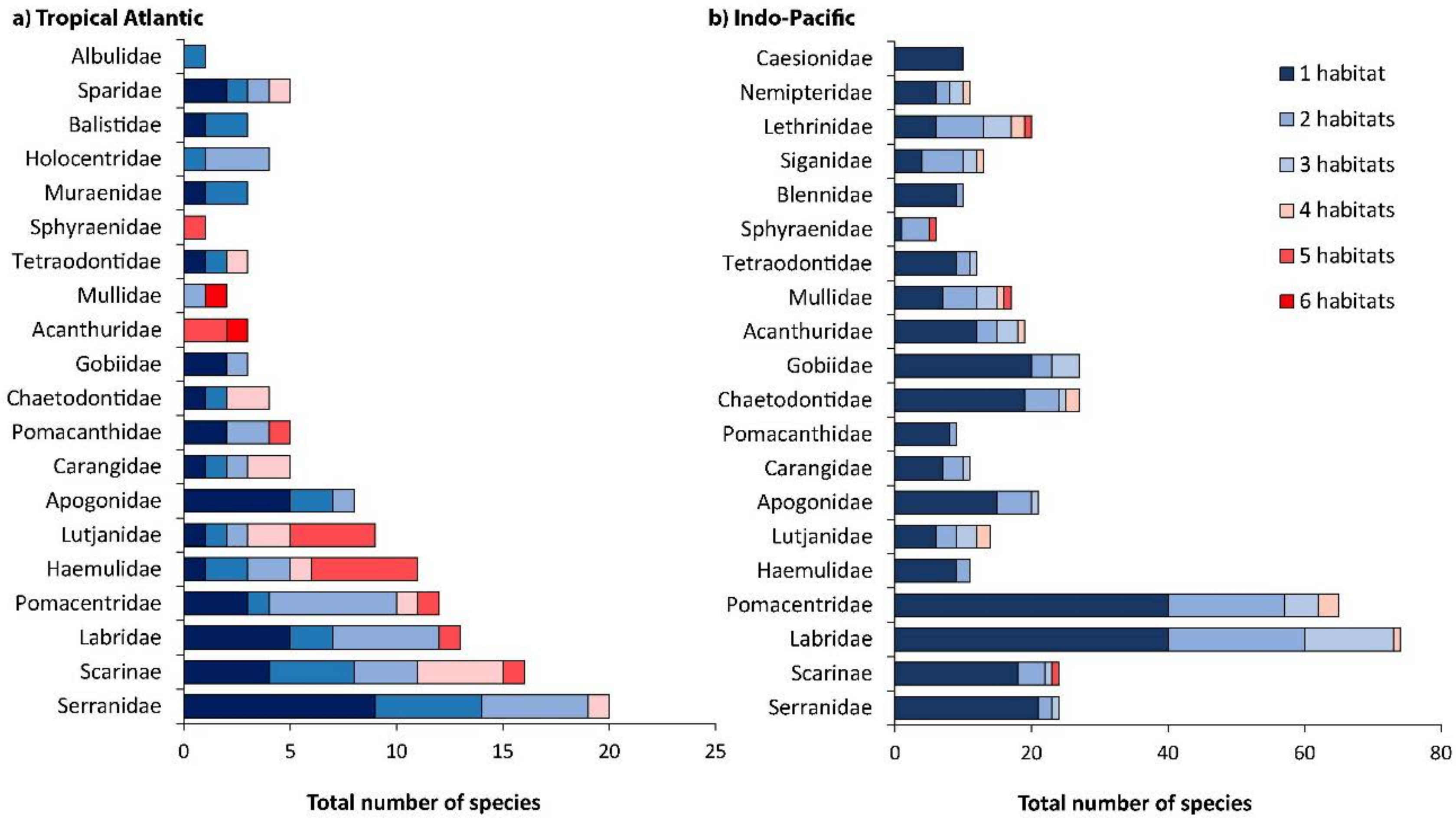


**Figure 2.2.** Prevalence of multiple habitat use among selected coral reef fish taxa in: a) the tropical Atlantic, and; b) the Indo-Pacific. The colours indicate the number of non-reef habitats (1-6) used by each species. In the tropical Atlantic, where a wide range of habitats have been surveyed, many species have been observed in four or more non-reef habitat types. In contrast, in the Indo-Pacific almost 60% of studies only surveyed coral reef fishes in one non-reef habitat.

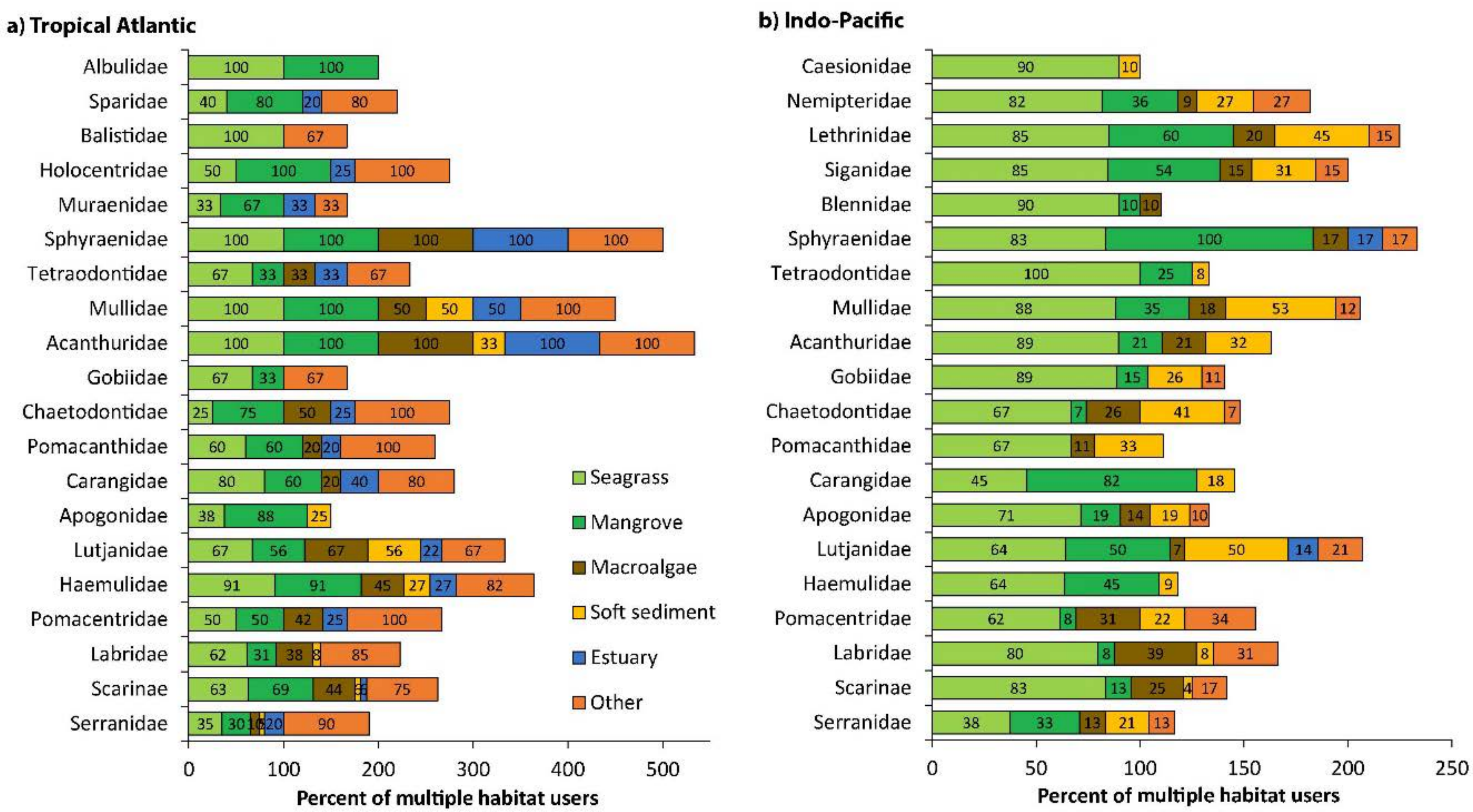


**Figure 2.3.** Habitat use among selected coral reef fish taxa in: a) the tropical Atlantic, and; b) the Indo-Pacific. Percentages represent the proportion of species within each taxa that are found within each habitat type. For example, for the Acanthuridae in the tropical Atlantic, 100% of the species identified as multiple habitat users were observed in seagrass, mangrove, macroalgae, estuary, and “other” habitat types and 33% of species were observed on soft sediments.

### *2.4.2 Comparison of the tropical Atlantic and Indo-Pacific*

Thirty-two fish families were common between the two biogeographic regions. Here four fish taxa of economic or ecological importance were selected to compare and contrast non-reef habitat use trends. Primarily observations were compared between mangrove and seagrass habitats because these habitat types have been most consistently surveyed across the two regions. Taxa with high numbers of species observed in multiple non-reef habitats in both the tropical Atlantic (TA) and Indo-Pacific (IP) include the Haemulidae (11 species in each region), Lutjanidae (9 species in TA, 14 in IP), Scarinae (16 in TA, 24 in IP) and Serranidae (20 in TA, 24 in IP). A similar trend in seagrass and mangrove observations emerged for three taxa (i.e., Haemulidae, Lutjanidae and Scarinae). In the tropical Atlantic, the majority of species from these groups were recorded in both seagrass and mangrove habitats, with fewer species only recorded in one habitat type. However, this pattern differed in the Indo-Pacific, where a greater proportion of species from these three groups were recorded in either mangrove or seagrass habitat types. For example, in the tropical Atlantic, of the 11 Haemulidae species for which data were available, nine species were recorded in both seagrass and mangrove habitat. In contrast in the Indo-Pacific, only one species, the two-striped sweetlips (*Plectorhinchus albovittatus*, Haemulidae), was recorded in both habitat types, five were recorded only in seagrass, and three only in mangroves. Two of the 11 species in the Indo-Pacific were not surveyed in both habitat types. Species from the Scarinae sub-family in the Indo-Pacific were almost sevenfold higher in seagrass habitats compared to mangroves (20 species vs. 3), whereas in the tropical Atlantic, a similar number of species was observed in seagrass and mangrove habitats (10 and 11 species respectively). Species from the Serranidae showed a different pattern to the other three taxa, but shared commonalities between both biogeographic regions. Fewer species of serranids were recorded in both mangrove and seagrass habitat, but comparable numbers of species were split between the two habitat types.

### *2.4.3 Adult and juvenile use of non-reef habitats*

Of the 107 studies that met the selection criteria, 29 contained information on the habitat use of both adult and juvenile life stages. From these 29 studies, 14 studies covered species in the tropical Atlantic and 16 studies the Indo-Pacific. Data were available for 170 species, 48 species from the tropical Atlantic and 122 from the Indo-Pacific. Both life stages showed a diverse range of habitat use in addition to coral reefs (Figure 2.4), with almost 75% of the 170 species observed as both adults and juveniles in non-reef habitats. In the tropical Atlantic, observations of juvenile reef fish species away from the reef were most common in seagrass (62.5%) and mangrove (64.6%) habitats (30 and 31 species, respectively), followed by macroalgae (33.3%, 16 species). In contrast, in the Indo-Pacific, juveniles were most commonly observed in seagrass beds (55.7%, 68 species), followed by “other” non-reef habitat types (40.2%, 49 species), macroalgal beds (24.6%, 30 species), and soft sediment (16.4%, 20 species) (Figure 2.4). For adults, the trends were slightly different. In the tropical Atlantic, adults from 26 species were recorded in “other” non-reef habitat types (54.2%), followed by seagrass (50%, 24 species), and then mangroves (35.4%, 17 species). In the Indo-Pacific, adults followed a similar pattern to that of juveniles with adults from 59 species observed in seagrass beds (48.4%), 54 species in “other” habitats (44.3%), and 18 species in soft sediments (14.8%).

To illustrate the diverse range of habitats used by adults and juveniles, this review focused on observations from six ecologically or economically important taxa, specifically Lutjanidae from both biogeographic regions, the Scarinae and Haemulidae from the tropical Atlantic, and Lethrinidae and Siganidae from the Indo-Pacific (Figure 2.5, Table A2.1). With the exception of the Lethrinidae, juveniles were consistently recorded in a wider range of non-reef habitats than adults from these species. 100% of lutjanids in the tropical Atlantic were observed as juveniles in mangroves, compared to 50% in the Indo Pacific, and 71.4% of juveniles were observed in seagrass habitats compared to 25% in the Indo-Pacific (Figure 2.5). In the tropical Atlantic, all six haemulid species for which adult and juvenile data were available have been recorded as juveniles in mangrove and seagrass habitats, compared to adults from only three species (Figure 2.5). Data were available for eight species of parrotfishes (Scarinae) in the tropical Atlantic (Figure 2.5). Juveniles from these species were more commonly recorded in mangrove and seagrass habitats than adults. In the Indo-Pacific, adults and juveniles from species in the Lethrinidae family were recorded in five non-reef habitats (i.e., seagrass, mangrove, macroalgae, soft sediment and “other”; Figure 2.5). Seagrass was the dominant habitat in which both adults and juveniles from these species were observed (i.e., juveniles from 7 species, adults from 4 species). Adult and juvenile data were available for seven Siganidae species; juveniles of these species have been recorded in five non-reef habitat types, compared to only two for adults (Figure 2.5). Similar to lethrinids, adults and juveniles from the Siganidae were most commonly observed in seagrass beds (i.e., 3 and 5 species respectively).

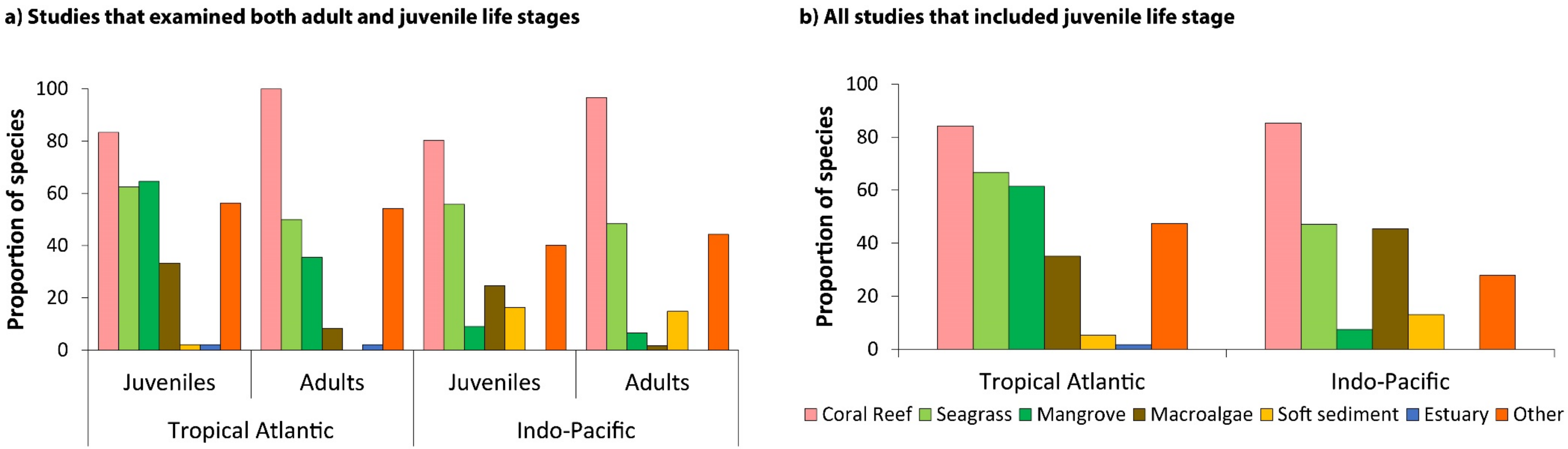


**Figure 2.4.** Proportion of species using coral reef and non-reef habitats by life stage in the tropical Atlantic and Indo-Pacific. (a) Proportion of adult and juvenile coral reef fish species recorded in coral reef and non-reef habitats. Based on data on 170 species from 29 studies that examined both adult and juvenile habitat use. In the tropical Atlantic, data were available for 48 species, and in the Indo-Pacific, data were available for 122 species; b) proportion of juveniles from 233 coral reef fish species observed in reef and non-reef habitats by biogeographic region. Based on the 29 studies that examined adult and juvenile habitat use and an addition 15 studies that examined juvenile habitat use only. In the tropical Atlantic, data were available for juveniles of 57 species, and in the Indo-Pacific, data were available for juveniles from 176 species.

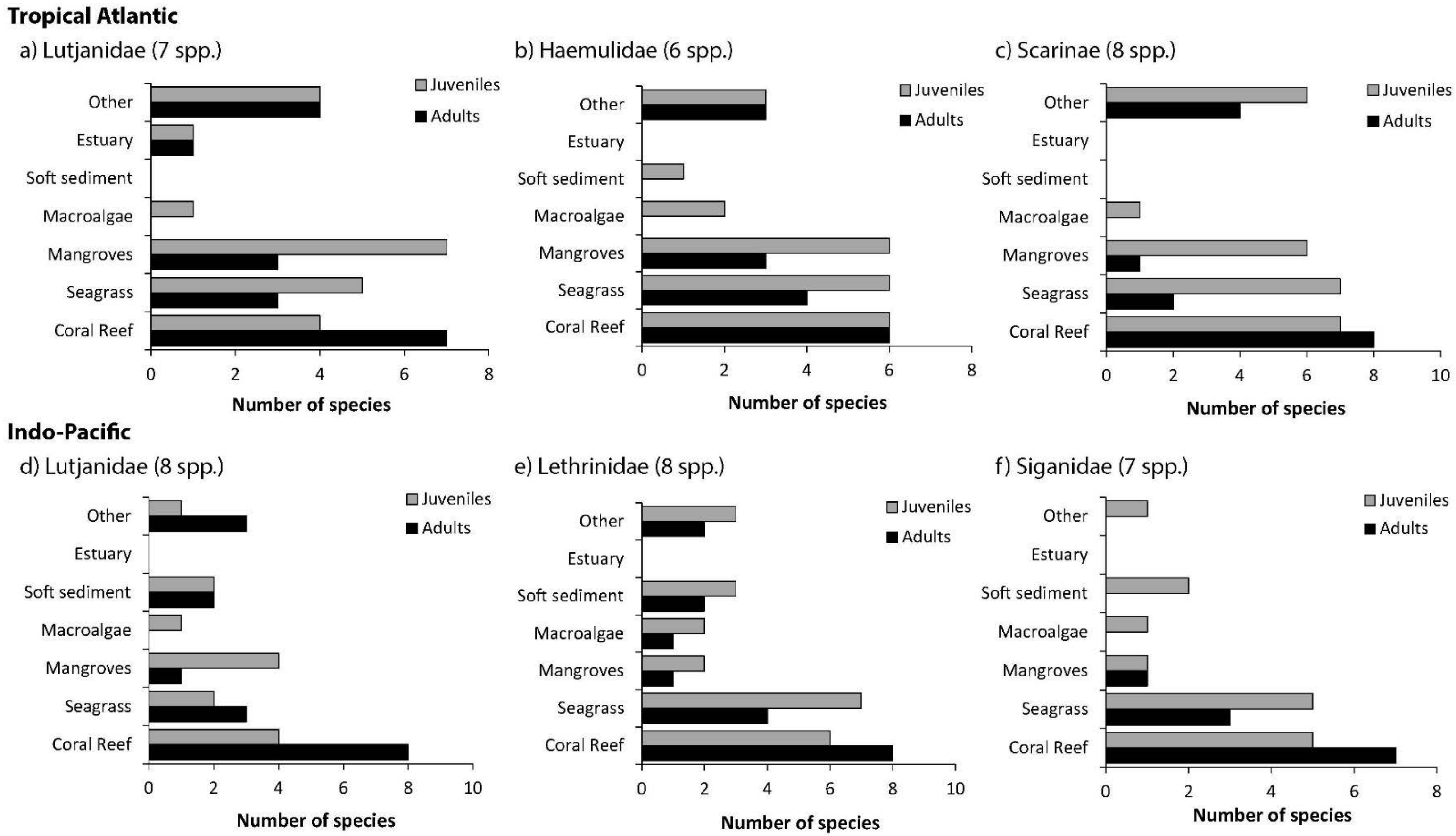


**Figure 2.5.** Observations of adult and juvenile coral reef fish species on coral reefs and in non-reef habitat for six ecologically and economically important groups in the tropical Atlantic: a) Lutjanidae, b) Haemulidae, c) Scarinae, and; in the Indo-Pacific: d) Lutjanidae, e) Lethrinidae, and f) Siganidae. Based on data from 29 studies that examined both adult and juvenile habitat use. Note that habitats have not been surveyed equitably so absences may be an artefact of sampling.

In addition to the 29 studies that collected data on both adult and juvenile reef fishes in non-reef habitats, a further 15 studies documented juveniles only. Two of these focused solely on macroalgal beds as well as coral reef (i.e., Wilson et al. 2010; Evans et al. 2014). When these 44 studies were combined, data were available on juveniles of 233 species, 57 species in the tropical Atlantic and 176 species in the Indo-Pacific (Figure 2.4). Habitat use was diverse; in the tropical Atlantic, juveniles from 66.7% of species were recorded in seagrass, 61.4% in mangroves, 47.4% in “other” non-reef habitat types, and 35.1% in macroalgal beds. In the Indo-Pacific, juveniles from 47.2% of species were recorded in seagrass, 45.5% in macroalgal beds, 27.8% in “other” non-reef habitat types, and 7.4% in mangroves.

### *2.4.4 Feeding guilds, body size and non-reef habitats*

There were similar patterns among regions by feeding guilds, with carnivorous species accounting for over half of all multiple habitat users in both regions (Figure 2.6). In the tropical Atlantic, the highest number of carnivorous species were recorded in “other” habitat types (76% of carnivores), followed by mangroves (60%) and seagrass (54%) (Figure 2.6). In contrast, in the Indo-Pacific, the highest number of carnivorous species was observed in seagrass beds (77%), followed by mangroves (30%), macroalgal beds and “other” habitat types (both 15% of carnivorous species) (Figure 2.6). In the tropical Atlantic, herbivores were relatively evenly distributed between seagrass, mangroves, macroalgae and “other” habitat types. In contrast in the Indo-Pacific, the highest number of herbivores was recorded in seagrass habitats (57 spp.), three- to four-fold higher than macroalgal beds (18 spp.) and mangrove habitats (15 spp.). A similar pattern for each region was observed for omnivores. The number of piscivorous species was low in both regions, but they were recorded in all habitat types except soft sediment. Planktivores were also recorded in all habitat types in the tropical Atlantic and Indo-Pacific except estuarine environments.

Species were recorded across the whole spectrum of body sizes in non-reef habitats, including many smaller-bodied species (Figure A2.4). The modal body size class, based on total length, was 10-19.9 cm. Over a third of the species (36%, 244 spp.) recorded in non-reef habitats have a maximum total length of <20 cm, 38% (257 spp.) can attain a maximum total length of 20-49.9 cm, 16% (110 spp.) can reach 50-99.9 cm, and 8.8% (59 spp.) of species have a maximum total length >100 cm.

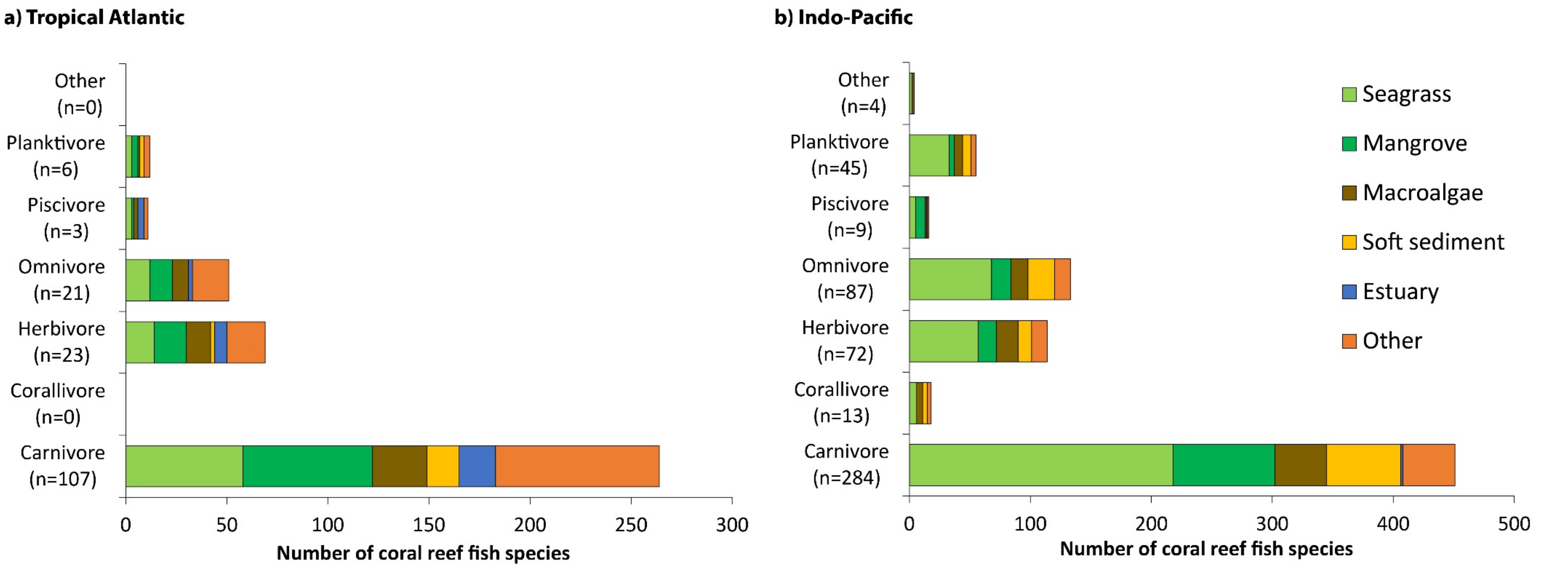


**Figure 2.6.** Feeding guilds of coral reef fishes and the non-reef habitats that they have been observed using for the: a) tropical Atlantic, and; b) Indo-Pacific. Feeding guilds assigned from *FishBase* (Froese & Pauly 2018).

### *2.4.5 Multi-habitat use by fisheries targets*

Across both biogeographic regions, 59% of the coral reef fish species (397 of 670 species) observed in non-reef habitats were potential fisheries targets (e.g., commercial, minor commercial, recreational and/or subsistence) (Figure 2.7). In each region, >90% of the multiple habitat users of interest to fisheries were categorised as being of commercial or minor commercial importance. In the Tropical Atlantic, 31% of fisheries species (30 of 96) were targets for recreational fisheries compared to 20% (66 of 305) in the Indo-Pacific. A limited number of species (>5%) were identified as important for subsistence fisheries in both regions. Patterns in the habitats where fisheries targets were recorded differed between the tropical Atlantic and Indo-Pacific regions, particularly for vegetated habitats. In the tropical Atlantic, fisheries species were evenly observed between mangroves (64 spp.), and seagrass beds (61 spp.), twofold higher than the 29 species observed in macroalgae beds (Figure 2.7). In contrast, in the Indo-Pacific, more than double the number of species were observed in seagrass beds compared to mangroves (238 vs. 109 spp.), and almost fivefold higher than the number observed in macroalgae beds (53 spp.) (Figure 2.7). This equates to 78% of fisheries targets observed in seagrass beds compared to 36% in mangrove habitats, and 17% in macroalgae beds in the Indo-Pacific.

### *2.4.6 Conservation status of multi-habitat users*

Several of the multi-habitat users identified from this synthesis are classified as endangered, near threatened or vulnerable (IUCN 2018). In the tropical Atlantic, 7.5% (12 of 160) of species observed in multiple habitat types are on the IUCN Red List. One species is classified as Endangered: the Nassau grouper (*Epinephelus striatus*, Serranidae), five as Vulnerable: tarpon (*Megalops atlanticus*, Elopidae), masked goby (*Coryphopterus personatus*, Gobiidae), hogfish (*Lachnolaimus maximus*, Labridae), mutton snapper (*Lutjanus analis*, Lutjanidae) and Cubera snapper (*Lutjanus cyanopterus*, Lutjanidae), and six as Near Threatened: bonefish (*Albula vulpes*, Albulidae), queen triggerfish (*Balistes vetula*, Balistidae), rainbow parrotfish (*Scarus guacamaia*, Scarinae), red grouper (*Epinephelus morio*, Serranidae), black grouper (*Mycteroperca bonaci*, Serranidae) and yellowfin grouper (*Mycteroperca venenosa*, Serranidae). In the Indo-Pacific, 3% of species recorded in multiple habitats (16 of 514) are classified on the IUCN Red List. Two species are classed as Endangered: humphead wrasse (*Cheilinus undulatus*, Labridae) and Banggai cardinal fish (*Pterapogon kauderni*, Apogonidae); five as Vulnerable: harlequin filefish (*Oxymonacanthus longirostris*,

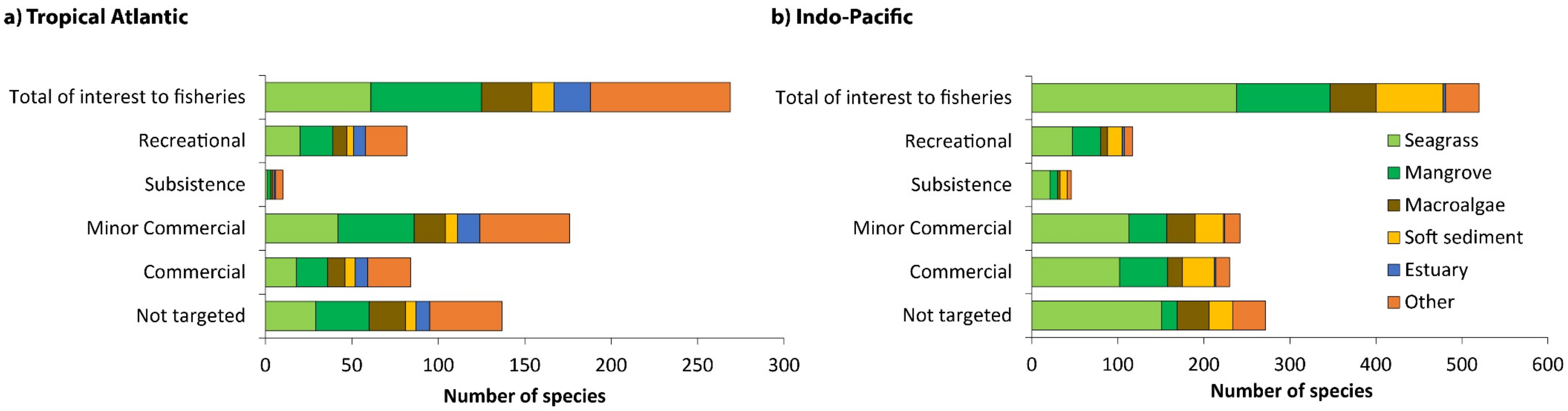


**Figure 2.7.** Coral reef fishes observed on coral reefs and in non-reef habitats and their interest to fisheries in the: a) tropical Atlantic, and; b) Indo-Pacific regions by habitat. Data on fisheries extracted using the five fisheries classifications available in *FishBase* (Froese & Pauly 2018).

Monacanthidae), bumphead parrotfish (*Bolbometopon muricatum*, Scarinae), giant grouper (*Epinephelus lanceolatus*, Serranidae), tiger tail seahorse (*Hippocampus comes*, Syngnathidae) and spiny seahorse (*Hippocampus histrix*, Syngnathidae), and nine as Near Threatened: chevron butterflyfish (*Chaetodon trifascialis*, Chaetodontidae), bluespotted ribbontail ray (*Taeniura lymma*, Dasyatidae), blackspot tuskfish (*Choerodon schoenleinii*, Labridae), whitesaddle goatfish (*Parupeneus porphyreus*, Mullidae), orange-spotted grouper (*Epinephelus coioides*, Serranidae), brown-marbled grouper (*Epinephelus fuscoguttatus*, Serranidae), Malabar grouper (*Epinephelus malabaricus*, Serranidae), camouflage grouper (*Epinephelus polyphekadion*, Serranidae), and coral trout (*Plectropomus leopardus*, Serranidae).

## 2.5 Discussion

This review found that a significant number of coral reef fishes, from a wide range of families, life stages and feeding guilds, are present in non-reef habitats; and that over half of those species are of interest to fisheries. To place the number of species into context, the findings suggest that almost 20% of the 2,642 species present in the highly diverse Coral Triangle region (Allen 2015) are likely to occur in reef and non-reef habitats. Furthermore, the estimate of 670 species recorded across the two biogeographic regions is highly likely to be conservative. This is because studies that did not survey reef fish on coral reefs as well as non-reef habitats were excluded (e.g., Nagelkerken et al. 2000c; Bradley et al. 2017; Tano et al. 2017), and summary statistics, rather than complete species lists, were provided for some studies that met the criteria (e.g., Mumby et al. 2008). Importantly, the review also highlights that many species utilise the wider seascape throughout their lives, with 80% of species for which data were available observed as both adults and juveniles in non-reef habitats. Whilst the use of non-reef habitats by reef fishes has been known for some time (e.g., Ogden & Zieman 1977; Birkeland 1985; Ogden 1988; Adams et al. 2006; Appeldoorn et al. 2009), this review is the first to quantify the sheer number of species across a broad spectrum of reef fish taxa that inhabit a diverse array of habitat types in addition to coral reefs.

The difference between biogeographic regions provides strong evidence in support of previous research that has highlighted a potential bias in research effort into multi-habitat use by coral reef fishes (e.g., Nagelkerken 2007; Pittman & Olds 2015; Olds et al. 2016). Over half of the studies were conducted in the tropical Atlantic, yet the Indo-Pacific region covers a much larger area. In the tropical Atlantic, significant research effort has focused on the use of non-reef habitats by coral reef fishes in the Caribbean (e.g., Nagelkerken et al. 2000b; Nagelkerken et al. 2001; Nagelkerken et al. 2002). As a result, many locations have been sampled on numerous occasions (e.g., Curaçao, Nagelkerken et al. 2000a; Nagelkerken & van der Velde 2002; Cocheret de la Morinière et al. 2002; Nagelkerken & van der Velde 2003; Pollux et al. 2007; Dorenbosch et al. 2009; Grol et al. 2014) and there is a relatively strong knowledge base for some of the species that use multiple habitats (e.g., French grunts, or schoolmaster snapper (*Lutjanus apodus*, Lutjanidae)). In contrast, few locations in the Indo-Pacific have been subjected to detailed examination. This indicates that we still have far more to learn about the use of multiple habitats by coral reef fishes in the Indo-Pacific region.

In addition to the large number of species observed away from reefs, the results highlight that coral reef fishes are using a diverse range of non-reef habitats; 44% of the 670 species were observed in multiple non-reef habitats. However, few studies, particularly in the Indo-Pacific, consider a broad range of habitats when investigating the use of non-reef habitats by coral reef fishes. It is only through synthesis of the data that we can begin to see that coral reef fishes have been observed in a much broader range of habitats across the seascape than previously considered. By extending the search for coral reef fishes to a wider range of habitats, we can build a more complete picture of which habitats are important for each species, and identify any species that may be quite singular in their use of non-reef habitats. For example, the night sergeant (*Abudefduf taurus*, Pomacentridae) has been searched for in habitats dominated by hard structures (i.e., corals, rocky boulders) and vegetation (i.e., seagrass, mangrove and macroalgae), but has only been observed in the hard structure habitats (Nagelkerken et al. 2000a). This indicates that the availability of hard structure, coral or otherwise, is likely to be more important for this species than the presence of vegetated habitat. Identifying the extent of habitat plasticity for a species, and the habitat characteristics that might be important, will provide us with a far greater insight into the impacts of changing seascapes (e.g., habitat loss; Wilson et al. 2010).

The findings are also predominantly based on single daytime observations of species distribution patterns. However, this approach fails to consider how tidal, diel, seasonal or annual variability may affect patterns of habitat use. In instances where studies have included a temporal component, changes to fish communities in the habitats of interest are common (e.g., tidal, Unsworth et al. 2007b; day-night shifts, Kopp et al. 2007; Hitt et al. 2011; seasonal and annual, Kimirei et al. 2011). Including a temporal aspect in studies that examine multiple habitat use in reef fishes, as well as considering additional non-reef habitats, may reveal even more extensive use of the seascape by certain species of coral reef fish.

Another interesting question is whether differences in habitat use by coral reef fishes exist both between and within the tropical Atlantic and Indo-Pacific regions. Drivers of differences in patterns of habitat use could include the type of non-reef habitats available within study locations (Dorenbosch et al. 2004; Mumby et al. 2004), proximity of habitats (Nakamura et al. 2009a; Nagelkerken et al. 2012; Olds et al. 2013), areal extent of non-reef habitats (Grober-Dunsmore et al. 2004; Gilby et al. 2016), and/or the tidal regime (Unsworth et al. 2007b; Igulu et al. 2014; Harborne et al. 2016a; Davis et al. 2017). For example, seagrass and mangrove habitats are absent from parts of the Indo-Pacific, which could increase the importance of other types of non-reef habitat (e.g., macroalgal beds) to coral reef fishes in this region. Tidal range may also play a role in the use of non-reef habitats by coral reef fishes. In the micro-tidal tropical Atlantic, such habitats are constantly inundated with water and therefore permanently available to fishes (Igulu et al. 2014). In contrast, the Indo-Pacific experiences micro-, meso- and macro-tidal conditions. For locations with larger tidal ranges, some non-reef habitats may be inaccessible at low tide and/or physiologically hostile due to rapid fluctuations in environmental variables (e.g., temperature, salinity; Sheaves 2005; Igulu et al. 2014). Despite this potential temporal constraint on habitat availability, >120 fish species were recorded in mangroves from the 19 studies that examined coral reef fishes in mangroves in the Indo-Pacific. This suggests that mangroves are still extensively used by coral reef fishes in this region. Few studies have, however, investigated how tides might influence the use of non-reef habitats by reef fishes in the Indo-Pacific in combination with surveys on the reef (but see Unsworth et al. 2007b).

More than >230 coral reef fish species were observed as juveniles in non-reef habitats. This figure is likely to be a conservative estimate because many studies did not differentiate between life history stages, and other studies exist that have examined juveniles of coral reef fishes in non-reef habitats but did not simultaneously quantify their use of adjacent coral reef habitat (e.g., Tano et al. 2017) and thus were excluded from this review. Vegetated habitats, particularly mangroves and seagrass beds, have frequently been reputed to provide an important nursery function for many coral reef fish species (Nagelkerken et al. 2000a; Nagelkerken et al. 2001; Sheaves et al. 2015), particularly those species of commercial interest to fisheries (Blaber 2009). However, in addition to observations in mangroves and seagrass beds, this review also confirms the widespread occurrence of juvenile coral reef fishes in macroalgae beds despite them currently being one of the least studied non-reef habitat types (13% of studies in this review). The potential importance of macroalgal beds as juvenile coral reef fish habitat is further supported by studies from north-eastern Brazil (Chaves et al. 2013) and Zanzibar, Tanzania (Tano et al. 2017). In particular, the use of macroalgal beds seems to be prevalent for labrids, pomacentrids, and siganids (Rossier & Kulbicki 2000; Adams & Ebersole 2002; Wilson et al. 2010; Hoey et al. 2013; Rasher et al. 2013; Evans et al. 2014). These findings are interesting, as it has been suggested that macroalgal-dominated reefs suppress recruitment in many coral reef fishes including pomacentrids, labrids and siganids (Dixson et al. 2014). Yet from this synthesis, it appears that at least for some species, macroalgal beds are a commonly utilised habitat by juveniles. Species of coral reef fish that use macroalgal beds as juveniles could have the potential to become more dominant on reefs experiencing regime-shifts or high macroalgae loads. To understand how this could affect ecosystem functioning on reefs in the future, we need a better understanding of patterns and drivers of macroalgal bed use by coral reef fishes and the contribution such species make to ecological processes on reefs.

There are a wide range of different factors that could influence non-reef habitat use by coral reef fishes, including key traits such as mobility, body size and feeding ecology. An individual's mobility will influence how it interacts with the wider seascape, and across what spatial and temporal scales. For some taxa, body size and mobility can be tightly coupled (Kramer & Chapman 1999; Sale et al. 2005). We might reasonably expect then, that large-bodied highly mobile species are more likely to use multiple habitat types than smaller-bodied, less mobile species. Many of the coral reef fishes using multiple habitats identified in this review were large-bodied, mobile carnivores or piscivores. Such species may have higher energetic demands that require larger home ranges to meet their resource requirements.

Comparing the results to the species list compiled as part of an extensive review on known movement patterns of coral reef fishes by Green et al. (2015), I found that movement data were available for 114 of the 670 species included in the review. Much of the data available explores only a single aspect of movement (e.g., spawning migrations), and hence likely fails to capture the full breadth of potential seascape usage. Moreover, movement data for many species is restricted to a single location which, whilst informative, fails to capture seascape variability. This information is needed, particularly for marine reserve design (Pittman & McAlpine 2003;

Green et al. 2015), because home range or daily movement patterns may vary considerably depending on individual behaviors and the spatial configuration and connectivity of habitat patches in the seascape (Hitt et al. 2011).

Contrary to expectations, a substantial proportion of the species observed in non-reef habitats were small-bodied species. Little, if any attention has been given to species typically thought of as permanent coral reef residents, or species with limited mobility, such as pomacentrids. Yet, large numbers of pomacentrid species were recorded in non-reef habitats, particularly in the Indo-Pacific, and these observations included both adults and juveniles. Moreover, many of these species were recorded using non-reef habitats from multiple studies and/or locations (e.g., beaugregory (*Stegastes leucostictus*, Pomacentridae) in the tropical Atlantic; Adams & Ebersole 2002; Christensen et al. 2003; Aguilar-Perera & Appeldoorn 2008; Harborne et al. 2008; and jewel damselfish (*Plectroglyphidodon lacrymatus*, Pomacentridae) in the Indo-Pacific; Wilson et al. 2010; Berkström et al. 2012; Kruse et al. 2016) indicating that the results are not location specific or due to chance (e.g., recruitment) events. Such species are unlikely to move considerable distances (e.g., pomacentrids, Turgeon et al. 2010) from where they settle. This suggests that there may be another, overlooked, category of coral reef fish species that can occur in non-reef habitats in addition to the standard explanations for non-reef habitat use (e.g., nursery, foraging etc.). Individuals in this alternate group may settle in non-reef habitats deliberately or because of an absence of more suitable habitat at the time of settlement. Once settled in a non-reef habitat, the limited mobility of such individuals would likely constrain them to that habitat for their entire life. Although abiotic and biotic conditions between reef and non-reef habitats are likely to differ substantially, trade-offs in terms of growth, survival and reproduction (Dahlgren & Eggleston 2000) between habitat types have received limited attention (but see Nakamura & Sano 2004a; Nakamura et al. 2007; Grol et al. 2008; Grol et al. 2011a, b; Grol et al. 2014). Given the widespread presence of small-bodied, and presumably less mobile coral reef fish in non-reef habitats documented in this review, the fitness consequences of living in reef versus non-reef habitats warrant further investigation.

Many species of herbivorous fishes were also observed in non-reef habitats. Herbivorous fishes perform a critical role on coral reefs (Nyström & Folke 2001; Scheffer et al. 2001; Rasher et al. 2013), by scraping and excavating the substratum, grazing on algal turfs, or browsing on macroalgae that help maintain a healthy balance between corals and macroalgae. Interestingly, several of the herbivorous species identified as multi-habitat users in this review have been identified as major contributors to herbivory on reefs, particularly species from the Acanthuridae (Hoey & Bellwood 2009; 2010a; Rasher et al. 2013; Chong-Seng et al. 2014) Siganidae (Fox & Bellwood 2008; Cvitanovic & Bellwood 2009; Cheal et al. 2010), and Scarinae (Bellwood et al. 2003; Mumby et al. 2006; Hoey & Bellwood 2008; Kuempel & Altieri 2017). The frequent presence of herbivores in non-reef habitats raises several interesting questions. For example, whilst larval replenishment from connected reefs following disturbance events has received considerable attention (e.g., Almany et al. 2007; Jones et al. 2009; Hogan et al. 2012), little consideration has been given to the potential role of non-reef habitats as support areas for the replenishment of reefs (but see Mumby & Hastings 2008; Edwards et al. 2010), or the links between larval dispersal and availability of nursery habitats (but see Brown et al. 2016). Such research is important given that the availability of nursery habitats for herbivores near to reefs has been implicated as a key factor on reefs that have repeatedly exhibited rapid recovery rates following coral loss (Adam et al. 2011). Another poorly explored topic is whether non-reef habitats could offer refuge for coral reef fish during disturbance events that differentially impact coral reefs (e.g., coral bleaching events). To date, the search for potential refugia for coral reef fishes has been reef-centric, typically looking at deeper reefs which may experience more stable abiotic conditions than shallow reefs (e.g., Bridge et al. 2013; Jankowski et al. 2015; MacDonald et al. 2016). However, there is evidence that deeper reefs may not be suitable refugia for some species, especially herbivores (Kahng et al. 2010). In light of the deteriorating conditions many reefs are facing, these are important future research subjects.

Much of the research into multi-habitat use has focused on species that use non-reef habitats as juveniles (e.g., Dennis 1992; Nagelkerken et al. 2000a, 2000b; Cocheret de la Morinière et al. 2002; Gillanders et al. 2003; Nagelkerken et al. 2012; Nakamura et al. 2012) or those that make short-term movements between reef and non-reef habitat to feed (e.g., Ogden 1976; Robblee & Zieman 1984; Meyer & Schultz 1985; Burke 1995). Families that contain species commonly associated with ontogenetic shifts from vegetated habitats as juveniles to coral reefs as adults include the Haemulidae (e.g., Tropical Atlantic: Nagelkerken & van der Velde 2004; Grol et al. 2014), Lethrinidae (e.g., Indo-Pacific: Mellin et al. 2007; Kimirei et al. 2013a) and Lutjanidae (e.g., Tropical Atlantic: Nagelkerken & van der Velde 2004; Aguilar-Perera & Appeldoorn 2007; Indo-Pacific: Nakamura et al. 2008; Kimirei et al. 2013b; Paillon et al. 2014), as well as some species from the Scarinae (e.g., Tropical Atlantic: Mumby et al. 2004; Dorenbosch et al. 2006b). Yet until recently, it has been challenging to provide direct, rather than correlative, evidence for ontogenetic shifts from non-reef habitats to coral reefs (Gillanders et al. 2003). This issue is now being addressed through the use of molecular approaches (e.g., stable isotope analysis) that can begin to quantify the contribution of non-reef habitat-using juveniles to adult populations on the reef (e.g., *Lutjanus ehrenbergii*, Lutjanidae), McMahon et al. 2012; *Lutjanus fulviflamma* (Lutjanidae), Paillon et al. 2014). However, in contrast to the many species of coral reef fishes that display an obligate relationship with reef habitat as juveniles (Jones et al. 2004; Wilson et al. 2008), few, if any, coral reef fishes appear to be functionally dependent on the availability of non-reef habitats as nurseries (Nagelkerken et al. 2000c, but see Mumby et al. 2004).

Another explanation for the presence of reef fishes in non-reef habitats is diel and/or tidal movement between feeding and shelter habitats. Several species of haemulids in the Caribbean have been documented making twilight feeding incursions away from reefs into seagrass beds to feed (see reviews by Appeldoorn et al. 2009; Krumme 2009) but there is little evidence that this behaviour is replicated by haemulids in the Indo-Pacific. Indeed, there is limited empirical data generally for the Indo-Pacific on this topic (but see Honda et al. 2016), although studies demonstrating tidal (e.g., Unsworth et al. 2007b) and diel (e.g., Unsworth et al. 2007a) changes to fish communities on reefs and in non-reef habitats indicate potential for regular feeding movements.

As well as direct uses, non-reef habitats can also play a role in supporting populations of reef fishes and influencing ecological processes on coral reefs through indirect mechanisms. This creates an additional level of complexity when attempting to evaluate the importance of non-reef habitats. For example, the Caribbean rainbow parrotfish (*Scarus guacamaia*) is widely considered to have a strong direct dependency on mangroves as juveniles, with adults absent from reefs more than 10 km away from mangrove habitats (e.g., Mumby et al. 2004; Dorenbosch et al. 2006b), although there are exceptions (Aguilar-Perera & Hernández-Landa 2017). In contrast, the presence of mangroves appears to indirectly support the Indo-Pacific bumphead parrotfish (*Bolbometopon muricatum*) by reducing sedimentation rates on inshore fringing reefs and hence protecting key coral microhabitats for juveniles (Hamilton et al. 2017). Other indirect effects can also be seen through the feeding incursions into vegetated habitats which can contribute nutrients to coral reef systems through defecation (Meyer & Schultz 1985; Hyndes et al. 2014; Shantz et al. 2015). In addition, it appears that whilst proximity to non-reef habitats can result in increased adult abundances of nursery-using species on reefs, it can have the opposite effect on reef-dependent species and, concomitantly alter key ecological processes (e.g., grazing; Harborne et al. 2016b). The potential for indirect effects (e.g., trophic and/or competitive cascades; Harborne et al. 2016b) to alter fish communities and ecological processes on reefs is therefore likely to be an important but understudied aspect of heterogeneous seascapes.

The findings from this review are highly relevant for fisheries management. Over half of all the species (60%) observed in non-reef habitats are fisheries targets in some capacity, and of these 50% were observed in two or more habitat types in addition to the reef. In particular, many commercially important species from the Carangidae, Haemulidae, Lethrinidae, Lutjanidae and Serranidae were identified as multiple habitat users. Coral reef fisheries provide an important source of income and protein, particularly in developing, or small island nations (Newton et al. 2007). To contribute towards long-term food security and sustainability of stocks, it essential that fisheries species at each stage of their life cycle are supported (Nagelkerken et al. 2015; Baker et al. 2018). Without adequate management of the entire seascape, loss of key non-reef habitats could have negative repercussions for fisheries productivity on coral reefs. However, for many fisheries species identified in this review, we still lack a comprehensive understanding of habitat use patterns and whether dependencies exist on particular habitats for different life history stages. These knowledge gaps limit our ability to effectively manage coral reef fisheries. Focusing management activities solely on reef environments may fail to protect the most vulnerable life stages, or neglect important feeding or spawning grounds which contribute towards population replenishment. Therefore, there is a need to better understand the importance of non-reef habitats for key fisheries species and broaden “coral reef” fisheries management to encompass the wider seascape (e.g., Unsworth et al. 2014; Baker et al. 2018).

From a conservation perspective, the review revealed that 28 of the species observed in non-reef habitats are currently considered at risk of extinction. To protect such vulnerable species, we need data on their direct and indirect habitat and resource requirements for each component of their life cycle, as well as short- and long-term movement patterns (Green et al. 2015). However, detecting rare species using conventional survey techniques can be challenging (Dulvy & Polunin 2004; Pikitch 2018), leading to an incomplete picture of species-habitat relationships. Environmental DNA (eDNA) is a non-destructive molecular technique that can detect the presence of rare species more time and cost efficiently than traditional sampling techniques (Rees et al. 2014; Pikitch 2018). Recent studies from coastal marine environments indicate that this tool could be applied to detect the presence of rare species across small spatial scales (50-100 m; Port et al. 2016; O'Donnell et al. 2017) which will be required for coral reef seascapes with a range of habitats in close proximity. As a relatively new molecular tool, there are uncertainties around the dynamics of eDNA across spatial and temporal scales (O'Donnell et al. 2017). However, assuming these uncertainties can be resolved satisfactorily, this approach could help in the future to unravel the mysteries of habitat use for species that are of conservation concern. Whilst there is much still to learn about habitat use by vulnerable species, this review provides insight into which 'at risk' species have been recorded in non-reef habitats to date, and provides a starting point for more extensive research to guide conservation efforts in the future.

Information on the four W's (what, when, where and why) is lacking or incomplete for many species. As a consequence, there is still much uncertainty and debate about the importance of non-reef habitats for coral reef fishes and the functional contribution of non-reef habitats to maintain or support ecological processes on coral reefs. Even the ability to group species into categories based on the reasons for use (e.g., nursery, food, shelter), their temporal (e.g., short- or long-term, diel, tidal etc.) or spatial scale of use (e.g., home ranges, spawning or foraging migrations) is restricted to a small number of species. Furthermore, it appears that there are two additional groups of multi-habitat users that have been largely neglected thus far. The first group are transients, specifically, highly mobile individuals or groups of individuals that interact regularly with different components of the seascape. I speculate that the ecological role of these transients should not be underestimated; passing through a habitat patch may also entail some form of habitat use or modification. For instance, transient individuals may specifically use structurally complex habitats, or habitat edges, as corridors for movement between different components of the seascape (Boström et al. 2011; Hitt et al. 2011; Nagelkerken et al. 2015; Davis et al. 2017). The importance of fish as mobile links between habitats has been acknowledged for some time (e.g., Nyström & Folke 2001; Lundberg & Moberg 2003), and highly mobile transients have the potential to be significant contributors to energy transfer between habitats. Opportunistic feeding by transients may influence community structure, individual behaviour and survivorship within non-reef habitats (Rooker et al. 2018), and defecation by transients, particularly for schooling species, could make a substantial contribution to nutrient exchange between habitats.

The second understudied group are individuals that may be able to complete their entire life cycle away from coral reefs. In both of these groups, populations of a species are likely to use multiple habitat types, but in the first instance, individuals will have the capacity to move between different components of the seascape, whereas in the second instance, individuals will settle and remain in a particular patch of habitat. To address the many gaps in our knowledge, a multi-faceted approach incorporating observational, experimental, molecular tools and acoustic telemetry is required. Combining such techniques can rapidly enhance our understanding of seascape usage at the species level (see Baker et al. 2018).

The future of coral reef ecosystems is increasingly uncertain due to a diverse range of stressors, namely elevated sea surface temperatures, severe storms, pollution, disease, and crown-of-thorns starfish outbreaks (Gardner et al. 2003; Osborne et al. 2011; De'ath et al. 2012; Hughes et al. 2017a; Unsworth et al. 2018). However, coral reefs are not the only coastal habitat threatened by anthropogenic and natural stressors. Globally, mangrove losses had reached around 35% two decades ago (Valiela et al. 2001; Duke et al. 2007) with recent estimates showing a continued, but reduced rate of decline (0.16-0.39% per year; Hamilton & Casey 2016), and seagrass has been disappearing at a rate of 110 $km^2$ per year since 1980 (Waycott et al. 2009). Faced with the deterioration of many coastal seascapes, it is imperative that we expand our understanding of how reef fishes use and depend on the range of habitats in the seascape. A seascape perspective is vital for understanding the strength and significance of connections between habitats, particularly because the loss and fragmentation of various habitats in the seascape is likely to alter functional and structural links between habitat patches in the seascape. Such information will help to more effectively manage coral reef seascapes and their associated fish populations in the future.

# Chapter 3

Broadening our horizons: seascape use by coral reef-associated fishes in Kavieng, Papua New Guinea, is common and diverse [2]

## 3.1 Abstract

There is increasing evidence that non-reef habitats in the seascape surrounding coral reefs are widely used by reef-associated fishes. However, our understanding of seascape use in the Indo-Pacific region is incomplete due to its large geographical range and as a consequence, considerable environmental variation (e.g., tidal regimes). Remote video cameras were used to survey reef-associated fishes within five habitat types (coral reef slope, coral reef flat, macroalgal beds, mangroves and seagrass meadows) around the Tigak Islands, Kavieng, Papua New Guinea. Of the 282 shallow-water reef-associated species observed across 360 videos, 35% (99 species) were recorded in non-reef habitats, the majority (78 species) on multiple occasions. Macroalgal beds dominated by low complexity algal genera (e.g., *Halimeda*, *Caulerpa*) were used extensively by reef-associated fishes, complementing previous research that has documented the use of canopy-forming macroalgae (e.g., *Sargassum*). Mean species richness and relative abundances (Max*N*) of reef-associated fishes were two-fold higher in macroalgal beds than mangroves or seagrass. Interestingly, mangroves contained the most distinct fish assemblage of the three non-reef habitats, including several reef-associated species that were not recorded from any other habitat type. This suggests that mangroves possess attributes not shared by other shallow non-reef, or even reef, habitats. Importantly, many of the fish families commonly found in non-reef habitats (i.e., lethrinids, lutjanids) are targeted by local fishers and are thus critical to sustaining local livelihoods. This study demonstrates non-reef habitat use is common for many reef-associated fishes and highlights the need to incorporate a range of habitats into study designs to better understand habitat use patterns in the Indo-Pacific. Given the widespread degradation of coral reefs and other shallow-water habitats, it is becoming more important to recognise that reefs are embedded within a mosaic

[2] This chapter is published as: **Sambrook K,** Bonin MC, Bradley M, Cumming GS, Duce S, Andréfouët S, Hoey AS (2020) Broadening our horizons: seascape use by coral reef-associated fishes in Kavieng, Papua New Guinea, is common and diverse. *Coral Reefs* 39: 1187-1197

of habitat types that influence patterns and processes, and scale management strategies appropriately.

## 3.2 Introduction

The influence of the wider landscape or seascape on patterns and processes observed within a habitat patch remains a long-standing and important question in ecology (Miller-Rushing et al. 2019). It has been proposed that the close proximity of particular kinds of habitat may have a range of effects on community composition, species diversity and ecosystem function (Fahrig et al. 2011). The effects of habitat adjacency on species diversity may occur directly, for example if a species requires resources that are found in both habitat types (e.g., different breeding and foraging habitats); or indirectly, via exchanges of nutrients and other subsidies between adjacent habitats (Alsterberg et al. 2017). Habitat adjacency and complementarity have long been recognised as important drivers of species abundance and distribution patterns in terrestrial systems (Fahrig et al. 2011), and a similar effect is increasingly evident from shallow-water coastal ecosystems (e.g., Dorenbosch et al. 2006a; Pittman et al. 2007; Olds et al. 2012a; Berkström et al. 2013a; Aller et al. 2014).

Many coral reef fish taxa use multiple habitat types throughout their life cycle (Nagelkerken et al. 2000c; Adams et al. 2006; Harborne et al. 2008). An understanding of the use of these habitats and the connections between them is critical to predict and manage the likely impacts of local and global disturbances (Berkström et al. 2012; Pittman & Olds 2015). Although numerous studies have documented the effects of coral loss on coral reef fish communities (e.g., Jones et al. 2004; Pratchett et al. 2011; Richardson et al. 2018), far fewer have considered how disturbances in the wider seascape can influence fish communities, despite many reef systems occurring within a mosaic of highly productive (Birkeland 1985) and extensive (Parrish 1989) non-reef habitat types such as mangroves and seagrass meadows. Much like coral reefs, these shallow-water ecosystems are undergoing rapid systemic change with widespread areal losses and degradation in recent decades (Valiela et al. 2001; Waycott et al. 2009; Hamilton & Casey 2016).

The number of coral reef-associated fish species that have been observed in non-reef habitats is substantial. Globally, at least 670 species of coral reef-associated fishes have been recorded in non-reef habitats in addition to reefs, representing approximately 20% of all coral reef fish species (Sambrook et al. 2019, **Chapter 2**). Reef fishes use the wider seascape for a range of reasons including foraging (Beets et al. 2003; Hitt et al. 2011), spawning (Pittman & McAlpine 2003), and as juvenile habitat before migrating to reefs as subadults or adults (Dahlgren & Eggleston 2000; Nagelkerken et al. 2000c; Nagelkerken et al. 2001; Adams et al. 2006; Jaxion-Harm et al. 2011). As a result, short- and long-term movements by reef fishes between different components of the seascape can contribute to ecosystem functioning on reefs through nutrient transfer (Meyer & Schultz 1985; Shantz et al. 2015), trophic subsidies and cascades (Heck et al. 2008; Harborne et al. 2016b), and population replenishment (Nakamura et al. 2008; McMahon et al. 2012).

Much of our knowledge about seascape use by reef-associated fishes comes from the Caribbean (Nagelkerken et al. 2000c; Aguilar-Perera & Appeldoorn 2008; Dorenbosch et al. 2009). Less is known about how, why and which reef fishes use non-reef habitats in the Indo-Pacific (Sambrook et al. 2019, **Chapter 2**). Our limited understanding in the Indo-Pacific is, in part, complicated because of its large spatial extent and biophysical variability. For instance, unlike the Caribbean where shallow-water habitats are permanently accessible to fishes, tidal regimes in the Indo-Pacific range from micro- to macro-tidal (Krumme 2009), affecting the accessibility of non-reef habitats to reef fishes (Igulu et al. 2014). As a consequence, understanding fish-habitat relationships in the Indo-Pacific requires exploration across a wider range of locations and tidal regimes.

Understanding habitat use patterns of coral reef fishes is also highly relevant when addressing concerns around long-term food security in the Indo-Pacific (Foale et al. 2013; Blasiak et al. 2017). This is because many of the coral reef fishes that are known to use non-reef habitats are common fisheries targets (Sambrook et al. 2019, **Chapter 2**) and the Indo-Pacific is home to a multitude of small island communities (Brodie et al. 2013) that rely on coral reef fisheries to satisfy daily nutritional requirements (Béné et al. 2007) and as a primary source of income (Bell et al. 2009). Many of these coastal communities are experiencing rapid population growth (Burke et al. 2011) which places increasing pressure on already stretched natural resources (Bell et al. 2009). By expanding our understanding of broader seascape use by coral reef fishes, we can identify essential fish habitats, combinations of habitats and/or target species that require better management or protection, which could contribute towards longer-term sustainable fisheries goals.

The objective of this study was to describe and compare reef-associated fish communities across five habitat types that are common in coastal tropical marine seascapes (i.e., coral reef flats, coral reef slopes, mangroves, seagrass meadows and macroalgae beds) in the Indo-Pacific. Specifically, the reef fish assemblages associated with the five habitat types were compared, the overlap in habitat use was quantified and the frequency of use of non-reef habitats identified in Kavieng, Papua New Guinea.

## 3.3 Methods

### *3.3.1 Study site*

The study was conducted around the Tigak Island Group within the Kavieng lagoon, New Ireland, Papua New Guinea (2° 34’ S, 150° 48’ E; Figure 3.1). The Kavieng lagoon is ~380 km$^2$ and contains a range of habitats. Extensive reef formations around islands are interspersed with seagrass meadows (predominantly *Enhalus* and *Thalassia* spp.), macroalgae beds (predominantly *Halimeda*, *Caulerpa* spp.) and mangrove forests (*Rhizophora* spp.). The annual water temperature ranges between 28.7°C and 31.6°C (NOAA 2019). Tides are mixed microtidal (Krumme 2009), with a maximum tidal range of 1.09 m. As a consequence, nearshore habitats (e.g., mangroves) are generally submerged, although inundation depths can be shallow (~30 cm).

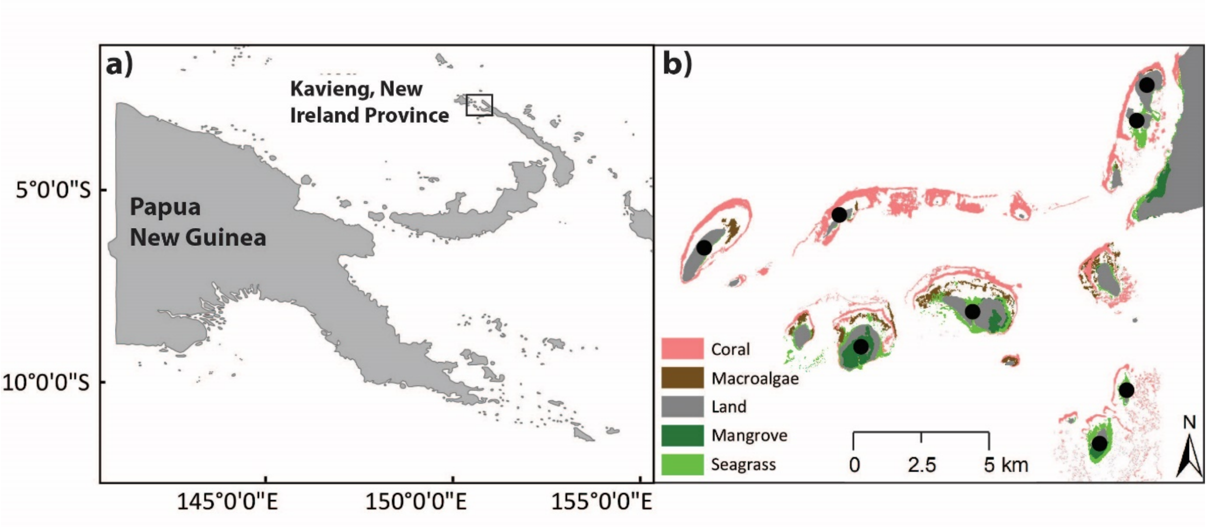


**Figure 3.1.** a) Map of Papua New Guinea with location of Kavieng, New Ireland Province, and b) study sites and habitats in the Tigak Island Group, Kavieng. Black circles denote the surveyed islands.

### *3.3.2 Data collection*

To quantify habitat use by coral reef-associated fishes, data were collected from five common habitat types, specifically: 1) shallow coral reef slopes (3-6 m depth), 2) reef flats containing hard structure (e.g., coral or rock), 3) macroalgal beds, 4) non-estuarine mangroves and, 5) seagrass meadows. Data on the use of these habitats by reef fishes were collected between 09:00 and 16:00 during April 2018, using unbaited underwater video cameras. This sampling method was chosen as it reduced any bias due to diver presence (Gotanda et al. 2009; Feary et al. 2011) and also due to the presence of saltwater crocodiles (*Crocodylus porosus*) in the area. The lack of baits on the cameras ensured that observations of habitat use were not influenced by attraction of fishes to bait (Bassett & Montgomery 2011).

Single video cameras (GoPros) mounted on steel frames were lowered to the substratum and GPS points were recorded for each camera drop. The use of single, as opposed to stereo, video systems precluded the collection of accurate body size data for fishes and prevented the separation of individual fishes into life stages based on body size. For mangrove and reef slope habitats, care was taken to ensure that cameras faced toward the habitat as opposed to adjacent open waters. Replicate camera drops were separated by a minimum of 50 m, both among and between the five habitat types. Each camera was deployed for a minimum of 20 minutes to enable high replication across broad-spatial scales within a relatively short time frame (e.g., Burge et al. 2012; Bradley et al. 2017; Pereira et al. 2017). The depth of the camera drops ranged from 0.3 to 5.5 m. In total 86 reef slope, 75 reef flat, 41 macroalgae, 58 mangrove and 100 seagrass videos were analysed. This variation was due to differences in the availability of each habitat type, and the exclusion of replicates with low video quality (camera fogging and limited underwater visibility).

### *3.3.3 Video analysis*

For each video, a 15-minute segment was analysed. Each segment began at least one minute after the camera had stabilised on the bottom and any sediment disturbed during placement had settled. From each video, species presence and the maximum number of individuals of a species observed in a single frame (Max*N*, *sensu* Cappo et al. 2004) were recorded. Max*N* is a common metric used as a conservative measure of relative abundance (Campbell et al. 2015). Cryptic (e.g., Blenniidae, Gobiidae) and surface-dwelling (e.g., Hemiramphidae) taxa were excluded because they were not able to be consistently counted using video. Individuals were identified to genus or species where possible. *FishBase* (Froese & Pauly 2019) was used to provide an objective assessment of which species were considered reef-associated, hereafter termed "reef fishes", or not reef-associated (following Sambrook et al. 2019, **Chapter 2**).

### *3.3.4 Data analysis*

Differences in the composition of fish assemblages between the five habitats were compared with a one-way Permutational Multivariate Analysis of Variance (PERMANOVA) using Type III sum of squares and 9999 permutations (Anderson et al. 2008). A zero-adjusted Bray-Curtis similarity matrix was used to account for the high number of zeros present in the Max*N* data and applied a fourth-root transformation (Clarke et al. 2006). Pair-wise tests were used to examine differences between habitats and visualised the data using non-metric multidimensional scaling (nMDS). The similarity percentages routine (SIMPER) was used to identify characteristic species for each habitat type.

Differences in the mean Max*N* (i.e., relative abundance) and species richness between habitats were compared with one-way ANOVAs, followed by Tukey's HSD post hoc tests using R. In addition, one-way ANOVAs were used to compare differences in mean Max*N* for common multi-habitat users to explore whether group sizes might differ between habitat types.

## 3.4 Results

Across the five habitat types (reef flat, reef slope, macroalgae, mangrove and seagrass), 15,492 individuals were recorded from a total of 319 taxa, of which 288 were identified to species. Across the five habitats surveyed, 282 out of the 288 species (98%) recorded were classed as reef fishes, with only six species observed on the videos considered non-reef associated. These six non-reef associated fish species were excluded from all further analyses.

In total, 35% of the reef fishes (99 of 282 species) observed in this study were recorded in non-reef habitats, with 20 species recorded in all three non-reef habitats (Figure 3.2a; Table A3.1). Although less speciose compared to the coral reef slope and flat habitats, the total number of reef fish species observed in each non-reef habitat was considerable (Table 3.1). A total of 53 reef fish species were observed in both seagrass meadows and mangroves and 60 species were observed in macroalgae beds (Figure 3.2; Table 3.1). While the total number of species observed was similar across the three non-reef habitat types, the mean species richness and relative abundance (i.e., mean Max*N*) of reef fish per video was approximately twofold higher in macroalgae beds compared to mangroves or seagrass meadows (Table 3.1; ANOVA $F_{2,196}$

= 15.002, $p$<0.001). The type and/or combination of non-reef habitats used by each of the 99 reef fish species varied widely. Over half of the species were observed in a single non-reef habitat (Figure 3.2), most commonly in macroalgae (22 spp.), followed by mangroves (18 spp.) and seagrass (12 spp.). However there was also considerable overlap in habitat use with almost half (47 of 99 species) recorded from two or more non-reef habitats (Figure 3.2).

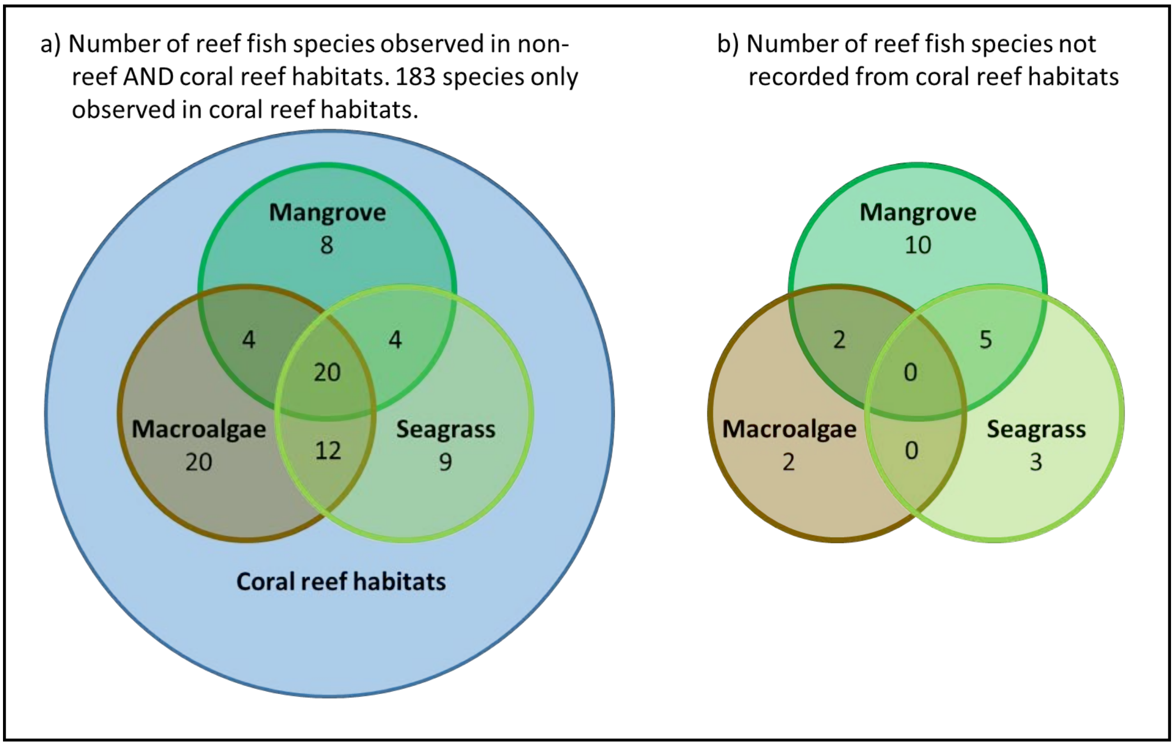


**Figure 3.2.** a) Number of reef fish species recorded in reef and non-reef habitats and overlap between non-reef habitats, and b) the number of species not recorded from coral reef habitats (reef slope and/or reef flat).

**Table 3.1.** The number of replicate video samples (n), total number of reef fish species observed across all videos, as well as the mean species richness and relative abundance (i.e., total Max$N$) of reef fish observed in each habitat type. Total Max$N$ calculated by summing the Max$N$ of each species recorded per video

| | Sample size *n* | Total no of reef fish species observed | Mean species richness per video ± SE (range) | Mean relative abundance (total Max$N$) per video ± SE (range) |
|---|---|---|---|---|
| Reef slope | 86 | 243 | 35.05 ± 1.19 (14-59) | 95.56 ± 7.07 (16-420) |
| Reef flat | 75 | 155 | 21.76 ± 0.83 (8-46) | 46.20 ± 2.57 (9-143) |
| Macroalgae | 41 | 60 | 13.12 ± 0.90 (3-36) | 31.24 ± 3.09 (4-70) |
| Mangrove | 58 | 53 | 6.84 ± 0.52 (1-19) | 16.69 ± 1.78 (1-56) |
| Seagrass | 100 | 53 | 5.43 ± 0.39 (0-16) | 15.6 ± 1.54 (0-72) |

### *3.4.1 Fish community differences between habitats*

Reef fish assemblages differed between the five habitats (PERMANOVA pseudo-$F_{4,355}$ = 38.926, $p$=0.0001, Figure 3.3), with each habitat type containing a distinct assemblage of reef fishes. Macroalgae beds were broadly characterised by several species of *Halichoeres*, the tuskfish *Choerodon anchorago*, the emperor *Lethrinus harak*, and the damselfish *Dischistodus chrysopoecilus*. *Lethrinus harak*, *C. anchorago* and *Halichoeres* spp., together with the rabbitfish *Siganus canaliculatus* were characteristic of seagrass habitats. Mangroves were characterised by a different suite of species including *Gerres oyena*, *Lutjanus ehrenbergii*, *Lutjanus fulviflamma*, the rabbitfish *Siganus lineatus* and the cardinalfish *Sphaeramia orbicularis.*

### *3.4.2 Habitat use patterns by reef fish family*

Two-thirds of the 41 families recorded during the surveys contained species that used non-reef habitats (27 families). Ten of these reef fish families contained a high proportion (≥50%) of species that were recorded in non-reef habitats including jacks (Carangidae), rabbitfishes (Siganidae), snappers (Lutjanidae), emperors (Lethrinidae) and sweetlips (Haemulidae) (Figure 3.4a). Patterns of habitat use (i.e., type and number of habitats) varied both among and within families. For example, species of snapper (Lutjanidae) ranged from being only recorded in coral reef habitats to being observed in both coral reef habitats and all three non-reef habitat types. In addition, several families contained species that were not recorded from either of the coral reef habitats (Figure 3.4b-d).

### *3.4.3 Species-level habitat use patterns*

The data revealed a wide variety of habitat usage patterns by the 99 reef fish species that were observed in non-reef habitats. Over three-quarters of the species were recorded on multiple occasions away from coral reef habitats. In addition, over half were observed more frequently in at least one non-reef habitat compared to either of the coral reef habitat types (e.g., Figure 3.5a, d, f-h; Table A3.2), while others occurred in similar frequencies across a range of reef and non-reef habitats (e.g., Figure 3.5b-c, e). Eighteen species were identified as widespread multi-habitat users and occurred in all five habitat types (Table A3.2). These ranged from larger-bodied species such as the emperor *Lethrinus harak*, the snapper *Lutjanus fulviflamma*, and the rabbitfish *Siganus canaliculatus* to smaller-bodied species such as the butterflyfish *Chaetodon vagabundus*, and the wrasses *Halichoeres scapularis* and *Stethojulis strigiventer*.

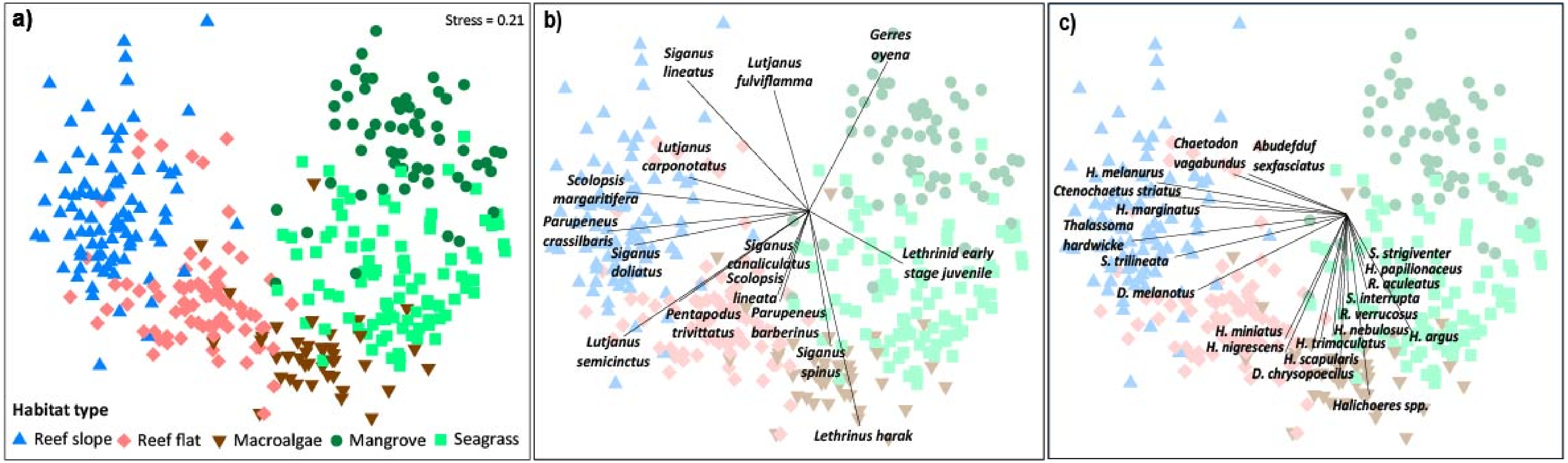


**Figure 3.3.** a) Non-metric multi-dimensional scaling plot showing the variation in the community structure of reef fishes recorded from remote underwater video in five habitat types (reef flat, reef slope, macroalgae, mangrove and seagrass). Each point represents a single video based on Max*N* data. Species where adults: b) ≥25 cm max length and c) <25 cm max length recorded on >10% of videos across all habitats or >25% of videos in a non-reef habitat type. Abbreviations of genera are *D.* = *Dischistodus*, *H.* = *Halichoeres*, *R.* = *Rhinecanthus*, *S.* = *Stethojulis.*

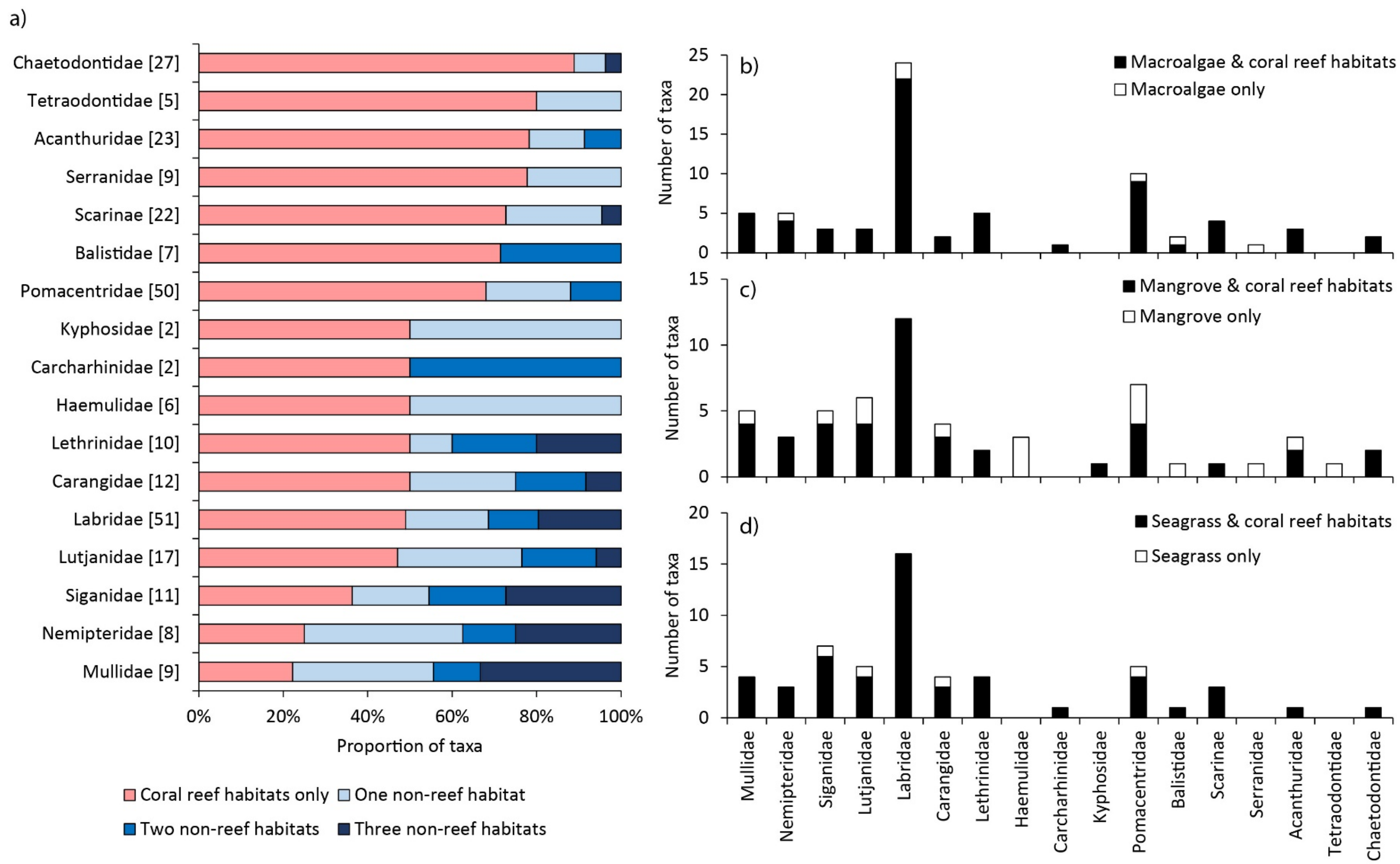


**Figure 3.4.** a) Habitat use patterns of common reef fish families showing proportion of taxa within each family only recorded from coral reefs and those recorded from one, two or three non-reef habitats. [x] denotes number of species observed in the study, b) reef fish taxa observed in macroalgal beds, c) mangroves, and, d) seagrass. Black bars represent species recorded in a non-reef habitat type and in coral reef habitats. White bars show the number of reef fish species that were not observed in coral reef habitats.

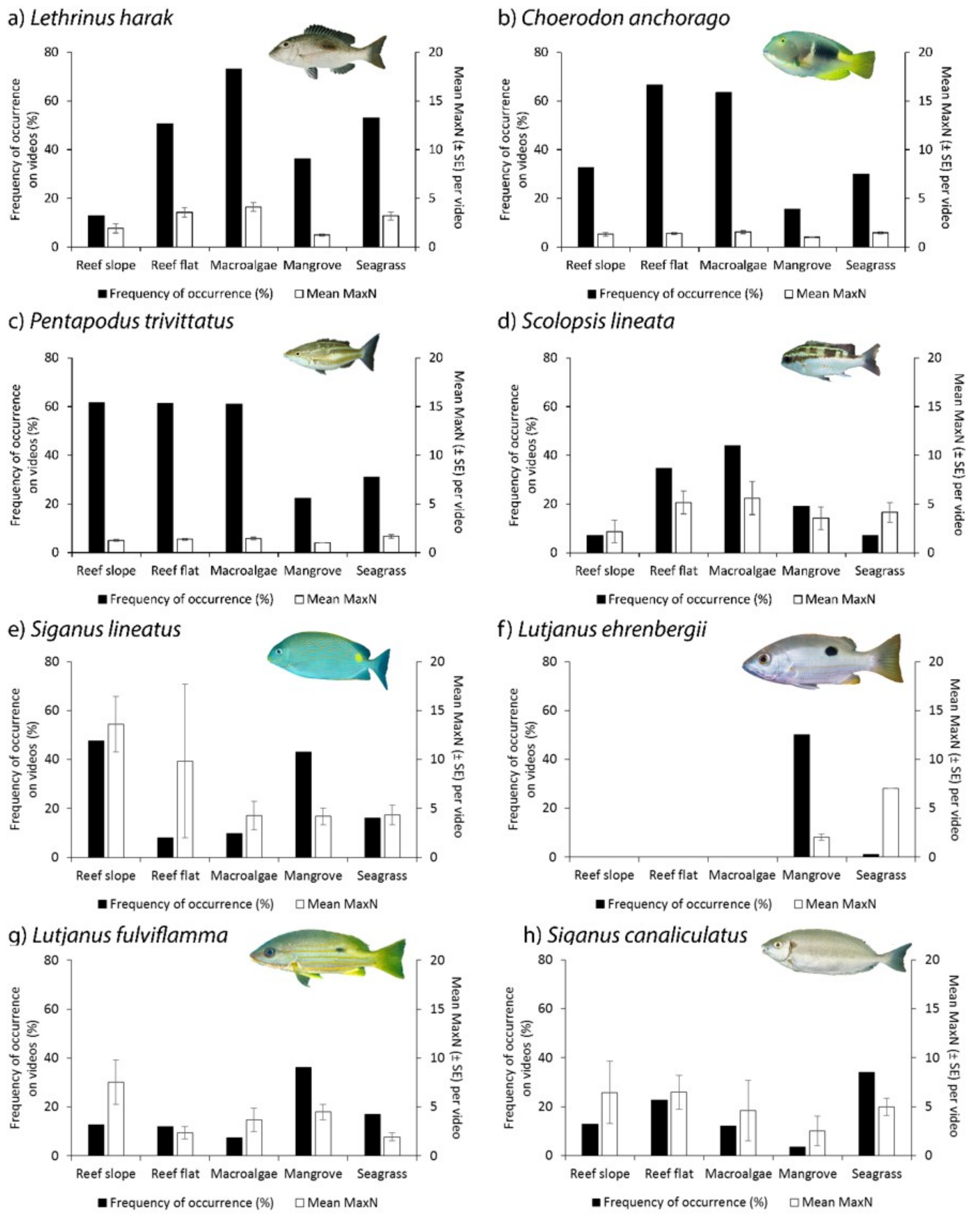


**Figure 3.5.** Species-specific habitat use patterns for eight common multi-habitat users. Black bars show the frequency of occurrence (%) on videos. White bars show the mean Max*N* (± 1 SE) calculated from videos where the species was recorded.

Comparing the relative abundance (i.e., Max*N*) for some of the most frequently observed and abundant multi-habitat users highlighted potential among habitat differences in group size

(Figure 3.5). For instance, the mean relative abundance for *Lethrinus harak* was significantly lower in mangroves (1.24 ± 0.10 SE) compared to reef flat, macroalgae and seagrass habitats (ANOVA $F_{4,158}$ = 4.68, p=0.01). The mean relative abundance for the rabbitfish *Siganus lineatus* was threefold higher on reef slopes compared to mangroves (ANOVA $F_{1,64}$ = 6.39, p=0.01), despite occurring on a similar number of occasions in each habitat, indicating that *S. lineatus* may occur in larger groups on reef slopes. Similarly, the snapper *Lutjanus fulviflamma* had a higher mean relative abundance on reef slopes (7.55 ± 2.26 SE) compared to all other habitat types, almost double the mean relative abundance in mangroves (4.48 ± 0.79 SE).

## 3.5 Discussion

There is increasing evidence of the widespread use of non-reef habitats by reef-associated fishes, with a recent systematic review suggesting that ~20% of reef fish species use non-reef habitats (Sambrook et al. 2019, **Chapter 2**). By comparing fish assemblages across five habitat types in Kavieng, Papua New Guinea, this study found that percentage to be even higher, with over a third (35%) of reef-associated fish species recorded in non-reef habitats, many of which occurred in multiple non-reef habitats. In addition, many of the species identified using multiple habitats are ecologically (e.g., the macroalgae browser *Siganus canaliculatus*) or economically important. These findings thus provide additional support for claims of widespread use of multiple habitat types by reef fishes and for the importance of better understanding habitat complementarity in coral reef ecosystems. The study also demonstrates the value of examining species distributions across a wider range of habitats at each study location in the Indo-Pacific, as has previously been noted for the Caribbean (Nagelkerken et al. 2000a; Harborne et al. 2008). Observed species-specific patterns of habitat use would have been incomplete had a more limited range of habitats been sampled.

Macroalgal beds contained, on average, more species and higher relative abundances of reef fish compared to mangroves or seagrass meadows, albeit considerably lower than the two reef habitats. This supports the growing number of studies that have documented high abundances and diversity of coral reef fishes in macroalgae beds (e.g., Rossier & Kulbicki 2000; Wilson et al. 2010; Chaves et al. 2013; Evans et al. 2014; Eggertsen et al. 2017; Tano et al. 2017). The majority of these studies have focused on beds of canopy-forming macroalgae, such as *Sargassum* (but see Rossier & Kulbicki 2000), finding that the structural complexity and canopy height of algae are important factors influencing its use by coral reef fishes, particularly juvenile life stages (Wilson et al. 2014; Fulton et al. 2019; Fulton et al. 2020; Tang et al. 2020).

In contrast, the macroalgal sites in this study were predominantly a mixture of *Halimeda* and *Caulerpa*, which are smaller and less structurally complex than *Sargassum*. Despite these differences, a similar suite of families (e.g., Labridae, Lethrinidae, Siganidae) to that reported from *Sargassum*-based studies were recorded. This suggests that factors other than structural complexity of the algae, such as the availability of food resources, visibility of predators, and proximity to other habitat types (e.g., van Lier et al. 2018) may also influence the suitability of macroalgae beds for coral reef fishes. Although fish assemblages in macroalgal beds were typically more speciose than seagrass meadows or mangroves, there was considerable overlap in species using macroalgae beds and seagrass meadows, indicating these two habitat types could act as complementary habitats for some fishes (Dunning et al. 1992). Seagrass meadows and macroalgal beds can be structurally similar (Gratwicke & Speight 2005), and contain comparable resources and refugia opportunities (Macreadie et al. 2017) which could drive similarities in habitat use.

In contrast, mangroves contained a distinct assemblage of reef fishes including some species (e.g., *Lutjanus argentimaculatus*) that were exclusive to this habitat. Although the methodology precluded the separation of the data into life stages based on body size, several individuals, particularly snappers (i.e., lutjanids), were observed with juvenile markings within mangrove habitats. These findings are interesting, but require additional research, given the debate about whether mangrove habitats in the Indo-Pacific are as important for coral reef fishes, particularly juveniles, as they are in the Caribbean (Blaber & Milton 1990; Thollot 1992; Dorenbosch et al. 2005a; Nakamura et al. 2008; Unsworth et al. 2009; Barnes et al. 2012; Kimirei et al. 2013a; Dubuc et al. 2019). Mangrove systems in the Indo-Pacific vary considerably depending on tidal regime (Krumme 2009; Igulu et al. 2014), geomorphological and spatial context (Blaber 2007; Unsworth et al. 2008; Olds et al. 2013; Bradley et al. 2019), as well as the size, composition and structural complexity of mangroves forests (Laegdsgaard & Johnson 2001; Nanjo et al. 2014), all of which can influence habitat use patterns (Sheaves 2017). Here, non-estuarine mangroves in a microtidal location were examined and it appears that under these conditions, mangroves might possess certain attributes (e.g., refuge, food availability) that are not provided by the other shallow non-reef, or even reef, habitats surveyed. Therefore the impact of mangrove loss or degradation could be greater for coral reef fishes that appear to selectively use mangroves compared to species that appear to use multiple habitats interchangeably.

Importantly, a substantial number (>50%) of the species using multiple habitat types belong to families (e.g., Carangidae, Lethrinidae, Lutjanidae, and Siganidae) caught by small-scale fisheries in the region (Papua New Guinea National Fisheries Authority 2005, 2007). Reef fishes have historically been, and continue to be, an important source of animal protein for Pacific Island communities (Dalzell et al. 1996; Pinca et al. 2012). However increasing human populations have placed pressure on reefs, and many island nation reef fisheries are considered to be operating at unsustainable levels (Newton et al. 2007). As reefs become more degraded, it has been suggested that the availability of non-reef habitats could play an important role in maintaining the productivity of reef fisheries (Rogers & Mumby 2019). Fishing around the Tigak Islands is largely restricted to inshore waters surrounding the islands, particularly during the monsoon season (Lawless & Frijlink 2016), with the only commercial fishing targeting tuna and other pelagic fishes in offshore waters. My findings suggest that this dependence on inshore waters for several months each year, combined with growing populations, requires careful management of the entire seascape, not just reefs, by local communities to protect food security into the future.

"Coral reef fishes" is a widely used term to describe fish assemblages that occupy waters in the vicinity of coral reefs, yet over one third of the fishes recorded from shallow-water habitats in the Kavieng Lagoon were present in one or more non-reef habitats. Many of these species were frequently encountered away from coral reef habitat and could be considered as "seascape users" or "habitat generalists" as opposed to "coral reef fish". Terminology aside, being flexible in habitat use could be advantageous given the widespread degradation of many shallow-water coastal habitats. As has been demonstrated from terrestrial landscapes (e.g., in birds, Salido et al. 2011), populations of such habitat generalists might be less vulnerable to the degradation of one habitat type. In contrast, species that obtain complementary resources from different habitats (e.g., food vs. shelter, Ries et al. 2004), may be negatively impacted by habitat disturbance or loss. However, the drivers of multiple habitat use are not well understood for many of the species identified here as multi-habitat users.

It is now widely recognised that coral reefs are moving into uncertain territory. However, efforts to predict how reefs might function in the future rarely consider that many reefs are embedded within, and consequently influenced by, a mosaic of other habitat types. Such connections may become increasingly important in the future both for supporting key ecological functions on reefs, and providing food security for nations with strong dependencies on coral reef fisheries.

# Chapter 4

## Relative importance of seascape versus within-habitat variables on the distribution of fishes in tropical seagrass beds [3]

### 4.1 Abstract

Indo-Pacific seagrass meadows, particularly those in the Coral Triangle, cover large areas of shallow water, harbour diverse fish communities and support coastal fisheries. These meadows are often located in complex seascapes containing a mosaic of habitat types. However, the relative influences of within-habitat variables (e.g., shoot density, canopy height) and the surrounding seascape (e.g., distance to coral reef or mangroves) in shaping fish communities in seagrass meadows are largely unknown. I used a multi-scale approach to examine the relative influence of within-habitat variables and seascape structure on the distribution patterns of 17 fish taxa (i.e., families and species), and life stages for two taxa, in 32 seagrass patches around the Tigak Islands, New Ireland, Papua New Guinea. Of the 21 fish groups examined, two-thirds were influenced more by seascape than within-habitat variables. Site-attached taxa were generally more influenced by within-habitat variables, while taxa with larger home ranges (e.g., rabbitfishes, snappers) and ontogenetic habitat-shifters (e.g., emperors) were generally more influenced by the surrounding seascape. Despite the majority of taxa being reef-associated, proximity to or area of adjacent coral reefs appeared to have limited influence on local abundances. Instead, proximity and area of hardground, macroalgae and mangroves emerged as more influential. The findings show that individual seagrass patches are not functionally equivalent and that the surrounding seascape is important in shaping tropical fish assemblages in seagrass beds. Adopting a multi-scale approach to examine species-habitat relationships will provide a more nuanced perspective, improving our ability to predict which seagrass patches are highly productive or important nurseries which can contribute towards to more refined spatial management strategies.

[3] Data from this chapter has been submitted as: **Sambrook K**, Andréfouët S, Aston EA, Bonin MC, Cumming GS, Duce S, Sievers KT, Hoey AS (in revision) Relative importance of seascape versus within-habitat variables on the distribution of fishes in tropical seagrass beds. *Estuarine, Coastal and Shelf Science*

## 4.2 Introduction

Understanding how distribution patterns of organisms are influenced and at what spatial scales is a fundamental goal of ecology (Levin 1992; Schneider 2001). An organism's habitat requirements are often dependent on traits such as body size, mobility, behavior, and vulnerability to predation, and these requirements can change during a species' lifecycle (Mittelbach 1981; Rayor & Uetz 1993; Nakazawa 2015). Furthermore, individuals may respond to variables operating across different spatial scales, ranging from within-habitat variables (e.g., structural complexity, food availability) to land- or seascape variables (e.g., composition and spatial configuration of habitats or patches surrounding a focal patch; Menge & Olson 1990; Dunning et al. 1992; Ries et al. 2004; Mayor et al. 2009; Thornton et al. 2011). Consequently, selecting ecologically meaningful scales at which to analyse influences on local distribution patterns can be challenging (Wiens 1989; Wheatley & Johnson 2009; Jackson & Fahrig 2015). One widely applied solution is to adopt a multi-scale approach that incorporates both within-habitat and broader land- or seascape variables (Kotliar & Wiens 1990; Kendall 2005; Mellin et al. 2009; Yeager et al. 2011).

Tropical shallow marine environments are composed of a mosaic of different habitat patches (e.g., coral reefs, mangroves, macroalgae beds, and seagrass meadows) interspersed across the seascape. Many fishes are known to use multiple habitats for a variety of reasons including short-term movements to foraging or spawning sites, and ontogenetic shifts among habitats (Adams et al. 2006; Appeldoorn et al. 2009; Nagelkerken 2009; Sambrook et al. 2019, **Chapter 2**). Although the use of multiple habitats by fishes has long been recognised (Ogden 1976; Parrish 1989), scaling up research from single habitats to incorporate the composition and configuration of multiple habitat types and patches in the surrounding seascape has begun to reveal the complexities of fish-habitat relationships (Grober-Dunsmore et al. 2009; Pittman & Brown 2011; Rees et al. 2018; van Lier et al. 2018). To date, the majority of this research in tropical marine environments has focused on coral reefs. It has found that seascape variables such as proximity to mangrove forests, seagrass meadows, and/or macroalgal beds can influence the distribution of some reef fish taxa on adjacent reefs (e.g., Dorenbosch et al. 2005b; Grober-Dunsmore et al. 2008; Berkström et al. 2013a; Martin et al. 2015). This is particularly evident for taxa that undertake ontogenetic shifts between habitats, and/or species with larger home ranges (e.g., sweetlips, snappers, emperors) that move between foraging and resting sites (Beets et al. 2003; Berkström et al. 2013b). In contrast, the distribution of more site-attached (e.g., damselfishes) or sedentary (e.g., groupers) taxa appears to be better explained by within-habitat variables (e.g., structural complexity, percent hard coral cover) (Grober-Dunsmore et al. 2007). For those fish taxa whose populations are influenced by the surrounding seascape, proximity to or area of seagrass meadows has often been identified as important (Dorenbosch et al. 2005b; Kendall 2005; Grober-Dunsmore et al. 2007; Olds et al. 2014).

Seagrasses occur in temperate and tropical ecosystems in both estuarine and marine environments. In temperate and tropical Atlantic systems, seagrass meadows are well-established as important fish habitat, particularly because of their role as nurseries for several key fisheries species (e.g., Atlantic cod (*Gadus morhua*), Lilley & Unsworth 2014; Tuya et al. 2014; McDevitt-Irwin et al. 2016). Until relatively recently, the value of seagrass habitat for fishes in tropical Indo-Pacific seascapes had received less attention (Orth et al. 2006; Duarte et al. 2008; Unsworth & Cullen 2010). Emerging social-ecological research has highlighted the significance of Indo-Pacific seagrass habitat in sustaining small-scale fisheries (de la Torre-Castro et al. 2014; Unsworth et al. 2014; Nordlund et al. 2018; Brodie et al. 2020), and hence its likely importance for populations of some tropical fishes.

The Indo-Pacific region is known for its high seagrass diversity, particularly in Pacific small island developing states such as Papua New Guinea and the Solomon Islands (Short et al. 2007; Waycott et al. 2009). In these areas the composition and structure of seagrass beds can be highly variable, even across relatively small areas (10s to 100s of metres) (McKenzie et al. 2020). While some studies have shown the importance of within-habitat features (e.g., canopy height, shoot density) in shaping fish assemblages within seagrass beds (Bell & Westoby 1986; Hyndes et al. 2003; Boström et al. 2006; Horinouchi 2007; Pogoreutz et al. 2012; Yeager & Hovel 2017), others have demonstrated the importance of neighbouring habitat types (e.g., coral reefs: Dorenbosch et al. 2005a; mangroves: Unsworth et al. 2008). Studies examining the relative influence of both within-habitat and seascape variables on fish distribution patterns in seagrass meadows are rare and confined to temperate systems (e.g., Staveley et al. 2017; Scapin et al. 2018; Olson et al. 2019) or the tropical Indian Ocean (Gullström et al. 2008; Aller et al. 2014). Given the potential ecological and economic value of many fishes that use tropical Indo-Pacific seagrass beds, identifying the variables that best predict their distribution merits greater consideration (Sambrook et al. 2020, **Chapter 3**). As well as improving our understanding of species distribution patterns, adopting a multi-scale approach has considerable value for spatial management strategies (e.g., reserve networks) that typically operate at broader spatial scales (i.e., 10s to 100s $km^2$).

I used a multi-scale approach to examine the relative influence of within-habitat variables and seascape structure on distribution patterns of fishes in seagrass beds in the Tigak Island Group, New Ireland Province, Papua New Guinea. Based on the underlying hypothesis that species occurrences will reflect a full set of resource needs, I predicted that within-habitat structure would exert a greater influence on the distribution patterns of less mobile and/or site-attached fish taxa (e.g., damselfishes), whereas the surrounding seascape would be more influential on taxa with larger home ranges and/or taxa that shift between habitats during ontogeny (e.g., emperors, snappers).

## 4.3 Methods

### *4.3.1 Study location*

The study was conducted around three island complexes (i.e., Enuk, Kabotteron, and Nusa) of the Tigak Island Group, Kavieng, New Ireland Province, Papua New Guinea (Figure 4.1). Each island has extensive seagrass meadows, with distinct patches, often in close proximity, that vary in their species composition, structural attributes (e.g., canopy height, shoot density, percent cover), and water depth. In addition to large expanses of seagrass, each island has a range of other habitat types (e.g., coral reefs, non-estuarine mangroves, macroalgal beds, sand) that vary in size and spatial configurations. This presents an ideal system to examine the influence of seascape and within-habitat variables on fish taxa in seagrass beds. The tidal regimen is mixed microtidal (Krumme 2009), with a tidal range of ~1.09 m.

### *4.3.2 Habitat mapping*

A benthic habitat map for the seascape surrounding each island was produced using high-resolution multispectral Worldview 2 imagery acquired in 2017 (Figure 4.1). The mapping process followed the user-oriented workflow described in Andréfouët (2008). Specifically, polygons of homogeneous colour and texture were photo-interpreted against the satellite images, and labelled based on a preliminary survey that investigated the diversity of shallow habitats throughout the Kavieng area in August 2014 (Andréfouët, unpublished data). Extensive ground-truthing using geo-referenced photographs (n = 1,470 photographs across 126 sites) was subsequently undertaken in September 2017 to verify the accuracy of initial habitat classifications. When necessary, the initial maps were corrected using the 2017 ground-truthing data to minimise any errors in habitat identification that could bias conclusions. I focused on eight broad benthic habitat categories: coral, deep water, hardground, heterogeneous, macroalgae, mangrove, seagrass and sand (Table 4.1). As benthic habitat maps derived from satellite imagery are restricted to shallow-water only (<20 m), I classified any unmapped regions surrounding islands as ‘deep water’. The classification ‘hardground’ included areas dominated by reef pavement, rock or rubble, and ‘heterogeneous’ encompassed predominantly small low relief patches of mixed composition including rubble, hard and soft coral, seagrass and algae. In addition, the high spatial resolution of the maps allowed for the identification of unique spectral signatures for different types of seagrass patches, predominantly based on seagrass density.

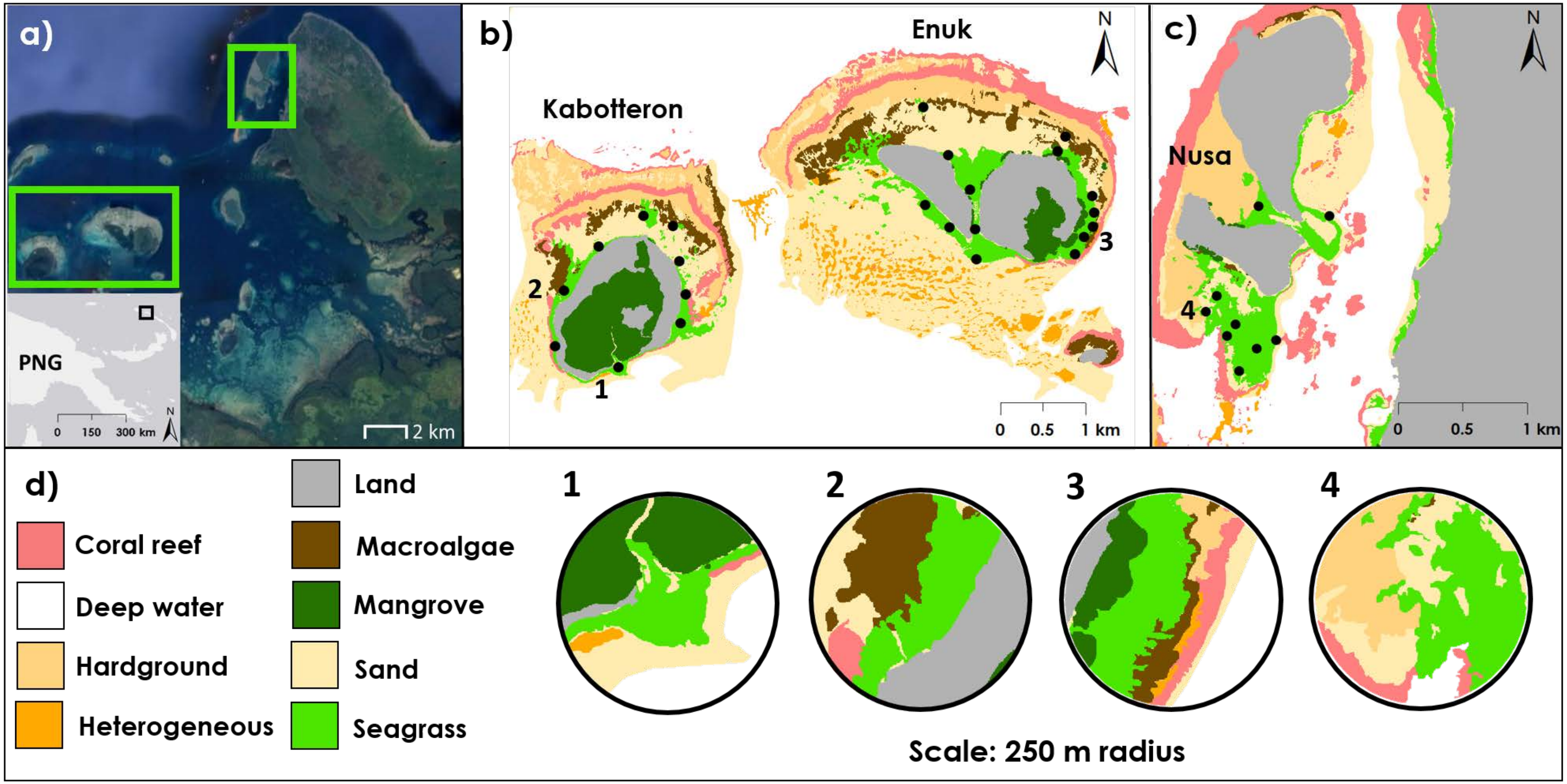


**Figure 4.1.** a) Map of Kavieng, New Ireland Province, with inset showing location within Papua New Guinea; b & c) the three focal island complexes and surrounding benthic habitats. Black circles denote the 32 seagrass survey sites, d) examples of different seascapes surrounding seagrass survey sites based on 250 m radii.

**Table 4.1.** Predictor variables used to examine the influence of within-habitat and seascape variables on the distribution of fishes in seagrass beds.

| Metric | Description | Unit | Mean | SE | Range |
|---|---|---|---|---|---|
| ***Within-habitat variables*** | | | | | |
| Depth | Measured at start & end of each transect | m | 0.80 | 0.04 | 0.25-2.30 |
| **Transect (25 m)** | | | | | |
| Coral | Percent cover | % | 1.8 | 0.58 | 0-39.22 |
| Macroalgae | Percent cover | % | 12.66 | 1.58 | 0-62.75 |
| Rock | Percent cover | % | 1.35 | 0.47 | 0-27.45 |
| Rubble | Percent cover | % | 0.61 | 0.29 | 0-21.57 |
| Sand | Percent cover | % | 14.30 | 1.80 | 0-80 |
| Seagrass | Percent cover | % | 69.26 | 2.59 | 5.88-100 |
| **Quadrat (5 x 0.25 m$^2$ per 25 m transect)** | | | | | |
| Shoot density | Seagrass shoot density in 5 x 0.01 m$^2$ sub-quadrats | | 19.10 | 0.97 | 0.33-42.67 |
| Canopy height | Tallest 5 seagrass blades in 5 x 0.01 m$^2$ sub-quadrats | cm | 13.64 | 0.97 | 4.03-60.68 |
| Algae | Mean percent cover | % | 15.78 | 1.51 | 0-60 |
| Seagrass | Mean percent cover | % | 41.91 | 2.84 | 0-96.67 |
| Epiphytes | Mean percent cover of epiphytes on seagrass blades | % | 34.53 | 2.01 | 10-90 |
| ***Seascape variables*** | | | | | |
| **Distance to nearest patch** | | | | | |
| Coral reef | Measured using Near function in ArcGIS. Edge-to-edge distance from seagrass patch to X habitat type avoiding crossing land | m | 256.41 | 25.26 | 4.76-1041.37 |
| Hardground | | m | 520.07 | 51.80 | 11.05-1728.45 |
| Heterogeneous | | m | 437.25 | 32.16 | 17.87-1168.57 |
| Macroalgae | | m | 457.37 | 48.42 | 0-1771.61 |
| Mangrove | | m | 415.25 | 34.88 | 17.34-1368.30 |
| **% area of habitat in 100, 250, 500 & 1000 m radii** (shown for 100 m scale only) | | | | | |
| Coral reef | | % | 3.84 | 0.81 | 0-27 |
| Deep water | | % | 0.88 | 0.28 | 0-11 |
| Hardground | | % | 3.09 | 0.82 | 0-30 |
| Heterogeneous | | % | 0.38 | 0.15 | 0-6 |
| Macroalgae | | % | 5.56 | 1.14 | 0-44 |
| Mangrove | | % | 1.88 | 0.63 | 0-34 |
| Seagrass | | % | 56.06 | 2.57 | 0-100 |
| Sand | | % | 22.34 | 2.28 | 0-80 |
| **Habitat richness** | | | | | |
| 100 m | Number of habitat types within buffer | N | 3.06 | 0.10 | 1-6 |
| 250 m | | N | 4.38 | 0.14 | 2-7 |
| 500 m | | N | 5.72 | 0.11 | 3-7 |
| 1000 m | | N | 6.66 | 0.07 | 5-7 |

### *4.3.3 Surveys*

I surveyed fish and benthic communities in 32 seagrass patches around the three island complexes (Figure 4.1) during April and May 2018. Seagrass patches were selected *a priori* from the initial benthic habitat map to represent a range of seagrass densities and seascape attributes (e.g., distance to mangroves). In each seagrass patch, fish and benthic communities were quantified along three replicate 25 m transects, with adjacent transects separated by a minimum of 10 m. Transects were positioned parallel to shore and placed ≥5 m away from the boundary of each patch to reduce potential confounding effects of edge habitats on fish communities. All surveys were carried out during daylight hours between 10:00 and 16:00.

All non-cryptic fishes were surveyed in seagrass patches using belt transects. Fish > 10 cm total length (TL) were identified, their TL estimated to the nearest 5 cm, and recorded within a 5 m wide belt as the transect was being placed to minimise any potential diver effects on fish counts. Fish <10 cm were identified, their TL estimated to the nearest 2.5 cm, and recorded within a 2 m wide belt during a return swim along the transect (Thompson & Mapstone 2002). Individuals were identified to genus or species where possible, and abundances standardised to 250 $m^2$.

### *4.3.4 Within-habitat structure*

Within-habitat variables were quantified along the same transects used to survey the fish community. I first quantified benthic composition using point-intercept transects, recording the substratum directly below the transect tape at 50 cm intervals (51 points per transect). The substratum was classified as seagrass, macroalgae, live coral, sand, rubble, or rock/pavement. Secondly, I placed five 0.25 $m^2$ quadrats at random points along each transect and estimated percent cover of seagrass, macroalgae and the percent epiphyte cover on seagrass blades. Within each quadrat, I also surveyed five smaller 'sub-quadrats' (0.01 $m^2$) to quantify the shoot density (i.e., number of shoots) and canopy height (i.e., height of the five longest seagrass blades per sub-quadrat) (Aller et al. 2014; Eggertsen et al. 2017). The depth at the start and end of each transect was recorded.

### *4.3.5 Seascape composition and configuration*

To explore the influence of seascape variables, I extracted spatial pattern metrics from the benthic habitat map using ArcGIS (v10.6.1). I quantified the proportion (area) of eight different habitat types (i.e., coral reef, deep water, hardground, heterogeneous, macroalgae, mangrove, seagrass, sand) and the number of habitat types (i.e., habitat richness) within 100 m, 250 m, 500 m and 1000 m radii of the survey sites (Figure 4.1, Table 4.1). Given the limited information on home ranges for common fish species at my study sites, radii were selected based on previous studies that have related fish abundance or diversity in other habitat types with the presence of seagrass beds (e.g., Grober-Dunsmore et al. 2007; Olds et al. 2012a; Van Wynsberge et al. 2012; Berkström et al. 2013a). I also measured the proximity (edge-to-edge distance) of the seagrass patch to the nearest polygon of one of five different habitat types (i.e., coral reef, hardground, heterogeneous, macroalgae and mangrove) using the Near function in ArcGIS (Table 4.1). Where the shortest route between a seagrass patch and a different habitat type crossed land, the shortest edge-to-edge distance between patches avoiding land was measured manually.

### *4.3.6 Spatial autocorrelation*

All response and predictor variables were tested for spatial autocorrelation using a standardised inverse distance weighted Global Moran's I with the threshold distance defined by the average distance from each site (n = 32 sites) to its eight nearest neighbours (average distance = 1,394 m). For variables where significant (pseudo-significance $P \leq 0.01$ calculated from 999 permutations) spatial autocorrelation was detected with a Moran's I value exceeding 0.4 (Hamylton & Barnes 2018), spatial patterns were further examined using cluster and outlier analysis (Anselin Local Moran's I) in ArcGIS. Two predictor variables at the seascape scale exhibited positive spatial autocorrelation, specifically, area of coral reef (Moran's I = 0.57, $P < 0.001$) and area of mangroves (Moran's I = 0.61, $P < 0.001$) within 1000 m radius. Cluster and outlier analysis revealed that these values were driven primarily by clustering of high values around the island of Nusalik that had a small area of mangroves and a larger area of coral reef habitat compared to sites around the other two islands (i.e., Enuk and Kabotteron). Only three of the 22 response variables were weakly spatially autocorrelated: adult parrotfishes (Scarinae; Moran's I = 0.182, P = 0.003, *Siganus spinus* (Moran's I = 0.251, P = 0.001) and *Stethojulis strigiventer* (Moran's I = 0.165, P = 0.000) (Table A4.2). The limited evidence of spatial autocorrelation in the data suggests that survey sites were spaced beyond the zone of spatial dependence (Hamylton 2017; McGarvey et al. 2010) and thus provide a representative characterisation of the spatial heterogeneity of the seascape.

### *4.3.7 Data analysis*

I used boosted regression trees (BRTs) to evaluate the influence of 12 within-habitat and 14 seascape predictor variables (Table 4.1) on the abundance and/or presence of each of 21 fish groups in seagrass beds (Table A4.1). BRTs are a powerful and increasingly popular technique to explore complex ecological datasets (Sekund & Pittman 2017) because they are capable of managing collinearity and can fit non-linear relationships (Elith et al. 2008). BRTs were fitted individually by fish group using functions from the *dismo* package (Hijmans & Elith 2017) in R v4.0.0 (R Core Team 2020).

Although BRTs are capable of managing multicollinearity, I followed (Zuur et al. 2010) and generated a collinearity matrix using Pearson's correlation coefficients in the R package *corrplot* to identify highly collinear (>0.7) predictor variables (Figures A4.1 & A4.2). Where high collinearity was identified, I ran a reduced BRT containing only the collinear variables (e.g., area of sand and area of seagrass within 100 m radius) using the gbm.step function for each response variable. From the reduced BRT, I retained the predictor variable with the highest relative influence for inclusion in subsequent modelling steps. Models were fitted with a Poisson distribution for count data for fish groups where >1,000 individuals were recorded across all surveys (e.g., parrotfishes, rabbitfishes, snappers, wrasses). Data for less abundant taxa (e.g., threadfin breams, goatfishes) were modelled using a Bernoulli distribution for presence.

An initial model was generated for each of the 21 fish groups allowing all non-collinear predictor variables to be evaluated using the gbm.step function in the *dismo* package. Following this initial model run, I used the function gbm.simplify (Elith & Leathwick 2017) to identify uninformative predictor variables. This process involves an iterative backwards stepwise removal using 10-fold cross-validation to identify the number and identity of predictor variables that can be removed from the model without affecting the model's predictive performance. Finally, I ran these simplified models through an optimisation loop in which three parameters were varied: bag fraction (0.5, 0.7, 0.8), learning rate (0.001, 0.0001, 0.00001) and tree complexity (1-5). Optimising these three parameters and using slow learning rates helps to counter overfitting issues associated with the use of multiple predictor variables and the generation of large numbers of trees (Elith et al. 2008). This optimisation process enabled the identification of the combination of parameters that produced the 'best' or lowest cross validation deviance (Aston et al. 2019) with the minimum number of trees set to 1,000 and maximum set to 10,000 trees (Elith et al. 2008). Models that explained <20% deviance were deemed unsatisfactory and excluded from further analysis. In total, models are reported for 17 fish taxa (Table A4.1) including family and species/genera, as well as juveniles and adults from two families (i.e., emperors and parrotfishes). Emperors and parrotfishes were the only taxa where adults and juveniles were easily distinguishable and occurred with sufficient frequency to explore distribution patterns discretely.

BRTs compute the relative influence of each predictor variable, resulting in a cumulative contribution of predictors summing to 100%. Influential predictor variables are identified by those selected in models more frequently than would be expected by chance. A higher relative influence (%) is therefore indicative that a predictor variable is influencing the response variable under investigation (Elith et al. 2008). On average, 5.9 ± 0.25 SE predictor variables were identified per model as influencing the distribution patterns (abundance or presence) of particular fish groups. For all subsequent analyses, I extracted only those predictor variables identified as more influential than expected by chance. Relationships between a response variable and influential predictor variables were visualised with partial dependency plots using the gbm.plot function (Elith & Leathwick 2017).

## 4.4 Results

A total of 9,746 individuals were recorded from 71 species (or species groups) representing 14 families (including the Scarinae; i.e., parrotfishes) across the 32 seagrass patches. Wrasses (Labridae) were the most abundant taxa, accounting for 50% of all individuals recorded, followed by parrotfishes (22%) and emperors (Lethrinidae: 9.5%; Figure 4.2). The majority of parrotfishes and emperors recorded were juveniles.

### *4.4.1 Seascape vs within-habitat variables*

The influence of seascape and within-habitat variables varied between fish groups. Of the 21 fish groups (e.g., family, species and life stage) examined, 13 (62%) were more strongly influenced by the surrounding seascape compared to within-habitat predictor variables, conversely within-habitat variables were more influential for the remaining eight groups.

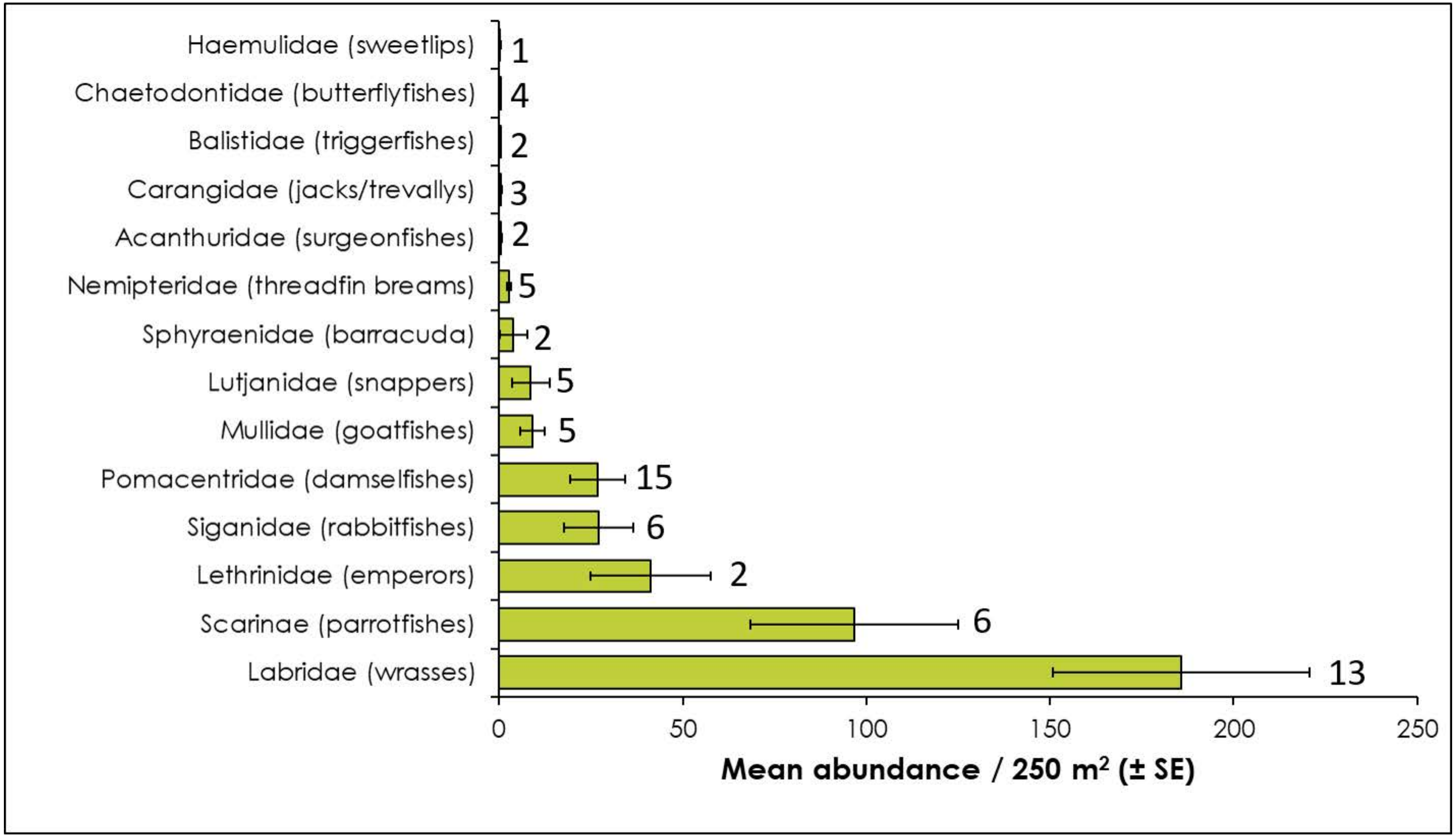


**Figure 4.2.** Mean abundance of individuals / 250 $m^2$ by family of selected taxa observed across 32 seagrass patches in Kavieng, Papua New Guinea. Note: parrotfishes from the subfamily Scarinae are presented separately from the Labridae family. Numbers above bar show number of taxa recorded in each family.

### 4.4.2 Family responses

Of the five families for which patterns of abundance were analysed, three families (i.e., rabbitfishes, wrasses, snappers) were primarily influenced by seascape variables while parrotfishes and damselfishes were more influenced by within-habitat attributes (Figure 4.3). For rabbitfishes and wrasses the influence of seascape characteristics on abundance was particularly strong, accounting for 82% and 76% of the most influential predictor variables. Specifically, the abundance of wrasses was predominantly influenced by distance to and area of macroalgae (Figure 4.3), being positively related to the proportion of macroalgae within 250 m. In contrast, rabbitfishes and snappers were primarily influenced by the proximity of mangroves. The abundance of both parrotfishes and damselfishes were positively related to the cover of live coral within seagrass patches.

Of the three families for which patterns of presence were analysed, emperors and threadfin breams were more strongly influenced by seascape variables (87% and 67% respectively), whereas goatfishes were more influenced by within-habitat characteristics. Threadfin breams were more likely to be present in seagrass patches proximal to mangroves, whereas emperors were less likely to be present as the proportion of mangrove within 500 m increased. Water depth was the most important predictor for goatfish presence (Figure 4.3), with this taxon more likely to be present as depth increased. All three families were influenced by distance to hardground and were less likely to be present when the seagrass patch was adjacent (<100 m) to hardground.

### 4.4.3 Species responses

Due to their high relative abundance, responses were compared for three species of wrasse (*Halichoeres trimaculatus*, *H. scapularis* and *Stethojulis strigiventer*), and a group of 'other' *Halichoeres* (including *H. argus*, *H. nebulosus* and *H. nigrescens*) that were difficult to differentiate in the field (Figure 4.4). The relative influence of seascape versus within-habitat variables on the abundance of these four wrasse taxa varied considerably (Figure 4.4). 'Other' *Halichoeres* responded most strongly to seascape variables (92%), with abundance negatively related to the area of sand within 100 m and positively related to either near (<100 m) or far (>1000 m) patches of macroalgae (Figure 4.4). In contrast, *H. trimaculatus* was more influenced by within-habitat variables (78%), particularly depth, percent cover of seagrass at the quadrat level, and canopy height (Figure 4.4). Seascape and within-habitat variables exerted broadly similar influences on the abundance of *H. scapularis* (43% vs. 57%) and *S. strigiventer*

(53% vs. 47%). *H. scapularis* abundance was negatively related to the canopy height of seagrass and positively related to the area of macroalgae within 250 m whereas *S. strigiventer* was negatively related to the area of mangrove habitat within 1000 m and positively related to the cover of macroalgae at the transect level.

The influence of seascape and within-habitat variables on the presence of three species of rabbitfishes were broadly similar (i.e., influence of seascape: *Siganus spinus* 64%, *S. canaliculatus* 60%, and *S. lineatus* 51%; Figure 4.4). Despite subtle differences in the relative importance of individual variables, the presence of all three species was influenced by distance to hardground (Figure 4.4), with *S. canaliculatus* and *S. spinus* being negatively related and *S. lineatus* positively related to the proximity of hardground. All three species were also influenced by the cover of macroalgae at the quadrat scale, however the nature of the relationship differed with *S. spinus* being positively related and, *S. canaliculatus* and *S. lineatus* negatively related to macroalgal cover. The presence of *Lutjanus fulviflamma* was more influenced by seascape than within-habitat variables (67% vs 33%), and was more likely to be present with increasing distance from coral reef and macroalgal habitat, and as the cover of seagrass increased. The presence of *Lethrinus harak* was more influenced by within-habitat variables (65%), and was positively related to the cover of seagrass and negatively related to the cover of macroalgae and sand within a seagrass patch.

### 4.4.4 Responses by life stage

Within-habitat variables had a greater influence on the presence of both adult and juvenile parrotfishes in seagrass beds (55% and 66% respectively) compared to seascape variables, however the relative importance of individual variables differed between life stages (Figure 4.5). Transect-level coral cover, and to a lesser extent water depth, were the important predictors for adult parrotfish presence, whereas quadrat-level macroalgae cover, seagrass density and epiphyte cover on seagrass blades were the most important predictors of juvenile parrotfish presence with juveniles being more likely to be present as these variables increased (Figure 4.5; Figure A4.3).

In contrast to parrotfish, the presence of adult and juvenile emperors were more influenced by seascape compared to within-habitat predictor variables (Figure 4.5). Juvenile emperors were more likely to occur with either low (<10%) or high (>45%) proportions of deep water habitat within 1000 m, and as depth of the seagrass patch increased but less likely to occur as the amount of coral reef within a 250 m radius increased (Figure A4.4). Adult emperors were more likely to be present in seagrass patches as the proportion of coral reef habitat within 1000 m increased.

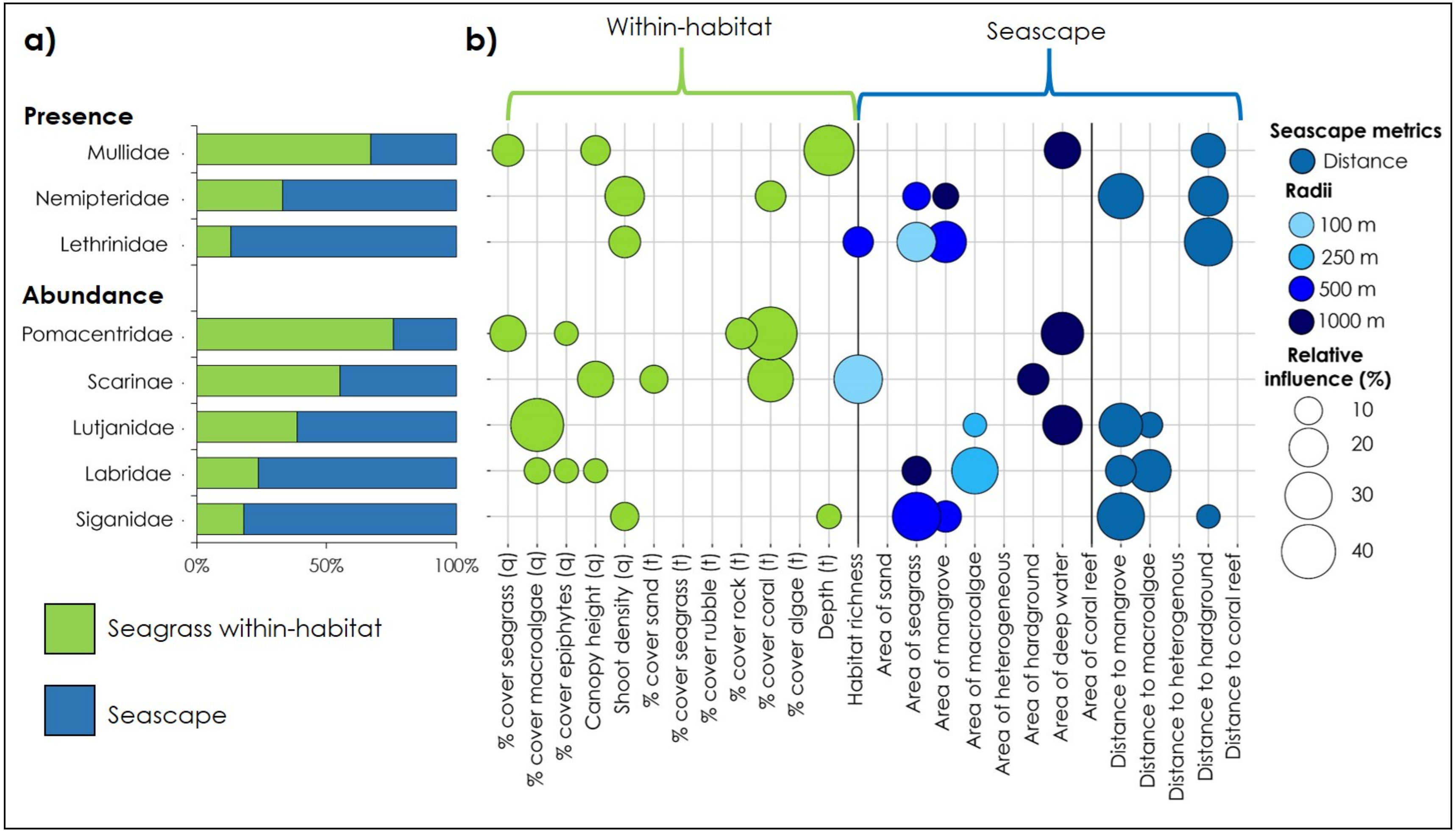


**Figure 4.3.** Relative influence of predictor variables contributing to the distribution of fish taxa in seagrass beds more than would be expected by chance: a) proportion of within-habitat and seascape variables and, b) relative influence of individual predictor variables. Circle sizes represent % relative influence. Green shows within-habitat and blue shows seascape predictor variables. Shades of blue represent different spatial scales identified as important. 'q' denotes variables quantified at quadrat level, and 't' variables quantified at transect level.

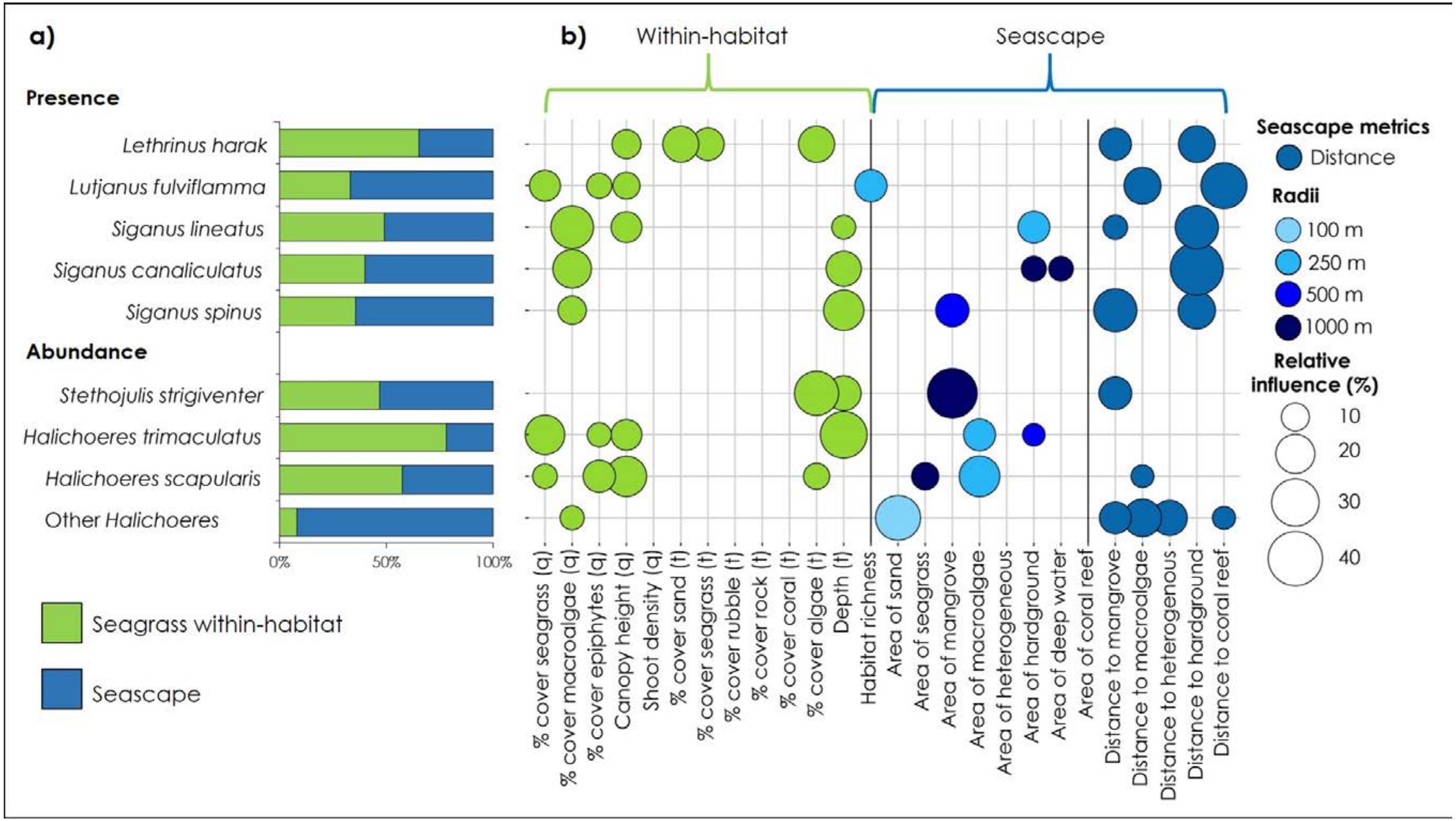


**Figure 4.4.** Relative influence of predictor variables contributing to fish species or species group abundance or presence in seagrass beds more than would be expected by chance: a) proportion of within-habitat and seascape variables and, b) relative influence of individual predictor variables. Circle sizes represent % relative influence. Green shows within-habitat and blue shows seascape predictor variables. Shades of blue represent different spatial scales identified as important. ‘q’ means measured at quadrat level, ‘t’ at transect level.

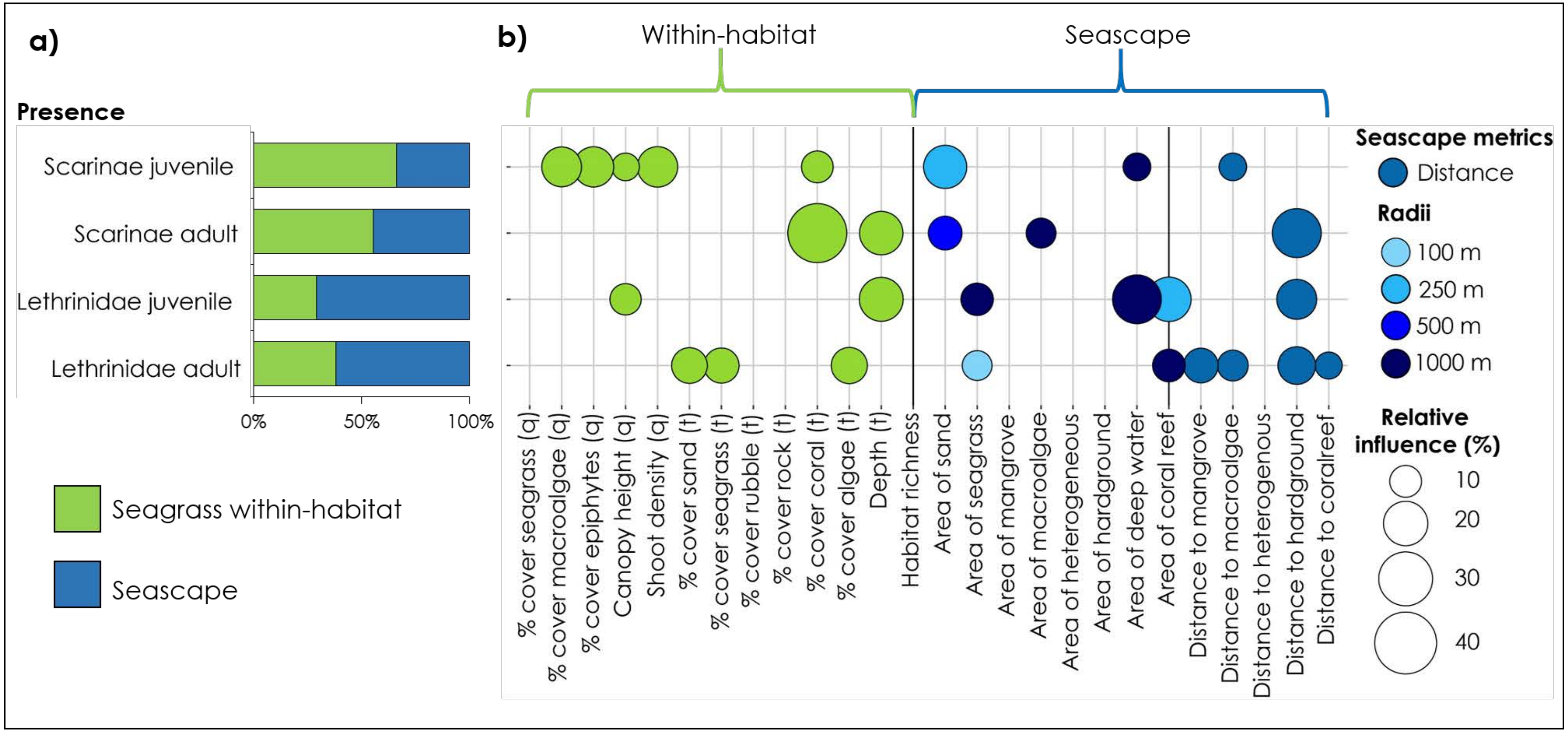


**Figure 4.5.** Relative influence of predictor variables contributing to the presence of adult and juvenile emperors (family: Lethrinidae) and parrotfishes (subfamily: Scarinae) in seagrass beds more than would be expected by chance: a) proportion of within-habitat and seascape variables and, b) relative influence of individual predictor variables. Circle sizes represent % relative influence. Green shows within-habitat and blue shows seascape predictor variables. Shades of blue represent different spatial scales identified as important. ‘q’ means measured at quadrat level, ‘t’ at transect level.

## 4.5 Discussion

Almost two-thirds of the fish groups recorded in seagrass beds were more strongly influenced by surrounding seascape configuration than within-habitat variables. As predicted, site-attached taxa (e.g., damselfishes) were more influenced by within-habitat variables such as coral cover, while taxa with larger home ranges (e.g., rabbitfishes, snappers) and those known to undertake ontogenetic shifts (e.g., emperors) were generally more influenced by the surrounding seascape, such as distance to mangrove. Interestingly, however, the differing habitat relationships of closely related taxa (e.g., species of *Halichoeres*) with similar movement capacities (Wainwright et al. 2002) suggested that underlying ecology, not simply mobility, also influences how species respond to the wider seascape.

Despite the majority of fish taxa recorded being considered to be reef-associated, proximity to or area of adjacent coral reefs appeared to have limited influence on fish distribution patterns within seagrass patches. Instead, other seascape features such as proximity and area of hardground, macroalgae and mangroves emerged as more influential. These results could be interpreted in two different ways. One perspective could be that these fish are less dependent on coral reefs than previously assumed. An alternative view could be that of hierarchical control, where the presence of these fish are determined by coral reef habitat in the surrounding seascape, but the nuanced dynamics of fish abundance and assemblage structure is subsequently driven by the within-habitat characteristics of seagrass and other aspects of the surrounding seascape.

I predicted that home range area and level of site attachment would influence how taxa responded to seascape and within-habitat variables. Variation in the abundance of damselfishes among seagrass patches was consistent with the hypothesis that site-attached, less mobile species would be shaped more by within-habitat variables. Damselfish typically settle directly to their adult habitat and remain in close association with their settlement site throughout juvenile and adult life stages (e.g., McCormick & Makey 1997). The abundance of damselfish within seagrass patches was primarily influenced by the amount of hard structure (i.e., coral and rock) within the seagrass patches. This is consistent with studies of damselfish on coral reefs that have demonstrated the importance of the structural complexity of habitats in providing refugia from predation and shaping adult populations (e.g., Beukers & Jones 1997; Nemeth 1998). Therefore features at scales greater than a few metres from their settlement site may have limited influence on their local abundances.

In contrast to damselfishes, wrasses (i.e., Labridae) were strongly influenced by the surrounding seascape and were more abundant when macroalgal beds were in close proximity or occupied a large proportion of the seascape within 250 m of the focal seagrass patch. Of the 13 taxa of wrasses recorded from seagrass beds, the most abundant were from the genera *Halichoeres* and *Stethojulis*. While many species of wrasse within these genera are considered highly mobile (Wainwright et al. 2002), home range area estimates for taxa similar to the most abundant species from the present study (i.e., *Halichoeres scapularis, H. trimaculatus,* 'other' *Halichoeres* and *Stethojulis strigiventer*) are typically small (e.g., <10 m, Jones 2005; Overholtzer-McLeod 2005; Green et al. 2015). Given this information, the strong collective response of wrasses to seascape factors was initially unexpected. However, the findings are similar to research from other tropical and temperate seascapes that also found that the spatial arrangement of the surrounding seascape can influence wrasse distribution and abundance patterns (e.g., Staveley et al. 2017; van Lier et al. 2018; Sievers et al. 2020a). Most attempts to quantify home ranges of wrasses have been conducted in coral reef habitats, where ready access to food and suitable hard structure as refugia may be important given the high predation rates associated with coral reefs (Hixon & Beets 1993; Beukers & Jones 1997). Home ranges may vary between habitat types due to differences in food and refugia availability. For instance, in macrophyte habitats, where the major habitat-forming organisms (i.e., seagrass, macroalgae) are flexible, and densities of predators are lower (Nakamura & Sano 2004a; Aller et al. 2014), individuals may not be as tightly linked to specific refuge sites and therefore may move greater distances. In this context, the characteristics of the immediate local habitat may become less critical than the attributes of the surrounding seascape.

Macroalgal and seagrass beds harbour diverse and abundant invertebrate communities that serve as a potential food source for fishes (Heck & Wetstone 1977; Nakamura & Sano 2005), but the composition of those communities can be quite distinct (e.g., Tano et al. 2016). Proximity to macroalgal beds, combined with less constrained movement, might allow wrasses to access supplementary dietary resources within adjacent macroalgal beds (Dunning et al. 1992). Alternatively, given the similar structural properties of seagrass and macroalgae (Gratwicke & Speight 2005), wrasses may not differentiate between these two habitat types and simply consider adjacent macroalgal patches to be an extension of the seagrass habitat. If this were true, I would have expected to find that area of seagrass also had a positive effect on wrasse abundance, yet the opposite was found. This could be because trophic spatial subsidies (e.g., transfer of invertebrate prey, Polis et al. 1997; Fagan et al. 1999) from macroalgal beds contribute towards wrasse abundance in adjacent seagrass patches. Density-dependent processes (e.g., inter- or intra-specific competition) operating in macroalgal beds could also contribute to the observed patterns. Macroalgae beds have recently gained recognition as important juvenile habitat for many reef fishes (Chaves et al. 2013; Eggertsen et al. 2017; Tano et al. 2017; Fulton et al. 2020; Tang et al. 2020), including wrasses (Evans et al. 2014; van Lier et al. 2018). As a consequence, high densities could lead to emigration of individuals (Grüss et al. 2011) from macroalgal beds into adjoining seagrass patches.

While wrasses were collectively most influenced by the proximity to and area of macroalgal beds, differential responses to seascape and within-habitat variables became apparent when distribution patterns for the most abundant species were examined. Here *H. scapularis* and *H. trimaculatus* were more influenced by within-habitat variables (e.g., canopy height and seagrass cover), 'other' *Halichoeres* was more influenced by seascape variables, and *Stethojulis strigiventer* was almost equally influenced by both. As one of the most diverse fish families, wrasses display a wide range of swimming, feeding and behavioural strategies (Fulton & Bellwood 2002; Wainwright et al. 2002; Bellwood et al. 2006a) which can include ontogenetic habitat (Green 1996) and diet (Nakamura et al. 2003) shifts. Such differential responses of wrasses to seascape and within-habitat variables in the present study may therefore be a reflection of the ecological versatility of particular taxa (Bellwood et al. 2006a).

Limited research has been conducted on the life history and ecology of threadfin breams (Nemipteridae) making it challenging to predict their response to seascape or within-habitat variables. One of the few studies to examine this taxon identified diel differences in foraging patterns between reef-associated adult and juvenile *Scolopsis bilineata* on Australia's Great Barrier Reef (Boaden & Kingsford 2012). Adults used daytime shelter sites on coral reefs and moved to nearby sand patches at night to feed on benthic invertebrates, whereas juveniles were associated with daytime feeding within sandy/rubble habitats. In the present study, threadfin breams (i.e., *Pentapodus trivittatus*, *Scolopsis lineatus*) were more likely to be present in seagrass beds close to mangroves, far from hardground and with low density seagrass. This information, combined with a previous study at this location that found threadfin breams were frequently observed in both seagrass and mangrove habitats during daylight hours (Sambrook et al. 2020, **Chapter 3**), suggests that these taxa may use seagrass or mangroves as shelter sites, with reef habitat being less important. In addition, by selecting for low density seagrass patches, there is also potential for daytime feeding in sandy interstices between seagrass shoots which could be important for juveniles.

I also found support for the hypothesis that taxa with larger home ranges are more influenced by seascape than within-habitat variables. Emperors, rabbitfishes, and snappers all responded strongly to seascape variables. Home ranges for some species from these families can exceed 1 km diameter (e.g., *Lethrinus harak*, Léopold et al. 2017), which could encompass up to seven different habitat types in my study system. In addition, individuals from these families have been previously recorded from multiple habitats at this study location (Sambrook et al. 2020, **Chapter 3**). Although many of these taxa could theoretically move between habitats in this study system given the distances involved, this still needs to be formally tested and would be a valuable area of future research. Foraging behaviour (e.g., diet, timing, shelter) may partially contribute towards explaining the strong responses by some of these taxa to seascape structure. Foraging behaviour can be driven by a range of factors including access to spatially separated resources (Dunning et al. 1992; Ries et al. 2004), resource partitioning (Berkström et al. 2013b), tracking of prey movements (e.g., during flood tides; Davis et al. 2017), predator avoidance (Rooker et al. 2018) or landscape structure (Redhead et al. 2016). With the exception of a few well-studied taxa (e.g., grunts, Haemulidae in the Caribbean, Beets et al. 2003; Appeldoorn et al. 2009), we know very little about cross-habitat foraging patterns, particularly in the Indo-Pacific (Sambrook et al. 2019, **Chapter 2**). Irrespective of the mechanisms involved, the strong responses to a wide range of seascape attributes indicate that these taxa could play an important role as mobile links (Lundberg & Moberg 2003) among habitats.

Given that some taxa move from juvenile to adult habitats, sometimes over considerable distances (e.g., >30 km, *Lutjanus ehrenbergii*, McMahon et al. 2012), I predicted that taxa known to undertake ontogenetic habitat shifts (e.g., emperors, Nakamura & Tsuchiya 2008; parrotfishes, Sievers et al. 2020b; rabbitfishes, Henderson et al. 2017; snappers, Nakamura et al. 2008; and wrasses, van Lier et al. 2018) would be more influenced by seascape characteristics than within-habitat variables. However, the findings suggest that the strength of these responses might differ depending on life stage. Within-habitat variables could be more important for juveniles as many are relatively site-attached and hence reliant on the quality of resources within a patch (e.g., food, refuge), whereas the presence of adults may be a function of both adult and juvenile habitats. I found contrasting results for the two taxa for which I was able to examine adult and juvenile distribution patterns (i.e., emperors and parrotfishes).

As expected, juvenile parrotfishes were more influenced by within-habitat rather than seascape variables, and contrary to expectations, adult parrotfishes responded similarly. However, juvenile parrotfishes were more influenced by small-scale seagrass variables (e.g., shoot density, percent cover epiphytes and canopy height), whereas adult parrotfishes were more likely to be present in seagrass beds that contained some hard coral cover and were close to hardground. These responses appear to reflect the feeding ecology of these distinct life stages in parrotfishes. For instance, newly settled juvenile parrotfishes from the *Scarus* genus are initially carnivorous feeding primarily on harpacticoid copepods (Bellwood 1988) which can be abundant in seagrass beds (Nakamura & Sano 2005) particularly those with high seagrass biomass (Vonk et al. 2010). Older juveniles then transition to an herbivorous feeding strategy where they target protein-rich epiphytes (Nakamura et al. 2003; Clements et al. 2017) which also supports my findings. In contrast, the presence of hard coral or hardground would be expected to be more important for adult parrotfish as most feed from carbonate surfaces (Bonaldo et al. 2014).

Adult and juvenile emperors were predominantly influenced by the surrounding seascape, but responded to different seascape metrics. Juvenile emperors were associated with deeper seagrass beds surrounded by limited coral reef habitats, whereas adults responded to a different suite of seascape metrics (e.g., distance to coral reef, hardground, mangrove) and in an opposite direction to juveniles (e.g., positive response to increased area of coral reef habitat). Emperors are known to use seagrass beds for feeding (Espadero et al. 2020), but can occur in a range of habitat types as adults. For juveniles, their presence in seagrass patches located away from coral reef habitats may reflect the higher predation risk associated with reefs compared to seagrass or mangrove habitats (e.g., Shulman 1985; Lugendo et al. 2006; Grol et al. 2014). In well-connected seascapes such as the Tigak Islands, the presence of seagrass beds away from coral reef habitat may therefore be important for juvenile survivorship and contribute to the replenishment of adults on reefs.

In addition to emperors and parrotfishes, juvenile rabbitfishes, snappers and sweetlips (Haemulidae) were also recorded in seagrass beds on several occasions (pers obs). All these taxa are important for local subsistence fisheries in Papua New Guinea (Papua New Guinea National Fisheries Authority 2007), as well as in other Indo-Pacific regions (Nordlund et al. 2018; Brodie et al. 2020). Fishing effort can be higher in seagrass compared to coral reefs, particularly during monsoon season where proximity to shore makes seagrass patches easier to access (de la Torre-Castro et al. 2014). As has occurred in Tanzania, this presents a sustainability risk whereby juvenile fish are extracted from seagrass beds and adults are taken from reefs (de la Torre-Castro et al. 2014). This process can erode fish populations and hence needs careful management. Improving our ability to predict which seagrass patches function as nurseries will lead to more evidence-based, spatially-refined management strategies (e.g., seasonal closures, restricted fishing gear) in the future.

Multi-scale studies are still relatively rare in aquatic environments, particularly in tropical seagrass ecosystems. However, as I demonstrate in this study, adopting a multi-scale approach to examine species-habitat relationships can provide a more nuanced perspective on factors that influence species distribution patterns. Given that two-thirds of the fish groups examined were influenced more by seascape than within-habitat variables, these findings highlight that seagrass patches are not functionally equivalent, can support quite distinct communities, and that the broader seascape is important in shaping tropical fish assemblages. Moreover, the taxa influenced by seascape variables included several ecologically and economically important taxa (e.g., emperors, parrotfishes and, rabbitfishes), which could have implications for ecological processes, both in seagrass patches and potentially the wider seascape, as well as for fisheries and spatial management strategies.

# Chapter 5

Influence of seascape and within-reef variables on a key ecosystem process, macroalgal browsing, on coral reefs in Papua New Guinea

## 5.1 Introduction

Tropical coral reefs are facing substantial changes to their structure and composition driven by climate change (e.g., thermal stress, ocean acidification) and other anthropogenic stressors (e.g., pollution, invasive species, overfishing, Aronson & Precht 2001; Hughes et al. 2003; Bellwood et al. 2004; Gardner et al. 2005; Hughes et al. 2018). Many of these stressors are predicted to increase in both frequency and intensity in the future (Hoegh-Guldberg et al. 2007; Frieler et al. 2013; Hoegh-Guldberg et al. 2017), placing growing pressure on an already vulnerable ecosystem. One of the major concerns is that collectively these pressures will markedly decrease the cover of live corals on reefs, disrupting the delicate balance between corals and macroalgae, and pushing reefs away from coral-dominated conditions towards alternative states, such as macroalgae-dominated reefs (Hughes et al. 2017b). As a result, taxa capable of removing macroalgae are considered a critical component of reef resilience (Hoey & Bellwood 2009; Graham et al. 2013a).

Herbivory has long been recognised as an important process on coral reefs, however the majority of herbivorous reef fish have limited capacity to remove tall canopy-forming macroalgae (e.g., *Sargassum*) that often dominates on degraded reefs. Instead it appears only a few species (i.e., macroalgal browsers) are capable of removing mature stands of macroalgae (e.g., Bellwood et al. 2006b; Hoey & Bellwood 2009). Moreover, the biomass of macroalgae removed by browsers (i.e., removal rates) and the composition of the browsing community appears to be context and site dependent. Differences in both the rates and agents (i.e., the species responsible for the consumption of macroalgal biomass) of browsing on reefs have been reported across a range of spatial scales including biogeographic region (Tebbett et al. 2020), latitude (Bennett & Bellwood 2011), inshore to offshore gradients (Hoey & Bellwood 2010a; Plass-Johnson et al. 2015; Bauman et al. 2017), among reef zones (e.g., Fox & Bellwood 2008; Hoey & Bellwood 2010b; Vergés et al. 2011; Loffler et al. 2015), and among sites (Cvitanovic & Bellwood 2009; Cvitanovic & Hoey 2010). Although these spatial differences in browsing activity have been described extensively, far less is known about what factors underpin these differences (Vergés et al. 2011; Nash et al. 2016; Roff et al. 2019). Identifying the factors that contribute towards this variability is a fundamental requirement for effective management of the browsing function on coral reefs.

The majority of studies that have investigated the potential drivers of variation in browsing fish assemblages, and/or their functional impact, have focused on within-reef variables. For instance, the composition of the coral community (Cvitanovic & Hoey 2010; Richardson et al. 2020), the cover of live hard coral or macroalgae (Cvitanovic & Hoey 2010; Chong-Seng et al. 2014; Bauman et al. 2017), and the structural complexity of reef habitats (Vergés et al. 2011) have all been linked to differences in browsing rates. Species-specific responses to such variables may be caused by preferences for particular types of reef habitat and/or the associated environmental conditions through their influence on resource availability (Nash et al. 2016), predation risk (Rizzari et al. 2014; Gil et al. 2017; Rasher et al. 2017), refuge potential (Bauman et al. 2019), as well as the provision of suitable recruitment habitat (Hoey et al. 2013).

Potential drivers of variation in browsing activity beyond within-reef variables have received limited attention. There is, however, a growing body of research showing that the seascape surrounding coral reefs (e.g., the presence of seagrass beds, mangroves) can exert a considerable influence on the composition and abundance of reef fish communities (e.g., Grober-Dunsmore et al. 2007; Olds et al. 2012a; Pittman & Olds 2015). More recently, research has shown that the seascape composition and configuration can also influence the delivery of certain ecological functions by fishes (e.g., grazing and bioeroding by parrotfishes, Eggertsen et al. 2019; 2020a; 2020b), and a similar response could occur in browsing fishes. For instance, the availability of alternative food sources for browsing fishes in close proximity to reefs (e.g., neighbouring macroalgal and seagrass beds) may affect the foraging behaviour and hence the realised rates and agents of browsing on reefs. Indeed, differences in browsing activity have been linked to seascape structure on subtropical reefs off Australia’s east coast, with browsing rates higher on isolated reefs compared to reefs in close proximity to each other (Martin et al. 2018), and further away from mangrove habitat (Yabsley et al. 2016). Given that many browsing species in tropical coral reef ecosystems are highly mobile (Meyer & Holland 2005; Welsh & Bellwood 2014), and are often observed in non-reef habitats as adults (e.g., siganids, Lugendo et al. 2005; Evans et al. 2014; **Chapters 3 & 4**), or juveniles (e.g., siganids, Hoey et al. 2013; Tang et al. 2020), it is reasonable to expect that the composition and spatial configuration of the seascape may directly influence browsing activity on coral reefs.

Here I investigate whether the seascape structure and within-reef benthic variables affect browsing activity on tropical coral reefs in the Tigak Islands, Papua New Guinea. Specifically, I examine which seascape and within-reef variables influence: 1) macroalgal removal rates, and 2) the agents of macroalgae removal among reef sites.

## 5.2 Methods

### *5.2.1 Study area*

The study was conducted on reefs surrounding six islands in the microtidal location of the Tigak Islands, Kavieng, New Ireland Province, Papua New Guinea (2° 38'S, 150° 43'E; Figure 5.1) during August 2019. At each island, four reef crest sites (1-3 m depth) were haphazardly selected from sheltered positions (i.e., away from the wave and wind exposed crest) (Figure 5.1b).

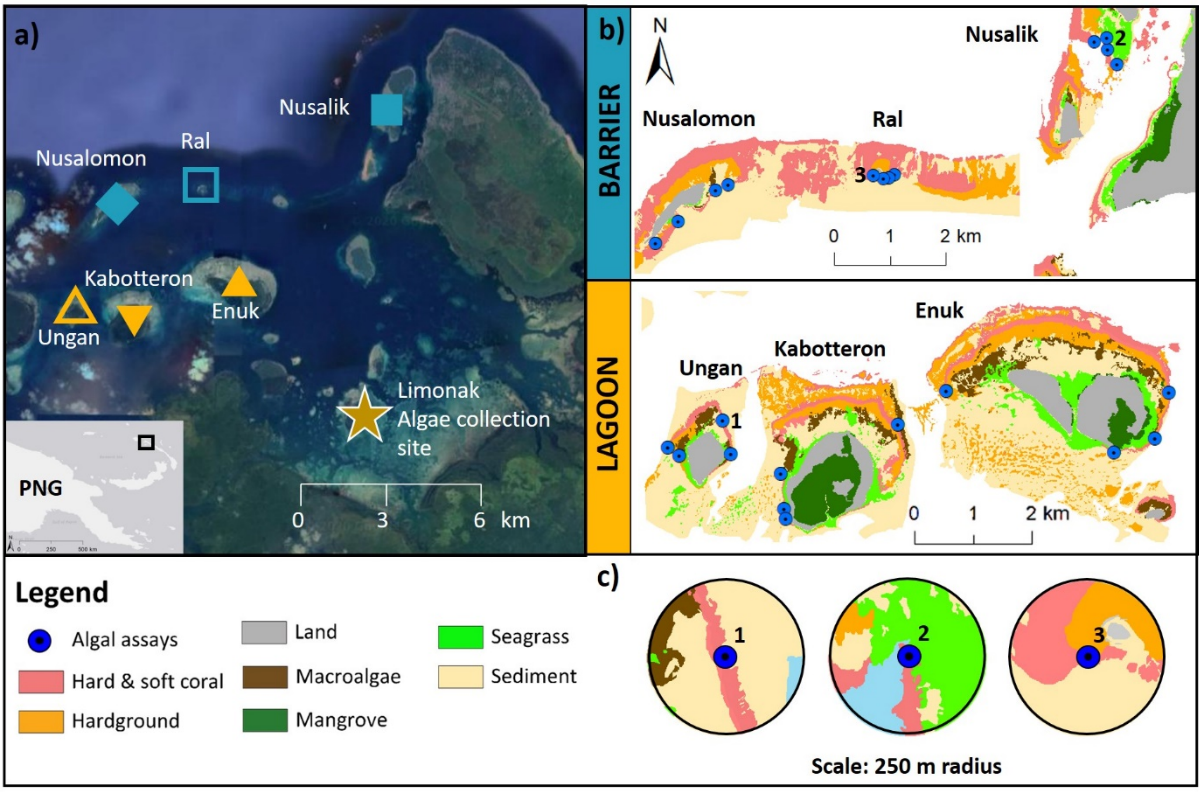


**Figure 5.1.** a) Map of the Tigak Islands, Kavieng, New Ireland Province with inset showing location in Papua New Guinea (PNG). The six study islands are shown with blue symbols for barrier reef islands and yellow symbols for lagoon islands (see results for distinction between island types). The star shows the macroalgae collection site, b) shallow water habitat types and macroalgal assay sites (blue circles) around each island and, c) examples of different seascapes (250 m radius) surrounding assay sites.

### *5.2.2 Macroalgal assays*

Assays of two locally abundant canopy-forming brown macroalgae (*Sargassum* sp. and *Cystoseira trinodis*) were used to quantify rates of macroalgae removal at each of the 24 reef sites. These taxa were selected because canopy-forming brown algae are often implicated in phase shifts from coral- to macroalgal-dominated reefs (Hughes 1994; Bellwood et al. 2006b; Hughes et al. 2007a; Hoey & Bellwood 2009). Algae were collected from the reef flat of an inner lagoon island, Limonak (Figure 5.1a), returned to the Nago Island Mariculture and Research Facility within 1 hour of collection and maintained in large (~1000L) circular aquaria with flow-through seawater and supplemental aeration for up to 3 days. Prior to deployment, thalli were spun for 30 seconds in a salad spinner to remove excess water, and the wet weight (g) and maximum height (cm) of each thallus was recorded. The mean initial weight and height were 57.2 g ± 1.7 SE and 50.2 cm ± 10.1 SE respectively for *Cystoseira* and 75.9 g ± 2.7 SE and 57.6 cm ± 13.4 SE for *Sargassum.*

Four randomly selected thalli of each macroalga (Chong-Seng et al. 2014) were deployed in pairs (i.e., one thallus of each macroalga) between 09:00 and 10:00 at each of the 24 sites. Three assay pairs were exposed to local herbivore communities, and one assay pair was placed inside an exclusion cage (~55 x 30 x 20 cm, 1 cm square mesh) to quantify any losses due to handling, translocation and hydrodynamic conditions at the site (following Hoey & Bellwood 2010b). Each thallus was attached to the substratum (i.e., dead coral or rock) using galvanised wire and an elastic band, with a small numbered plastic tag used to identify individual thalli (following Hoey & Bellwood 2010b). After four hours (i.e., 13:00-14:00) assays were collected, spun in a salad spinner for 30 seconds, and thallus weight and height recorded. To account for reductions in algal weight due to handling rather than herbivory, the weight of macroalgae consumed from the exposed assays was standardised using Equation 1:

$$[T_o \times (C_f/C_o) - T_f] \qquad \textbf{Equation 1.}$$

where $T_o$ and $T_f$ are the initial and final weights for the exposed thalli, and $C_o$ and $C_f$ are the initial and final weights for the cage control (Cronin & Hay 1996).

### *5.2.3 Agents of macroalgal removal*

To identify the agents of macroalgae consumption and quantify their contribution to macroalgal removal, a small video camera (GoPro 4) mounted on a dive weight was positioned approximately 1 m from one of the assay pairs at each of the 24 sites. At the start of each recording, a small scale bar was held adjacent to each assay and used to calibrate the size of fishes in the video footage. For each video, the first two hours of video footage were viewed, and the identity, total length (to nearest cm) and number of bites on each macroalga by individual fish were recorded. Given that the bite impact of an individual is influenced by body size, bites were subsequently converted to mass standardised bites (total number of bites per species x biomass) $hr^{-1}$ (following Bellwood et al. 2006b) using published length-weight relationships (Kulbicki et al. 1993; Kulbicki et al. 2005; Froese & Pauly 2021).

To quantify the herbivorous fish assemblages at each site the first two hours of video footage from each assay was viewed and the presence and maximum number of individuals observed on a single frame (Max*N*) for species belonging to the families Acanthuridae, Kyphosidae, Siganidae and subfamily Scarinae (family Labridae) were recorded. Max*N* was used as a conservative measure of relative abundance of species observed during the video recording period (Cappo et al. 2004).

### *5.2.4 Characterising the within-reef benthic community composition and seascape structure*

To examine the influence of within-reef benthic variables on rates and agents of macroalgal removal, the benthic community was surveyed along four 25-m point-intercept transects at each site (depth 1-3 m). Each transect was placed along the reef crest separated by a minimum of 5 m between adjacent transects. The substratum directly beneath the transects at 25 random points was recorded. The substratum was recorded as hard (scleractinian) coral, macroalgae, soft coral, epilithic algal matrix (EAM), crustose coralline algae (CCA), sand, rubble, and ‘other’ which included bare rock, recently dead coral, seagrass and other sessile invertebrates. Hard corals were identified to genus and morphotype where possible, and macroalgae were identified to genus.

Features of the seascape surrounding each of the 24 sites were quantified from a benthic habitat map of each island (see **Chapter 4** for detail of map production). The proportion of five broad habitat types identified as influencing different aspects of the reef fish community in **Chapter 4**, specifically hard and soft coral reef structure, hardground (e.g., pavement), macroalgae beds, sand, and seagrass beds in the surrounding seascape was quantified. Mangroves were excluded from analysis due to their limited distribution among study sites (i.e., present around only six sites compared to a minimum of 13 sites for other habitat types), and because browsing species were not recorded from mangrove habitat in this study region (**Chapter 3**), and are rarely observed in mangrove habitats elsewhere (**Chapter 2**). ArcGIS (v10.6.1) was used to quantify the proportion by area of each habitat type within a 250 m radius of each site. The 250 m radius size was chosen based on available home range data for browsing species (e.g., browsing siganids, Ebrahim et al. 2020; *Naso unicornis*, Meyer & Holland 2005), and given the close proximity of some sites around islands that would have resulted in spatial overlap of seascape characteristics leading to high spatial autocorrelation. In addition, distance from each site to open ocean was measured using the Near function in ArcGIS. If the route crossed land, the shortest distance was measured manually avoiding land.

### *5.2.5 Data analysis*

Distance-based linear models (DISTLM, McArdle & Anderson 2001; Anderson et al. 2008) and distance-based redundancy analyses (dbRDA) were used to identify and visualise which of the 16 benthic and 6 seascape variables (Table A5.1) best predicted spatial patterns of macroalgal removal and browsing activity. No predictor variables were identified as collinear (Pearson's $r > 0.7$) based on pairwise Pearson's correlations obtained from draftsman plots. Predictor variables were $\log(x+1)$ transformed and normalised to account for different scales of measurement. All possible combinations of predictor variables were fitted using the *Best* procedure (Anderson et al. 2008). Models were selected using the Akaike's Information Criterion adjusted for small sample sizes (AICc). In addition, given the potential risk of overfitting associated with AICc values, model outcomes were checked for consensus against the more conservative Bayesian Information Criterion (BIC) (Anderson et al. 2008).

Following analysis of model outputs, the six islands were subsequently separated into two groups, based on their position and proximity to open ocean. Three islands, hereafter termed "barrier reef islands" were directly adjacent to and near to open ocean (<2.2 km) and three islands, termed "lagoon islands", were further from open ocean (>5 km) and situated behind the barrier reef islands (Figure 5.1b).

The amount of macroalgae removed from assays was compared using a univariate three-factor nested permutational analysis of variance (PERMANOVA) with reef position (i.e., barrier or lagoon) as a fixed factor, island as a nested random factor within reef position, and site as a nested random factor within island. Analyses were based on zero-adjusted Bray-Curtis similarity resemblance matrices that were constructed from untransformed data. The PERMANOVA (Type III sums of squares) analysis was performed using 9999 permutations of residuals under a reduced model (Anderson et al. 2008). The PERMDISP routine was used to verify that any differences were primarily due to location rather than dispersion effects. Similar patterns of removal were observed for both *Cystoseira* and *Sargassum* (Figure A5.1) and data were subsequently pooled for analysis and visualisation.

Species that accounted for >1% of mass standardised bites on assays were identified, and their macroalgal consumption patterns (i.e., mass standardised bites) were subsequently analysed to explore the influence of within-reef and seascape variables on browsing community activity. Differences in the browsing community (Max*N*) and function (i.e., mass standardised bites) were compared using a two-factor nested permutational analysis of variance (PERMANOVA) with reef position as a fixed factor and island as a nested random factor within reef position, following the same procedure described above. Analyses were based on zero-adjusted Bray-Curtis similarity resemblance matrices that were constructed using square-root transformed data. Where the number of possible permutations was <100, results were interpreted cautiously using the more conservative Monte Carlo p-value. Results were visualised using principal coordinates analysis (PCO) plots. A SIMPER (similarity percentage) analysis was used to identify the browsing taxa driving any differences in the browsing community between lagoon and barrier reef islands. The relationship between the relative abundance of each browsing species and mass standardised bites was examined using Pearson's correlation coefficient (r).

Univariate analyses were conducted in R v4.0.0 (R Core Team 2020) and all multivariate data analyses were performed using the software PRIMER v7 with PERMANOVA+ (Anderson et al. 2008).

### *5.2.6 Spatial autocorrelation*

Each response and seascape predictor variable was checked for spatial autocorrelation using a standardised inverse distance weighted Global Moran's I conceptualisation of spatial relationships based on the average distance to each site's four nearest neighbours (average distance = 3,459 m; Table A5.2). Where spatial autocorrelation values were significant (pseudo-significance $P \leq 0.01$ calculated from 999 permutations) and Moran's I values >0.4 (Hamylton & Barnes 2018), relationships were visually examined using cluster and outlier analysis (Anselin Local Moran's I) in ArcGIS. Only one seascape predictor variable was significantly spatially autocorrelated suggesting that our sampling sites were far enough apart to each represent independent samples. The area of sand within 250 m radius was significantly, but not strongly, spatial autocorrelated (Moran's I = 0.48, P = 0.001). Cluster and outlier analysis showed one high-low outlier at Enuk (lagoon) indicating the seascape surrounding one site had a high proportion of sand within 250 m compared to other neighbouring sites, one low-high outlier (i.e., low value for one site compared to neighbouring sites) and two high-high clusters at Nusalomon (barrier) and two low-low clusters at Nusalik (barrier). Three response variables exhibited positive spatial autocorrelation, specifically, total mass standardised bites (Moran's I = 0.626, P <0.001), *Naso lituratus* mass standardised bites (Moran's I = 0.598, P <0.001) and mean % macroalgae consumed (Moran's I = 0.686, P <0.001). These were driven by differential consumption rates by species among islands (see Results).

## 5.3 Results

The proportion of macroalgae removed was lower and more variable on lagoon reefs, than on barrier reefs (Figure 5.2). For instance, algal consumption at sites around Enuk ranged from 28.1% ± 4.9 (mean ± SE) to 70.0% ± 5.7, and from 16.4% ± 5.7 to 66.6% ± 9.9 at Ungan. Macroalgae removal was two-fold higher on barrier (71.2% ± 2.0) compared to lagoon reefs (35.0% ± 3.3) (Figure 5.2). However, one barrier reef island, Nusalik, had considerably less macroalgae consumed on average (57.1% ± 3.9) compared to the other two other barrier reef islands (i.e., Nusalomon 81.4% ± 1.6, Ral 75.8% ± 2.1). The mean handling loss was 12.2% ± 1.0 (6.3 g ± 0.7) for *Cystoseira* and 7.1% ± 0.8 (4.9 g ± 0.7) for *Sargassum*.

The best fit distance-based linear model for macroalgal removal rates included eight predictor variables. Distance to open ocean was the only seascape variable included in the top model, with the remaining seven related to within-reef benthic community composition (Figure 5.3). Together these eight predictor variables explained 90% of the variation in macroalgal removal rates among sites (Table 5.1). Lower macroalgal removal rates were strongly correlated with increasing distance from open ocean and this variable alone explained 51% of the variance. The cover of rubble, sand and massive *Porites* at each site was negatively related to removal rates, while the cover of crustose coralline algae (CCA) and *Acropora* (digitate, staghorn, and tabulate growth forms) was positively related.

From the video footage, 23 fish species were observed taking a total of 61,014 bites from the macroalgal assays (4,086.25 total mass standardised bites). Six species were responsible for >99% of the mass standardised (ms) bites: the orange-spine unicornfish *Naso lituratus* (59.2%), the rabbitfishes *Siganus canaliculatus* (13.5%) and *Siganus doliatus* (10.3%), the blue-spine unicornfish *Naso unicornis* (7.0%), and two species of chub, *Kyphosus cinerascens* (5.3%) and *Kyphosus vaigiensis* (3.9%). A total of 61.6% of the variance was explained by the best fit

DISTLM for mass standardised bites of the browsing community (Table 5.1). The best fit model included five predictor variables: distance from open ocean, area (%) of seagrass within a 250 m radius, and the cover of encrusting corals, sand, and other *Acropora* at each site (Figure 5.4). Distance to open ocean explained the majority (25.9%) of the variance. Lower browsing activity was typically recorded further away from open ocean and at sites with higher cover of sand, with *S. canaliculatus*, *K. cinerascens* and *K. vaigiensis* absent from sites with this combination of attributes (Figure 5.4). Area of seagrass within 250 m of each site also influenced the browsing community bite rates. At sites with higher amounts of seagrass within 250 m, *S. canaliculatus* and the two kyphosid species were responsible for more bites than *N. lituratus* or *N. unicornis* which were either absent or took few bites on assays (Figure 5.4).

The browsing community structure and feeding of browsing fish assemblages differed between lagoon and barrier reef islands (Figure 5.5, Table 5.2, Figure A5.2). The structure of the browsing communities around lagoon islands was variable with low similarity among sites (SIMPER average similarity = 26.9), compared to barrier reef sites (average similarity = 54.9). Only a single species contributed towards the similarity between lagoon islands, the rabbitfish *S. doliatus*, whereas browsing fish communities around barrier reef islands were characterised by three species, primarily *N. lituratus*, followed by *S. doliatus* and *S. canaliculatus*.

The browsing species most frequently recorded from video footage were: *S. doliatus* (83% of videos), *N. lituratus* (67%), and *S. canaliculatus* (58%). Five of the six key browsing species were more frequently observed at barrier compared to lagoonal reef sites. The dominant browsing species, *N. lituratus*, was six times more abundant (Max*N* = 12.3 individuals ± 3.0 SE) and took 73 times more ms bites (198.8 ms bites ± 60.3 SE) at barrier reef sites compared to lagoon sites (Max*N* = 2.0 ± 1.1 SE, ms bites = 2.6 ± 1.2 SE). Similarly, the relative abundance of the rabbitfish *Siganus canaliculatus* was four-fold higher, and the bite rate was 30 times more, on macroalgal assays at barrier reef sites compared to lagoon islands. *K. vaigiensis* was the only species that had similar abundances and browsing rates among barrier reef and lagoon islands.

Importantly, the presence of a browsing species at a site did not always equate to browsing activity (Figure 5.6). On several occasions, individuals or groups of browsers were observed on the video footage but not recorded feeding on assays, the only exception being *N. unicornis* which was always recorded browsing on assays whenever it was observed (Figure 5.6). While browsing activity was related to relative abundance for three of the six browsing species (*K.*

*cinerascens*, *N. unicornis* and *S. doliatus*), the remaining three browsing species (*K. vaigiensis*, *N. lituratus* and *S. canaliculatus*) showed no significant relationship between relative abundance and browsing activity (Figure 5.6) indicating that presence was not necessarily a strong predictor of function for all browsing taxa. In addition, the positive correlation between relative abundance and bites for *K. cinerascens* was driven by a single outlier.

Despite the overall dominance of *N. lituratus* in terms of ms bites, its dominance was largely attributable to extensive feeding at two barrier reef islands, Nusalomon and Ral. Elsewhere, *K. cinerascens* took, on average, the highest number of ms bites at Nusalik (barrier reef), *N. unicornis* was responsible for the most ms bites at Ungan (lagoon reef), and *S. doliatus* took the most bites at Enuk and Kabotteron (lagoon reefs).

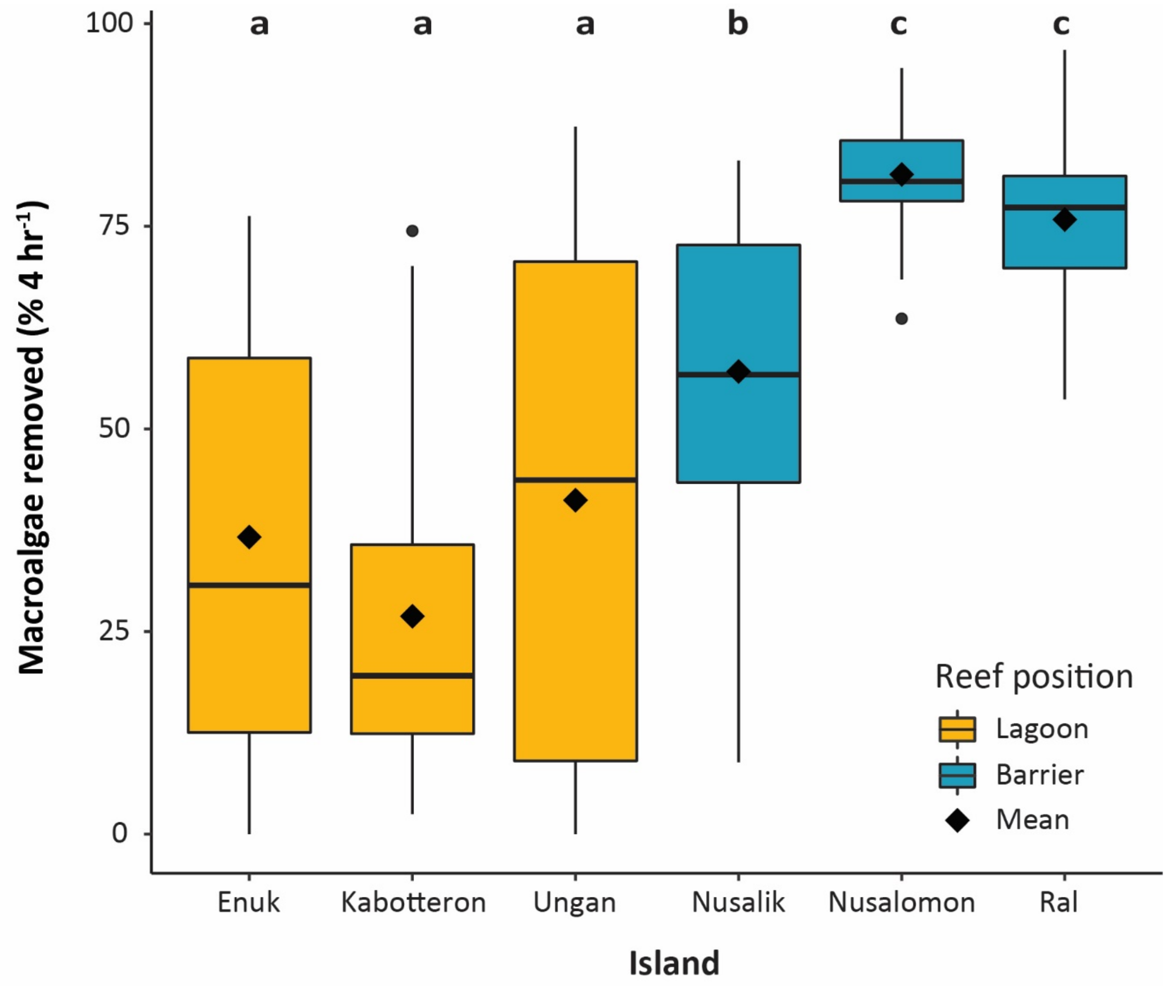


**Figure 5.2.** Differences in macroalgal removal (%) between lagoon and barrier reefs. Median and 25% quantiles are shown on the boxplot with black dots as outliers. Diamond symbol represents the mean macroalgal removed (%) from assays for each island. Letters above

boxplots denote similar groups in terms of mean macroalgal removal identified by PERMANOVA pairwise tests ($p < 0.01$, Table A5.3).

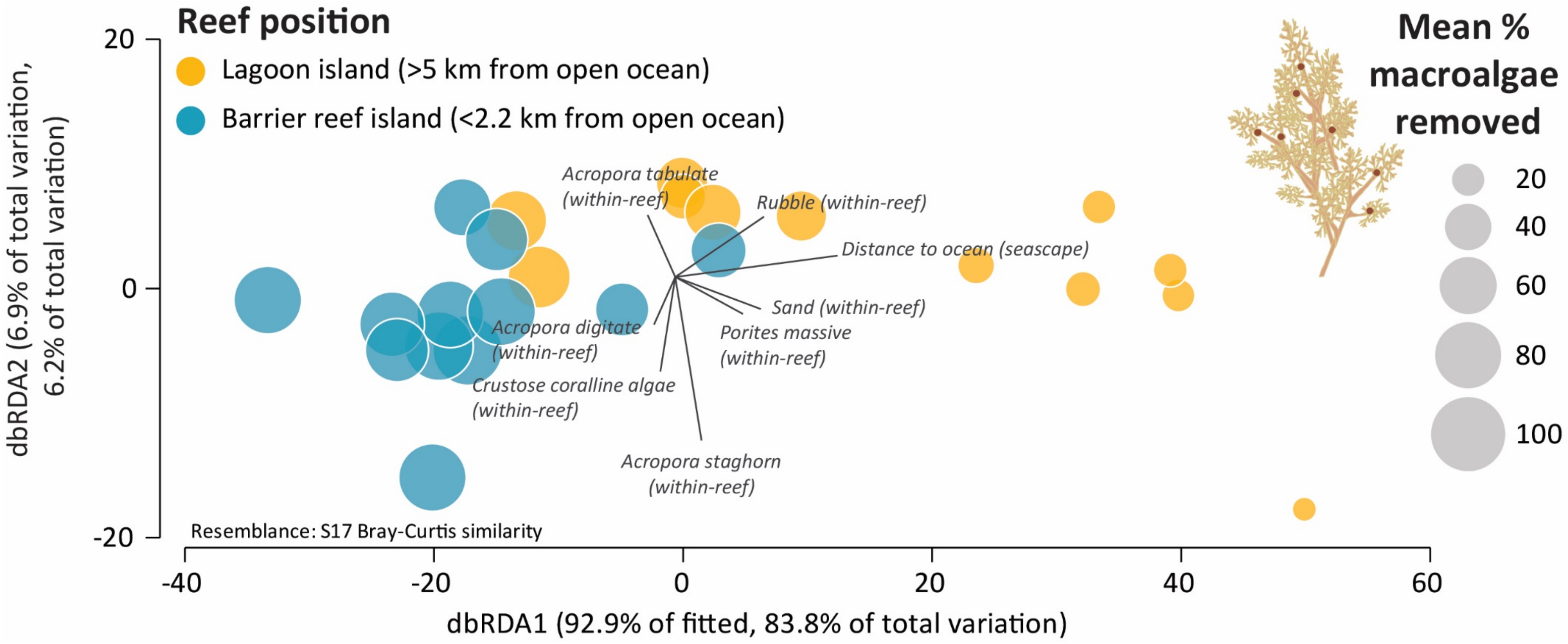


**Figure 5.3.** Distance-based redundancy analysis (dbRDA) ordination showing the predictor variables identified in the top model (DISTLM) as influencing macroalgal removal rates. Yellow = lagoon sites, blue = barrier reef sites. Image credit: Tracey Saxby, Integration and Application Network.

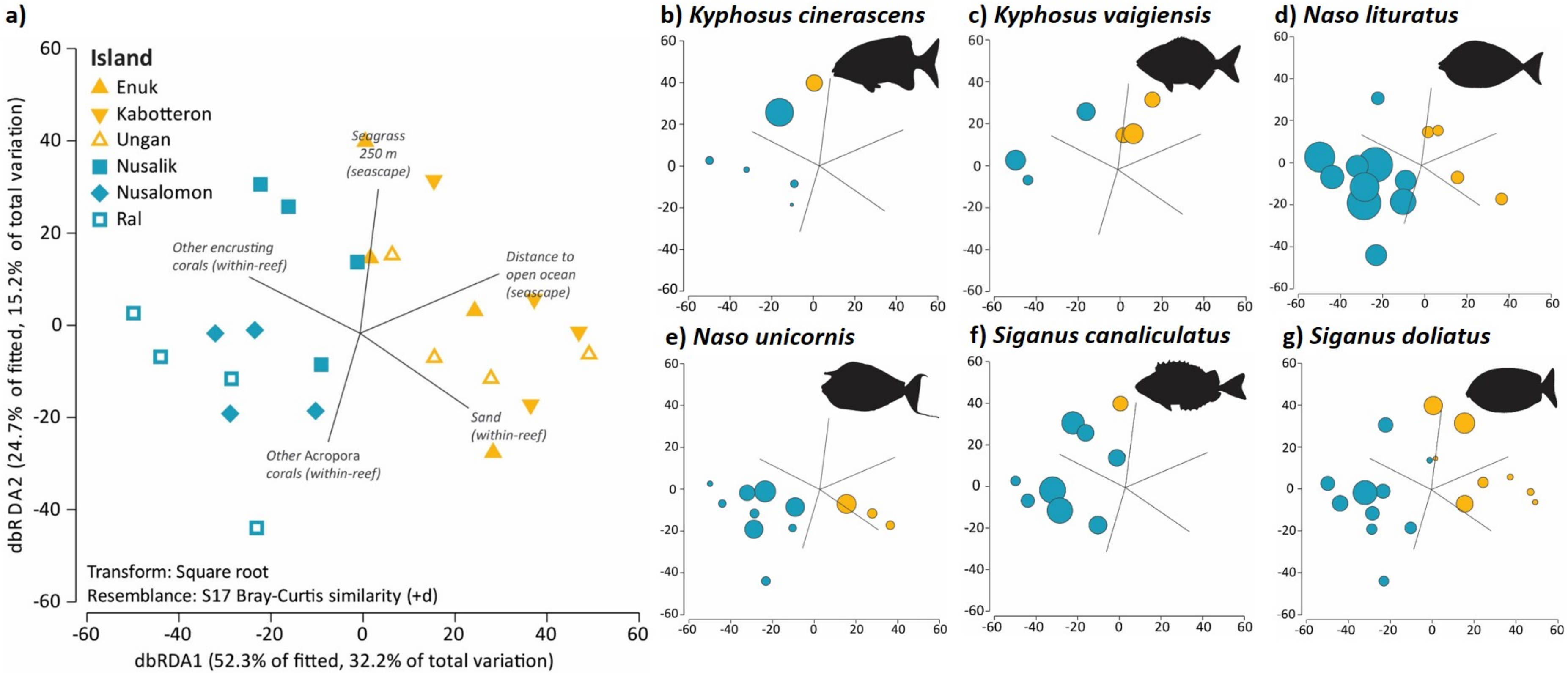


**Figure 5.4.** Distance-based redundancy analysis (dbRDA) ordination showing the predictor variables identified in the best fit model (DISTLM) as influencing browsing community mass standardised bites at each site. Smaller panels (b-g) show presence of six main browsing taxa in relation to vectors described in panel (a). Bubble size represents the square-root transformed ms bites for each individual taxa at sites where they were observed feeding. Yellow = lagoon sites, blue = barrier reef sites.

**Table 5.1.** Top model of benthic and seascape variables influencing macroalgal removal rates and mass standardised bites of browsing community. Results given for AICc and BIC models from distance-based linear modelling (DISTLM).

| Model | $R^2$ | AICc | BIC |
|---|---|---|---|
| **Macroalgal removal rates** | | | |
| ***Seascape variables:*** Distance to open ocean | 0.90 | 130.7 | 128.44 |
| ***Within-reef benthic variables***: sand, rubble, crustose coralline algae, *Porites* massive, *Acropora* staghorn, *Acropora* tabulate, *Acropora* digitate | | | |
| **Mass standardised bites of browsing community** | | | |
| ***Seascape variables***: Distance to open ocean, area of seagrass 250 m | 0.62 | 181.52 | 186.47 |
| ***Within-reef benthic variables:*** other encrusting corals, other *Acropora*, sand | | | |

**Table 5.2.** PERMANOVA results for comparing differences between reef position (fixed), islands (random nested within reef position) and sites (random nested within islands) for macroalgal removal rates, and differences between reef position (fixed) and islands (random nested within reef position) for mass standardised bites of the browsing community. *ECV denotes percent estimated components of variation.

| | df | SS | MS | Pseudo-*F* | P(perm) | ECV* |
|---|---|---|---|---|---|---|
| **Macroalgal removal rates** | | | | | | |
| Reef position | 1 | 38942 | 38942 | 16.179 | **0.0423** | 36.5% |
| Island(Reef position) | 4 | 9636.3 | 2409.1 | 1.419 | 0.2202 | 2.1% |
| Site(Island(Reef position) | 18 | 30664 | 1703.6 | 2.351 | **0.0003** | 11.6% |
| Residual | 115 | 83338 | 724.68 | | | |
| Total | 138 | 163950 | | | | |
| **Mass standardised bites of browsing community** | | | | | | |
| Reef position | 1 | 15376 | 15376 | 9.4826 | **0.0011** | 36.8% |
| Island(Reef position) | 4 | 6486.2 | 1621.5 | 0.7344 | 0.7344 | 3.7% |
| Residual | 18 | 37599 | 2088.8 | | | |
| Total | 23 | 59461 | | | | |
| **Relative abundance (Max*N*) of browsers** | | | | | | |
| Reef position | 1 | 5452.9 | 5452.9 | 3.7883 | **0.0336** | 19.1% |
| Island(Reef position) | 4 | 5757.7 | 1439.4 | 1.0197 | 0.4531 | 0.4% |
| Residual | 18 | 25409 | 1411.6 | | | |
| Total | 23 | 36619 | | | | |

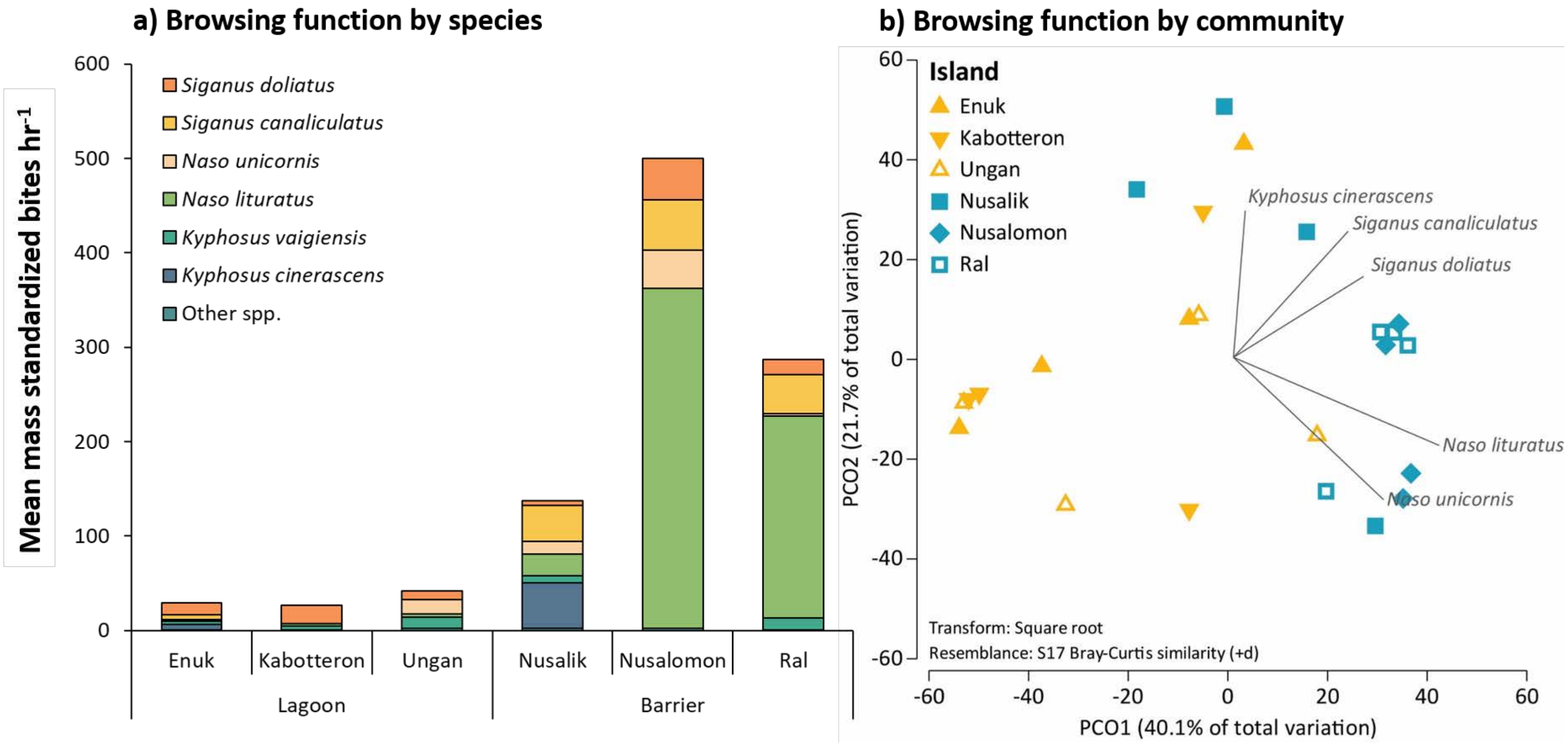


**Figure 5.5.** Browsing rates by: a) the six species each accounting for >1% of mass standardised bites and all other species (n = 17 spp.), and b) PCO plot to visualise the browsing function at the browsing community level. Vectors show species contributing to community patterns. Yellow = lagoon sites, blue = barrier reef sites.

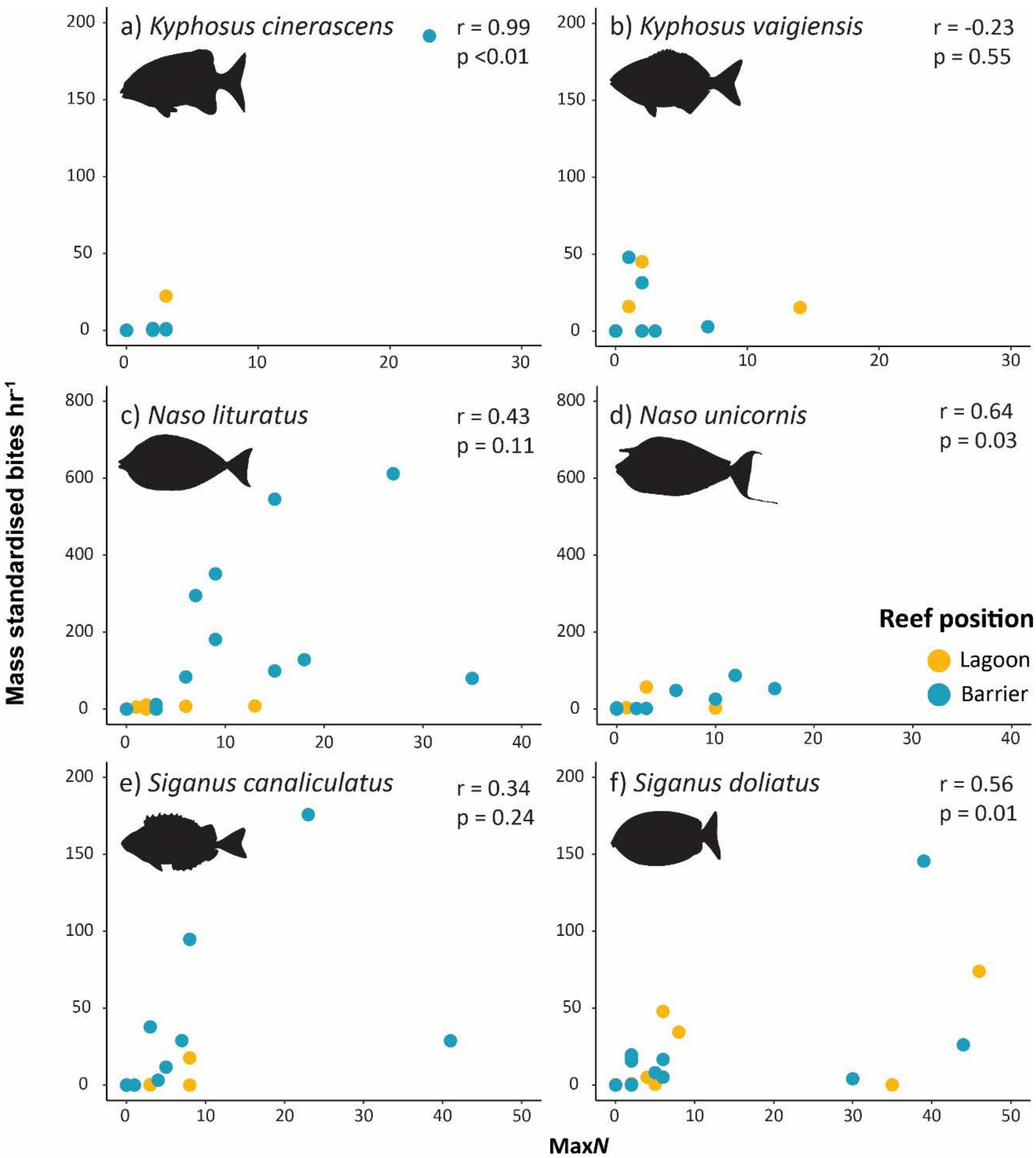


**Figure 5.6.** Relationship between relative abundance (Max*N*) of the six most common browsing species and their realised impact (i.e., mass standardised bites $hr^{-1}$). a) *Kyphosus cinerascens*, b) *K. vaigiensis*, c) *Naso lituratus*, d) *N. unicornis*, e) *Siganus canaliculatus*, and f) *S. doliatus*. Yellow = lagoon sites, blue = barrier reef sites. R value = Pearson's correlation coefficient.

## 5.4 Discussion

Both rates and agents of macroalgal removal on shallow water reefs were most strongly influenced by distance to oceanic environment, but exhibited differential responses to other seascape and benthic variables. Macroalgal removal rates were higher on reefs closer to open ocean compared to those further inside the lagoon, and greater at sites containing higher cover of *Acropora* spp. and crustose coralline algae than sites with higher cover of sand, rubble and/or massive *Porites.* Similarly, the agents of macroalgal removal (i.e., fish species recorded feeding on the macroalgal assays) were influenced by distance to open ocean, the area of seagrass within 250 m, and encrusting corals, *Acropora* spp., and sand. Assay consumption on two of the reefs closest to open ocean was dominated by a single browser, the orange-spine unicornfish *Naso lituratus,* however, there was considerable variation in the species responsible for browsing across the study system, particularly around the three lagoon reefs.

### *5.4.1 Environmental drivers of rates and agents of browsing*

Distance to open ocean was the most important variable explaining differences in both macroalgal removal rates and browsing activity among sites, with the highest removal rates at reefs proximal to the open ocean. Environmental and physical gradients are frequently evident between inshore and offshore reef systems including changes in pollutant loads, turbidity, sedimentation, wave energy, depth, and productivity (Bellwood & Wainwright 2001; Larcombe et al. 2001; De'ath & Fabricius 2010; Fisher et al. 2015; Bainbridge et al. 2018). These gradients can have concomitant effects on both benthic (Wismer et al. 2009; De'ath & Fabricius 2010; Baum et al. 2015; Draisma et al. 2018) and fish communities (Williams 1982; Williams & Hatcher 1983; Mallela et al. 2007) on coral reefs, and therefore it seems reasonable to expect that these differences would also translate to differential delivery of a key ecological function, such as browsing. Yet few studies have explicitly examined how browsing patterns on reefs can change across an inshore-offshore gradient (for exceptions see Hoey & Bellwood 2010a - Great Barrier Reef (GBR); Plass-Johnson et al. 2015 - Indonesia). Comparing findings among studies does however begin to reveal some consistent patterns across regions. Similar to this study, others have shown that outer reefs appear to support a higher biomass or relative abundance of browsers and browsing communities are often dominated by species from the acanthurid genus *Naso* (Hoey & Bellwood 2010a; Plass-Johnson et al. 2015). In contrast, the browsing community composition on inshore reefs appears to be more variable, as observed in this study and others (e.g., Cvitanovic & Bellwood 2009). Potential mechanisms for these inshore-offshore differences in browsing fish assemblages are difficult to ascertain, but may be related to differences in dietary resource availability, predation, and the availability of preferred habitats.

Rates of macroalgal removal may be driven by the availability of macroalgal resources on reefs (e.g., Cvitanovic & Hoey 2010; Hoey & Bellwood 2010a; Nash et al. 2016), and/or the availability of alternative resources elsewhere in the seascape (e.g., Hoey & Bellwood 2010a; Bennett & Bellwood 2011; Bellwood et al. 2018). In the present study, there was no relationship between macroalgal removal rates and within-reef macroalgae cover, potentially because macroalgae cover was generally low (<10%) on reefs across all sites. Similarly, no relationship emerged between removal rates and the presence of macroalgal beds in the surrounding (250 m buffer) seascape. This was despite lagoon reefs, where removal rates were consistently lower than barrier reefs, often being situated in the vicinity of macroalgal beds. One explanation for this lack of relationship may be that several, but not all, of the macroalgal beds around the lagoon islands are dominated by green algae (e.g., *Halimeda*, *Caulerpa*) which may be a less attractive or palatable resource than brown macroalgae (e.g., *Sargassum*) for many browsing taxa (e.g., *Kyphosus vaigiensis*, Loffler et al. 2015; *Naso unicornis*, Rasher et al. 2013). Future steps to gain greater insight into the influence of resource availability on browsing patterns should include examining whether different types of macroalgal beds in the surrounding seascape can affect outcomes, and conducting experimental assays across a breadth of vegetated habitats (e.g., seagrass, green and brown macroalgal beds) as well as on reefs.

The rapid rate of assay consumption at the barrier reef sites compared to reefs around the lagoon islands could indicate resource limitation. The two barrier reefs with the highest macroalgal removal rates (i.e., Nusalomon and Ral), had little vegetated habitat, and instead were surrounded by a low complexity matrix dominated by sand and hardground which browsers may be reluctant to move across (Turgeon et al. 2010; Gil et al. 2017) to find alternative resources. As a consequence, browsers located at these two reefs may be less dispersed and have fewer foraging options leading to higher intensity of browsing where macroalgae assays are offered.

While the availability of sufficient resources is essential for survival, foraging decisions also need to be carefully balanced against the risk of predation. Habitat structure quantified at seascape and within-reef scales could influence predation risk by altering predator-prey dynamics (Catano et al. 2016; Gaynor et al. 2019). How browsers respond to the threat of predation will be contingent on species identity, body size, foraging behaviour and propensity to form groups (Rizzari et al. 2014; Catano et al. 2016). In the current study, browsers, particularly *Naso lituratus* and *N. unicornis*, tended to occur in larger groups around the barrier reefs compared to lagoonal reefs, which is a common behavioural strategy in predator-rich environments (Magurran 1990; Michael et al. 2013; Gil et al. 2017). High predation risk can in turn affect foraging behaviour (Rizzari et al. 2014; Nash et al. 2016) by leading to faster feeding rates (Catano et al. 2016) when suitable resources are located which may be the case around two of the barrier reef islands (i.e., Nusalomon and Ral). However, elevated predation risk can also suppress feeding in less structurally complex habitats by limiting refuge potential (Fox & Bellwood 2007; Hoey & Bellwood 2011; Graham & Nash 2013; Gil et al. 2017), and/or requiring increased vigilance (Brown 1999), and this may be contributing towards the lower browsing activity around the lagoonal reef sites with higher amounts of sand.

### *5.4.2 Differential responses of browsing agents across the seascape*

Species-specific habitat preferences may disproportionately influence the maintenance or delivery of browsing on coral reefs (Ruttenberg et al. 2019). Although 23 species were recorded taking bites on macroalgae, only six species accounted for the majority of browsing activity (99% of bites). Importantly, the spatial distribution of those six browsing species differed considerably across the seascape and their differential distribution patterns translated into variation in the structure of the browsing community and browsing rates.

The orange-spine unicornfish *Naso lituratus* was responsible for the highest browsing rates on reefs but its distribution, and therefore realised impact, was largely confined to two reefs that were close to open ocean (i.e., Nusalomon and Ral). Such apparent habitat specificity by *N. lituratus* for outer, as opposed to inshore, reefs has been reported elsewhere (e.g., GBR, Cheal et al. 2012; McClure et al. 2019; Indonesia, Plass-Johnson et al. 2015) although in the present study this habitat preference was evident across a relatively compressed inshore-offshore system (e.g., <10 km between reefs near and far from open ocean as compared to >50 km in the GBR and Indonesia studies). In addition, *N. lituratus* occurred predominantly at sites that supported benthic communities typically found in higher energy reef environments (e.g., dominated by CCA, *Acropora* spp., encrusting corals, Dollar 1982; Fabricius & De’ath 2001; Wismer et al. 2009; Gove et al. 2015). These findings lend strong support for the notion that

*N. lituratus* has a tightly coupled relationship with the physical or environmental properties associated with outer reef habitats (Cheal et al. 2012).

The blue-spined unicornfish *N. unicornis* also followed a similar distribution pattern to *N. lituratus* but was less abundant and took fewer bites. However, these findings were unexpected given that *N. unicornis* is found in a wide range of reef environments on other Indo-Pacific reefs and is often the dominant browser (e.g., Hoey & Bellwood 2009; Vergés et al. 2012; Rasher et al. 2013; Plass-Johnson et al. 2015; Tebbett et al. 2020). Lower abundances may be an artefact of overexploitation as, although both *Naso* species are heavily targeted by fisheries across the Indo-Pacific, *N. unicornis* appears less resilient to fishing pressure (Bejarano et al. 2013; Ford et al. 2016; but see Taylor et al. 2019).

The white-spotted rabbitfish *Siganus canaliculatus* is generally considered an inshore species (Fox & Bellwood 2008; Cvitanovic & Bellwood 2009; Hoey et al. 2013) and is rarely recorded from outer reefs on the GBR (Cheal et al. 2012; Hoey et al. 2013; McClure et al. 2019). However, that pattern was reversed around the Tigak Islands where *S. canaliculatus* was more abundant and took more bites at sites that were closer to open ocean (<2 km) and/or surrounded by extensive seagrass beds (>17% of 250 m radii). The difference in distribution patterns may be a result of the compressed inshore-offshore gradient enabling *S. canaliculatus* individuals to occupy habitats otherwise unavailable to them. For instance, the configuration of habitat patches in Kavieng may facilitate movement from juvenile seagrass nursery habitats (Grandcourt et al. 2007; Lin et al. 2019) to preferred open ocean spawning grounds (Hasse et al. 1977) which may not be feasible across the cross-shelf distances of the GBR. The findings that this species appeared to use two reef habitats with differing seascape structures in this location (e.g., close to open ocean and/or surrounded by extensive seagrass beds) could be indicative of such an ontogenetic habitat shift but detailed size-based studies would be needed to test this hypothesis. The fewer bites and observations of *S. canaliculatus* around lagoon islands could also reflect the availability of other dietary resources in adjacent habitats (Hoey & Bellwood 2010a; Bennett & Bellwood 2011) given that *S. canaliculatus* can feed on seagrass as well as macroalgae (Lam 1974), and vegetated habitat patches are more common inside the lagoon compared to the barrier reef sites. Future research that compares juvenile abundances and feeding activity across a range of habitats (e.g., coral reefs, macroalgal and seagrass beds) may help us to obtain a more complete picture of distribution and browsing patterns for this species.

Of the six key browsing species, only the rabbitfish *Siganus doliatus* was widely distributed across all reefs around the Tigak Islands. Indeed *S. doliatus* had no apparent preference for a particular benthic community or seascape type, which supports the notion that *S. doliatus* is more of a habitat generalist on reefs than other browsing species (Bennett & Bellwood 2011; Richardson et al. 2020). Such flexibility is likely attributable to its varied diet as it is known to feed on a diverse range of algae (Fox et al. 2009; Hoey et al. 2013; Loffler et al. 2015), as well as its small body size compared to the other key browsers which may enable it to access more cryptic alga in structurally complex habitats (Bennett & Bellwood 2011; Richardson et al. 2020). *S. doliatus* was also the only species consistently recorded browsing around lagoon islands, and accounted for the majority of browsing activity at two of the lagoon islands (i.e., Enuk and Kabotteron). This suggests that this species might be important for maintaining the coral-algal balance around lagoon sites. However, *S. doliatus* is recognised as primarily a cropper of red and green algae, and its efficacy in the removal of brown, fleshy macroalgae has been questioned on several occasions (Fox et al. 2009; Streit et al. 2015). Rather, it is hypothesised that its bites are targeting epiphytes on the macroalgae rather than the algae (Streit et al. 2015). Therefore, its ability to make a significant contribution to macroalgal removal on lagoonal reefs is likely to be limited.

The third key family of browsers recorded from this location were kyphosids. Of the two species recorded (i.e., *Kyphosus cinerascens* and *K. vaigiensis*), both were patchily distributed and no clear patterns emerged to indicate whether these species were responding to certain aspects of the benthic community or seascape structure. Data on the ecology of tropical kyphosids is relatively limited but *K. vaigiensis* is often a significant contributor to macroalgal removal on reefs (e.g., Hoey & Bellwood 2011; Bennett & Bellwood 2011; Vergés et al. 2012; Michael et al. 2013) and is recognised as a true browser of brown macroalgae (Clements & Choat 1997; Choat et al. 2004). In contrast, little is known about the ecology or movement patterns of *K. cinerascens*, but its diet on the GBR has been reported to primarily consist of filamentous and foliose red and green algae (Choat et al. 2004). For *K. vaigiensis*, its patchy distribution around the Tigak Islands may be a reflection of its high mobility (>2 km daily movements, Welsh & Bellwood 2014) and efficiency at finding cryptic resources throughout the seascape (Hoey & Bellwood 2010a). For highly mobile species with such opportunistic feeding strategies, more temporal and spatially extensive sampling approaches will be necessary to identify whether benthic or seascape variables influence spatial distribution and browsing patterns.

### *5.4.3 Limitations*

The study was conducted over a relatively short timeframe (2 weeks), and as such provides a snapshot into the process of macroalgal removal in this system. Trophic subsidies, primary productivity and physical conditions can change between habitats and seasons (Polis et al. 1997; Marczak et al. 2007; Bejarano et al. 2017) which may in turn alter browser behaviour or distribution patterns. Extending the study across a longer time period would provide greater insight into the consistency of the patterns observed, and the stability of browsing fish assemblages. However, despite the limited temporal scale, it was still possible to detect trends in the data such as the dominant species, and higher macroalgal removal rates around barrier reef islands, and these results were comparable with studies elsewhere. In addition, only one spatial scale at the seascape level (i.e., 250 m) was considered here, however, individuals can respond to their environment across different spatial scales depending on life history stage, ecology and movement capabilities (Jackson & Fahrig 2015; **Chapter 4**). Evaluating browsing activity across a greater range of spatial scales in the future may provide additional insights into macroalgal removal on coral reefs.

### *5.4.4 Conclusions*

Browsers perform a critical function on reefs by removing the large, fleshy macroalgae that have been linked to phase shifts on coral reefs (e.g., Bellwood et al. 2006b). However, browsing activity is often patchily distributed across space (Cvitanovic & Bellwood 2009) with limited understanding about the drivers behind this variability. Here, I show that processes operating across different spatial scales, including the surrounding seascape, contribute to the function of browsing on tropical coral reefs. Distance to open ocean appeared particularly important for browsing activity with macroalgal removal higher at sites closer to open ocean. However, this was strongly influenced by a single species (*Naso lituratus*) with a high bite rate that exhibited a clear preference for higher energy outer reef sites. As coral reefs reconfigure and reassemble under an increasing number and intensity of anthropogenic stressors (Graham et al. 2013b; Williams & Graham 2019), it is imperative to better understand habitat preferences of key browsing species to identify what factors might affect the critical ecosystem function of browsing. Adopting a seascape perspective will provide additional insight into what factors drive spatial patterns of both rates and agents of browsing on tropical coral reefs.

# Chapter 6

General Discussion

## 6.1 Thesis contribution and key findings

Coral reef ecosystems are recognised as hyperdiverse environments (Barlow et al. 2018), with high cultural, ecological and economic values (Moberg & Folke 1999), but they face an uncertain future due to the effects of anthropogenic-induced disturbances (e.g., climate change, Hughes et al. 2017b). In many locations, significant changes to coral reef communities have already occurred, including coral loss (Bruno & Selig 2007; Hughes et al. 2018), flattening of reef structures (Alvarez-Filip et al. 2009) and the reconfiguration of coral communities into novel assemblages (Graham et al. 2013b; Williams & Graham 2019). These changes to coral reef habitats have caused substantial changes in the composition and functional structure of fish communities (Jones et al. 2004; Graham et al. 2006; Pratchett et al. 2008; Pratchett et al. 2011; Richardson et al. 2018; Stuart-Smith et al. 2018). But coral reefs rarely exist in isolation and are typically surrounded by a range of other habitat types (e.g., mangrove forests, seagrass beds, Ogden 1988; Parrish 1989) which are also subject to ongoing losses, fragmentation and degradation (Halpern et al. 2019). Yet we still know comparatively little about how reef fish taxa interact with, and are influenced by, other habitats in the seascape. This thesis provides novel insights into the ubiquity of multiple-habitat use among tropical reef fishes, the relative importance of seascape versus within habitat patch attributes in shaping tropical fish assemblages and how the spatial context of a reef can influence the delivery of a key ecological function. Collectively the findings of this thesis build upon an emerging body of research on seascape ecology (e.g., Boström et al. 2011; Pittman et al. 2011; Olds et al. 2016; Pittman 2018) and highlights the need to adopt a broader seascape perspective when evaluating ecological patterns and processes on coral reefs.

Over the last few years, seascape ecology has burgeoned into an exciting, fast-paced discipline that has the potential to transform the way we think about and manage marine ecosystems. Narrowing our perspective to a single habitat type using a patch-centric approach (Luckhurst & Luckhurst 1978; Heck & Orth 1980; Roberts & Ormond 1987; Sale 1991) is becoming out-dated. Indeed, studies using a seascape ecology framework have revealed that the spatial arrangement and composition of habitat types and patches can have a significant influence on species distribution and abundance patterns (e.g., Pittman & Olds 2015; Pittman 2018; van Lier et al. 2018; Berkström et al. 2020). Despite its utility, there has been a relatively slow uptake of seascape ecology perspectives among coral reef ecologists, where the majority of research continues to focus almost exclusively on reef habitat, either within-reef (e.g., coral cover, Russ et al. 2021; structural complexity, Darling et al. 2017; Agudo-Adriani et al. 2019) or between-reefs (e.g., larval dispersal, Abesamis et al. 2017; Almany et al. 2017; Harrison et al. 2020) when measuring the effects of habitat composition and structure on fish community structure and ecosystem functioning.

A potential hurdle to the widespread adoption of a broader seascape perspective in the discipline of coral reef fish ecology is a limited understanding of the prevalence of multiple habitat use among reef fishes. Prior to this thesis, data on multiple habitat use had never been synthesised to examine the diversity of reef fish taxa that are observed outside of coral reef habitats or to describe species-specific habitat use patterns. **Chapter 2** addressed this fundamental knowledge gap by providing the first global synthesis of non-reef habitat use among fishes commonly associated with coral reef habitats. The synthesis revealed that non-reef habitat use is extensive and widespread among reef fish taxa, and includes ecologically important herbivores (e.g., parrotfishes and rabbitfishes), economically important fishes (e.g., emperors, grunts, and snappers) as well as species threatened with extinction (e.g., Nassau grouper and Mäori wrasse). I estimated that approximately 20% of fish species classified as "reef-associated" are also using non-reef habitats, and suggest that this figure is likely conservative and may be considerably higher. In **Chapter 3**, the conservative nature of this estimate of non-reef habitat use was further supported by an in-depth examination of shallow-water habitat use in a diverse seascape in Kavieng, Papua New Guinea. In this study location, 35% of the reef-associated fish species were observed in non-reef habitats. Findings from these two thesis chapters (**Chapters 2 & 3**) suggest that we are almost certainly underestimating the importance of non-reef habitats and the broader seascape on coral reef systems, and consequently, predictions about the future outlook of coral reefs and their associated fish communities could be biased by an incomplete picture.

One of the common hypotheses to explain the observed use of multiple habitats by reef fishes is that non-reef habitats are primarily the domain of juveniles, with these habitats serving as nurseries (Nagelkerken et al. 2002; Dorenbosch et al. 2006b). My thesis provided evidence to support the use of non-reef habitats by juvenile fishes through both the global synthesis (**Chapter 2**), and video and diver-based surveys (**Chapters 3 & 4**) that showed juveniles from a wide variety of taxa occur in non-reef habitats, often frequently. Significantly, by applying seascape ecology principles that consider the spatial configuration of different habitats and adopting a multi-scale approach, **Chapter 4** is one of the first studies to show that the distribution patterns of both juvenile emperors and parrotfishes within seagrass patches is influenced, at least to some degree, by the spatial arrangement and type of habitats within the surrounding seascape. Moreover, juveniles from these two families responded to different seascape variables suggesting that nursery habitat selection is more complex than simply locating and settling into a particular habitat type. Adopting a more mechanistic approach to examine why juveniles are using different habitats and habitat patches (e.g., enhanced growth, refugia from predation, Grol et al. 2011b, Grol et al. 2014), will help us to better understand the drivers of settlement across a broader range of fish taxa and can help design strategies for the potential replenishment of reef fish populations.

In temperate reef environments, macroalgae has long been recognised as important habitat for fishes, particularly as settlement habitat for some species (e.g., Anderson 1994; Carr 1989). Yet in tropical coral reef seascapes, macroalgae is widely viewed as a sign of reef degradation. Areas of macroalgae cover on reefs are often associated with deteriorating reef conditions or phase-shifts (Hughes 1994; McCook 1999; Cheal et al. 2010; Graham et al. 2015) and macroalgae cover impedes coral recruitment and hence recovery of coral populations (e.g., Kuffner et al. 2006; Hughes et al. 2007b). However, its natural occurrence as a habitat in its own right is sometimes overlooked (but see Tano et al. 2017; Fulton et al. 2020), particularly by coral reef scientists. Throughout this thesis macroalgal beds were identified as important habitat for some fishes or were influential in explaining species distribution patterns across the seascape (**Chapters 2, 3 & 4**). Interestingly, while the global synthesis (**Chapter 2**) identified differences in habitat use patterns for seagrass and mangroves between the Tropical Atlantic and Indo-Pacific, there was consensus in terms of macroalgal bed use. Macroalgae beds were predominantly used by juvenile rather than adult reef fishes, indicating that macroalgal beds could play an important, though currently underappreciated, nursery role for tropical fishes. In **Chapter 3**, using the Tigak Island seascapes in Papua New Guinea, I showed that macroalgal beds contained more species and higher abundances than mangrove and seagrass habitat types, and the presence of macroalgal beds had a positive effect on the abundance of wrasses in neighbouring seagrass patches (**Chapter 4**). Together, these findings lend strong support to a growing body of research (Eggertsen et al. 2017; Fulton et al. 2019; Fulton et al. 2020) showing that naturally occurring macroalgal beds are a key habitat for many fish species and that their presence can have positive effects on fish abundance in multiple habitat types found in tropical seascapes.

### 6.2 Conservation and management implications

The sizeable number of fish species identified as multi-habitat users, including many that are ecologically important, fisheries targets, and/or threatened with extinction, highlights the importance of holistic approaches that consider multiple aspects of the seascape to inform the effective conservation and management of shallow-water tropical seascapes. Scaling up research to understand fish-seascape relationships (**Chapters 2, 3 & 4**), how these might influence ecological processes (**Chapter 5**) and contribute to ecosystem integrity will be critical in the development and implementation of spatial management strategies that are fit for purpose.

This thesis provides new insights into why it is so critically important to include a range of habitat types in spatial management plans. Designing marine protected area networks based on the CAR principles (Comprehensiveness, Adequacy and Representative) has become common practice (e.g., Great Barrier Reef Marine Park, Australia, Fernandes et al. 2005). The underlying theory in this approach is that by incorporating multiple habitat types and patches of different sizes, spatial configurations and locations, there is a greater chance of capturing the full complement of biodiversity within a seascape, protecting critical support areas for growth, reproduction or survival (e.g., juvenile nurseries), maintaining ecological integrity, and supporting population viability (Margules & Pressey 2000; Day et al. 2002). Until recently, we knew little about the extent to which these assumptions were true. The widespread use of multiple habitat types by such a significant portion of the fish community documented in this thesis provides strong support for including a range of habitat types in spatial management plans. However, it also revealed new insights that could be used to refine spatial planning strategies that incorporate multiple habitats. Discrete patches of the same habitat type can support quite distinct fish communities (**Chapter 4**), both in terms of taxonomic and functional composition, and differences in the spatial context of a patch can flow through to the delivery of key ecological functions (e.g., browsing, **Chapter 5**). The findings of this thesis indicate that the positioning and placement of marine protected areas, or the choice of which habitat patch to protect will need to be tailored to the objectives of the reserve or reserve network (e.g., to conserve biodiversity, maintain ecosystem integrity, protect essential fish nursery habitat or to manage fisheries).

The findings from this thesis are also relevant for fisheries management. For example at my study site in the Tigak Islands, seagrass meadows, macroalgal beds and mangrove habitats were extensively used by both adult and juvenile reef fishes (**Chapters 3 & 4**), and the majority of multiple habitat-using taxa are fisheries targets (e.g., emperors, snappers). Moreover, my findings also suggest that some habitat patches may support higher abundances and diversity of fisheries species than other patches of the same habitat type (**Chapter 4**). Human communities in this location, like many across the Indo-Pacific, are heavily reliant on healthy marine ecosystems and fisheries stocks (Bell et al. 2009; Gillet 2014). Although a lot of attention is given to coral reef fisheries, it is vital to recognise that other habitats are also important in their own right, and in the context of coral reef fisheries management. Both seagrass beds and mangroves support highly productive fisheries (e.g., mangroves, Sheaves 2017; Carrasquilla-Henao et al. 2019; seagrass, Nordlund et al. 2018), and are accessible year round unlike coral reefs which can be challenging to access during adverse weather conditions, making sheltered vegetated habitat types a more predictable source of fish protein (e.g., during monsoon season). In addition, if we assume connectivity between habitat patches, then mangroves, macroalgal and seagrass beds are not only a valuable resource for fisheries in their own right, but could also enhance fish populations on reefs. Therefore, adopting a seascape perspective for fisheries management may be critical for longer term food security, particularly for the Pacific Island Countries and Territories that have extensive nearshore vegetated habitats.

The long-term viability of many tropical shallow-water habitats is uncertain given the diverse range of stressors these habitats are exposed to (e.g., coastal developments, elevated sea surface temperatures, severe storms, pollution, Jackson et al. 2001; Bellwood et al. 2004; Halpern et al. 2019). These threats have led conservation and management efforts to focus on maintaining key functions to enhance resilience and support recovery processes (e.g., Nyström & Folke 2001; Harun-or-Rashid et al. 2009; Graham et al. 2011; Rasheed et al. 2014). While some approaches to build resilience have considered connectivity between different habitat types (e.g., MPA networks, Green et al. 2009; Bernhardt & Leslie 2013; Torres-Pulliza et al. 2013), others have focused on implementing measures within a single habitat type. For instance, one measure that has been repeatedly proposed is to restrict fishing of taxa that perform key ecological roles (e.g., herbivores, McCook 1999; Hughes et al. 2007b; Graham et al. 2013a; MacNeil et al. 2015; Williams et al. 2019; Mumby et al. 2021), but solely on reefs rather than the range of habitats used by herbivores. Yet the findings from this thesis suggest quite strongly that there will be considerable value in thinking about herbivore management, and other resilience building strategies, within a seascape context. For example, herbivores such as parrotfishes and rabbitfishes were revealed to use multiple habitat types, not just coral reefs, throughout their lives (**Chapters 2 & 3**), and their spatial distribution (**Chapter 4)** and the functional impact of browsers was influenced by seascape structure (**Chapter 5)**. Management strategies that seek to conserve herbivores, for example threatened species that have distinct juvenile habitats (e.g., the bumphead parrotfish *Bolbometopon muricatum*, Hamilton et al. 2017; and the rainbow parrotfish *Scarus guacamaia*, Mumby et al. 2006), in order to promote reef resilience will be more effective if they incorporate connections between different habitat types in the seascape.

As well as resilience building, there is a growing need for active interventions to restore habitats or critical ecosystem functions (Bosire et al. 2008; Hein et al. 2021; Sinclair et al. 2021). However until recently, restoration was focused on a single habitat type rather than considering the value of interactions among multiple habitat types found in the seascape mosaic (Gilby et al. 2018; Pittman et al. 2021). One prominent effect of habitat loss is that habitat patches may become smaller, more fragmented and increasingly isolated, which can cause the breakdown of critical relationships between habitats (Saunders et al. 1991; Steffan-Dewenter & Tscharntke 1999; Fischer & Lindenmayer 2007; Fahrig 2013). As we enter the UN Decade of Ecosystem Restoration (Waltham et al. 2020), spatially explicit approaches that consider aspects such as the composition of the surrounding matrix may be more effective in restoring habitats and associated fauna than single habitat approaches by re-establishing functional connections (Hale et al. 2020), such as seascape nurseries (Nagelkerken et al. 2015). However, the success of seascape restoration approaches will ultimately depend on whether we address the dominant stressor of climate change given it will particularly impact shallow-water ecosystems, especially those in close proximity to the coast (Duarte et al. 2020; Kleypas et al. 2021).

## 6.3 Future research

The findings of this thesis open up an interesting interface between traditional ecological theory and landscape perspectives. Our understanding about how multiple habitat or patch use, and spatial context can affect individual fitness is limited. As a consequence, incorporating spatially explicit approaches into empirical tests of key ecological theories (e.g., optimal foraging, landscape of fear) may reveal new and valuable insights into population and community dynamics. As a relatively new field, there are also many fruitful avenues of seascape research to be pursued which will progress the field from testing landscape ecology principles, to developing a framework more suitable for marine environments, and ultimately facilitating the transition into a solutions-oriented science that can support the long-term persistence and health of marine environments. Indeed, a recent horizon scan has identified some of the most pressing seascape-related questions among academics and practitioners that need to be addressed to advance the field (Pittman et al. 2021). Themes identified as important include changing seascapes, connectivity, ecosystem-based management (EBM), restoration, and seascape goods and services (Pittman et al. 2021), with knowledge gained from this thesis directly contributing to several of these. The findings from this thesis have provided some novel insights and made a valuable contribution to expanding our appreciation about the influence of the seascape on the structure and function of tropical fish communities. However, the thesis has also identified some key knowledge gaps that should form the basis of future research to more fully understand the implications of changing seascapes.

### *6.3.1 Multiple habitat users, early life history, and the seascape mosaic*

One sizeable and longstanding knowledge gap is our limited understanding about the reasons for multiple habitat use for the vast majority of fish species. I found evidence of extensive use of multiple habitat types in many species but we do not yet understand the extent to which the use of multiple habitat types makes these species more or less vulnerable to habitat loss and changing seascapes. If species that use multiple habitats have obligate dependencies on specific resources in each habitat type then we might expect to see detrimental effects on populations if critical habitats or habitat patches are lost, whereas if the use of multiple habitats in the seascape is an indication of high levels of resource flexibility then changing seascapes may have little impact. This is likely to differ by species, such that species with greater habitat flexibility will be more likely to cope with changing conditions (e.g., Colossi Brustolin et al. 2019; Kingsbury et al. 2019; Stuart-Smith et al. 2021), and importantly may hold the key to future diversification across longer evolutionary timeframes (Gajdzik et al. 2019). Multiple habitat users may increase response diversity by responding to environmental perturbations at different spatial scales than species constrained to a single habitat type (Elmqvist et al. 2003), with the potential to relocate away from patches if conditions become suboptimal (Lenihan et al. 2001), only returning when conditions become more favourable. Through their habitat flexibility, some multiple habitat users could contribute towards recovery processes through larval supply, population replenishment into depauperate habitat patches, or by performing an essential role that can support recovery (e.g., grazing).

Processes operating during early life stages may be important drivers of multiple habitat use in many taxa. Juveniles from a wide range of taxa were recorded using multiple habitat types (**Chapter 2**), particularly from families that are economically (e.g., emperors) or ecologically important (e.g., herbivorous fishes). In addition, juveniles from separate families (e.g., emperors and parrotfishes) appeared to use different types of seagrass beds depending on the seascape context and within-patch attributes (**Chapter 4**). However, it is currently impossible to determine whether these patterns are a result of active habitat patch selection at settlement and/or differential post-settlement survival in different habitat types and patches. Few studies have directly quantified settlement of fishes into a range of habitat types (but see Rooker et al. 1996; Nakamura et al. 2009b, Hedberg et al 2018), and even fewer within a seascape context (but see Nakamura et al. 2009a). In part, progress in this area has been impeded due to the challenge of accurate identification to species level for some early life stages (e.g., juvenile parrotfishes). However, advances in DNA analyses are helping to overcome this issue and have begun to reveal interesting insights into habitat use patterns of early stage juveniles (e.g., Sievers et al. 2020a).

Collecting data from a wider range of habitats, habitat patches, and seascapes situated in different environmental and spatial contexts will be important in furthering our understanding of multiple habitat use patterns by tropical fishes. One way this is likely to be achieved is through the increased use of remote video cameras in combination with the rapidly advancing field of computer vision. Deploying cameras across a more extensive range of habitats and habitat patches will be less time intensive than traditional diver-led surveys, can capture habitat use patterns of diver-averse taxa, and is easily replicable across different seascapes (Mallet & Pelletier 2014; Weinstein 2018). Moreover, a number of projects are currently underway to improve battery performance and night-vision capabilities so that data collection can occur across longer time periods (e.g., Coro & Bjerregaard Walsh 2021), particularly useful for species that undertake day-night shifts between habitat types. Progress in computer vision technology (e.g., onboard processing, motion detection for more efficient data capture, automated detection of species, body sizes, and relative abundances) will also considerably reduce the time traditionally involved in manual data extraction from videos (Wäldchen & Mäder 2018; Lopez-Marcano et al. 2020; Coro & Bjerregaard Walsh 2021). In addition to video data, molecular techniques will also help unravel habitat use patterns of rare species (e.g., eDNA, Budd et al. 2021) and cryptic life stages (e.g., Sievers et al. 2020a). Scaling up research using more spatially extensive approaches such as remote cameras will lead to more accurate predictive models about species distribution patterns that can inform future spatially explicit conservation and management strategies.

More intensive research that explores the underlying drivers of habitat use patterns is essential in order to interpret findings emerging from seascape research in an ecologically meaningful way and to fully comprehend the implications of changing seascapes. For instance, delving into why discrete taxa and life stages were using different types of seagrass patches (**Chapter 4**) is an important next step emerging from this thesis. Identifying mechanisms underpinning multiple habitat use will necessitate a combination of field, laboratory, and modelling techniques such as quantifying larval supply into a range of habitats and habitat patches, testing habitat preferences; evaluating survival and growth rates of post-settlement fishes (e.g., food availability, predation, competition) and; examining how the intervening matrix between juvenile and adult habitats influences thresholds of connectivity. Progressing beyond observational studies towards more mechanistic approaches will help us to evaluate whether coral reef-associated taxa will be able to switch to, or persist in, non-reef habitat types, and better predict the consequences of habitat loss or fragmentation on individual taxa.

### *6.3.2 Behavioural seascape ecology*

Another key area for future research is improving our knowledge about how the seascape structure can affect patterns of movement. This thesis found that different taxa and life stages responded to different spatial scales (e.g., from metres to 1 km radii), similar to other seascape studies (e.g., Yeager et al. 2011; Olds et al. 2012a; Sievers et al. 2020b). Although the spatial scales examined in seascape studies are often similar, there can be considerable variability in the spatial scale identified as influential for species distribution and abundance patterns, between study locations and even taxa. These differences among studies may be caused by differences in the spatial arrangement and composition of habitat patches within the focal seascape, however this topic has not yet been explored. Greater information on species-specific movement patterns, as well as intra-specific variability may therefore be valuable to help us identify features that might facilitate or impede movement (Taylor et al. 1993). Acoustic tracking capabilities have become increasingly refined in recent years and will be useful to shed light on this topic given that manually (i.e., divers) following individual fishes over long periods is not feasible. However, despite recent advances in satellite, underwater and aerial drone imagery capture and processing, it remains challenging to produce high resolution, accurate mapping of seascape habitats across broad areas (Benoist et al. 2019; Joyce et al. 2019; Lyons et al. 2020). Therefore few movement ecology studies have explicitly examined movement between different habitats (but see Hitt et al. 2011; Rooker et al. 2018; Ebrahim et al. 2020; Heidmann et al. 2021), instead quantifying movement patterns in terms of migration distances or home ranges. More study designs that enable individuals to be tracked between different habitats are therefore needed. One of the few studies to explore movement in two common reef fishes within a seascape context found that predator avoidance influenced movement patterns and patch occupation (Rooker et al. 2018). Moreover, few studies have formally tested for matrix effects on movement patterns, despite the fact that the type of matrix has been implicated in declines in species numbers away from nursery habitats (e.g., deep water, sand, Berkström et al. 2020 but see Pagès et al. 2014), as well as the potential for certain types of matrix to act as a movement corridor between two spatially separated patches (Davis et al. 2017). Clearly, there is much to learn about the factors that influence movement patterns for fishes in coastal marine seascapes.

### *6.3.3 Seascape ecology and ecosystem functioning*

Understanding how the spatial arrangement and composition of habitat patches influences ecosystem dynamics and functioning across seascapes, and differing spatial scales, should be a priority area for future research. To date, few studies have considered how the wider seascape can influence ecosystem functioning, and even in terrestrial systems, matching ecological processes with spatial patterns remains a challenging research frontier (Turner & Gardener 2015). Rather, there is a tendency to make assumptions based on fish-seascape patterns which may not be a robust substitute for function. This thesis found that the spatial context of a focal reef influences macroalgal browsing rates on coral reefs, with higher browsing rates on outer reefs with little vegetated habitat nearby (**Chapter 5**). Based on these findings, future areas of research should include examining macroalgal removal on reefs from similar spatial contexts (e.g., similar distances from open ocean) but with differing availabilities of vegetated habitat types (e.g., seagrass, macroalgal beds), as well as examining feeding behaviour across a range of habitat types including reefs to determine foraging flexibility among browsing taxa. Expanding this approach to examine other types of herbivorous fishes should be a priority for future research. For instance, grazing parrotfishes perform a critical role by preventing the establishment of macroalgae (Bellwood et al. 2004; Mumby et al. 2006; Burkepile & Hay 2008; Adam et al. 2011), commonly use non-reef habitats (Campbell et al. 2011; Sambrook et al. 2020; Sievers et al. 2020a; **Chapters 3 & 4**), and have been implicated in reef recovery following disturbance events (Mumby & Hastings 2008; Adam et al. 2011; Harborne et al. 2016b). Therefore understanding how the surrounding seascape can influence grazing patterns on reefs warrants greater attention.

The application of big data approaches (e.g., global datasets) will allow us to address some of these knowledge gaps and rapidly advance our understanding of patterns, processes, and scales within a seascape context. One of the major challenges for advancing seascape ecology is the difficulty associated with collecting and analysing sufficient amounts of data from underwater environments. This can limit our ability to detect relationships, identify commonalities and differences between seascapes, and test predictions. Much of the data that could enable us to test out seascape-related hypotheses across greater spatial extents may already exist but will require collaboration, multi-disciplinary teams and access to historical satellite imagery. For instance, herbivory on both coral reefs and in seagrass beds has been extensively explored across multiple locations (e.g., coral reef: Great Barrier Reef & Ningaloo, Australia, Vergés et al. 2012, Fiji, Rasher et al. 2013; Indonesia, Plass-Johnson et al. 2015; Singapore, Bauman et al. 2017; Tanzania, Eggertsen et al. 2019; Palau, Roff et al. 2019; and seagrass herbivory: Indonesia, Unsworth et al. 2007c; Puerto Rico, Swindells et al. 2017; Tanzania, Eggertsen et al. 2019; Australia, Vanderklift et al. 2021). Bringing these data together and examining different types of herbivory within a seascape context may reveal valuable insights and hidden connections between different elements of the seascape.

## 6.4 Concluding remarks

Overall, this thesis has demonstrated that multiple habitat use by tropical fishes is widespread, perhaps more so than previously recognised, and that by looking in a wider range of habitat types, we can gain a deeper understanding of fish-habitat relationships. In addition, this thesis has shown that patches of the same habitat type may not be functionally equivalent, with the taxa and life stage of fish occupying a patch, and the delivery of their function also moderated by seascape context. Finally, this thesis demonstrated that the spatial context of a reef is an important driver of a key ecological process (i.e., macroalgae browsing) on reefs. As a body of work, this thesis demonstrates that the seascape matters and supports growing calls to transition from a habitat- or patch-centric approach, to approaches that encompass the surrounding seascape. Adopting a seascape ecology approach will give us a more complete picture of connections between habitats, how such connections might influence patterns and processes, and what that might mean as seascapes continue to change into the future.

## References

Abesamis RA, Saenz-Agudelo P, Berumen ML, Bode M, Jadloc CRL, Solera LA, Villanoy CL, Bernardo LPC, Alcala AC, Russ GR (2017) Reef-fish larval dispersal patterns validate no-take marine reserve network connectivity that links human communities. *Coral Reefs* 36: 791-801

Adam TC, Schmitt RJ, Holbrook SJ, Brooks AJ, Edmunds PJ, Carpenter RC, Bernardi G (2011) Herbivory, connectivity, and ecosystem resilience: response of a coral reef to a large-scale perturbation. *PLoS ONE* 6: e23717

Adams AJ, Dahlgren CP, Kellison GT, Kendall MS, Layman CA, Ley JA, Nagelkerken I, Serafy JE (2006) Nursery function of tropical back-reef systems. *Marine Ecology Progress Series* 318: 287-301

Adams AJ, Ebersole JP (2002) Use of back-reef and lagoon habitats by coral reef fishes. *Marine Ecology Progress Series* 228: 213-226

Addicott JF, Aho JM, Antolin MF, Padilla DK, Richardson JS, Soluk DA (1987) Ecological neighborhoods: scaling environmental patterns. *Oikos* 49: 340-346

Ager AA, Johnson BK, Kern JW, Kie JG (2003) Daily and seasonal movements and habitat use by female Rocky Mountain elk and mule deer. *Journal of Mammalogy* 84: 1076-1088

Agudo-Adriani EA, Cappelletto J, Cavada-Blanco F, Cróquer A (2019) Structural complexity and benthic cover explain reef-scale variability of fish assemblages in Los Roques National Park, Venezuela. *Frontiers in Marine Science* 6: 690

Aguilar-Perera A, Appeldoorn RS (2007) Variation in juvenile fish density along the mangrove-seagrass-coral reef continuum in SW Puerto Rico. *Marine Ecology Progress Series* 348: 139-148

Aguilar-Perera A, Appeldoorn RS (2008) Spatial distribution of marine fishes along a cross-shelf gradient containing a continuum of mangrove-seagrass-coral reefs off southwestern Puerto Rico. *Estuarine, Coastal and Shelf Science* 76: 378–394

Aguilar-Perera A, Hernández-Landa RC (2017) The rainbow parrotfish (*Scarus guacamaia*) does not depend on mangroves as nursery habitats in the Parque Nacional Arrecife Alacranes, Southern Gulf of Mexico. *Marine Biodiversity* 47: 13-14

Allen GR (2015) Review of Indo-Pacific coral reef fish systematics: 1980 to 2014. *Ichthyological Research* 62: 2-8

Aller EA, Gullström M, Maarse FKJE, Gren M, Nordlund LM, Jiddawi N, Eklöf JS (2014) Single and joint effects of regional- and local-scale variables on tropical seagrass fish assemblages. *Marine Biology* 161: 2395-2405

Almany GR, Berumen ML, Thorrold SR, Planes S, Jones GP (2007) Local replenishment of coral reef fish populations in a marine reserve. *Science* 316: 742-744

Almany GR, Planes S, Thorrold SR, Berumen ML, Bode M, Saenz-Agudelo P, Bonin MC, Frisch AJ, Harrison HB, Messmer V, Nanninga GB, Priest MA, Srinivasan M, Sinclair-Taylor T, Williamson DH, Jones GP (2017) Larval fish dispersal in a coral-reef seascape. *Nature Ecology and Evolution* 1: 1-7

Alsterberg C, Roger F, Sundbäck K, Juhanson J, Hulth S, Hallin S, Gamfeldt L (2017) Habitat diversity and ecosystem multifunctionality – the importance of direct and indirect effects. *Science Advances* 3: e1601475

Alvarez-Filip L, Dulvy NK, Gill JA, Côté IM, Watkinson AR (2009) Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings of the Royal Society B* 276: 3019-3025

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: Guide to software and statistical methods. PRIMER-E: Plymouth, UK

Anderson TW (1994) Role of macroalgal structure in the distribution and abundance of a temperate reef fish. *Marine Ecology Progress Series* 113: 279-290

Andréfouët S (2008) Coral reef habitat mapping using remote sensing: a user vs producer perspective. Implications for research, management and capacity building. *Journal of Spatial Science* 53: 113-129

Appeldoorn RS, Aguilar-Perera A, Bouwmeester BLK, Dennis GD, Hill RL, Merten W, Recksiek CW, Williams SJ (2009) Movement of fishes (Grunts: Haemulidae) across the coral reef seascape: a review of scales, patterns and processes. *Caribbean Journal of Science* 45: 304-316

Aronson RB, Precht WF (2001) White-band disease and the changing face of Caribbean coral reefs. *Hydrobiologia* 460: 25-38

Ashworth JS, Bruce OE, El Hellw M (2006) Fish assemblages of Red Sea backreef biotopes. *Aquatic Conservation: Marine and Freshwater Ecosystems* 16: 593-609

Aston EA, Williams GJ, Mattias Green JA, Davies AJ, Wedding LM, Gove JM, Jouffray JB, Jones TT, Clark J (2019) Scale-dependent spatial patterns in benthic communities around a tropical island seascape. *Ecography* 42: 578-590

Bainbridge Z, Lewis S, Bartley R, Fabricius K, Collier C, Waterhouse J, Garzon-Garcia A, Robson B, Burton J, Wenger A, Brodie J (2018) Fine sediment and particulate organic matter: a review and case study on ridge-to-reef transport, transformations, fates, and impacts on marine ecosystems. *Marine Pollution Bulletin* 135: 1205-1220

Baker R, Barnett A, Bradley M, Abrantes K, Sheaves M (2018) Contrasting seascape use by a coastal fish assemblage: a multi-methods approach. *Estuaries and Coasts* 42: 292-307

Barlow J, França F, Gardner TA, Hicks CC, Lennox GD, Berenguer E, Castello L, Economo EP, Ferreira J, Guénard B, Gontijo Leal C, Isaac V, Lees AC, Parr CL, Wilson SK, Young PJ, Graham NAH (2018) The future of hyperdiverse tropical ecosystems. *Nature* 559: 517-526

Barnes L, Bellwood DR, Sheaves M, Tanner JK (2012) The use of clear-water non-estuarine mangroves by reef fishes on the Great Barrier Reef. *Marine Biology* 159: 211-220

Bassett DK, Montgomery JC (2011) Investigating nocturnal fish populations *in situ* using baited underwater video: with special reference to their olfactory capabilities. *Journal of Experimental Marine Biology and Ecology* 409: 194-199

Baum G, Januar HI, Ferse SA, Kunzmann A (2015) Local and regional impacts of pollution on coral reefs along the Thousand Islands north of the megacity Jakarta, Indonesia. *PLoS ONE* 10: e0138271

Bauman AG, Hoey AS, Dunshea G, Feary DA, Low J, Todd PA (2017) Macroalgal browsing on a heavily degraded, urbanized equatorial reef system. *Scientific Reports* 7: 1-8

Bauman AG, Seah JCL, Januchowski-Hartley FA, Hoey AS, Fong J, Todd PA (2019) Fear effects associated with predator presence and habitat structure interact to alter herbivory on coral reefs. *Biology Letters* 15: 20190409

Beck MW, Heck KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MP (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *BioScience* 51: 633-641

Beets J, Muehlstein L, Haught K, Schmitges H (2003) Habitat connectivity in coastal environments: patterns and movements of Caribbean coral reef fishes with emphasis on bluestriped grunt, *Haemulon sciurus*. *Gulf and Caribbean Research* 14:29-42

Bejarano S, Golbuu Y, Sapolu T, Mumby PJ (2013) Ecological risk and the exploitation of herbivorous reef fish across Micronesia. *Marine Ecology Progress Series* 482: 197-215

Bejarano S, Jouffray J-B, Chollett I, Allen R, Roff G, Marshell A, Steneck R, Ferse SCA, Mumby PJ (2017) The shape of success in a turbulent world: wave exposure filtering of coral reef herbivory. *Functional Ecology* 31: 1312-1324

Bell JD, Kronen M, Vunisea A, Nash WJ, Keeble G, Demmke A, Pontifex S, Andréfouët S (2009) Planning the use of fish for food security in the Pacific. *Marine Policy* 33: 64-76

Bell JD, Westoby M (1986) Importance of local changes in leaf height and density to fish and decapods associated with seagrasses. *Journal of Experimental Marine Biology and Ecology* 104: 249-274

Bellwood DR (1988) Ontogenetic changes in the diet of early post-settlement *Scarus* species (Pisces: Scaridae). *Journal of Fish Biology* 33: 213-219

Bellwood DR, Hoey AS, Choat JH (2003) Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecology Letters* 6: 281-285

Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. *Nature* 429: 827-833

Bellwood DR, Hughes TP, Hoey AS (2006b) Sleeping functional group drives coral-reef recovery. *Current Biology* 16: 2434-2439

Bellwood DR, Tebbett SB, Bellwood O, Mihalitsis M, Morais RA, Streit RP, Fulton CJ (2018) The role of the reef flat in coral reef trophodynamics: past, present, and future. *Ecology and Evolution* 8: 4108-4119

Bellwood DR, Wainwright PC (2001) Locomotion in labrid fishes: implications for habitat use and cross-shelf biogeography on the Great Barrier Reef. *Coral Reefs* 20: 139-150

Bellwood DR, Wainwright PC, Fulton CJ, Hoey AS (2006a) Functional versatility supports coral reef biodiversity. *Proceedings of the Royal Society B* 273: 101-107

Béné C, Macfadyen G, Allison EH (2007) Increasing the contribution of small-scale fisheries to poverty alleviation and food security. FAO Fisheries Technical Paper 481

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

Benoist NMA, Morris KJ, Bett BJ, Durden JM, Huvenne VAI, Le Bas TP, Wynn RB, Ware SJ, Ruhl HA (2019) Monitoring mosaic biotopes in a marine conservation zone by autonomous underwater vehicle. *Conservation Biology* 5: 1174-1186

Berkström C, Eggertsen L, Goodell W, Cordeiro CAMM, Lucena MB, Gustafsson R, Bandeira S, Jiddawi N, Ferreira CEL (2020) Thresholds in seascape connectivity: the spatial arrangement of nursery habitats structure fish communities on nearby reefs. *Ecography* 43: 882-896

Berkström C, Gullström M, Lindborg R, Mwandya AW, Yahya SAS, Kautsky N, Nyström M (2012) Exploring ‘knowns’ and ‘unknowns’ in tropical seascape connectivity with insights from East African coral reefs. *Estuarine, Coastal and Shelf Science* 107: 1–21

Berkström C, Jörgensen TL, Hellström M (2013b) Ecological connectivity and niche differentiation between two closely related fish species in the mangrove-seagrass-coral reef continuum. *Marine Ecology Progress Series* 477: 201-215

Berkström C, Lindborg R, Thyresson M, Gullström M (2013a) Assessing connectivity in a tropical embayment: fish migrations and seascape ecology. *Biological Conservation* 166: 43-53

Bernhardt JR, Leslie HM (2013) Resilience to climate change in coastal marine ecosystems. *Annual Review of Marine Science* 5: 371-392

Beukers JS, Jones GP (1997) Habitat complexity modifies the impact of piscivores on a coral reef fish population. *Oecologia* 114: 50-59

Birkeland C (1985) Ecological interactions between tropical coastal ecosystems. *UNEP Regional Seas Reports and Studies* 73: 1–26

Blaber SJM (2007) Mangroves and fishes: issues of diversity, dependence, and dogma. *Bulletin of Marine Science* 80: 457-472

Blaber SJM (2009) Relationships between tropical coastal habitats and (offshore) fisheries. In: Nagelkerken I (Ed). *Ecological connectivity among tropical coastal ecosystems.* Springer Dordrecht pp 533-563

Blaber SJM, Milton DA (1990) Species composition, community structure and zoogeography of fishes of mangrove estuaries in the Solomon Islands. *Marine Biology* 105: 259-267

Blasiak R, Spijkers J, Tokunaga K, Pittman J, Yagi N, Österblom (2017) Climate change and marine fisheries: least developed countries top global index of vulnerability. *PLoS ONE* 12: e0179632

Boaden AE, Kingsford MJ (2012) Diel behavior and trophic ecology of *Scolopsis bilineatus* (Nemipteridae). *Coral Reefs* 31: 871-883

Bonaldo RM, Hoey AS, Bellwood DR (2014) The ecosystem roles of parrotfishes on tropical reefs. *Oceanography and Marine Biology: An Annual Review* 52: 81-132

Bonin MC, Almany GR, Jones GP (2011) Contrasting effects of habitat loss and fragmentation on coral-associated reef fishes. *Ecology* 92: 1503-1512

Bosire JO, Dahdouh-Guebas F, Walton M, Crona BI, Lewis III RR, Field C, Kairo JG, Koedam N (2008) Functionality of restored mangroves: a review. *Aquatic Botany* 89: 251-259

Boström C, Jackson EL, Simenstad CA (2006) Seagrass landscapes and their effects on associated fauna: a review. *Estuarine, Coastal and Shelf Science* 68: 383-403

Boström C, Pittman SJ, Simenstad C, Kneib RT (2011) Seascape ecology of coastal biogenic habitats: advances, gaps, and challenges. *Marine Ecology Progress Series* 427: 191-217

Bradley M, Baker R, Nagelkerken I, Sheaves M (2019) Context is more important than habitat type in determining use by juvenile fish. *Landscape Ecology* 34: 427-442

Bradley M, Baker R, Sheaves M (2017) Hidden components in tropical seascapes: deep-estuary habitats support unique fish assemblages. *Estuaries and Coasts* 40: 1195-1206

Bridge TCL, Hughes TP, Guinotte JM, Bongaerts P (2013) Call to protect all coral reefs. *Nature Climate Change* 3: 528-530

Brodie G, Holland E, De Ramon N'Yeurt A, Soapi K, Hills J (2020) Seagrasses and seagrass habitats in Pacific small island developing states: potential loss of benefits via human disturbance and climate change. *Marine Pollution Bulletin* 160: 111573

Brodie G, Pikacha P, Tuiwawa M (2013) Biodiversity and conservation in the Pacific Islands: why are we not succeeding? In: Sodhi NS, Gibson L, Raven PH (Eds) *Conservation Biology: Voices from the Tropics.* John Wiley & Sons pp 181-187

Brooks TM, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Rylands AB, Konstant WR, Flick P, Pilgrim J, Oldfield S, Magin G, Hilton-Taylor C (2002) Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology* 16: 909-923

Brown CJ, Harborne AR, Paris CB, Mumby PJ (2016) Uniting paradigms of connectivity in marine ecology. *Ecology* 97: 2447-2457

Brown JS (1999) Vigilance, patch use and habitat selection: foraging under predation risk. *Evolutionary Ecology Research* 1: 49-71

Brown JS, Laundré JW, Gurung M (1999) The ecology of fear: optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy* 80: 385-399

Bruno JF, Selig ER (2007) Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS ONE* 2: e711

Budd AM, Cooper MK, Le Port A, Schils T, Mills MS, Deinhart ME, Huerlimann R, Strugnell JM (2021) First detection of critically endangered scalloped hammerhead sharks (*Sphyrna lewini*) in Guam, Micronesia, in five decades using environmental DNA. *Ecological Indicators* 107649

Burge EJ, Atack JD, Andrews C, Binder BM, Hart ZD, Wood AC, Bohrer LE, Jagannathan K (2012) Underwater video monitoring of groupers and the associated hard-bottom reef fish assemblage of North Carolina. *Bulletin of Marine Science* 88: 15-38

Burke JS, Kenworthy WJ, Wood LL (2009) Ontogenetic patterns of concentration indicate lagoon nurseries are essential to common grunt stocks in a Puerto Rican bay. *Estuarine, Coastal and Shelf Science* 81: 533-543

Burke L, Reytar K, Spalding M, Perry A (2011) Reefs at risk revisited. World Resources Institute, 130 p

Burke NC (1995) Nocturnal foraging habitats of French and bluestriped grunts, *Haemulon flavolineatum* and *H. sciurus*, at Tobacco Caye, Belize. *Environmental Biology of Fishes* 42: 365-374

Burkepile DE, Hay ME (2008) Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proceedings of the National Academy of Sciences of the United States of America* 105: 16201-16206

Byrnes JE, Reed DC, Cardinale BJ, Cavanaugh KC, Holbrook SJ, Schmitt RJ (2011) Climate-driven increases in storm frequency simplify kelp forest food webs. *Global Change Biology* 17: 2513-2524

Cadotte MW, Carscadden K, Mirotchnick N (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology* 48: 1079-1087

Campbell MD, Pollack AG, Gledhill CT, Switzer TS, DeVries DA (2015) Comparison of relative abundance indices calculated from two methods of generating video count data. *Fisheries Research* 170: 125-133

Campbell SJ, Kartawijaya T, Sabarini EK (2011) Connectivity in reef fish assemblages between seagrass and coral reef habitats. *Aquatic Biology* 13: 65-77

Cappo M, Speare P, De'ath G (2004) Comparison of baited remote underwater video stations (BRUVS) and prawn (shrimp) trawls for assessments of fish biodiversity in inter-reefal areas of the Great Barrier Reef Marine Park. *Journal of Experimental Marine Biology and Ecology* 302: 123-152

Carr MH (1989) Effects of macroalgal assemblages on the recruitment of temperate zone reef fishes. *Journal of Experimental Marine Biology and Ecology* 126: 59-76

Carrasquilla-Henao M, Ban N, Rueda M, Juanes F (2019) The mangrove-fishery relationship: a local ecological perspective. *Marine Policy* 108: 103656

Carroll JM, Peterson BJ (2013) Ecological trade-offs in seascape ecology: bay scallop survival and growth across a seagrass seascape. *Landscape Ecology* 28: 1401-1413

Catano LB, Rojas MC, Malossi RJ, Peters JR, Heithaus MR, Fourqurean JW, Burkepile DE (2016) Reefscapes of fear: predation risk and reef heterogeneity interact to shape herbivore foraging behaviour. *Journal of Animal Ecology* 85: 146-156

Chaves LTC, Pereira PHC, Feitosa JLL (2013) Coral reef fish association with macroalgal beds on a tropical reef system in North-eastern Brazil. *Marine and Freshwater Research* 64: 1101-1111

Cheal A, Emslie M, Miller I, Sweatman H (2012) The distribution of herbivorous fishes on the Great Barrier Reef. *Marine Biology* 159: 1143-1154

Cheal AJ, MacNeil MA, Cripps E, Emslie MJ, Jonker M, Schaffelke B, Sweatman H (2010) Coral-macroalgal phase shifts or reef resilience: links with diversity and functional roles of herbivorous fishes on the Great Barrier Reef. *Coral Reefs* 29: 1005-1015

Chesson P (2000) General theory of competitive coexistence in spatially-varying environments. *Theoretical Population Biology* 58: 211-237

Choat JH, Robbins WD, Clements KD (2004) The trophic status of herbivorous fishes on coral reefs. II. Food processing modes and trophodynamics. *Marine Biology* 145: 445-454

Chong-Seng KM, Nash KL, Bellwood DR, Graham NAJ (2014) Macroalgal herbivory on recovering versus degrading coral reefs. *Coral Reefs* 33: 409-419

Christensen JD, Jeffrey CFG, Caldow C, Monaco ME, Kendall MS, Appeldoorn RS (2003) Cross-shelf habitat utilization patterns of reef fishes in Southwestern Puerto Rico. *Gulf and Caribbean Research* 14: 9-27

Clarke KR, Somerfield PJ, Chapman MG (2006) On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. *Journal of Experimental Marine Biology and Ecology* 330: 55-80

Clements KD, Choat JH (1997) Comparison of herbivory in the closely-related marine fish genera *Girella* and *Kyphosus*. *Marine Biology* 127: 579-586

Clements KD, German DP, Piché J, Tribollet A, Choat JH (2017) Integrating ecological roles and trophic diversification on coral reefs: multiple lines of evidence identify parrotfishes as microphages. *Biological Journal of the Linnean Society* 120: 729-751

Cocheret de la Morinière E, Pollux BJA, Nagelkerken I, van der Velde G (2002) Post-settlement life cycle migration patterns and habitat preference of coral reef fish that use seagrass and mangrove habitats as nurseries. *Estuarine, Coastal and Shelf Science* 55: 309-321

Colossi Brustolin M, Nagelkerken I, Moitinho Ferreira C, Urs Goldenberg S, Ullah H, Fonseca G (2019) Future ocean climate homogenizes communities across habitats through diversity loss and rise of generalist species. *Global Change Biology* 25: 3539-3548

Connell JH (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42: 710-723

Connell JH (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. *The American Naturalist* 122: 661-696

Coro G, Bjerregaard Walsh M (2021) An intelligent and cost-effective remote underwater video device for fish size monitoring. *Ecological Informatics* 63: 101311

Cronin G, Hay ME (1996) Susceptibility to herbivores depends on recent history of both the plant and animal. *Ecology* 77: 1531-1543

Cushman SA (2006) Effects of habitat loss and fragmentation on amphibians: a review and prospectus. *Biological Conservation* 128: 231-240

Cvitanovic C, Bellwood DR (2009) Local variation in herbivore feeding activity on an inshore reef of the Great Barrier Reef. *Coral Reefs* 28: 127-133

Cvitanovic C, Hoey AS (2010) Benthic community composition influences within-habitat variation in macroalgal browsing on the Great Barrier Reef. *Marine and Freshwater Research* 61: 999-1005

Dahlgren CP, Eggleston DB (2000) Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology* 81: 2227-2240

Dahlgren CP, Kellison GT, Adams AJ, Gillanders BM, Kendall MS, Layman CA, Ley JA, Nagelkerken I, Serafy JE (2006) Marine nurseries and effective juvenile habitats: concepts and applications. *Marine Ecology Progress Series* 312: 291-295

Dalzell P, Adams TJH, Polunin NVC (1996) Coastal fisheries in the Pacific Islands. *Oceanography and Marine Biology: an Annual Review* 34: 395-531

Darling ES, Graham NAJ, Januchowski-Hartley FA, Nash KL, Pratchett MS, Wilson SK (2017) Relationships between structural complexity, coral traits, and reef fish assemblages. *Coral Reefs* 36: 561-575

Davis JP, Pitt JA, Olds AD, Harborne AR, Connolly RM (2017) Seagrass corridors and tidal state modify how fish use habitats on intertidal coral reef flats. *Marine Ecology Progress Series* 581: 135-147

Day J, Fernandes L, Lewis A, De'ath G, Slegers S, Barnett B, Kerrigan B, Breen D, Innes J, Oliver J, Ward T, Lowe D (2002) The Representative Areas Program for protecting biodiversity in the Great Barrier Reef World Heritage Area. In *Proceedings of the Ninth International Coral Reef Symposium, Bali, 23-27 October 2000* pp 687-696

de la Torre-Castro M, Di Carlo G, Jiddawi NS (2014) Seagrass importance for a small-scale fishery in the tropics: the need for seascape management. *Marine Pollution Bulletin* 83: 398-407

De'ath G, Fabricius K (2010) Water quality as a regional driver of coral biodiversity and macroalgae on the Great Barrier Reef. *Ecological Applications* 20: 840-850

De'ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proceedings of the National Academy of Sciences of the United States of America* 109: 17995-17999

Dennis GD (1992) Island mangrove habitats as spawning and nursery areas for commercially important fishes in the Caribbean. *Proceedings of the 41st Gulf and Caribbean Fisheries Institute* 205-225

Dixson DL, Abrego D, Hay ME (2014) Chemically mediated behavior of recruiting corals and fishes: a tipping point that may limit reef recovery. *Science* 345: 892-897

Dollar SJ (1982) Wave stress and coral community structure in Hawaii. *Coral Reefs* 1: 71-81

Dorenbosch M, Grol MGG, Christianen MJA, Nagelkerken I, van der Velde G (2005a) Indo-Pacific seagrass beds and mangroves contribute to fish density and diversity on adjacent coral reefs. *Marine Ecology Progress Series* 302: 63-76

Dorenbosch M, Grol MGG, de Groene A, van der Velde G, Nagelkerken I (2009) Piscivore assemblages and predation pressure affect relative safety of some back-reef habitats for juvenile fish in a Caribbean bay. *Marine Ecology Progress Series* 379: 181–196

Dorenbosch M, Grol MGG, Nagelkerken I, van der Velde G (2005b) Distribution of coral reef fishes along a coral reef-seagrass gradient: edge effects and habitat segregation. *Marine Ecology Progress Series* 299: 277-288

Dorenbosch M, Grol MGG, Nagelkerken I, van der Velde G (2006a) Different surrounding landscapes may result in a different fish assemblages in East African seagrass beds. *Hydrobiologia* 563: 45-60

Dorenbosch M, Grol MGG, Nagelkerken I, van der Velde G (2006b) Seagrass beds and mangroves as potential nurseries for the threatened Indo-Pacific humphead wrasse, *Cheilinus undulatus* and Caribbean rainbow parrotfish, *Scarus guacamaia*. *Biological Conservation* 129: 277-282

Dorenbosch M, van Riel MC, Nagelkerken I, van der Velde G (2004) The relationship of reef fish densities to the proximity of mangrove and seagrass nurseries. *Estuarine, Coastal and Shelf Science* 60: 37-48

Dormann CF, Schweiger O, Augenstein I, Bailey D, Billeter R, de Blust G, DeFilippi R, Frenzel M, Henrickx F, Herzog F, Klotz S, Liira J, Maelfait JP, Schmidt T, Speelmans M, van Wingerden WKRE, Zobel M (2007) Effects of landscape structure and land-use intensity on similarity of plant and animal communities. *Global Ecology and Biogeography* 16: 774-787

Draisma SGA, Prud'homme van Reine WF, Herandarudewi SMC, Hoeksema BW (2018) Macroalgal diversity along an inshore-offshore environmental gradient in the Jakarta Bay – Thousand Islands reef complex, Indonesia. *Estuarine, Coastal and Shelf Science* 200: 258-269

Drew CA, Eggleston DB (2008) Juvenile fish densities in Florida Keys mangroves correlate with landscape characteristics. *Marine Ecology Progress Series* 362: 233-243

Duarte CM, Agusti S, Barbier E, Britten GL, Castilla JC, Gattuso J-P, Fulweiler RW, Hughes TP, Knowlton N, Lovelock CE, Lotze HK, Predragovic M, Poloczanska E, Roberts C, Worm B (2020) Rebuilding marine life. *Nature* 580: 39-51

Duarte CM, Dennison WC, Orth RJW, Carruthers TJB (2008) The charisma of coastal ecosystems: addressing the balance. *Estuaries and Coasts* 31: 233-238

Dubuc A, Walthan NJ, Baker R, Marchand C, Sheaves M (2019) Patterns of fish utilization in a tropical Indo-Pacific mangrove-coral seascape, New Caledonia. *PLoS One* 14: e0207168

Duke NC, Meynecke J-O, Dittman S, Ellison AM, Anger K, Berger U, Cannicci S, Diele K, Ewel KC, Field CD, Koedam N, Lee SY, Marchand C, Nordhaus I, Dahdouh-Guebas F (2007) A world without mangroves? *Science* 317: 41-42

Dulvy NK, Polunin NVC (2004) Using informal knowledge to infer human-induced rarity of a conspicuous reef fish. *Animal Conservation* 7: 365-374

Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological processes that affect populations in complex landscapes. *Oikos* 65: 169-175

Ebrahim A, Bijoux JP, Mumby PJ, Tibbetts IR (2020) The commercially important shoemaker spinefoot, *Siganus sutor*, connects coral reefs to neighbouring seagrass meadows. *Journal of Fish Biology* 96: 1034-1044

Edwards HJ, Elliott IA, Pressey RL, Mumby PJ (2010) Incorporating ontogenetic dispersal, ecological processes and conservation zoning into reserve design. *Biological Conservation* 143: 457-470

Eggertsen L, Ferreira CEL, Fontoura L, Kautsky N, Gullström M, Berkström C (2017) Seaweed beds support more juvenile reef fish than seagrass beds in a south-western Atlantic tropical seascape. *Estuarine, Coastal and Shelf Science* 196: 97-108

Eggertsen M, Chacin DH, Åkerlund C, Halling C, Berkström C (2019) Contrasting distribution and foraging patterns of herbivorous and detritivorous fishes across multiple habitats in a tropical seascape. *Marine Biology* 166: 1-16

Eggertsen M, Chacin DH, van Lier J, Eggertsen L, Fulton CJ, Wilson S, Halling C, Berkström C (2020a) Seascape configuration and fine-scale habitat complexity shape parrotfish distribution and function across a coral reef lagoon. *Diversity* 12: 391

Eggertsen L, Goodell W, Cordeiro CAMM, Mendes TC, Longo GO, Ferreira CEL, Berkström C (2020b) Seascape configuration leads to spatially uneven delivery of parrotfish herbivory across a Western Indian Ocean seascape. *Diversity* 12:434

Elith J, Leathwick J (2017) Boosted Regression Trees for ecological modeling. R Documentation. Available online: https://cran. r-project.org/web/packages/dismo/vignettes/brt.pdf

Elith J, Leathwick JR, Hastie T (2008) A working guide to boosted regression trees. *Journal of Animal Ecology* 77: 802-813

Ellison AM, Bank MS, Clinton BD, Colburn EA, Elliott K, Ford CR, Foster DR, Kloeppel BD, Knoepp JD, Lovett GM, Mohan J, Orwig DA, Rodenhouse NL, Sobczak WV, Stinson KA, Stone JK, Swan CM, Thompson J, Von Holle B, Webster JR (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment.* 2: 479-486

Elmqvist T, Folke C, Nyström M, Peterson G, Bengtsson J, Walker B, Norberg J (2003) Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment* 9: 488-494

Emlen JM (1966) The role of time and energy in food preference. *The American Naturalist* 100: 611-617

Espadero ADA, Nakamura Y, Uy WH, Tongnunui P, Horinouchi M (2020) Tropical intertidal seagrass beds: an overlooked foraging habitat for fishes revealed by underwater videos. *Journal of Experimental Marine Biology and Ecology* 526: 151353

Estes JA, Palmisano JF (1974) Sea otters: their role in structuring nearshore communities. *Science* 185: 1058-1060

Evans RD, Wilson SK, Field SN, Moore JAY (2014) Importance of macroalgal fields as coral reef fish nursery habitat in north-west Australia. *Marine Biology* 161: 599-607

Fabricius K, De'ath G (2001) Environmental factors associated with the spatial distribution of crustose coralline algae on the Great Barrier Reef. *Coral Reefs* 19: 303-309

Fagan WF, Cantrell RS, Cosner C (1999) How habitat edges change species interactions. *The American Naturalist* 153: 165-182

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34: 487-515

Fahrig L (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography* 40: 1649-1663

Fahrig L, Baudry J, Brotons L, Burel FG, Crist TO, Fuller RJ, Sirami C, Siriwardena GM, Martin J (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters* 14: 101-112

Feary DA, Cinner JE, Graham NAJ, Januchowski-Hartley FA (2011) Effects of customary marine closures on fish behavior, spear-fishing success, and underwater visual surveys. *Conservation Biology* 25: 341-349

Fernandes L, Day J, Lewis A, Slegers S, Kerrigan B, Breen D, Cameron D, Jago B, Hall J, Lowe D, Innes J, Tanzer J, Chadwick V, Thompson L, Gorman K, Simmons M, Barnett B, Sampson K, De'ath G, Mapstone B, Marsh H, Possingham H, Ball I, Ward T, Dobbs K, Aumend J, Slater D, Stapleton K (2005) Establishing representative no-take areas in the Great Barrier Reef: large-scale implementation of theory on Marine Protected Areas. *Conservation Biology* 19: 1733-1744

Fischer J, Lindenmayer DB (2007) Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography* 16: 265-280

Fisher R, Stark C, Ridd P, Jones R (2015) Spatial patterns in water quality changes during dredging in tropical environments. *PLoS ONE* 10: e0143309

Foale S, Adhuri D, Aliño P, Allison EH, Andrew N, Cohen P, Evans L, Fabinyi M, Fidelman P, Gregory C, Stacey N, Tanzer J, Weeratunge N (2013) Food security and the Coral Triangle Initiative. *Marine Policy* 38: 174-183

Ford AK, Bejarano S, Marshell A, Mumby PJ (2016) Linking the biology and ecology of key herbivorous unicornfish to fisheries management in the Pacific. *Aquatic Conservation: Marine and Freshwater Ecosystems* 26: 790-805

Fox RJ, Bellwood DR (2007) Quantifying herbivory across a coral reef depth gradient. *Marine Ecology Progress Series* 339: 49-59

Fox RJ, Bellwood DR (2008) Remote video bioassays reveal the potential feeding impact of the rabbitfish *Siganus canaliculatus* (f: Siganidae) on an inner-shelf reef of the Great Barrier Reef. *Coral Reefs* 27: 605-615

Fox RJ, Sunderland TL, Hoey AS, Bellwood DR (2009) Estimating ecosystem function: contrasting roles of closely related herbivorous rabbitfishes (Siganidae) on coral reefs. *Marine Ecology Progress Series* 385: 261-269

Fretwell SD, Lucas HL (1970) On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* 19: 16-36

Frieler K, Meinshausen M, Golly A, Mengel M, Lebek K, Donner SD, Hoegh-Guldberg O (2013) Limiting global warming to 2°C is unlikely to save most coral reefs. *Nature Climate Change* 3: 165-170

Froese R, Pauly D (Eds) (2018) *FishBase*. www.fishbase.org

Froese R, Pauly D (Eds) (2019) *FishBase*. www.fishbase.org

Froese R, Pauly D (Eds) (2021) *FishBase*. www.fishbase.org

Fulton CJ, Abesamis RA, Berkström C, Depczynski M, Graham NAJ, Holmes TH, Kulbicki M, Noble MM, Radford BT, Tano S, Tinkler P, Wernberg T, Wilson SK (2019) Form and function of tropical macroalgal reefs in the Anthropocene. *Functional Ecology* 33: 989-999

Fulton CJ, Bellwood DR (2002) Patterns of foraging in labrid fishes. *Marine Ecology Progress Series* 226: 135-142

Fulton CJ, Berkström C, Wilson SK, Abesamis RA, Bradley M, Åkerlund C, Barrett LT, Bucol AA, Chacin DH, Chong-Seng KM, Coker DJ, Depczynski M, Eggertsen L, Eggertsen M, Ellis D, Evans RD, Graham NAH, Hoey AS, Holmes TH, Kulbicki M, Leung PTY, Lam PKS, van Lier J, Matis PA, Noble MM, Pérez-Matus A, Piggott C, Radford BT, Tano S, Tinkler P (2020) Macroalgal meadow habitats support fish and fisheries in diverse tropical seascapes. *Fish and Fisheries* 00: 1-18

Gajdzik L, Aguilar-Medrano R, Frédérich B (2019) Diversification and functional evolution of reef fish feeding guilds. *Ecology Letters* 22: 572-582

Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. *Science* 301: 958-960

Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR (2005) Hurricanes and Caribbean coral reefs: impacts, recovery patterns, and role in long-term decline. *Ecology* 86: 174-184

Gaynor KM, Brown JS, Middleton AD, Power ME, Brashares JS (2019) Landscapes of fear: spatial patterns of risk perception and response. *Trends in Ecology and Evolution* 34: 355-368

Gil MA, Zill J, Ponciano JM (2017) Context-dependent landscape of fear: algal density elicits risky herbivory in a coral reef. *Ecology* 98: 534-544

Gilby BL, Olds AD, Connolly RM, Henderson CJ, Schlacher TA (2018) Spatial restoration ecology: placing restoration in a landscape context. *BioScience* 68: 1007-1019

Gilby BL, Tibbetts IR, Olds AD, Maxwell PS, Stevens T (2016) Seascape context and predators override water quality effects on inshore coral reef fish communities. *Coral Reefs* 35: 979-990

Gillanders BM, Able KW, Brown JA, Eggleston DB, Sheridan PF (2003) Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. *Marine Ecology Progress Series* 247: 281-295

Gillet R (2014) Pacific Perspectives on fisheries and sustainable development. United Nations Economic and Social Commission for Asia and the Pacific, Fiji p 62

Goldberg L, Lagomasino D, Thomas N, Fatoyinbo T (2020) Global declines in human-driven mangrove loss. *Global Change Biology* 26: 5844-5855

Gotanda KM, Turgeon K, Kramer DL (2009) Body size and reserve protection affect flight initiation distances in parrotfishes. *Behavioral Ecology and Sociobiology* 63: 1563-1572

Gove JM, Williams GJ, McManus MA, Clark SJ, Ehses JS, Wedding LM (2015) Coral reef benthic regimes exhibit non-linear threshold responses to natural physical drivers. *Marine Ecology Progress Series* 522: 33-48

Graham NAJ, Bellwood DR, Cinner JE, Hughes TP, Norström AV, Nyström M (2013a) Managing resilience to reverse phase shifts in coral reefs. *Frontiers in Ecology and the Environment* 11: 541-548

Graham NAJ, Cinner JE, Norström AV, Nyström M (2013b) Coral reefs as novel ecosystems: embracing new futures. *Current Opinion in Environmental Sustainability 7*: 9-14

Graham NAJ, Jennings S, MacNeil MA, Mouillot D, Wilson SK (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature* 518: 94-97

Graham NAJ, Nash KL (2013) The importance of structural complexity in coral reef ecosystems. *Coral Reefs* 32: 315-326

Graham NAJ, Nash KL, Kool JT (2011) Coral reef recovery dynamics in a changing world. *Coral Reefs* 30: 283-294

Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Bijoux JP (2006) Dynamic fragility of oceanic coral reef ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* 103: 8425-8429

Grandcourt E, Al Abdessalaam T, Francis F, Al Shamsi A (2007) Population biology and assessment of the white-spotted spinefoot, *Siganus canaliculatus* (Park, 1797), in the southern Arabian Gulf. *Journal of Applied Ichthyology* 23: 53-59

Gratwicke B, Speight MR (2005) The relationships between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *Journal of Fish Biology* 66: 650-667

Green A, Smith SE, Lipsett-moore G, Groves C, Peterson N, Sheppard S, Lokani P, Hamilton R, Almany J, Aitsi J, Bualia L (2009) Designing a resilient network of marine protected areas for Kimbe Bay, Papua New Guinea. *Oryx* 43: 488-498

Green AL (1996) Spatial, temporal and ontogenetic patterns of habitat use by coral reef fishes (Family Labridae). *Marine Ecology Progress Series* 133: 1-11

Green AL, Maypa AP, Almany GR, Rhodes KL, Weeks R, Abesamis RA, Gleason MG, Mumby PJ, White AT (2015) Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biological Reviews* 90: 1215-1247

Green BC, Smith DJ, Underwood GJC (2012) Habitat connectivity and spatial complexity differentially affect mangrove and salt marsh fish assemblages. *Marine Ecology Progress Series* 466: 177-192

Grober-Dunsmore R, Frazer TK, Beets J, Funicelli N, Zwick PD (2004) The significance of adjacent habitats on reef fish assemblage structure: are relationships detectable and quantifiable at a landscape-scale? *55th Gulf and Caribbean Fisheries Institute* 713-734

Grober-Dunsmore R, Frazer TK, Beets JP, Lindberg WJ, Zwick P, Funicelli NA (2008) Influence of landscape structure on reef fish assemblages. *Landscape Ecology* 23: 37-53

Grober-Dunsmore R, Frazer TK, Beets JP, Lindberg WJ, Zwick P, Funicelli NA (2007) Reef fish and habitat relationships in a Caribbean seascape: the importance of reef context. *Coral Reefs* 26: 201-216

Grober-Dunsmore R, Pittman SJ, Caldow S, Kendall MS, Frazer TK (2009) A landscape ecology approach for the study of ecological connectivity across tropical marine seascapes. In: Nagelkerken I (Ed). *Ecological connectivity among tropical coastal ecosystems.* Springer Dordrecht pp 493-530

Grol MGG, Dorenbosch M, Kokkelmans EM, Nagelkerken I (2008) Mangroves and seagrass beds do not enhance growth of early juveniles of a coral reef fish. *Marine Ecology Progress Series* 366: 137-146

Grol MGG, Nagelkerken I, Bosch N, Meesters EH (2011a) Preference of early juveniles of a coral reef fish for distinct lagoonal microhabitats is not related to common measures of structural complexity. *Marine Ecology Progress Series* 432: 221-233

Grol MGG, Nagelkerken I, Rypel AL, Layman CA (2011b) Simple ecological trade-offs give rise to emergent cross-ecosystem distributions of a coral reef fish. *Oecologia* 165: 79-88

Grol MGG, Rypel AL, Nagelkerken I (2014) Growth potential and predation risk drive ontogenetic shifts among nursery habitats in a coral reef fish. *Marine Ecology Progress Series* 502: 229-244

Grüss A, Kaplan DM, Guénette S, Roberts CM, Botsford LW (2011) Consequences of adult and juvenile movement for marine protected areas. *Biological Conservation* 144: 692-702

Gullström M, Bodin M, Nilsson PG, Öhman MC (2008) Seagrass structural complexity and landscape configuration as determinants of tropical fish assemblage composition. *Marine Ecology Progress Series* 363: 241-255

Hairston NG, Smith FE, Slobodkin LB (1960) Community structure, population control, and competition. *The American Naturalist* 94: 421-425

Hale R, Blumstein DT, Mac Nally R, Swearer SE (2020) Harnessing knowledge of animal behaviour to improve habitat restoration outcomes. *Ecosphere* 11: e03104

Halpern BS, Frazier M, Afflerbach J, Lowndes JS, Micheli F, O'Hara C, Scarborough C, Selkoe KA (2019) Recent pace of change in human impact on the world's ocean. *Scientific Reports* 9: 1-8

Hamilton RJ, Almany GR, Brown CJ, Pita J, Peterson NA, Choat JH (2017) Logging degrades nursery habitat for an iconic coral reef fish. *Biological Conservation* 210: 273-280

Hamilton SE, Casey D (2016) Creation of a high spatio-temporal resolution global database of continuous mangrove forest cover for the 21st century (CGMFC-21). *Global Ecology and Biogeography* 25: 729-738

Hamylton SM (2017) Spatial analysis of coastal environments. Cambridge University Press, Cambridge, United Kingdom

Hamylton SM, Barnes RSK (2018) The effect of sampling effort on spatial autocorrelation in microbenthic intertidal invertebrates. *Hydrobiologia* 811: 239-250

Harborne AR, Mumby PJ, Kappel CV, Dahlgren CP, Micheli F, Holmes KE, Brumbaugh DR (2008) Tropical coastal habitats as surrogates of fish community structure, grazing, and fisheries value. *Ecological Applications* 18: 1689–1701

Harborne AR, Mumby PJ, Kennedy EV, Ferrari R (2011) Biotic and multi-scale abiotic controls of habitat quality: their effect on coral-reef fishes. *Marine Ecology Progress Series* 437: 201-214

Harborne AR, Nagelkerken I, Wolff NH, Bozec Y-M, Dorenbosch M, Grol MGG, Mumby PJ (2016a) Direct and indirect effects of nursery habitats on coral-reef fish assemblages, grazing pressure and benthic dynamics. *Oikos* 125: 957-967

Harborne AR, Talwar B, Brooks EJ (2016a) The conservation implications of spatial and temporal variability in the diurnal use of Bahamian tidal mangrove creeks by transient predatory fishes. *Aquatic Conservation: Marine and Freshwater Ecosystems* 26: 202-211

Harrison HB, Bode M, Williamson DH, Berumen ML, Jones GP (2020) A connectivity portfolio effect stabilizes marine reserve performance. *Proceedings of the National Academy of Sciences of the United States of America* 117: 25595-25600

Harun-or-Rashid S, Biswas SR, Böcker R, Kruse M (2009) Mangrove community recovery potential after catastrophic disturbances in Bangladesh. *Forest Ecology and Management* 257: 923-930

Hasse JJ, Madraisau BB, McVey JP (1977) Some aspects of the life history of *Siganus canaliculatus* (Park) (Pisces: Siganidae) in Palau. *Micronesica* 13: 297-312

Heck Jr KL, Carruthers TJB, Duarte CM, Hughes AR, Kendrick G, Orth RJ, Williams SW (2008) Trophic transfers from seagrass meadows subsidize diverse marine and terrestrial consumers. *Ecosystems* 11: 1198-1210

Heck Jr KL, Orth RJ (1980) Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and mobile macro- invertebrate assemblages. In: Kennedy VS (Ed) *Estuarine Perspectives*. Academic Press, New York, pp 449-462

Heck KL, Wetstone GS (1977) Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. *Journal of Biogeography* 4: 135-142

Hedberg P, Rybak FF, Gullström M, Jiddawi NS, Winder M (2018) Fish larvae distribution among different habitats in coastal East Africa. *Journal of Fish Biology* 94: 29-39

Heidmann SL, Jossart J, Kimble M, Nemeth RS (2021) Home range characteristics and diel patterns in space use of mutton snapper, *Lutjanus analis*, in St. Thomas, US Virgin Islands. *Animal Biotelemetry* 9: 15

Hein MY, Vardi T, Shaver EC, Pioch S, Boström-Einarsson L, Ahmed M, Grimsditch G, McLeod IM (2021) Perspectives on the use of coral reef restoration as a strategy to support and improve reef ecosystem services. *Frontiers in Marine Science* 8: 618303

Henderson CJ, Olds AD, Lee SY, Gilby BL, Maxwell PS, Connolly RM, Stevens T (2017) Marine reserves and seascape context shape fish assemblages in seagrass ecosystems. *Marine Ecology Progress Series* 566: 135-144

Hijmans RJ, Elith J (2017) Species distribution modelling with R. R CRAN Project

Hitt S, Pittman SJ, Nemeth RS (2011) Diel movements of fishes linked to benthic seascape structure in a Caribbean coral reef ecosystem. *Marine Ecology Progress Series* 427: 275-291

Hixon MA, Beets JP (1993) Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs* 63: 77-101

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME (2007) Coral reefs under rapid climate change and ocean acidification. *Science* 318: 1737-1742

Hoegh-Guldberg O, Poloczanska ES, Skirving W, Dove S (2017) Coral reef ecosystems under climate change and ocean acidification. *Frontiers in Marine Science* 4: 158

Hoekstra JM, Boucher TM, Ricketts TH, Roberts C (2005) Confronting a biome crisis: global disparities of habitat loss and protection. *Ecology Letters* 8: 23-29

Hoey AS, Bellwood DR (2008) Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. *Coral Reefs* 27: 37-47

Hoey AS, Bellwood DR (2009) Limited functional redundancy in a high diversity system: single species dominates key ecological process on coral reefs. *Ecosystems* 12: 1316-1328

Hoey AS, Bellwood DR (2010a) Cross-shelf variation in browsing intensity on the Great Barrier Reef. *Coral Reefs* 29: 499-508

Hoey AS, Bellwood DR (2010b) Among-habitat variation in herbivory on *Sargassum* spp. on a mid-shelf reef in the northern Great Barrier Reef. *Marine Biology* 157: 189-200

Hoey AS, Bellwood DR (2011) Suppression of herbivory by macroalgal density: a critical feedback on coral reefs? *Ecology Letters* 14: 267-273

Hoey AS, Bonaldo RM (2018) *Biology of parrotfishes.* Taylor & Francis, London, UK

Hoey AS, Brandl SJ, Bellwood DR (2013) Diet and cross-shelf distribution of rabbitfishes (f. Siganidae) on the northern Great Barrier Reef: implications for ecosystem function. *Coral Reefs* 32: 973-984

Hogan JD, Thiessen RJ, Sale PF, Heath DD (2012) Local retention, dispersal and fluctuating connectivity among populations of a coral reef fish. *Oecologia* 168: 61-71

Holbrook SJ, Carr MG, Schmitt RJ, Coyer JA (1990) Effect of giant kelp on local abundance of reef fishes: the importance of ontogenetic resource requirements. *Bulletin of Marine Science* 47: 104-114

Holland JD, Bert DG, Fahrig L (2004) Determining the spatial scale of species' response to habitat. *BioScience* 54: 227-233

Honda K, Uy WH, Baslot DI, Pantallano ADS, Nakamura Y, Nakaoka M (2016) Diel habitat-use patterns of commercially important fishes in a marine protected area in the Philippines. *Aquatic Biology* 24: 153-174

Horinouchi M (2007) Review of the effects of within-patch scale structural complexity on seagrass fishes. *Journal of Experimental Marine Biology and Ecology* 350: 111-129

Hughes L (2000) Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution* 15: 56-61

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

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nyström M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate change, human impacts, and the resilience of coral reefs. *Science* 301: 929-933

Hughes TP, Barnes ML, Bellwood DR, Cinner JE, Cumming GS, Jackson JBC, Kleypas J, van de Leemput IA, Lough JM, Morrison TH, Palumbi SR, van Nes EH, Scheffer M (2017b) Coral reefs in the Anthropocene. *Nature* 546: 82-90

Hughes TP, Bellwood DR, Folke CS, McCook LJ, Pandolfi JM (2007b) No-take areas, herbivory, and coral reef resilience. *Trends in Ecology and Evolution* 22: 1-3

Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, Baird AH, Babcock RC, Beger M, Bellwood DR, Berkelmans R, Bridge TC, Butler IR, Byrne M, Cantin NE, Comeau S, Connolly SR, Cumming GS, Dalton SJ, Diaz-Pulido G, Eakin CM, Figueira WF, Gilmour JP, Harrison HB, Heron SF, Hoey AS, Hobbs JA, Hoogenboom MO, Kennedy EV, Kuo C, Lough JM, Lowe RJ, Liu G, McCulloch MT, Malcolm HA, McWilliam MJ, Pandolfi JM, Pears RJ, Pratchett MS, Schoepf V, Simpson T, Skirving WJ, Sommer B, Torda G, Wachenfeld DR, Willis BL, Wilson SK (2017a) Global warming and recurrent mass bleaching of corals. *Nature* 543: 373-377

Hughes TP, Kerry JT, Baird AH, Connolly SR, Dietzel A, Eakin CM, Heron SF, Hoey AS, Hoogenboom MO, Liu G, McWilliam MJ, Pears RJ, Pratchett MS, Skirving WJ, Stella JS, Torda G (2018) Global warming transforms coral reef assemblages. *Nature* 556: 492-496

Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L, Moltschaniwskyj N, Pratchett MS, Steneck RS, Willis B (2007a) Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology* 17: 360-365

Hunt JC, Seibel BA (2000) Life history of *Gonatus onyx* (Cephalopoda: Teuthoidea): ontogenetic changes in habitat, behaviour and physiology. *Marine Biology* 136: 543-552

Hutchinson GE (1957) Population studies: animal ecology and demography: concluding remarks. *Cold Spring Harbour Symposium on Quantitative Biology* 22: 415-427

Hyndes GA, Kendrick AJ, MacArthur LD, Stewart E (2003) Differences in the species- and size-composition of fish assemblages in three distinct seagrass habitats with differing plant and meadow structure. *Marine Biology* 142: 1195-1206

Hyndes GA, Nagelkerken I, McLeod RJ, Connolly RM, Lavery PS, Vanderklift MA (2014) Mechanisms and ecological role of carbon transfer within coastal seascapes. *Biological Reviews* 89: 232-254

Igulu MM, Nagelkerken I, Dorenbosch M, Grol MGG, Harborne AR, Kimirei IA, Mumby PJ, Olds AD, Mgaya YD (2014) Mangrove habitat use by juvenile reef fish: meta-analysis reveals that tidal regime matters more than biogeographic region. *PLoS ONE* 9: e114715

IUCN (2018) The IUCN Red List of Threatened Species. Version 2018-1. www.iucnredlist.org

Jackson HB, Fahrig L (2015) Are ecologists conducting research at the optimal scale? *Global Ecology and Biogeography* 24: 52-63

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293: 629-637

Jackson MV, Carrasco LR, Choi CY, Li J, Ma Z, Melville DS, Mu T, Peng HB, Woodworth BK, Yang Z, Zhang L, Fuller RA (2019) Multiple habitat use by declining migratory birds necessitates joined-up conservation. *Ecology and Evolution* 9: 2505-2515

Jankowski MW, Graham NAJ, Jones GP (2015) Depth gradients in diversity, distribution and habitat specialisation in coral reef fishes: implications for the depth-refuge hypothesis. *Marine Ecology Progress Series* 540: 203-215

Jaxion-Harm J, Saunders J, Speight MR (2011) Distribution of fish in seagrass, mangroves and coral reefs: life-stage dependent habitat use in Honduras. *Revista de Biología Tropical* 60: 683-698

Jones GP, Almany GR, Russ GR, Sale PF, Steneck RS, van Oppen MJH, Willis BL (2009) Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. *Coral Reefs* 28: 307-325

Jones GP, McCormick MI, Srinivasan M, Eagle JV (2004) Coral decline threatens fish biodiversity in marine reserves. *Proceedings of the National Academy of Sciences of the United States of America* 101: 8251-8253

Jones KMM (2005) Home range areas and activity centres in six species of Caribbean wrasses (Labridae). *Journal of Fish Biology* 66: 150-166

Joyce KE, Duce S, Leahy SM, Leon J, Maier SW (2018) Principles and practice of acquiring drone-based image data in marine environments. *Marine and Freshwater Research* 70: 952-963

Kahng SE, Garcia-Sais JR, Spalding HL, Brokovich E, Wagner D, Weil E, Hinderstein L, Toonen RJ (2010) Community ecology of mesophotic coral reef ecosystems. *Coral Reefs* 29: 255-275

Kendall MS (2005) A method for investigating seascape ecology of reef fish. *56th Gulf and Caribbean Fisheries Institute* 355-366

Kendall MS, Miller TJ, Pittman SJ (2011) Patterns of scale-dependency and the influence of map resolution on the seascape ecology of reef fish. *Marine Ecology Progress Series* 427: 259-274

Kimirei IA, Nagelkerken I, Griffioen B, Wagner C, Mgaya YD (2011) Ontogenetic habitat use by mangrove/seagrass-associated coral reef fishes shows flexibility in time and space. *Estuarine, Coastal and Shelf Science* 92: 47-58

Kimirei IA, Nagelkerken I, Mgaya YD, Huijbers CM (2013a) The mangrove nursery paradigm revisited: otolith stable isotopes support nursery-to-reef movements by Indo-Pacific fishes. *PLoS ONE* 8: e66320

Kimirei IA, Nagelkerken I, Trommelen M, Blankers P, van Hoytema N, Hoeijmakers D, Huijbers CM, Mgaya YD, Rypel AL (2013b) What drives ontogenetic niche shifts of fishes in coral reef ecosystems? *Ecosystems* 16: 783-796

Kingsbury KM, Gillanders BM, Booth DJ, Nagelkerken I (2019) Trophic niche segregation allows range-extending coral reef fishes to co-exist with temperate species under climate change. *Global Change Biology* 26: 721-733

Klemetsen A, Amundsen PA, Dempson JB, Jonsson B, Jonsson N, O'Connell MF, Mortensen E (2003) Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish* 12: 1-59

Kleypas J, Allemand D, Anthony K, Baker AC, Beck MW, Zeitlin Hale L, Hilmi N, Hoegh-Guldberg O, Hughes T, Kaufman L, Kayanne H, Magnan AK, Mcleod E, Mumby P, Palumbi S, Richmond RH, Rinkevich B, Steneck RS, Voolstra CR, Wachenfeld D, Gattuso J-P (2021) Designing a blueprint for coral reef survival. *Biological Conservation* 257: 109107

Kopp D, Bouchon-Navaro Y, Louis M, Bouchon C (2007) Diel differences in the seagrass fish assemblages of a Caribbean island in relation to adjacent habitat types. *Aquatic Botany* 87: 31-37

Kotliar NB, Wiens JA (1990) Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59: 253-260

Kramer DL, Chapman MR (1999) Implications of fish home range size and relocation for marine reserve function. *Environmental Biology of Fishes* 55: 65-79

Kremen C, Williams NM, Aizen MA, Gemmill-Herren B, LeBuhn G, Minckley R, Packer L, Potts SG, Roulston T, Steffan-Dewenter I, Vázquez P, Winfree R, Adams L, Crone EE, Greenleaf SS, Keitt TH, Klein AM, Regetz J, Ricketts TH (2007) Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology Letters* 10: 299-314

Krumme U (2009) Diel and tidal movements by fish and decapods linking tropical coastal ecosystems. In: Nagelkerken I (Ed). *Ecological connectivity among tropical coastal ecosystems.* Springer Dordrecht pp 271-324

Kruse M, Taylor M, Muhando CA, Reuter H (2018) Lunar, diel, and tidal changes in fish assemblages in an East African marine reserve. *Regional Studies in Marine Science* 3: 49-57

Kuempel CD, Altieri AH (2017) The emergent role of small-bodied herbivores in pre-empting phase shifts on degraded coral reefs. *Nature Scientific Reports* 7: 39670

Kuffner IBLJ, Walters MA, Becerro VJ, Paul R, Ritson-Williams, Beach KS (2006) Inhibition of coral recruitment by macroalgae and cyanobacteria. *Marine Ecology Progress Series* 323: 107-117

Kulbicki M, Guillemot N, Amand M (2005) A general approach to length-weight relationships for New Caledonia lagoon fishes. *Cybium* 29: 235-252

Kulbicki M, Mou-Tham G, Thollot P, Wantiez L (1993) Length-weight relationships of fish from the lagoon of New Caledonia. *NAGA* 16: 26-30

Laegdsgaard P, Johnson C (2001) Why do juvenile fish utilise mangrove habitats? *Journal of Experimental Marine Biology and Ecology* 257: 229-253

Lam TJ (1974) Siganids: their biology and mariculture potential. *Aquaculture* 3: 325-354

Larcombe P, Costen A, Woolfe KJ (2001) The hydrodynamic and sedimentary setting of nearshore coral reefs, central Great Barrier Reef shelf, Australia: Paluma Shoals, a case study. *Sedimentology* 48: 811-835

Laundré JW, Hernández L, Altendorf KB (2001) Wolves, elk, and bison: re-establishing the "landscape of fear" in Yellowstone National Park, USA. *Canadian Journal of Zoology* 79: 1401-1409

Laundré JW, Hernández L, Ripple WJ (2010) The landscape of fear: ecological implications of being afraid. *The Open Ecology Journal* 3: 1-7

Laurance WF, Dell B, Turton SM, Lawes MJ, Hutley LB, McCallum H, Dale P, Bird M, Hardy G, Prideaux G, Gawne B, McMahon CR, Yu R, Hero J, Schwarzkopf L, Krockenberger A, Douglas M, Silvester E, Mahony M, Vella K, Saikia U, Wahren C, Xu Z, Smith B, Cocklin C (2011) The 10 Australian ecosystems most vulnerable to tipping points. *Biological Conservation* 144: 1472-1480

Lawless S, Frijlink S (2016) Socioeconomic assessment of villages in the Tigak and Tsoi islands, northern New Ireland Province, Papua New Guinea. Wildlife Conservation Society, Papua New Guinea, 37 p

Lenihan HS, Peterson CH, Byers JE, Grabowski JH, Thayer GW, Colby DR (2001) Cascading of habitat degradation: oyster reefs invaded by refugee fishes escaping stress. *Ecological Applications* 11: 764-782

Léopold M, Chateau O, Gabriault H, Ham J, Andréfouët S, Raubani J, Dumas P (2017) Fish movements within community-managed fishery reserve networks: an acoustic survey of *Lethrinus harak* in Vanuatu. *Marine Ecology Progress Series* 571: 153-168

Levin SA (1992) The problem of pattern and scale in ecology. *Ecology* 73: 1943-1967

Lilley RJ, Unsworth RKF (2014) Atlantic Cod (*Gadus morhua*) benefits from the availability of seagrass (*Zostera marina*) nursery habitat. *Global Ecology and Conservation* 2: 367-377

Lin U, Roa-Ureta RH, Rabaoui L, Grandcourt EM, Maneja RH, Al-Abdulkader K, Qurban MA (2019) Association to vegetated habitats and different vulnerability to habitat degradation for two fish species, *Epinephelus areolatus* (Serranidae) and *Siganus canaliculatus* (Siganidae), from the western Arabian Gulf. *Marine Pollution Bulletin* 141: 482-492

Loffler Z, Bellwood DR, Hoey AS (2015) Among-habitat algal selectivity by browsing herbivores on an inshore coral reefs. *Coral Reefs* 34: 597-605

Lopez-Marcano S, Brown CJ, Sievers M, Connolly RM (2021) The slow rise of technology: computer vision techniques in fish population connectivity. *Aquatic Conservation: Marine and Freshwater Ecosystems* 31: 210-217

Lubchenco J, Gaines SD (1981) A unified approach to marine plant-herbivore interactions. I. Populations and communities. *Annual Review of Ecology and Systematics* 12: 405-437

Luckhurst BE, Luckhurst K (1978) Analysis of the influence of substrate variables on coral reef fish communities. *Marine Biology* 49: 317-323

Lugendo BR, Nagelkerken I, van der Velde G, Mgaya YD (2006) The importance of mangroves, mud and sand flats, and seagrass beds as feeding areas of juvenile fishes in Chwaka Bay, Zanzibar: gut content and staple isotope analyses. *Journal of Fish Biology* 69: 1639-1661

Lugendo BR, Pronker A, Cornelissen I, de Groene A, Nagelkerken I, Dorenbosch M, van der Velde G, Mgaya YD (2005) Habitat utilisation by juveniles of commercially important fish species in a marine embayment in Zanzibar, Tanzania. *Aquatic Living Resources* 18: 149-158

Lundberg J, Moberg F (2003) Mobile link organisms and ecosystem functioning: implications for ecosystem resilience and management. *Ecosystems* 6: 87-98

Lyons MB, Roelfsema CM, Kennedy EV, Kovacs EM, Borrego-Acevedo R, Markey K, Roe M, Yuwono DM, Harris DL, Phinn SR, Asner GP, Li J, Knapp DE, Fabina NS, Larsen K, Traganos D, Murray NJ (2020) Mapping the world's coral reefs using a global multiscale earth observation framework. *Remote Sensing in Ecology and Conservation* 6: 557-568

MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. *The American Naturalist* 100: 603-609

MacDonald C, Bridge TCL, Jones GP (2016) Depth, bay position and habitat structure as determinants of coral reef fish distributions: are deep reefs a potential refuge? *Marine Ecology Progress Series* 561: 217-231

MacNeil MA, Graham NAJ, Cinner JE, Wilson SK, Williams ID, Maina J, Newman S, Friedlander AM, Jupiter S, Polunin NVC, McClanahan TR (2015) Recovery potential of the world's coral reef fishes. *Nature* 520: 341-344

Macreadie PI, Jarvis J, Trevathan-Tackett SM, Bellgrove A (2017) Seagrasses and macroalgae: importance, vulnerability and impacts. In: Phillips BF, Pérez-Ramírez M (Eds) *Climate change impacts on fisheries and aquaculture: a global analysis Volume II*. John Wiley & Sons Ltd, pp 729-770

Magurran AE (1990) The adaptive significance of schooling as an anti-predator defence in fish. In *Annales Zoologici Fennici*. Finnish Zoological Publishing Board, Finnish Academy of Sciences, pp 51-66

Mallela J, Roberts C, Harrod C, Goldspink CR (2007) Distributional patterns and community structure of Caribbean coral reef fishes within a river-impacted bay. *Journal of Fish Biology* 70: 523-537

Mallet D, Pelletier D (2014) Underwater video techniques for observing coastal marine biodiversity: a review of sixty years of publications (1952-2012). *Fisheries Research* 154: 44-62

Marczak LB, Thompson RM, Richardson JS (2007) Meta-analysis: trophic level, habitat, and productivity shape the food web effects of resource subsidies. *Ecology* 88: 140-148

Margules CR, Pressey RL (2000) Systematic conservation planning. *Nature* 405: 243-253

Martin TSH, Olds AD, Olalde ABH, Berkström C, Gilby BL, Schlacher TA, Butler IA, Yabsley NA, Zann M, Connolly RM (2018) Habitat proximity exerts opposing effects on key ecological functions. *Landscape Ecology* 33: 1273-1286

Martin TSH, Olds AD, Pitt KA, Johnston AB, Butler IR, Maxwell PS, Connolly RM (2015) Effective protection of fish on inshore coral reefs depends on the scale of mangrove-reef connectivity. *Marine Ecology Progress Series* 527: 157-165

Massol F, Gravel D, Mouquet N, Cadotte MW, Fukami T, Leibold MA (2011) Linking community and ecosystem dynamics through spatial ecology. *Ecology Letters* 14: 313-323

Mayor SJ, Schneider DC, Schaefer JA, Mahoney SP (2009) Habitat selection at multiple scales. *Ecoscience* 16: 238-247

McAlpine C, Lunney D, Melzer A, Menkhorst P, Phillips S, Phalen D, Ellis W, Foley W, Baxter G, de Villiers D, Kavanagh R, Adams-Hosking C, Todd C, Whisson D, Molsher R, Walter M, Lawler I, Close R (2015) Conserving koalas: a review of the contrasting regional trends, outlooks and policy challenges. *Biological Conservation* 192: 226-236

McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82: 290-297

McClure EC, Richardson LE, Graba-Landry A, Loffler Z, Russ GR, Hoey AS (2019) Cross-shelf differences in the response of herbivorous fish assemblages to severe environmental disturbances. *Diversity* 11: 23

McCook LJ (1999) Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs* 18: 357-367

McCormick MI, Makey LJ (1997) Post-settlement transition in coral reef fishes: overlooked complexity in niche shifts. *Marine Ecology Progress Series* 153: 247-257

McDevitt-Irwin JM, Iacarella JC, Baum JK (2016) Reassessing the nursery role of seagrass habitats from temperate to tropical regions: a meta-analysis. *Marine Ecology Progress Series* 557: 133-143

McGarvey R, Feenstra JE, Mayfield S, Sautter EV (2010) A diver survey method to quantify the clustering of sedentary invertebrates by the scale of spatial autocorrelation. *Marine and Freshwater Research* 61: 153-162

McKenzie LJ, Nordlund LM, Jones BL, Cullen-Unsworth LC, Roelfsema C, Unsworth RKF (2020) The global distribution of seagrass meadows. *Environmental Research Letters* 15: 074041

McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution* 14: 450-453

McMahon KW, Berumen ML, Thorrold SR (2012) Linking habitat mosaics and connectivity in a coral reef seascape. *Proceedings of the National Academy of Sciences of the United States of America* 109: 15372-15376

Mellin C, Andréfouët S, Kulbici M, Dalleau M, Vigliola L (2009) Remote sensing and fish-habitat relationships in coral reef ecosystems: review and pathways for systematic multi-scale hierarchical research. *Marine Pollution Bulletin* 58: 11-19

Mellin C, Kulbicki M, Ponton D (2007) Seasonal and ontogenetic patterns of habitat use in coral reef fishes. *Estuarine, Coastal and Shelf Science* 75: 481-491

Menge BA (2000) Top-down and bottom-up community regulation in marine rocky intertidal habitats. *Journal of Experimental Marine Biology and Ecology* 250: 257-289

Menge BA, Olson AM (1990) Role of scale and environmental factors in regulation of community structure. *Trends in Ecology and Evolution* 5: 52-57

Meyer CG, Holland KN (2005) Movement patterns, home range size and habitat utilization of the bluespine unicornfish, *Naso unicornis* (Acanthuridae) in a Hawaiian marine reserve. *Environmental Biology of Fishes* 73: 201-210

Meyer JL, Schultz ET (1985) Migrating haemulid fishes as a source of nutrients and organic matter on coral reefs. *Limnology and Oceanography* 30: 146-156

Michael PJ, Hyndes GA, Vanderklift MA, Vergés A (2013) Identity and behaviour of herbivorous fish influence large-scale spatial patterns of macroalgal herbivory in a coral reef. *Marine Ecology Progress Series* 482: 227-240

Miguet P, Jackson HB, Jackson ND, Martin AE, Fahrig L (2016) What determines the spatial extent of landscape effects on species? *Landscape Ecology* 31: 1177-1194

Miller-Rushing AJ, Primack RB, Devictor V, Corlett RT, Cumming GS, Loyola R, Maas B, Pejchar L (2019) How does habitat fragmentation affect biodiversity? A controversial question at the core of conservation biology. *Biological Conservation* 232: 271-273

Mittelbach GG (1981) Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology* 62: 1370-1386

Mittelbach GG, Osenberg CW (1993) Stage-structured interactions in bluegill: consequences of adult resource variation. *Ecology* 74: 2381-2394

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

Moore CH, Van Niel K, Harvey ES (2011) The effect of landscape composition and configuration on the spatial distribution of temperate demersal fish. *Ecography* 34: 425-435

Mumby PJ, Broad K, Brumbaugh DR, Dahlgren CP, Harborne AR, Hastings A, Holmes KE, Kappel CV, Micheli F, Sanchirico JN (2008) Coral reef habitats as surrogates of species, ecological functions, and ecosystem services. *Conservation Biology* 22: 941-951

Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Broad K, Sanchirico JN, Buch K, Box S, Stoffle RW, Gill AB (2006) Fishing, tropical cascades, and the process of grazing on coral reefs. *Science* 311: 98-101

Mumby PJ, Edwards AJ, Arias-González JE, Lindeman KC, Blackwell PG, Gall A, Gorczynska MI, Harborne AR, Pescod CL, Renken H, Wabnitz CCC, Llewellyn G (2004) Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* 427: 533-536

Mumby PJ, Hastings A (2008) The impact of ecosystem connectivity on coral reef resilience. *Journal of Applied Ecology* 45: 854-862

Mumby PJ, Steneck RS, Roff G, Paul VJ (2021) Marine reserves, fisheries ban, and 20 years of positive change in a coral reef ecosystem. *Conservation Biology* doi: 10.111/cobi.13738

Naeem S, Thompson LJ, Lawler SP, Lawton JH, Woodfin RM (1994) Declining biodiversity can alter the performance of ecosystems. *Nature* 368: 734-737

Nagelkerken I (2007) Are non-estuarine mangroves connected to coral reefs through fish migration? *Bulletin of Marine Science* 80: 595-607

Nagelkerken I (2009) Evaluation of nursery function of mangroves and seagrass beds for tropical decapods and reef fishes: patterns and underlying mechanisms. In: Nagelkerken I (Ed). *Ecological connectivity among tropical coastal ecosystems* Springer Dordrecht pp 357-399

Nagelkerken I, Blaber SJM, Bouillon S, Green P, Haywood M, Kirton LG, Meynecke JO, Pawlik J, Penrose HM, Sasekumar A, Somerfield PJ (2008) The habitat function of mangroves for terrestrial and marine fauna: a review. *Aquatic Botany* 89: 155-185

Nagelkerken I, Dorenbosch M, Verberk WCEP, Cocheret de la Morinière E, van der Velde G (2000a) Importance of shallow-water biotopes of a Caribbean bay for juvenile coral reef fishes: patterns in biotope association, community structure and spatial distribution. *Marine Ecology Progress Series* 202: 175-192

Nagelkerken I, Dorenbosch M, Verberk WCEP, Cocheret de la Morinière E, van der Velde G (2000b) Day-night shifts of fishes between shallow-water biotopes of a Caribbean bay, with emphasis on the nocturnal feeding of Haemulidae and Lutjanidae. *Marine Ecology Progress Series* 194: 55-64

Nagelkerken I, Grol MGG, Mumby PJ (2012) Effects of marine reserves versus nursery habitat availability on structure of reef fish communities. *PLoS ONE* 7: e36906

Nagelkerken I, Kleijnen S, Klop T, van den Brand RACJ, Cocheret de la Morinière E, van der Velde G (2001) Dependence of Caribbean reef fishes on mangroves and seagrass beds as nursery habitats: a comparison of fish faunas between bays with and without mangroves/seagrass beds. *Marine Ecology Progress Series* 214: 225-235

Nagelkerken I, Roberts CM, van der Velde G, Dorenbosch M, van Riel MC, Cocheret de la Morinière E, Nienhuis PH (2002) How important are mangroves and seagrass beds for coral-reef fish? The nursery hypothesis tested on an island scale. *Marine Ecology Progress Series* 244: 299-305

Nagelkerken I, Sheaves M, Baker R, Connolly RM (2015) The seascape nursery: a novel spatial approach to identify and manage nurseries for coastal marine fauna. *Fish and Fisheries* 16: 362-371

Nagelkerken I, van der Velde G (2002) Do non-estuarine mangroves harbour higher densities of juvenile fish than adjacent shallow-water and coral reef habitats in Curaçao (Netherlands Antilles)? *Marine Ecology Progress Series* 245: 191-204

Nagelkerken I, van der Velde G (2003) Connectivity between coastal habitats of two oceanic Caribbean islands as inferred from ontogenetic shifts by coral reef fishes. *Gulf and Caribbean Research* 14: 43-59

Nagelkerken I, van der Velde G (2004) A comparison of fish communities of subtidal seagrass beds and sandy seagrass beds in 13 marine embayments of a Caribbean island, based on species, families, size distribution and functional groups. *Journal of Sea Research* 52: 127-147

Nagelkerken I, van der Velde G, Gorissen MW, Meijer GJ, van't Hof T, den Hartog C (2000c) Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. *Estuarine, Coastal and Shelf Science* 51: 31-44

Nakamura Y, Hirota K, Shibuno T, Watanabe Y (2012) Variability in nursery function of tropical seagrass beds during fish ontogeny: timing of ontogenetic habitat shift. *Marine Biology* 159: 1305-1315

Nakamura Y, Horinouchi M, Nakai T, Sano M (2003) Food habits of fishes in a seagrass bed on a fringing coral reef at Iriomote Island, southern Japan. *Ichthyological Research* 50: 15-22

Nakamura Y, Horinouchi M, Shibuno T, Tanaka Y, Miyajima T, Koike I, Kurokura H, Sano M (2008) Evidence of ontogenetic migration from mangroves to coral reefs by black-tail snapper *Lutjanus fulvus*: stable isotope approach. *Marine Ecology Progress Series* 355: 257-266

Nakamura Y, Kawasaki H, Sano M (2007) Experimental analysis of recruitment patterns of coral reef fishes in seagrass beds: effects of substrate type, shape and rigidity. *Estuarine, Coastal and Shelf Science* 71: 559-568

Nakamura Y, Sano M (2004a) Is there really lower predation risk for juvenile fishes in a seagrass bed compared with an adjacent coral area? *Bulletin of Marine Science* 74: 477-482

Nakamura Y, Sano M (2004) Overlaps in habitat use of fishes between a seagrass bed and adjacent coral and sand areas at Amitori Bay, Iriomote Island, Japan: importance of the seagrass bed as juvenile habitat. *Fisheries Science* 70: 788-803

Nakamura Y, Sano M (2005) Comparison of invertebrate abundance in a seagrass bed and adjacent coral and sand areas at Amitori Bay, Iriomote Island, Japan. *Fisheries Science* 71: 543-550

Nakamura Y, Shibuno T, Lecchini D, Kawamura T, Watanabe Y (2009a) Spatial variability in habitat associations of pre- and post-settlement stages of coral reef fishes at Ishigaki Island, Japan. *Marine Biology* 156: 2413-2419

Nakamura Y, Shibuno T, Lecchini D, Watanabe Y (2009b) Habitat selection by emperor fish larvae. *Aquatic Biology* 6: 61-65

Nakamura Y, Tsuchiya M (2008) Spatial and temporal patterns of seagrass habitat use by fishes at the Ryukyu Islands, Japan. *Estuarine, Coastal and Shelf Science* 76: 345-356

Nakazawa T (2015) Ontogenetic niche shifts matter in community ecology: a review and future perspectives. *Population Ecology* 57: 347-354

Nanjo K, Kohno H, Nakamura Y, Horinouchi M, Sano M (2014) Effects of mangrove structure on fish distribution patterns and predation risks. *Journal of Experimental Marine Biology and Ecology* 461:216-225

Nash KL, Abesamis RA, Graham NAJ, McClure EC, Moland E (2016) Drivers of herbivory on coral reefs: species, habitat and management effects. *Marine Ecology Progress Series* 554: 129-140

Nemeth RS (1998) The effect of natural variation in substrate architecture on the survival of juvenile bicolor damselfish. *Environmental Biology of Fishes* 53: 129-141

Newbold T, Hudson LN, Arnell AP, Contu S, De Palma A, Ferrier S, Hill SLL, Hoskins AJ, Lysenko I, Phillips HRP, Burton VJ, Chng CWT, Emerson S, Gao D, Pask-Hale G, Hutton J, Jung M, Sanchez-Ortiz K, Simmons BI, Whitmee S, Zhang H, Scharlemann JPW, Purvis A (2016) Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. *Science* 353: 288-291

Newton K, Côté IM, Pilling GM, Jennings S, Dulvy NK (2007) Current and future sustainability of island coral reef fisheries. *Current Biology* 17: 655–658

Nordlund LM, Unsworth RKF, Gullström M, Cullen-Unsworth LC (2018) Global significance of seagrass fishery activity. *Fish and Fisheries* 19: 399-412

Nyström M, Folke C (2001) Spatial resilience of coral reefs. *Ecosystems* 4: 406-417

O'Donnell JL, Kelly RP, Shelton AO, Samhouri JF, Lowell NC, Williams GD (2017) Spatial distribution of environmental DNA in a nearshore marine environment. *Peer J* 5: e3044

Ogden JC (1976) Some aspects of herbivore-plant relationships on Caribbean reefs and seagrass beds. *Aquatic Botany* 2: 103-116

Ogden JC (1988) The influence of adjacent systems on the structure and function of coral reefs. *Proceedings of the Sixth International Coral Reef Symposium* 123-129

Ogden JC, Buckman NS (1973) Movements, foraging groups, and diurnal migrations of the striped parrotfish *Scarus croicensis* bloch (Scaridae). *Ecology* 54: 589-596

Ogden JC, Zieman JC (1977) Ecological aspects of coral reef-seagrass bed contacts in the Caribbean. *Proceedings of the Third International Coral Reef Symposium* 377-382

Olds AD, Albert S, Maxwell PS, Pitt KA, Connolly RM (2013) Mangrove-reef connectivity promotes the effectiveness of marine reserves across the western Pacific. *Global Ecology and Biogeography* 22: 1040-1049

Olds AD, Connolly RM, Pitt KA, Maxwell PS (2012a) Primacy of seascape connectivity effects in structuring coral reef fish assemblages. *Marine Ecology Progress Series* 462: 191-203

Olds AD, Connolly RM, Pitt KA, Maxwell PS, Aswani S, Albert S (2014) Incorporating surrogate species and seascape connectivity to improve marine conservation outcomes. *Conservation Biology* 28: 982-991

Olds AD, Connolly RM, Pitt KA, Pittman SJ, Maxwell PS, Huijbers CM, Moore BR, Albert S, Rissik D, Babcock RC, Schlacher TA (2016) Quantifying the conservation value of seascape connectivity: a global synthesis. *Global Ecology and Biogeography* 25: 3-15

Olds AD, Pitt KA, Maxwell PS, Connolly RM (2012b) Synergistic effects of reserves and connectivity on ecological resilience. *Journal of Applied Ecology* 49: 1195-1203

Oliver TH (2016) How much biodiversity loss is too much? *Science* 353: 220-221

Olson AM, Hessing-Lewis M, Haggarty D, Juanes F (2019) Nearshore seascape connectivity enhances seagrass meadow nursery function. *Ecological Applications* 29: e01897

Orians GH, Pearson NE (1979) On the theory of central place foraging. In Horn DJ, Mitchell RD, Stairs GR (Eds) *Analysis of ecological systems*, Ohio State University Press, Columbus, Ohio, USA

Orians GH, Wittenberger JF (1991) Spatial and temporal scales in habitat selection. *The American Naturalist* 137: 29-49

Orth RJ, Carruthers TJB, Dennison WC, Duarte CM, Fourqurean JW, Heck KL, Hughes AR, Kendrick GA, Kenworthy WJ, Olyarnik S, Short FT, Waycott M, Williams SL (2006) A global crisis for seagrass ecosystems. *BioScience* 56: 987–996

Osborne K, Dolman AM, Burgess SC, Johns KA (2011) Disturbance and the dynamics of coral cover on the Great Barrier Reef (1995-2009). *PLoS ONE* 6: e17516

Overholtzer-McLeod KL (2005) Post-settlement emigration affects mortality estimates for two Bahamian wrasses. *Coral Reefs* 24: 283-291

Pagès JF, Gera A, Romero J, Alcoverro T (2014) Matrix composition and patch edges influence plant-herbivore interactions in marine landscapes. *Functional Ecology* 28: 1440-1448

Paillon C, Wantiez L, Kulbicki M, Labonne M, Vigliola L (2014) Extent of mangrove nursery habitats determines the geographic distribution of a coral reef fish in a South-Pacific archipelago. *PLoS ONE* 9: e105158

Paine RT (1966) Food web complexity and species diversity. *The American Naturalist* 100: 65-75

Paine RT, Levin SA (1981) Intertidal landscapes: disturbance and the dynamics of pattern. *Ecological Monographs* 51: 145-178

Papua New Guinea National Fisheries Authority (2005) Small-scale fisheries in New Ireland Province: landing, market and buyer surveys in Kavieng. National Fisheries Authority and Coastal Fisheries Management and Development Project, 77 p

Papua New Guinea National Fisheries Authority (2007) A review of fisheries and marine resources in New Ireland Province, Papua New Guinea. National Fisheries Authority and Coastal Fisheries Management and Development Project, 40 p

Parnell PE (2015) The effects of seascape pattern on algal patch structure, sea urchin barrens, and ecological processes. *Journal of Experimental Marine Biology and Ecology* 465: 64-76

Parrish JD (1989) Fish communities of interacting shallow-water habitats in tropical oceanic regions. *Marine Ecology Progress Series* 58: 143-160

Pereira PHC, dos Santos MVB, Lippi DL, de Paula Silva PH, Barros B (2017) Difference in the trophic structure of fish communities between artificial and natural habitats in a tropical estuary. *Marine and Freshwater Research* 68: 473-483

Perry D, Staveley TA, Gullström M (2018) Habitat connectivity of fish in temperate shallow-water seascapes. *Frontiers in Marine Science* 4: 440

Phua MH, Minowa M (2005) A GIS-based multi-criteria decision making approach to forest conservation planning at a landscape scale: a case study in the Kinabalu Area, Saba, Malaysia. *Landscape and Urban Planning* 71: 207-222

Pikitch EK (2018) A tool for finding rare marine species. *Science* 360: 1180-1182

Pinca S, Kronen M, Magron F, McArdle B, Vigliola L, Kulbicki M, Andréfouët S (2012) Relative importance of habitat and fishing in influencing reef fish communities across seventeen Pacific Island Countries and Territories. *Fish and Fisheries* 13: 361-379

Pittman SJ (2018) *Seascape ecology*. John Wiley & Sons Ltd, West Sussex, United Kingdom

Pittman SJ, Brown KA (2011) Multi-scale approach for predicting fish species distributions across coral reef seascapes. *PLoS ONE* 6: e20583

Pittman SJ, Caldow C, Hile SD, Monaco ME (2007) Using seascape types to explain the spatial patterns of fish in the mangroves of SW Puerto Rico. *Marine Ecology Progress Series* 348: 273-284

Pittman SJ, Kneib RT, Simenstad CA (2011) Practicing coastal seascape ecology. *Marine Ecology Progress Series* 427: 187-190

Pittman SJ, McAlpine CA (2003) Movement of marine fish and decapod crustaceans: process, theory and application. *Advances in Marine Biology* 44: 205-294

Pittman SJ, McAlpine CA, Pittman KM (2004) Linking fish and prawns to their environment: a hierarchical landscape approach. *Marine Ecology Progress Series* 283: 233-254

Pittman SJ, Olds AD (2015) Seascape ecology of fishes on coral reefs. In: C Mora (Ed) *Ecology of fishes on coral reefs*. Cambridge, UK: Cambridge University Press, pp 274-282

Pittman SJ, Yates KL, Bouchet PJ, Alvarez-Berastegui D, Andréfouët S, Bell SS, Berkström C, Boström C, Brown CJ, Connolly RM, Devillers R, Eggleston D, Gilby BL, Gullström M, Halpern BS, Hidalgo M, Holstein D, Hovel K, Huettmann F, Jackson EL, James WR, Kellner JB, Kot CY, Lecours V, Lepczyk C, Nagelkerken I, Nelson J, Olds AD, Santos RO, Scales KL, Schneider DC, Schilling HT, Simenstad C, Suthers IM, Treml EA, Wedding LM, Yates P, Young M (2021) Seascape ecology: identifying research priorities for an emerging ocean sustainability science. *Marine Ecology Progress Series* 663: 1-29

Plass-Johnson JG, Ferse SCA, Jompa J, Wild C, Teichberg M (2015) Fish herbivory as key ecological function in a heavily degraded coral reef system. *Limnology and Oceanography* 60: 1382-1391

Pogoreutz C, Kneer D, Litaay M, Asmus H, Ahnelt H (2012) The influence of canopy structure and tidal level of fish assemblages in tropical Southeast Asian seagrass meadows. *Estuarine, Coastal and Shelf Science* 107: 58-68

Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28: 289-316

Pollux BJA, Verberk WCEP, Dorenbosch M, Cocheret de la Morinière E, Nagelkerken I, van der Velde G (2007) Habitat selection during settlement of three Caribbean coral reef fishes: indications for directed settlement to seagrass beds and mangroves. *Limnology and Oceanography* 52: 903-907

Pope SE, Fahrig L, Merriam HG (2000) Landscape complementation and metapopulation effects on Leopard frog populations. *Ecology* 81: 2498-2508

Port JA, O'Donnell JL, Romero-Maraccini OC, Leary PR, Litvin SY, Nickols KJ, Yamahara KM, Kelly RP (2016) Assessing vertebrate biodiversity in a kelp forest ecosystem using environmental DNA. *Molecular Ecology* 25: 527-241

Powers RP, Jetz W (2019) Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. *Nature Climate Change* 9: 323-329

Pratchett MS, Hoey AS, Wilson SK, Messmer V, Graham NAJ (2011) Changes in biodiversity and functioning of reef fish assemblages following coral bleaching and coral loss. *Diversity* 3: 424-452

Pratchett MS, Munday PL, Wilson SK, Graham NAJ, Cinner JE, Bellwood DR, Jones GP, Polunin NVC, McClanahan TR (2008) Effects of climate-induced coral bleaching on coral-reef fishes – ecological and economic consequences. *Oceanography and Marine Biology: An Annual Review* 46: 251-296

Pressey RL, Cabeza M, Watts ME, Cowling RM, Wilson KA (2007) Conservation planning in a changing world. *Trends in Ecology and Evolution* 22: 583-592

Pulliam HR, Dunning JB, Liu J (1992) Population dynamics in complex landscapes: a case study. *Ecological Applications* 2: 165-177

Pyke GH (1984) Optimal foraging theory: a critical review. *Annual Review of Ecology and Systematics* 15: 523-575

Randall JE (1965) Grazing effect on sea grasses by herbivorous reef fishes in the West Indies. *Ecology* 46: 255-260

Rasheed MA, McKenna SA, Carter AB, Coles RG (2014) Contrasting recovery of shallow and deep water seagrass communities following climate associated losses in tropical north Queensland, Australia. *Marine Pollution Bulletin* 83: 491-499

Rasher DB, Hoey AS, Hay ME (2013) Consumer diversity interacts with prey defences to drive ecosystem function. *Ecology* 94: 1347-1358

Rasher DB, Hoey AS, Hay ME (2017) Cascading predator effects in a Fijian coral reef ecosystem. *Scientific Reports* 7: 15684

Rayor LS, Uetz GW (1993) Ontogenetic habitat shifts within the selfish herd: predation risk and foraging trade-offs change with age in colonial web-building spiders. *Oecologia* 95: 1-8

Redhead JW, Dreier S, Bourke AFG, Heard MS, Jordan WC, Sumner S, Wang J, Carvell C (2016) Effects of habitat composition and landscape structure on worker foraging distances of five bumble bee species. *Ecological Applications* 26: 726-739

Rees HC, Maddison BC, Middleditch DJ, Patmore JRM, Gough KC (2014) The detection of aquatic animal species using environmental DNA – a review of eDNA as a survey tool in ecology. *Journal of Applied Ecology* 51: 1450-1459

Rees MJ, Knott NA, Davis AR (2018) Habitat and seascape patterns drive spatial variability in temperate fish assemblages: implications for marine protected areas. *Marine Ecology Progress Series* 607: 171-186

Ricart AM, Sanmartí N, Pérez M, Romero J (2018) Multilevel assessments reveal spatially scaled landscape patterns driving coastal fish assemblages. *Marine Environmental Research* 140: 210-220

Richards DR, Friess DA (2016) Rates and drivers of mangrove deforestation in Southeast Asia, 2000-2012. *Proceedings of the National Academy of Sciences of the United States of America* 113: 344-349

Richardson LE, Graham NAJ, Hoey AS (2020) Coral species composition drives key ecosystem function on coral reefs. *Proceedings of the Royal Society B* 287: 20192214

Richardson LE, Graham NAJ, Pratchett MS, Eurich JG, Hoey AS (2018) Mass coral bleaching causes biotic homogenization of reef fish assemblages. *Global Change Biology* 24: 3117-3129

Richardson LE, Graham NAJ, Pratchett MS, Hoey AS (2017) Structural complexity mediates functional structure of reef fish assemblages among coral habitats. *Environmental Biology of Fishes* 100: 193-207

Ricketts TH (2001) The matrix matters: effective isolation in fragmented landscapes. *The American Naturalist* 158: 87-99

Ries L, Fletcher RJ, Battin J, Sisk TD (2004) Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution and Systematics* 35: 491-522

Rizzari JR, Frisch AJ, Hoey AS, McCormick MI (2014) Not worth the risk: apex predators suppress herbivory on coral reefs. *Oikos* 123: 829-836

Robblee MB, Zieman JC (1984) Diel variation in the fish fauna of a tropical seagrass feeding ground. *Bulletin of Marine Science* 34: 335-345

Roberts CM, Ormond RF (1987) Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Marine Ecology Progress Series* 41: 1-8

Roff G, Bejarano S, Priest M, Marshell A, Chollett I, Steneck RS, Doropoulos C, Golbuu Y, Mumby PJ (2019) Seascapes as drivers of herbivore assemblages in coral reef ecosystems. *Ecological Monographs* 89: e01336

Rogers A, Mumby PJ (2019) Mangroves reduce the vulnerability of coral reef fisheries to habitat degradation. *PLoS Biology* 17: e3000510

Rooker JR, Dance MA, Wells RJD, Quigg A, Hill RL, Appeldoorn RS, Ferreira BP, Boswell KM, Sanchez PJ, Moulton DL, Kitchens LL, Rooker GJ, Aschenbrenner A (2018) Seascape connectivity and the influence of predation risk on the movement of fishes a inhabiting back-reef ecosystem. *Ecosphere* 9: e02200

Rooker JR, Dennis GD, Goulet D (1996) Sampling larval fishes with a nightlight lift-net in tropical inshore waters. *Fisheries Research* 26: 1-15

Rossier O, Kulbicki M (2000) A comparison of fish assemblages from two types of algal beds and coral reefs in the south-west lagoon of New Caledonia. *Cybium* 24: 3-26

Russ GR, Rizzari JR, Abesamis RA, Alcala AC (2021) Coral cover a stronger driver of reef fish trophic biomass than fishing. *Ecological Applications* 31: e02224

Ruttenberg BI, Adam TC, Duran A, Burkepile DE (2019) Identity of coral reef herbivores drives variation in ecological processes over multiple spatial scales. *Ecological Applications* 29: e01893

Sale PF (1991) The ecology of fishes on coral reefs. Academic Press, San Diego

Sale PF, Cowen RK, Danilowicz BS, Jones GP, Kritzer JP, Lindeman KC, Planes S, Polunin NVC, Russ GR, Sadovy YJ, Steneck RS (2005) Critical science gaps impede use of no-take fishery reserves. *Trends in Ecology and Evolution* 20: 74-80

Salido L, Purse BV, Marrs R, Chamberlain DE, Shultz S (2011) Flexibility in phenology and habitat use act as buffers to long-term population declines in UK passerines. *Ecography* 35: 604-613

Sambrook K, Bonin MC, Bradley M, Cumming GS, Duce S, Andréfouët S, Hoey AS (2020) Broadening our horizons: seascape use by coral reef-associated fishes in Kavieng, Papua New Guinea, is common and diverse. *Coral Reefs* 39: 1187-1197

Sambrook K, Hoey AS, Andréfouët S, Cumming GS, Duce S, Bonin MC (2019) Beyond the reef: the widespread use of non-reef habitats by coral reef fishes. *Fish and Fisheries* 20: 903-920

Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5: 18-32

Sbrocco EJ, Barber PH (2013) MARSPEC: ocean climate layers for marine spatial ecology. *Ecology* 94: 979

Scapin L, Zucchetta M, Sfriso A, Franzoi P (2018) Local habitat and seascape structure influence seagrass fish assemblages in the Venice Lagoon: the importance of conservation at multiple spatial scales. *Estuaries and Coasts* 41: 2410-2425

Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. *Nature* 413: 591-596

Schneider DC (2001) The rise of the concept of scale in ecology. *BioScience* 51: 545-553

Schoener TW (1971) Theory of feeding strategies. *Annual Review of Ecology and Systematics* 2: 369-404

Schreiber S, Rudolf VHW (2008) Crossing habitat boundaries: coupling dynamics of ecosystems through complex life cycles. *Ecology Letters* 11: 576-587

Sekund L, Pittman S (2017) Explaining island-wide geographical patterns of Caribbean fish diversity: a multi-scale seascape ecology approach. *Marine Ecology* 38: e12434

Shantz AA, Ladd MC, Schrack E, Burkepile DE (2015) Fish-derived nutrient hotspots shape coral reef benthic communities. *Ecological Applications* 25: 2142-2152

Sheaves M (2005) Nature and consequences of biological connectivity in mangrove systems. *Marine Ecology Progress Series* 302: 293-305

Sheaves M (2009) Consequences of ecological connectivity: the coastal ecosystem mosaic. *Marine Ecology Progress Series* 391: 107-115

Sheaves M (2017) How many fish use mangroves? The 75% rule an ill-defined and poorly validated concept. *Fish and Fisheries* 18: 778-789

Sheaves M, Baker R, Nagelkerken I, Connolly RM (2015) True value of estuarine and coastal nurseries for fish: incorporating complexity and dynamics. *Estuaries and Coasts* 38: 401-414

Short F, Carruthers T, Dennison W, Waycott M (2007) Global seagrass distribution and diversity: a bioregional model. *Journal of Experimental Marine Biology and Ecology* 350: 3-20

Shulman MJ (1985) Recruitment of coral reef fishes: effects of distribution of predators and shelter. *Ecology* 66: 1056-1066

Sievers KT, Abesamis RA, Bucol AA, Russ GR (2020b) Unravelling seascape patterns of cryptic life stages: non-reef habitat use in juvenile parrotfishes. *Diversity* 12: 376

Sievers KT, Barr RJ, Maloney JM, Driscoll NW, Anderson TW (2016) Impact of habitat structure on fish populations in kelp forests at a seascape scale. *Marine Ecology Progress Series* 557: 51-63

Sievers KT, McClure EC, Abesamis RA, Russ GR (2020a) Non-reef habitats in a tropical seascape affect density and biomass of fishes on coral reefs. *Ecology and Evolution* 10: 13673-13686

Sinclair EA, Sherman CDH, Statton J, Copeland C, Matthews A, Waycott M, van Dijk K-J, Vergés A, Kajlich L, McLeod IM, Kendrick GA (2021) Advances in approaches to seagrass restoration in Australia. *Ecological Management and Restoration* 22: 10-21

Staveley TAB, Hernvall P, Stjärnkvist N, van der Meijs F, Wikström SA, Gullström M (2017) Seascape structure and complexity influence temperate seagrass fish assemblage composition. *Ecography* 40: 936-946

Steffan-Dewenter I, Tscharntke T (1999) Effects of habitat isolation on pollinator communities and seed set. *Oecologia* 121: 432-440

Streit RP, Hoey AS, Bellwood DR (2015) Feeding characteristics reveal functional distinctions among browsing herbivorous fishes on coral reefs. *Coral Reefs* 34: 1037-1047

Stuart-Smith RD, Brown CJ, Ceccarelli DM, Edgar GJ (2018) Ecosystem restructuring along the Great Barrier Reef following mass coral bleaching. *Nature* 560: 92-96

Stuart-Smith RD, Mellin C, Bates AE, Edgar GJ (2021) Habitat loss and range shifts contribute to ecological generalization among reef fishes. *Nature Ecology and Evolution* 5: 656-662

Swadling DS, Knott NA, Rees MJ, Davis AR (2019) Temperate zone coastal seascapes: seascape patterning and adjacent seagrass habitat shape the distribution of rocky reef fish assemblages. *Landscape Ecology* 34: 2337-2352

Swindells KL Murdoch RJ, Bazen WD, Harman NW, Unsworth RKF (2017) Habitat configuration alters herbivory across the tropical seascape. *Frontiers in Marine Science* 4: 48

Tang S, Graba-Landry A, Hoey AS (2020) Density and height of *Sargassum* influence rabbitfish (f. Siganidae) settlement on inshore reef flats of the Great Barrier Reef. *Coral Reefs* 39: 467-473

Tano S, Eggertsen M, Wikström SA, Berkström C, Buriyo AS, Halling C (2016) Tropical seaweed beds are important habitats for mobile invertebrate epifauna. *Estuarine, Coastal and Shelf Science* 183: 1-12

Tano SA, Eggertsen M, Wikström SA, Berkström C, Buriyo AS, Halling C (2017) Tropical seaweed beds as important habitats for juvenile fish. *Marine and Freshwater Research* 68: 1921-1934

Taylor BM, Choat JH, DeMartini EE, Hoey AS, Marshell A, Priest MA, Rhodes KL, Meekan MG (2019) Demographic plasticity facilitates ecological and economic resilience in a commercially important reef fish. *Journal of Animal Ecology* 88: 1888-1900

Taylor BM, Mills JS (2013) Movement and spawning migration patterns suggest small marine reserves can offer adequate protection for exploited emperorfishes. *Coral Reefs* 32: 1077-1087

Taylor PD, Fahrig L, Hennein K, Merriam G (1993) Connectivity is a vital element of landscape structure. *Oikos* 68: 571-573

Tebbett SB, Hoey AS, Depczynski M, Wismer S, Bellwood DR (2020) Macroalgae removal on coral reefs: realised ecosystem functions transcend biogeographic locations. *Coral Reefs* 39: 203-214

Thollot P (1992) Importance of mangroves for Pacific reef fish species, myth or reality? *Proceedings of the Seventh International Coral Reef Symposium* 2: 934-941

Thollot P, Kulbicki M, Wantiez L (1990) Temporal patterns of fish populations in three habitats of the St Vincent Bay area (New Caledonia): coral reefs, soft bottoms and mangroves. *Proceedings ISRS Congress, Noumea* 122-136

Thompson AA, Mapstone BD (2002) Intra- versus inter-annual variation in counts of reef fishes and interpretations of a long-term monitoring studies. *Marine Ecology Progress Series* 232: 247-257

Thornton DH, Branch LC, Sunquist ME (2011) The influence of landscape, patch, and within-patch factors on species presence and abundance: a review of focal patch studies. *Landscape Ecology* 26: 7-18

Tilman D, Downing JA (1994) Biodiversity and stability in grasslands. *Nature* 367: 363-365

Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E (1997) The influence of functional diversity and composition on ecosystem processes. *Science* 277: 1300-1301

Torney CJ, Grant C, Hopcraft J, Morrison TA, Couzin ID, Levin SA (2018) From single steps to mass migration: the problem of scale in the movement ecology of the Serengeti wildebeest. *Philosophical Transactions of the Royal Society B* 373: 20170012

Torres-Pulliza D, Wilson JR, Darmawan A, Campbell SJ (2013) Ecoregional scale seagrass mapping: a tool to support resilient MPA network design in the Coral Triangle. *Ocean and Coastal Management* 80: 55-64

Tscharntke T, Tylianakis JM, Rand TA, Didham RK, Fahrig L, Batáry P, Bengtsson J, Clough Y, Crist TO, Dormann CF, Ewers RM, Fründ J, Holt RD, Holzschuh A, Klein AM, Kleijn D, Kremen C, Landis DA, Laurance W, Lindenmayer D, Scherber C, Sodhi N, Steffan-Dewenter I, Thies C, van der Putten WH, Westphal C (2012) Landscape moderation of biodiversity patterns and processes – eight hypotheses. *Biological Reviews* 87: 661-685

Turgeon K, Robillard A, Grégoire J, Duclos V, Kramer DL (2010) Functional connectivity from a reef fish perspective: behavioral tactics for moving in a fragmented landscape. *Ecology* 91: 3332-3342

Turner MG (1989) Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics* 20: 171-197

Turner MG (2005) Landscape ecology: what is the state of the science? *Annual Review of Ecology, Evolution, and Systematics* 36: 319-344

Turner MG (2010) Disturbance and landscape dynamics in a changing world. *Ecology* 91: 2833-2849

Turner MG, Gardner RH (2015) Landscape ecology in theory and practice. 2nd Edition, Springer-Verlag, New York

Turner SJ, Hewitt JE, Wilkinson MR, Morrisey DJ, Thrush SF, Cummings CJ, Funnell G (1999) Seagrass patches and landscapes: the influence of wind-wave dynamics and hierarchical arrangements of spatial structure on macrofaunal seagrass communities. *Estuaries* 22: 1016-1032

Tuya F, Haroun R, Espino F (2014) Economic assessment of ecosystem services: monetary value of seagrass meadows for coastal fisheries. *Ocean and Coastal Management* 96: 181-187

Unsworth RKF, Bell JJ, Smith DJ (2007b) Tidal fish connectivity of reef and sea grass habitats in the Indo-Pacific. *Journal of the Marine Biological Association of the UK* 87: 1287-1296

Unsworth RKF, Cullen LC (2010) Recognising the necessity for Indo-Pacific seagrass conservation. *Conservation Letters* 3: 63-73

Unsworth RKF, Garrard SL, De León PS, Cullen LC, Smith DJ, Sloman KA, Bell JJ (2009) Structuring of Indo-Pacific fish assemblages along the mangrove-seagrass continuum. *Aquatic Biology* 5: 85-95

Unsworth RKF, Hinder SL, Bodger OG, Cullen-Unsworth LC (2014) Food supply depends on seagrass meadows in the Coral Triangle. *Environmental Research Letters* 9: 094005

Unsworth RKF, McKenzie LJ, Nordlund LM, Cullen-Unsworth LC (2018) A changing climate for seagrass conservation? *Current Biology* 28: 1229-1232

Unsworth RKF, Salinas De León P, Garrard SL, Jompa J, Smith DJ, Bell JJ (2008) High connectivity of Indo-Pacific seagrass fish assemblages with mangrove and coral reef habitats. *Marine Ecology Progress Series* 353: 213-224

Unsworth RKF, Taylor JD, Powell A, Bell JJ, Smith DJ (2007) The contribution of scarid herbivory to seagrass ecosystem dynamics in the Indo-Pacific. *Estuarine, Coastal and Shelf Science* 74: 53-62

Unsworth RKF, Wylie E, Smith DJ, Bell JJ (2007a) Diel trophic structuring of seagrass bed fish assemblages in the Wakatobi Marine National Park, Indonesia. *Estuarine, Coastal and Shelf Science* 72: 81-88

Valiela I, Bowen JL, York JK (2001) Mangrove forests: One of the world's threatened major tropical environments. *BioScience* 51: 807–815

van Lier JR, Wilson SK, Depcynski M, Wenger LN, Fulton CJ (2018) Habitat connectivity and complexity underpin fish community structure across a seascape of tropical macroalgae meadows. *Landscape Ecology* 33: 1287-1300

Van Wynsberge S, Andréfouët S, Hamel MA, Kulbicki M (2012) Habitats as surrogates of taxonomic and functional fish assemblages in coral reef ecosystems: a critical analysis of factors driving effectiveness. *PLoS ONE* 7: e40997

Vanderklift MA, Pillans RD, Hutton M, De Wever L, Kendrick GA, Zavala-Perez A, Vergés A, Garthwin R, Oades D, McCarthy P, George K, Sampi T, George D, Sampi C, Edgar Z, Dougal K, Howard A (2021) High rates of herbivory in remote northwest Australian seagrass meadows by rabbitfish and green turtles. *Marine Ecology Progress* Series 665: 63-73

Vergés A, Bennett S, Bellwood DR (2012) Diversity among macroalgae-consuming fishes on coral reefs: a transcontinental comparison. *PLoS ONE* 7: e45543

Vergés A, Vanderklift MA, Doropoulos C, Hyndes GA (2011) Spatial patterns in herbivory on a coral reef are influenced by structural complexity but not by algal traits. *PLoS ONE* 6: e17115

Vonk JA, Christianen MJA, Stapel J (2010) Abundance, edge effect, and seasonality of fauna in mixed-species seagrass meadows in southwest Sulawesi, Indonesia. *Marine Biology Research* 6: 282-291

Wainwright PC, Bellwood DR, Westneat MW (2002) Ecomorphology of locomotion in labrid fishes. *Environmental Biology of Fishes* 65: 47-62

Wäldchen J, Mäder P (2018) Machine learning for image based species identification. *Methods in Ecology and Evolution* 9: 2216-2225

Walker B, Kinzig A, Langridge J (1999) Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* 2: 95-113

Waltham NJ, Elliott M, Yip Lee S, Lovelock C, Duarte CM, Buelow C, Simenstad C, Nagelkerken I, Claassens L, Wen CKC, Barletta M, Connolly RM, Gillies C, Mitsch WJ, Ogburn MB, Purandare J, Possingham H, Sheaves M (2020) UN Decade on Ecosystem Restoration 2021-2030 – What chance for success in restoring coastal ecosystems? *Frontiers in Marine Science* 7: 71

Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B, Roy DB, Telfer MG, Jeffcoate S, Harding P, Jeffcoate G, Willis SG, Greatorex-Davies JN, Moss D, Thomas CD

(2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* 414: 65-69

Waycott M, Duarte CM, Carruthers TJB, Orth RJ, Dennison WC, Olyarnik S, Calladine A, Fourqurean JW, Heck KL, Hughes AR, Kendrick GA, Kenworthy WJ, Short FT, Williams SL (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* 106: 12377-12381

Wedding LM, Friedlander AM (2008) Determining the influence of seascape structure on coral reef fishes in Hawaii using a geospatial approach. *Marine Geodesy* 31: 246-266

Wedding LM, Lepczyk CA, Pittman SJ, Friedlander AM, Jorgensen S (2011) Quantifying seascape structure: extending terrestrial spatial patterns metrics to the marine realm. *Marine Ecology Progress Series* 427: 219-232

Weinstein BG (2018) A computer vision for animal ecology. *Journal of Animal Ecology* 87: 533-545

Welsh JQ, Bellwood DR (2014) Herbivorous fishes, ecosystem function and mobile links on coral reefs. *Coral Reefs* 33: 303-311

Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* 15: 393-425

Wheatley M, Johnson C (2009) Factors limiting our understanding of ecological scale. *Ecological Complexity* 6: 150-159

Whittaker RH (1965) Dominance and diversity in land plant communities. *Science* 147: 250-260

Wiens JA (1976) Population responses to patchy environments. *Annual Review of Ecology and Systematics* 7: 81-120

Wiens JA (1989) Spatial scaling in ecology. *Functional Ecology* 3: 385-397

Wiens JA (2007) Does conservation need landscape ecology? A perspective from both sides of the divide. In Lindenmayer DB, Hobbs RJ (Eds) *Managing and designing landscapes for conservation: moving from perspectives to principles*. Blackwell Publishing pp 479-493

Wiens JA, Stenseth NC, Van Horne B, Ims RA (1993) Ecological mechanisms and landscape ecology. *Oikos* 66: 369-380

Williams DM (1982) Patterns in the distribution of fish communities across the central Great Barrier Reef. *Coral Reefs* 1: 35-43

Williams DM, Hatcher AI (1983) Structure of fish communities on outer slopes of inshore, mid-shelf and outer shelf reefs of the Great Barrier Reef. *Marine Ecology Progress Series* 10: 239-250

Williams GJ. Graham NAJ (2019) Rethinking coral reef functional futures. *Functional Ecology* 33: 942-947

Williams ID, Kindinger TL, Couch CS, Walsh WJ, Minton D, Oliver TA (2019) Can herbivore management increase the persistence of Indo-Pacific coral reefs? *Frontiers in Marine Science* 6: 557

Williams SE, Bolitho EE, Fox S (2003) Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Proceedings of the Royal Society B* 270: 1887-1892

Wilson SK, Burgess SC, Cheal AJ, Emslie M, Fisher R, Miller I, Polunin NVC, Sweatman HPA (2008) Habitat utilization by coral reef fish: implications for specialists vs. generalists in a changing environment. *Journal of Animal Ecology* 77: 220-228

Wilson SK, Depczynski M, Fisher R, Holmes TH, O'Leary RA, Tinkler P (2010) Habitat associations of juvenile fish at Ningaloo Reef, Western Australia: the importance of coral and algae. *PLoS ONE* 5: e15185

Wilson SK, Depczynski M, Holmes TH, Noble MM, Radford BT, Tinkler P, Fulton CJ (2017) Climatic conditions and nursery habitat quality provide indicators of reef fish recruitment strength. *Limnology and Oceanography* 65: 1868-1880

Wilson SK, Fulton CJ, Depczynski M, Holmes TH, Noble MM, Radford B, Tinkler P (2014) Seasonal changes in habitat structure underpins shifts in macroalgae-associated tropical fish communities. *Marine Biology* 161: 2597-2607

Wismer S, Hoey AS, Bellwood DR (2009) Cross-shelf benthic community structure on the Great Barrier Reef: relationships between macroalgal cover and herbivore biomass. *Marine Ecology Progress Series* 376: 45-54

Wu J, Loucks OL (1995) From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. *The Quarterly Review of Biology* 70: 439-466

Yabsley NA, Olds AD, Connolly RM, Martin TSH, Gilby BL, Maxwell PS, Huijbers CM, Schoeman DS, Schlacher TA (2016) Resource type influences the effects of reserves and connectivity on ecological functions. *Journal of Animal Ecology* 85: 437-444

Yeager LA, Layman CA, Allgeier JC (2011) Effects of habitat heterogeneity at multiple spatial scales on fish community assembly. *Oecologia* 167: 157-168

Yeager ME, Hovel KA (2017) Structural complexity and fish body size interactivity affect habitat optimality. *Oecologia* 185: 257-267

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1: 3-14

# Appendices

## Appendix A: Supplementary materials for Chapter 2

### *Beyond the reef: the widespread use of non-reef habitats by coral reef fishes*

**Table A2.1.** Coral reef fish species observed in non-reef habitats by life stage. Habitat categories: SG = seagrass, MG = mangrove, MA = macroalgae beds, SS = soft sediment, E = estuarine environments, OT = Other (includes non-coral dominated channels, gorgonian plains, mudflats, boulders, notches and transition habitat between reef and seagrass). Observations were recorded as follows: X = observed in habitat, 0 = habitat surveyed but species not observed, - = habitat not surveyed. Criteria for inclusion in table: 1) in each study, individuals were observed on coral reefs AND in non-reef habitat, and; 2) species were classed as coral reef-associated (*FishBase*; Froese & Pauly 2018).

| | **All** | | | | | | **Juveniles** | | | | | | **Adults** | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **References** |
| **<u>Tropical Atlantic</u>** | | | | | | | | | | | | | | | | | | | |
| Acanthuridae | | | | | | | | | | | | | | | | | | | |
| *Acanthurus bahianus* | X | X | X | 0 | X | X | X | X | X | - | - | X | X | 0 | 0 | - | - | 0 | 1, 2, 3, 4, 5, 6, 7, 8, 9. 10, 11, 12, 13, 14,,15,16,17,18,19 |
| *Acanthurus chirurgus* | X | X | X | X | X | X | X | X | X | - | - | X | X | X | 0 | - | - | X | 1,2,3,4,5,6,7,8,10,11,12,13,14,15,16,18,19,20 |
| *Acanthurus coeruleus* | X | X | X | 0 | X | X | X | X | X | - | - | X | 0 | 0 | 0 | - | - | 0 | 2,4,6,7,8,10,12,13,14,15,16,19,21,22 |
| Albulidae | | | | | | | | | | | | | | | | | | | |
| *Albula vulpes* | X | X | - | - | - | - | X | X | - | - | - | - | - | - | - | - | - | - | 23 |
| Apogonidae | | | | | | | | | | | | | | | | | | | |
| *Apogon binotatus* | 0 | X | - | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 24 |
| *Apogon lachneri* | X | X | - | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 24 |
| *Apogon maculatus* | X | X | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 24 |
| *Apogon planifrons* | 0 | X | - | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 24 |
| *Apogon townsendi* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 18 |

| | All | | | | | | Juveniles | | | | | | Adults | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **References** |
| *Phaeoptyx conklini* | 0 | X | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 24 |
| *Phaeoptyx pigmentaria* | 0 | X | - | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 24 |
| *Phaeoptyx xenus* | 0 | X | - | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 24 |
| Atherinidae | | | | | | | | | | | | | | | | | | | |
| *Atherinomorus stipes* | X | X | - | X | - | - | X | X | - | X | - | - | - | - | - | - | - | - | 25 |
| Aulostomidae | | | | | | | | | | | | | | | | | | | |
| *Aulostomus maculatus* | X | X | 0 | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 8,14,26 |
| Balistidae | | | | | | | | | | | | | | | | | | | |
| *Balistes vetula* | X | 0 | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 4,8 |
| *Melichthys niger* | 0 | 0 | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 8 |
| Blennidae | | | | | | | | | | | | | | | | | | | |
| *Ophioblennius trinitatis* | 0 | - | X | - | - | - | 0 | - | 0 | - | - | - | 0 | - | X | - | - | - | 6 |
| Carangidae | | | | | | | | | | | | | | | | | | | |
| *Carangoides bartholomaei* | X | - | X | - | X | X | X | - | X | - | - | - | 0 | - | 0 | - | - | - | 4,6,8,16 |
| *Caranx crysos* | X | X | - | - | - | 0 | - | - | - | - | - | - | - | - | - | - | - | - | 7,8 |
| *Caranx latus* | X | X | 0 | - | X | X | - | - | - | - | - | - | - | - | - | - | - | - | 14,16 |
| *Caranx ruber* | X | X | 0 | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 4,7,8,14,18 |
| *Seriola rivoliana* | 0 | 0 | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 8 |
| Chaetodontidae | | | | | | | | | | | | | | | | | | | |
| *Chaetodon capistratus* | X | X | X | - | - | X | X | X | - | - | - | X | X | X | - | - | - | X | 2,4,7,8,9,12,13,14,15,18,19,22,27 |
| *Chaetodon ocellatus* | 0 | X | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 7,8,27 |
| *Chaetodon striatus* | 0 | X | X | 0 | X | X | 0 | - | X | - | - | - | 0 | - | 0 | - | - | - | 1,2,6,7,8,16,27 |
| *Prognathodes aculeatus* | 0 | 0 | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 8 |
| Cirrhitidae | | | | | | | | | | | | | | | | | | | |
| *Amblycirrhitus pinos* | 0 | 0 | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 8 |
| Dasyatidae | | | | | | | | | | | | | | | | | | | |
| *Hypanus americanus* | X | 0 | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 7,8 |
| Diodontidae | | | | | | | | | | | | | | | | | | | |
| *Diodon holocanthus* | X | X | X | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 2,14 |
| *Diodon hystrix* | X | X | 0 | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 2,14,21 |

| Species | All | | | | | | Juveniles | | | | | | Adults | | | | | | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | SG | MG | MA | SS | E | OT | SG | MG | MA | SS | E | OT | SG | MG | MA | SS | E | OT | |
| Engraulidae | | | | | | | | | | | | | | | | | | | |
| *Anchoa lyolepis* | X | X | - | X | - | - | X | X | - | X | - | - | - | - | - | - | - | - | 25 |
| Ephippidae | | | | | | | | | | | | | | | | | | | |
| *Chaetodipterus faber* | - | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | 16 |
| Gerreidae | | | | | | | | | | | | | | | | | | | |
| *Gerres cinereus* | X | X | X | X | X | X | X | X | - | - | - | X | X | X | - | - | - | X | 1,2,4,8,9,12,13,14,16,20,21,22,28 |
| Gobiidae | | | | | | | | | | | | | | | | | | | |
| *Coryphopterus glaucofraenum* | X | X | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 4,7,18 |
| *Coryphopterus personatus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 18 |
| *Gnatholepis thompsoni* | - | 0 | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 4 |
| Grammatidae | | | | | | | | | | | | | | | | | | | |
| *Gramma loreto* | 0 | 0 | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 8 |
| Haemulidae | | | | | | | | | | | | | | | | | | | |
| *Anisotremus surinamensis* | 0 | X | 0 | - | - | 0 | 0 | - | 0 | - | - | - | 0 | - | 0 | - | - | - | 6,8,14 |
| *Anisotremus virginicus* | X | X | 0 | - | X | X | - | - | - | - | - | - | - | - | - | - | - | - | 2,4,7,14,16,18 |
| *Haemulon album* | X | 0 | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 8 |
| *Haemulon aurolineatum* | X | X | X | - | X | X | X | X | 0 | - | - | - | 0 | 0 | 0 | - | - | - | 2,3,4,6,7,9,10,16 |
| *Haemulon carbonarium* | X | X | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 8,10,27 |
| *Haemulon chrysargyreum* | X | X | 0 | - | - | X | X | X | - | - | - | X | X | X | - | - | - | X | 12,13,14 |
| *Haemulon flavolineatum* | X | X | X | X | - | X | X | X | - | X | - | X | X | X | - | - | - | X | 1,2,4,5,7,8,9,10,11,12,13,14,15,18,19,20,21,22,27,28,29,30,31,32,33,34,35 |
| *Haemulon macrostomum* | X | X | - | - | - | 0 | - | - | - | - | - | - | - | - | - | - | - | - | 4,7 |
| *Haemulon parra* | X | X | X | - | X | X | X | X | X | - | - | 0 | X | X | 0 | - | - | 0 | 2,6,7,8,12,16,20,22,28 |
| *Haemulon plumierii* | X | X | X | X | - | X | X | X | X | - | - | - | 0 | 0 | 0 | - | - | - | 1,2,4,6,7,8,9,10,11,13,14,21,22,27,29,30,36,37 |
| *Haemulon sciurus* | X | X | X | X | - | X | X | X | - | - | - | X | X | X | - | - | - | X | 2,3,4,5,7,8,9,12,13,14,15,20,21,22,27,28,29,30,31,33,38,39 |
| Holocentridae | | | | | | | | | | | | | | | | | | | |

| | All | | | | | | Juveniles | | | | | | Adults | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **References** |
| *Holocentrus adscensionis* | 0 | X | 0 | - | X | X | 0 | 0 | - | - | - | X | 0 | 0 | - | - | - | X | 2,8,14,16,20 |
| *Holocentrus rufus* | X | X | 0 | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 2,4,8,14 |
| *Myripristis jacobus* | 0 | X | 0 | - | - | 0 | - | - | - | - | - | - | - | - | - | - | - | - | 4,8,14 |
| *Sargocentron vexillarium* | X | X | 0 | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 2,14 |
| Kyphosidae | | | | | | | | | | | | | | | | | | | |
| *Kyphosus sectatrix* | 0 | X | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 2,7,8 |
| Labridae | | | | | | | | | | | | | | | | | | | |
| *Bodianus rufus* | 0 | 0 | 0 | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 8,14 |
| *Clepticus parrae* | 0 | 0 | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 8 |
| *Halichoeres bivittatus* | X | X | X | X | - | X | X | X | - | - | | X | X | X | - | - | | X | 1,2,4,7,8,9,12,14,18,40,41 |
| *Halichoeres brasiliensis* | 0 | - | X | - | - | - | 0 | - | 0 | - | - | - | 0 | - | 0 | - | - | - | 6 |
| *Halichoeres garnoti* | X | X | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 2,4,8 |
| *Halichoeres maculipinna* | X | 0 | X | 0 | - | X | X | 0 | - | - | - | X | X | 0 | - | - | - | X | 1,8,12,14 |
| *Halichoeres pictus* | 0 | 0 | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 8 |
| *Halichoeres poeyi* | X | 0 | X | 0 | - | X | X | 0 | X | - | - | - | X | 0 | X | - | - | - | 1,2,4,6,8,9,14 |
| *Halichoeres radiatus* | X | X | 0 | 0 | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 1,7,8,14 |
| *Lachnolaimus maximus* | X | 0 | 0 | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 2,7,8,14 |
| *Thalassoma bifasciatum* | X | X | 0 | - | - | X | X | X | - | - | - | X | X | X | - | - | - | X | 2,4,7,8,9,12,14,18,41 |
| *Xyrichtys martinicensis* | - | 0 | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 4 |
| *Xyrichtys splendens* | X | - | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 |
| Labrisomidae | | | | | | | | | | | | | | | | | | | |
| *Labrisomus nuchipinnis* | 0 | - | X | - | - | - | 0 | - | X | - | - | - | 0 | - | 0 | - | - | - | 6 |
| *Malacoctenus triangulatus* | 0 | X | X | - | - | - | 0 | - | 0 | - | - | - | 0 | - | X | - | - | - | 4,6,18 |
| Lutjanidae | | | | | | | | | | | | | | | | | | | |
| *Lutjanus alexandrei* | - | X | X | X | - | - | - | X | - | - | - | - | - | 0 | - | - | - | - | 42,43 |
| *Lutjanus analis* | X | X | X | X | - | X | X | X | - | - | - | 0 | 0 | 0 | - | - | - | X | 1,2,7,8,13,14,20,29 |
| *Lutjanus apodus* | X | X | X | X | - | X | X | X | - | - | - | X | X | X | - | - | - | X | 2,3,4,5,7,8,9,12,13,14,15,17,18,20,21,22,26,27,28,31,44,45 |
| *Lutjanus cyanopterus* | 0 | X | - | - | - | 0 | - | - | - | - | - | - | - | - | - | - | - | - | 8 |

| | All | | | | | | Juveniles | | | | | | Adults | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **References** |
| *Lutjanus griseus* | X | X | X | - | - | X | X | X | - | - | - | X | X | X | - | - | - | X | 2,3,4,5,7,8,9,12,13,14,20,21,28,46 |
| *Lutjanus jocu* | 0 | X | - | - | X | - | - | X | - | - | X | - | - | 0 | - | - | X | - | 2,16,29,42,47 |
| *Lutjanus mahogoni* | X | X | X | X | - | X | X | X | - | - | - | X | X | X | - | - | - | X | 1,2,4,8,10,11,12,13,14,15,19,20,22,31 |
| *Lutjanus synagris* | X | X | - | - | X | X | - | - | - | - | - | - | - | - | - | - | - | - | 4,7,8,16,27,36 |
| *Ocyurus chrysurus* | X | X | X | X | - | X | X | X | X | - | - | X | 0 | 0 | 0 | - | - | 0 | 1,2,4,5,6,7,8,9,10,11,12,13,14,15,17,20,22,27,29,33,36,48 |
| Malacanthidae | | | | | | | | | | | | | | | | | | | |
| *Malacanthus plumieri* | X | 0 | X | X | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 1,4,8 |
| Megalopidae | | | | | | | | | | | | | | | | | | | |
| *Megalops atlanticus* | 0 | X | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 7 |
| Monacanthidae | | | | | | | | | | | | | | | | | | | |
| *Aluterus schoepfii* | 0 | 0 | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 8 |
| *Cantherhines macrocerus* | 0 | 0 | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 8 |
| *Monacanthus tuckeri* | X | 0 | - | - | - | 0 | - | - | - | - | - | - | - | - | - | - | - | - | 7,49 |
| Mullidae | | | | | | | | | | | | | | | | | | | |
| *Mulloidichthys martinicus* | X | X | 0 | - | - | X | X | X | - | - | - | 0 | X | X | - | - | - | X | 2,4,8,12,14 |
| *Pseudupeneus maculatus* | X | X | X | X | X | X | 0 | - | X | - | - | - | X | - | X | - | - | - | 1,2,4,6,8,14,16 |
| Muraenidae | | | | | | | | | | | | | | | | | | | |
| *Gymnothorax funebris* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 |
| *Gymnothorax moringa* | 0 | X | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 2,8 |
| *Gymnothorax vicinus* | - | - | - | - | X | - | - | - | - | - | - | - | - | - | | - | - | - | 16 |
| Ophichthidae | | | | | | | | | | | | | | | | | | | |
| *Myrichthys ocellatus* | - | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | 16 |
| Opistognathidae | | | | | | | | | | | | | | | | | | | |
| *Opistognathus aurifrons* | - | 0 | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 4 |
| Ostraciidae | | | | | | | | | | | | | | | | | | | |
| *Acanthostracion polygonius* | 0 | X | 0 | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 8,14 |
| *Lactophrys bicaudalis* | X | X | X | 0 | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 1,8,14 |
| *Lactophrys triqueter* | 0 | X | X | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 14 |
| Pomacanthidae | | | | | | | | | | | | | | | | | | | |

| | All | | | | | | Juveniles | | | | | | Adults | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **References** |
| *Holacanthus bermudensis* | 0 | 0 | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 7 |
| *Holacanthus ciliaris* | X | X | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 2,7 |
| *Holacanthus tricolor* | 0 | 0 | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 8 |
| *Pomacanthus arcuatus* | X | X | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 2,4,7,8 |
| *Pomacanthus paru* | X | X | X | - | X | X | 0 | - | X | - | - | - | X | - | 0 | - | - | - | 1,6,7,8,14,16 |
| Pomacentridae | | | | | | | | | | | | | | | | | | | |
| *Abudefduf saxatilis* | X | X | X | - | X | X | 0 | X | X | - | - | - | 0 | 0 | 0 | - | - | - | 2,4,6,7,8,9,13,14,16, 18,19,27,28 |
| *Abudefduf taurus* | 0 | 0 | 0 | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 14 |
| *Chromis cyanea* | 0 | 0 | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 8 |
| *Chromis multilineata* | 0 | 0 | 0 | - | - | X | 0 | 0 | - | - | - | 0 | 0 | 0 | - | - | - | X | 8,12,14 |
| *Microspathodon chrysurus* | 0 | 0 | X | - | - | X | 0 | - | X | - | - | - | 0 | - | 0 | - | - | - | 6,8 |
| *Stegastes adustus* | X | X | 0 | - | - | X | 0 | X | - | - | - | 0 | 0 | X | - | - | - | X | 2,4,8,12,14,18 |
| *Stegastes diencaeus* | X | X | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 4,8 |
| *Stegastes fuscus* | 0 | 0 | X | - | X | X | 0 | - | X | - | - | - | 0 | - | X | - | - | - | 6,7,16 |
| *Stegastes leucostictus* | X | X | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1,2,4,8 |
| *Stegastes partitus* | X | X | 0 | - | - | X | 0 | 0 | - | - | - | X | 0 | 0 | - | - | - | X | 1,2,4,7,8,12,14,41 |
| *Stegastes planifrons* | X | X | 0 | 0 | - | X | 0 | 0 | - | - | - | X | X | X | - | - | - | X | 2,4,8,9,12,14,41,50 |
| *Stegastes variabilis* | 0 | 0 | X | - | X | X | 0 | - | X | - | - | - | 0 | - | X | - | - | - | 6,7,8,16 |
| Scarine | | | | | | | | | | | | | | | | | | | |
| *Cryptotomus roseus* | - | 0 | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 4 |
| *Nicholsina usta usta* | 0 | X | - | - | - | 0 | - | - | - | - | - | - | - | - | - | - | - | - | 8 |
| *Scarus coeruleus* | X | 0 | - | - | - | X | X | 0 | - | - | - | X | 0 | 0 | - | - | - | 0 | 12,13,20 |
| *Scarus guacamaia* | X | X | - | - | - | X | X | X | - | - | - | X | 0 | 0 | - | - | | 0 | 7,8,12,13,28,39,51 |
| *Scarus iseri* | X | X | X | 0 | - | X | X | X | - | - | - | X | X | X | - | - | - | X | 1,3,4,5,7,8,9,10,11,1 2,13,18,20,31,33 |
| *Scarus taeniopterus* | X | X | X | 0 | - | X | 0 | X | - | - | - | - | 0 | 0 | - | - | - | - | 1,2,5,7,8,10,22 |
| *Scarus vetula* | 0 | X | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 7,8,21 |
| *Sparisoma amplum* | 0 | - | X | - | - | - | 0 | - | X | - | - | - | 0 | - | 0 | - | - | - | 6 |
| *Sparisoma atomarium* | X | X | 0 | 0 | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 1,4,8 |
| *Sparisoma aurofrenatum* | X | X | X | 0 | - | X | X | X | - | - | - | X | X | 0 | - | - | - | X | 2,3,7,8,9,10,12,18,3 1 |
| *Sparisoma axillare* | X | - | X | - | X | - | X | - | X | - | - | - | 0 | - | 0 | - | - | - | 6,16,52 |
| *Sparisoma chrysopterum* | X | X | - | - | - | X | X | X | - | - | - | X | X | 0 | - | - | - | X | 4,7,8,12,13,20,27 |

| | All | | | | | | Juveniles | | | | | | Adults | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **References** |
| *Sparisoma frondosum* | 0 | - | X | - | - | - | 0 | - | X | - | - | - | 0 | - | 0 | - | - | - | 6 |
| *Sparisoma radians* | X | X | X | X | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 1,4,7,8 |
| *Sparisoma rubripinne* | 0 | X | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 2,7,8,27 |
| *Sparisoma viride* | X | X | X | 0 | - | X | X | X | - | - | - | X | 0 | 0 | - | - | - | X | 1,2,3,4,7,8,12,13,15, 18,19,21,50 |
| Sciaenidae | | | | | | | | | | | | | | | | | | | |
| *Equetus punctatus* | 0 | 0 | 0 | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 14 |
| *Pareques acuminatus* | X | 0 | X | - | - | X | 0 | - | X | - | - | - | 0 | - | 0 | - | - | - | 6,7 |
| Scorpaenidae | | | | | | | | | | | | | | | | | | | |
| *Pterois volitans* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 53,54,55,56 |
| *Scorpaena plumieri* | 0 | X | 0 | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 14 |
| Serranidae | | | | | | | | | | | | | | | | | | | |
| *Cephalopholis cruentata* | 0 | 0 | 0 | - | - | X | 0 | 0 | - | - | - | 0 | 0 | 0 | - | - | - | X | 8,12,14 |
| *Cephalopholis fulva* | X | 0 | 0 | - | X | X | X | - | 0 | - | - | - | - | - | - | - | - | - | 8,16,57 |
| *Epinephelus adscensionis* | X | - | 0 | - | X | - | X | - | 0 | - | - | - | - | - | - | - | - | - | 16,57 |
| *Epinephelus guttatus* | X | 0 | X | 0 | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 1,8 |
| *Epinephelus morio* | 0 | 0 | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 7 |
| *Epinephelus striatus* | X | X | X | 0 | - | X | X | - | 0 | - | - | - | - | - | - | - | - | - | 8,36,50,57 |
| *Hypoplectrus aberrans* | 0 | 0 | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 8 |
| *Hypoplectrus chlorurus* | 0 | X | 0 | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 2,4,8,14 |
| *Hypoplectrus guttavarius* | 0 | 0 | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 8 |
| *Hypoplectrus indigo* | 0 | 0 | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 8 |
| *Hypoplectrus puella* | X | X | 0 | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 2,4,7,8,14,18 |
| *Hypoplectrus unicolor* | X | X | 0 | - | - | X | X | X | - | - | - | X | X | X | - | - | - | X | 2,12,14 |
| *Mycteroperca bonaci* | 0 | X | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 7,8 |
| *Mycteroperca tigris* | 0 | 0 | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 8 |
| *Mycteroperca venenosa* | 0 | 0 | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 8 |
| *Rypticus maculatus* | 0 | X | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 7 |
| *Rypticus saponaceus* | 0 | 0 | 0 | - | X | X | - | - | - | - | - | - | - | - | - | - | - | - | 14,16 |
| *Serranus flaviventris* | - | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | 16 |
| *Serranus tabacarius* | 0 | 0 | 0 | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 14 |
| *Serranus tigrinus* | X | 0 | 0 | X | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 1,8,18 |
| Sparidae | | | | | | | | | | | | | | | | | | | |

| | All | | | | | | Juveniles | | | | | | Adults | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **References** |
| *Archosargus rhomboidalis* | X | X | - | - | X | X | - | - | - | - | - | - | - | - | - | - | - | - | 2,7,16,21,23 |
| *Calamus bajonado* | 0 | X | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 7,8,21 |
| *Calamus calamus* | X | X | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 8,21 |
| *Calamus pennatula* | - | 0 | 0 | 0 | 0 | X | - | - | - | - | - | - | - | - | - | - | - | - | 4 |
| *Lagodon rhomboides* | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 28 |
| Sphyraenidae | | | | | | | | | | | | | | | | | | | |
| *Sphyraena barracuda* | X | X | X | - | X | X | X | X | - | - | - | X | X | X | - | - | - | 0 | 2,3,8,12,13,14,15,16 ,20,28 |
| Synodontidae | | | | | | | | | | | | | | | | | | | |
| *Synodus intermedius* | X | 0 | 0 | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 2,4,14 |
| Tetraodontidae | | | | | | | | | | | | | | | | | | | |
| *Canthigaster rostrata* | X | X | X | 0 | - | X | 0 | 0 | - | - | - | X | 0 | 0 | - | - | - | X | 1,2,4,8,12,14,18 |
| *Sphoeroides greeleyi* | - | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | 16 |
| *Sphoeroides spengleri* | X | 0 | 0 | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 2,4,14 |
| ***<u>Indo-Pacific</u>*** | | | | | | | | | | | | | | | | | | | |
| **Species** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | |
| Acanthuridae | | | | | | | | | | | | | | | | | | | |
| *Acanthurus auranticavus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Acanthurus blochii* | X | X | X | - | 0 | - | X | X | - | 0 | - | - | 0 | 0 | - | 0 | - | - | 58,59,60,61,62 |
| *Acanthurus dussumieri* | X | X | X | X | - | - | - | - | X | - | | - | - | - | - | - | | - | 58,60,61,63,64,65 |
| *Acanthurus grammoptilus* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 65 |
| *Acanthurus leucosternon* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58,66,67 |
| *Acanthurus mata* | X | X | - | X | - | - | X | - | - | 0 | - | - | 0 | - | - | 0 | - | - | 58,61,64,68,69 |
| *Acanthurus nigricauda* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Acanthurus nigrofuscus* | X | 0 | X | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | 58,60,67,70,71 |
| *Acanthurus thompsoni* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Acanthurus xanthopterus* | X | X | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 61,64,72 |
| *Ctenochaetus binotatus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 67 |
| *Ctenochaetus striatus* | X | 0 | - | X | - | - | X | - | - | - | - | - | - | - | - | - | - | - | 58,67,71,73,74 |
| *Ctenochaetus strigosus* | X | 0 | - | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | 58 |

| | All | | | | | | Juveniles | | | | | | Adults | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **References** |
| *Naso brevirostris* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Naso unicornis* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 66 |
| *Zebrasoma desjardini* | - | 0 | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 64 |
| *Zebrasoma scopas* | X | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 67,74 |
| *Zebrasoma veliferum* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58,71 |
| *Zebrasoma xanthurum* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| Antennariidae | | | | | | | | | | | | | | | | | | | |
| *Antennarius pictus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Histrio histrio* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| Apogonidae | | | | | | | | | | | | | | | | | | | |
| *Apogon ishigakiensis* | X | - | - | - | - | - | X | - | - | - | - | - | X | - | - | - | - | - | 59 |
| *Apogon sangiensis* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Apogonichthyoides taeniatus* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Archamia fucata* | 0 | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Cheilodipterus lachneri* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Cheilodipterus macrodon* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Cheilodipterus novemstriatus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Cheilodipterus quinquelineatus* | X | 0 | X | X | - | - | X | - | X | 0 | - | - | X | - | - | 0 | - | - | 58,59,63,64,65,68,69,72 |
| *Fibramia ambionensis* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Fibramia thermalis* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Fowleria aurita* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Jaydia catalai* | - | 0 | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 64 |
| *Ostorhinchus aureus* | X | 0 | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58,64 |
| *Ostorhinchus compressus* | 0 | - | - | - | - | X | 0 | - | - | - | - | X | 0 | - | - | - | - | X | 75 |
| *Ostorhinchus cyanosoma* | X | 0 | - | - | - | X | X | - | - | - | - | 0 | 0 | - | - | - | - | X | 58,71,75 |
| *Ostorhinchus rueppellii* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 65 |
| *Ostorhinchus wassinki* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 65 |
| *Pristiapogon fraenatus* | - | 0 | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 64 |
| *Pterapogon kauderni* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 76 |
| *Sphaeramia orbicularis* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 63 |
| *Zoramia leptacantha* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |

| | All | | | | | | Juveniles | | | | | | Adults | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **References** |
| Atherinidae | | | | | | | | | | | | | | | | | | | |
| *Atherinomorus lacunosus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58,71 |
| Aulostomidae | | | | | | | | | | | | | | | | | | | |
| *Aulostomus chinensis* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58,67,68,72 |
| Balistidae | | | | | | | | | | | | | | | | | | | |
| *Balistapus undulatus* | X | 0 | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58,74 |
| *Balistoides viridescens* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Melichthys niger* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Pseudobalistes fuscus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Rhinecanthus aculeatus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Sufflamen albicaudatum* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Sufflamen chrysopterum* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Sufflamen fraenatum* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| Belonidae | | | | | | | | | | | | | | | | | | | |
| *Strongylura leiura* | 0 | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Tylosurus crocodilus crocodilus* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| Blennidae | | | | | | | | | | | | | | | | | | | |
| *Atrosalarias fuscus* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 65 |
| *Ecsenius frontalis* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Ecsenius gravieri* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Meiacanthus grammistes* | X | - | - | 0 | - | - | 0 | - | - | 0 | - | - | X | - | - | 0 | - | - | 69 |
| *Meiacanthus mossambicus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58,67 |
| *Meiacanthus migrolineatus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Petroscirtes breviceps* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Petroscirtes mitratus* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Salarias guttatus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 77 |
| Caesionidae | | | | | | | | | | | | | | | | | | | |
| *Caesio caerulaurea* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Caesio lunaris* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58,71 |
| *Caesio suevica* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Caesio teres* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |

| | All | | | | | | Juveniles | | | | | | Adults | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **References** |
| *Caesio varilineata* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Caesio xanthonota* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Pterocaesio chrysozona* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Pterocaesio marri* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Pterocaesio pisang* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Pterocaesio tile* | - | 0 | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 64 |
| Carangidae | | | | | | | | | | | | | | | | | | | |
| *Alectis ciliaris* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Carangoides ferdau* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Carangoides fulvoguttatus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Caranx ignobilis* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58,61,78 |
| *Caranx melampygus* | X | X | - | X | - | - | - | X | - | 0 | - | - | - | 0 | - | 0 | - | - | 61,62,72,79 |
| *Caranx papuensis* | 0 | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58,61 |
| *Caranx sexfasciatus* | 0 | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Gnathanodon speciosus* | 0 | X | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58,80 |
| *Scomberoides commersonnianus* | 0 | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Scomberoides tol* | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 61 |
| *Trachinotus blochii* | 0 | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| Centriscidae | | | | | | | | | | | | | | | | | | | |
| *Aeoliscus strigatus* | - | 0 | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 64 |
| Chaetodontidae | | | | | | | | | | | | | | | | | | | |
| *Chaetodon aureofasciatus* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 81 |
| *Chaetodon auriga* | X | X | X | X | - | - | X | - | X | X | - | - | - | X | - | X | - | - | 58,61,62,64,65,66,70,71,73,82 |
| *Chaetodon austriacus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Chaetodon baronessa* | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 74 |
| *Chaetodon bennetti* | - | 0 | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 64 |
| *Chaetodon ephippium* | X | 0 | - | X | - | - | X | - | - | - | - | - | - | - | - | - | - | - | 64,73 |
| *Chaetodon falcula* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Chaetodon fasciatus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Chaetodon flavirostris* | - | 0 | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 64 |

| | All | | | | | | Juveniles | | | | | | Adults | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **References** |
| *Chaetodon guttatissimus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 67 |
| *Chaetodon kleinii* | X | 0 | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58,67,74 |
| *Chaetodon lineolatus* | - | 0 | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 64 |
| *Chaetodon lunulatus* | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 74 |
| *Chaetodon melannotus* | X | 0 | - | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | 58,71,73,82 |
| *Chaetodon octofasciatus* | 0 | - | - | - | - | X | 0 | - | - | - | - | X | 0 | - | - | - | - | X | 75 |
| *Chaetodon paucifasciatus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Chaetodon plebeius* | X | 0 | X | X | - | - | X | - | X | - | - | - | - | - | - | - | - | - | 64,65,73 |
| *Chaetodon speculum* | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | 73 |
| *Chaetodon trifascialis* | 0 | - | X | - | - | X | 0 | - | X | - | - | 0 | 0 | - | - | - | - | X | 65,75 |
| *Chaetodon trifasciatus* | X | 0 | X | - | - | - | X | - | X | - | - | - | - | - | - | - | - | - | 58,65,67,73 |
| *Chaetodon vagabundus* | X | - | - | X | - | - | X | - | - | 0 | - | - | X | - | - | 0 | - | - | 68,69,74 |
| *Chaetodon xanthocephalus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Chelmon marginalis* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 81 |
| *Hemitaurichthys zoster* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Heniochus acuminatus* | X | 0 | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 58,60,61,62,81 |
| *Heniochus diphreutes* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Heniochus intermedius* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| Clupeidae | | | | | | | | | | | | | | | | | | | |
| *Spratelloides delicatulus* | 0 | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| Dasyatidae | | | | | | | | | | | | | | | | | | | |
| *Neotrygon kuhlii* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Taeniura lymma* | X | X | - | - | - | X | 0 | - | - | - | - | X | 0 | - | - | - | - | 0 | 58,75 |
| Diodontidae | | | | | | | | | | | | | | | | | | | |
| *Cyclichthys spilostylus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Diodon hystrix* | X | X | 0 | X | - | X | - | 0 | - | 0 | - | - | - | 0 | - | X | - | - | 58,61,62 |
| *Diodon liturosus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| Echeneidae | | | | | | | | | | | | | | | | | | | |
| *Echeneis naucrates* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| Ephippidae | | | | | | | | | | | | | | | | | | | |
| *Platax orbicularis* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58,61 |

| | All | | | | | | Juveniles | | | | | | Adults | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **References** |
| *Platax teira* | 0 | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| Fistularidae | | | | | | | | | | | | | | | | | | | |
| *Fistularia commersonii* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58,63,67,71 |
| *Fistularia petimba* | X | X | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58,64,83 |
| Gerreidae | | | | | | | | | | | | | | | | | | | |
| *Gerres filamentosus* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Gerres longirostris* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Gerres oblongus* | 0 | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Gerres oyena* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58,73,82 |
| Gobiidae | | | | | | | | | | | | | | | | | | | |
| *Amblyeleotris steinitzi* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Amblyeleotris sungami* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Amblygobius albimaculatus* | X | X | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58,72 |
| *Amblygobius phalaena* | X | - | - | X | - | X | X | - | - | X | - | - | X | - | - | 0 | - | - | 68,69,83,84 |
| *Amblygobius semicinctus* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Asterropteryx semipunctata* | X | - | - | X | - | X | X | - | - | 0 | - | - | X | - | - | 0 | - | X | 68,69,72,83,84 |
| *Bathygobius fuscus* | 0 | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Callogobius hasseltii* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 77 |
| *Ctenogobiops feroculus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 77 |
| *Ctenogobiops formosa* | 0 | - | - | X | - | - | 0 | - | - | X | - | - | 0 | - | - | X | - | - | 69 |
| *Ctenogobiops maculosus* | X | - | - | 0 | - | - | X | - | - | 0 | - | - | X | - | - | 0 | - | - | 69 |
| *Ctenogobiops pomastictus* | X | - | - | X | - | - | X | - | - | X | - | - | X | - | - | X | - | - | 68,69 |
| *Eviota infulata* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 77 |
| *Eviota queenslandica* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 77 |
| *Eviota sigillata* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 77 |
| *Fusigobius aureus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 77 |
| *Fusigobius neophytus* | X | X | - | X | - | - | X | - | - | 0 | - | - | X | - | - | X | - | - | 58,68,69,77 |
| *Gnatholepis anjerensis* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Gnatholepis cauerensis* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 77 |
| *Gobiodon oculolineatus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 77 |
| *Gobiodon unicolor* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 77 |
| *Macrodontogobius wilburi* | X | - | - | 0 | - | - | X | - | - | 0 | - | - | X | - | - | 0 | - | - | 69 |

| | All | | | | | | Juveniles | | | | | | Adults | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **References** |
| *Phyllogobius platycephalops* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 77 |
| *Pleurosicya muscarum* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 77 |
| *Valenciennea muralis* | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 84 |
| *Valenciennea puellaris* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| Haemulidae | | | | | | | | | | | | | | | | | | | |
| *Diagramma pictum* | X | 0 | - | X | - | - | - | 0 | - | X | - | - | - | 0 | - | 0 | - | - | 58,62,64 |
| *Plectorhinchus albovittatus* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58,85 |
| *Plectorhinchus chaetodonoides* | X | - | - | 0 | - | - | X | - | - | 0 | - | - | 0 | - | - | 0 | - | - | 69 |
| *Plectorhinchus flavomaculatus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58,66,67,82 |
| *Plectorhinchus gaterinus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58,82 |
| *Plectorhinchus gibbosus* | 0 | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58,85 |
| *Plectorhinchus lineatus* | 0 | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 61,63 |
| *Plectorhinchus obscurus* | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 61 |
| *Plectorhinchus plagiodesmus* | 0 | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Plectorhinchus schotaf* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58,66 |
| *Plectorhinchus vittatus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58,68 |
| Hemiramphidae | | | | | | | | | | | | | | | | | | | |
| *Hemiramphus far* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 61,79 |
| *Hyporhamphus dussumieri* | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 61 |
| Holocentridae | | | | | | | | | | | | | | | | | | | |
| *Myripristis murdjan* | X | - | - | - | - | X | 0 | - | - | - | - | X | 0 | - | - | - | - | 0 | 71,75 |
| *Neoniphon sammara* | X | X | - | 0 | - | - | - | 0 | - | 0 | - | - | - | X | - | 0 | - | - | 58,61,62 |
| *Sargocentron diadema* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58,71 |
| *Sargocentron rubrum* | - | X | - | 0 | - | - | - | 0 | - | 0 | - | - | - | X | - | 0 | - | - | 61,62 |
| Kyphosidae | | | | | | | | | | | | | | | | | | | |
| *Kyphosus cinerascens* | 0 | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Kyphosus vaigiensis* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |

| | All | | | | | | Juveniles | | | | | | Adults | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **References** |
| Labridae | | | | | | | | | | | | | | | | | | | |
| *Anampses caeruleopunctatus* | X | 0 | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 58, 65, 71 |
| *Anampses geographicus* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 65, 81 |
| *Anampses meleagrides* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Anampses twistii* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Bodianus anthioides* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Bodianus axillaris* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Cheilinus chlorourus* | X | 0 | X | X | - | - | X | - | X | 0 | - | - | X | - | - | 0 | - | - | 58, 63, 64, 65, 67, 68, 69, 72, 79 |
| *Cheilinus fasciatus* | X | - | - | 0 | - | X | 0 | - | - | - | - | X | 0 | - | - | - | - | X | 72, 75, 82 |
| *Cheilinus lunulatus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Cheilinus oxycephalus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Cheilinus trilobatus* | X | 0 | X | - | - | X | 0 | - | X | - | - | X | 0 | - | - | - | - | 0 | 58, 65, 66, 67, 74, 75, 82 |
| *Cheilinus undulatus* | X | 0 | X | - | - | - | X | - | X | - | - | - | - | - | - | - | - | - | 51, 58, 66, 79, 82, 85, 86 |
| *Cheilio inermis* | X | 0 | X | 0 | - | - | X | - | X | 0 | - | - | X | - | - | 0 | - | - | 58, 59, 63, 65, 66, 68, 69, 71, 72, 79, 82, 83 |
| *Choerodon anchorago* | X | X | - | 0 | - | X | X | - | - | 0 | - | X | X | - | - | 0 | - | X | 63, 68, 69, 75, 79, 85, 87 |
| *Choerodon cauteroma* | X | - | X | - | - | X | X | - | X | - | - | X | X | - | - | - | - | X | 81, 88 |
| *Choerodon cyanodus* | X | - | X | - | - | X | X | - | X | - | - | X | X | - | - | - | - | X | 81, 88 |
| *Choerodon monostigma* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 81 |
| *Choerodon schoenleinii* | X | - | X | - | - | X | X | - | X | - | - | X | X | - | - | - | - | X | 81, 88 |
| *Cirrhilabrus rubriventralis* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Coris aygula* | X | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 65, 71 |
| *Coris batuensis* | X | - | - | - | - | X | 0 | - | - | - | - | X | 0 | - | - | - | - | 0 | 68, 75 |
| *Coris caudimacula* | X | 0 | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 58, 65, 67, 71 |
| *Coris formosa* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 67 |
| *Coris variegata* | X | - | - | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71, 83 |
| *Diproctacanthus xanthurus* | 0 | - | - | - | - | X | 0 | - | - | - | - | X | 0 | - | - | - | - | X | 75 |
| *Epibulus insidiator* | X | - | - | - | - | X | 0 | - | - | - | - | X | X | - | - | - | - | X | 75 |
| *Gomphosus caeruleus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 67, 71 |

| Species | All | | | | | | Juveniles | | | | | | Adults | | | | | | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **References** |
| *Gomphosus varius* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 65 |
| *Halichoeres argus* | X | X | - | - | - | - | X | - | - | - | - | - | X | - | - | - | - | - | 59, 63, 68 |
| *Halichoeres chloropterus* | X | - | - | - | - | X | X | - | - | - | - | X | X | - | - | - | - | X | 75 |
| *Halichoeres hortulanus* | X | 0 | - | X | - | X | 0 | - | - | - | - | X | 0 | - | - | - | - | 0 | 58, 63, 67, 74, 75 |
| *Halichoeres leucurus* | 0 | - | - | - | - | X | 0 | - | - | - | - | X | 0 | - | - | - | - | X | 75 |
| *Halichoeres margaritaceus* | X | 0 | - | 0 | - | X | X | - | - | - | - | X | X | - | - | - | - | X | 63, 72, 75 |
| *Halichoeres marginatus* | X | 0 | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 58, 65 |
| *Halichoeres melanochir* | 0 | - | - | - | - | X | 0 | - | - | - | - | X | 0 | - | - | - | - | X | 75 |
| *Halichoeres melanurus* | X | - | - | X | - | X | X | - | - | 0 | - | 0 | X | - | - | 0 | - | X | 69, 74, 75 |
| *Halichoeres miniatus* | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 87 |
| *Halichoeres nebulosus* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 65, 81 |
| *Halichoeres richmondi* | 0 | - | - | - | - | X | 0 | - | - | - | - | 0 | 0 | - | - | - | - | X | 75 |
| *Halichoeres scapularis* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 63 |
| *Halichoeres trimaculatus* | X | - | X | 0 | - | - | X | - | X | 0 | - | - | X | - | - | 0 | - | - | 59, 65, 68, 69, 72 |
| *Halichoeres vrolikii* | 0 | - | - | - | - | X | 0 | - | - | - | - | X | 0 | - | - | - | - | X | 75 |
| *Halichoeres zeylonicus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Hemigymnus fasciatus* | X | 0 | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 58, 65, 71 |
| *Hemigymnus melapterus* | X | - | X | - | - | X | X | - | X | - | - | X | X | - | - | - | - | X | 65, 71, 81 |
| *Hologymnosus annulatus* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 65, 71 |
| *Labrichthys unilineatus* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 65 |
| *Labroides dimidiatus* | X | 0 | X | - | - | X | 0 | - | X | - | - | X | 0 | - | - | - | - | X | 58, 65, 67, 71, 75 |
| *Larabicus quadrilineatus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Macropharyngodon bipartitus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Macropharyngodon negrosensis* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 81 |
| *Macropharyngodon ornatus* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 65 |
| *Novaculichthys taeniourus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Oxycheilinus arenatus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Oxycheilinus bimaculatus* | X | 0 | - | X | - | - | X | - | - | 0 | - | - | X | - | - | 0 | - | - | 58, 59, 64, 69 |
| *Oxycheilinus celebicus* | 0 | - | - | - | - | X | 0 | - | - | - | - | 0 | 0 | - | - | - | - | X | 75 |
| *Oxycheilinus digramma* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 71 |
| *Oxycheilinus mentalis* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Paracheilinus octotaenia* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |

| | All | | | | | | Juveniles | | | | | | Adults | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **References** |
| *Pseudocheilinus evanidus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Pseudocheilinus hexataenia* | X | - | - | X | - | X | 0 | - | - | - | - | 0 | 0 | - | - | - | - | X | 67, 71, 74, 75 |
| *Pteragogus cryptus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Pteragogus flagellifer* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Stethojulis albovittata* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 71 |
| *Stethojulis bandanensis* | X | 0 | X | 0 | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 58, 65, 67, 72, 79 |
| *Stethojulis interrupta* | X | 0 | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 58, 65, 71, 81 |
| *Stethojulis strigiventer* | X | X | X | 0 | - | - | X | - | X | 0 | - | - | X | - | - | 0 | - | - | 58, 59, 65, 68, 69, 72, 81, 83 |
| *Stethojulis trilineata* | X | X | - | - | - | X | X | - | - | - | - | X | X | - | - | - | - | X | 63, 75 |
| *Thalassoma amblycephalum* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 67 |
| *Thalassoma hardwicke* | X | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 65, 67 |
| *Thalassoma hebraicum* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 67 |
| *Thalassoma lunare* | X | 0 | X | X | - | X | 0 | - | X | - | - | 0 | 0 | - | - | - | - | X | 64, 65, 67, 71, 74, 75 |
| *Thalassoma lutescens* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 65 |
| *Thalassoma rueppellii* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| Lethrinidae | | | | | | | | | | | | | | | | | | | |
| *Gnathodentex aureolineatus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Gymnocranius grandoculis* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58,66 |
| *Lethrinus atkinsoni* | X | - | X | 0 | - | - | X | - | X | 0 | - | - | 0 | - | - | 0 | - | - | 59, 65, 68, 69, 83, 89, 90 |
| *Lethrinus erythropterus* | 0 | X | - | - | - | X | 0 | - | - | - | - | X | 0 | - | - | - | - | X | 75,85 |
| *Lethrinus genivittatus* | X | X | - | X | - | - | X | - | - | - | - | - | 0 | - | - | - | - | - | 58,59,64,80 |
| *Lethrinus harak* | X | X | X | X | - | X | X | X | - | X | - | 0 | X | X | - | X | - | X | 58, 59, 61, 62, 63, 66, 67, 68, 69, 79, 82, 85, 87, 89, 91, 92, 93, 94, 95, 96 |
| *Lethrinus lentjan* | X | X | - | X | - | X | X | X | - | - | - | 0 | X | 0 | - | - | - | X | 58, 61, 64, 66, 82, 91, 92, 93 |
| *Lethrinus mahsena* | X | X | - | X | - | - | X | - | - | X | - | - | - | - | - | - | - | - | 58, 66, 67, 70, 82 |
| *Lethrinus microdon* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 66 |
| *Lethrinus miniatus* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |

| | All | | | | | | Juveniles | | | | | | Adults | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **References** |
| *Lethrinus nebulosus* | X | X | X | X | - | - | X | - | X | X | - | - | X | - | - | - | - | - | 58, 59, 61, 64, 66, 70, 83, 90, 97 |
| *Lethrinus obsoletus* | X | X | - | X | - | - | X | - | - | X | - | - | X | - | - | X | - | - | 58, 59, 61, 66, 67, 68, 83, 89, 94 |
| *Lethrinus olivaceus* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Lethrinus ornatus* | X | - | - | - | - | - | X | - | - | - | - | - | 0 | - | - | - | - | - | 59, 68 |
| *Lethrinus punctulatus* | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 80 |
| *Lethrinus rubrioperculatus* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 61 |
| *Lethrinus semicinctus* | - | 0 | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 64 |
| *Lethrinus variegatus* | X | X | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 58, 82, 90 |
| *Lethrinus xanthochilus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Monotaxis grandoculis* | X | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71, 74 |
| Lutjanidae | | | | | | | | | | | | | | | | | | | |
| *Lutjanus argentimaculatus* | X | X | - | X | - | - | - | X | - | 0 | - | - | - | X | - | 0 | - | - | 58, 61, 62, 64, 66, 82, 85, 87, 89 |
| *Lutjanus bohar* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 66, 67 |
| *Lutjanus carponotatus* | X | - | X | X | - | X | X | - | X | - | - | 0 | 0 | - | - | - | - | X | 75, 80, 81 |
| *Lutjanus decussatus* | X | X | - | - | - | X | 0 | - | - | - | - | X | X | - | - | - | - | X | 63, 75 |
| *Lutjanus ehrenbergii* | X | X | - | - | - | - | 0 | X | - | - | - | - | - | - | - | - | - | - | 58, 82, 98, 99, 100 |
| *Lutjanus fulviflamma* | X | X | - | X | - | 0 | X | X | - | - | - | 0 | X | 0 | - | - | - | 0 | 58, 61, 63, 64, 66, 67, 75, 82, 85, 87, 91, 92, 93, 98, 101 |
| *Lutjanus fulvus* | 0 | X | - | 0 | - | - | - | X | - | 0 | - | - | - | 0 | - | 0 | - | - | 58, 61, 62, 85, 102 |
| *Lutjanus gibbus* | X | 0 | - | X | - | - | X | - | - | X | - | - | X | - | - | X | - | - | 58, 59, 66, 68, 69, 82, 83, 94 |
| *Lutjanus kasmira* | X | 0 | - | X | X | X | - | - | - | - | - | - | - | - | - | - | - | - | 58, 64, 103 |
| *Lutjanus lutjanus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 66 |
| *Lutjanus monostigma* | 0 | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 63 |
| *Lutjanus quinquelineatus* | - | 0 | - | X | - | - | - | 0 | - | 0 | - | - | - | 0 | - | X | - | - | 62, 64 |
| *Lutjanus russellii* | - | X | - | 0 | - | - | - | X | - | 0 | - | - | - | 0 | - | 0 | - | - | 61, 62 |
| *Lutjanus vitta* | - | 0 | - | X | - | - | - | 0 | - | X | - | - | - | 0 | - | X | - | - | 62 |
| Monacanthidae | | | | | | | | | | | | | | | | | | | |
| *Aluterus scriptus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |

| | All | | | | | | Juveniles | | | | | | Adults | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **References** |
| *Amanses scopas* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 67, 71 |
| *Cantherhines pardalis* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 67, 71 |
| *Oxymonacanthus longirostris* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 65 |
| *Pervagor randalli* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| Mullidae | | | | | | | | | | | | | | | | | | | |
| *Mulloidichthys flavolineatus* | X | X | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 64, 68, 71, 72, 79, 82 |
| *Mulloidichthys vanicolensis* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 66 |
| *Parupeneus barberinoides* | X | - | X | 0 | - | - | X | - | X | - | - | - | X | - | - | - | - | - | 59, 65, 68, 81, 83 |
| *Parupeneus barberinus* | X | X | - | X | - | X | X | - | - | 0 | - | X | X | - | - | 0 | - | X | 58, 59, 63, 66, 68, 69, 72, 74, 75, 79, 82, 83 |
| *Parupeneus ciliatus* | X | 0 | - | 0 | - | - | X | - | - | 0 | - | - | X | - | - | 0 | - | - | 58, 59, 68, 69 |
| *Parupeneus cyclostomus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 71 |
| *Parupeneus forsskali* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Parupeneus heptacanthus* | - | 0 | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 64 |
| *Parupeneus indicus* | X | X | - | X | - | - | X | - | - | X | - | - | X | - | - | X | - | - | 58, 59, 61, 62, 64, 66, 68, 69, 82, 94 |
| *Parupeneus macronemus* | X | X | - | X | - | - | X | - | - | X | - | - | - | - | - | - | - | - | 58, 66, 67, 70, 71, 82 |
| *Parupeneus multifasciatus* | X | - | - | X | - | - | X | - | - | 0 | - | - | X | - | - | 0 | - | - | 59, 68, 69, 72, 74, 83 |
| *Parupeneus pleurostigma* | X | 0 | - | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 66, 72, 82 |
| *Parupeneus porphyreus* | X | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 72, 104 |
| *Parupeneus rubescens* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 61, 66, 82 |
| *Parupeneus spilurus* | - | 0 | X | X | - | - | - | 0 | X | X | - | - | - | 0 | - | X | - | - | 62, 64, 65 |
| *Upeneus taeniopterus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 79 |
| *Upeneus tragula* | X | X | X | X | - | X | X | - | - | X | - | X | X | X | - | X | - | X | 58, 59, 60, 61, 62, 64, 75, 87 |
| Muraenidae | | | | | | | | | | | | | | | | | | | |
| *Echidna nebulosa* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Gymnothorax griseus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Gymnothorax nudivomer* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |

| | All | | | | | | Juveniles | | | | | | Adults | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **References** |
| *Gymnothorax pictus* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| Nemipteridae | | | | | | | | | | | | | | | | | | | |
| *Pentapodus trivittatus* | X | - | - | - | - | X | X | - | - | - | - | 0 | X | - | - | - | - | X | 75 |
| *Scolopsis affinis* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 63 |
| *Scolopsis bilineata* | X | X | X | X | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 60, 63, 65, 74, 79 |
| *Scolopsis bimaculata* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Scolopsis ciliata* | X | X | - | X | - | 0 | 0 | - | - | - | - | 0 | X | - | - | - | - | 0 | 63, 74, 75 |
| *Scolopsis ghanam* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 66, 71, 82 |
| *Scolopsis lineata* | X | X | - | 0 | - | X | X | - | - | 0 | - | 0 | X | - | - | 0 | - | X | 63, 69, 75, 79 |
| *Scolopsis margaritifera* | 0 | - | - | - | - | X | 0 | - | - | - | - | 0 | 0 | - | - | - | - | X | 75 |
| *Scolopsis monogramma* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 79 |
| *Scolopsis temporalis* | - | 0 | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 64 |
| *Scolopsis trilineata* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 79 |
| Ophichthidae | | | | | | | | | | | | | | | | | | | |
| *Myrichthys colubrinus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| Ostraciidae | | | | | | | | | | | | | | | | | | | |
| *Lactoria cornuta* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Lactoria fornasini* | 0 | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Ostracion cubicus* | X | 0 | - | X | - | - | - | 0 | - | 0 | - | - | - | 0 | - | X | - | - | 58, 62, 64, 71 |
| *Ostracion cyanurus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| Pinguipedidae | | | | | | | | | | | | | | | | | | | |
| *Parapercis cylindrica* | X | X | X | X | - | - | X | 0 | - | X | - | - | X | 0 | - | X | - | - | 59, 60, 62, 63, 64, 68, 69, 83 |
| *Parapercis hexophtalma* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| Platycephalidae | | | | | | | | | | | | | | | | | | | |
| *Papilloculiceps longiceps* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Thysanophrys chiltonae* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| Plotosidae | | | | | | | | | | | | | | | | | | | |
| *Plotosus lineatus* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| Pomacanthidae | | | | | | | | | | | | | | | | | | | |
| *Apolemichthys xanthotis* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |

| Species | All | | | | | | Juveniles | | | | | | Adults | | | | | | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | SG | MG | MA | SS | E | OT | SG | MG | MA | SS | E | OT | SG | MG | MA | SS | E | OT | |
| *Centropyge multispinis* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 71 |
| *Centropyge tibicen* | - | 0 | - | X | - | - | - | 0 | - | X | - | - | - | 0 | - | X | - | - | 62 |
| *Centropyge vrolikii* | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 74 |
| *Genicanthus caudovittatus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Pomacanthus chrysurus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Pomacanthus imperator* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Pomacanthus sexstriatus* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 81 |
| *Pygoplites diacanthus* | X | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71, 71 |
| Pomacentridae | | | | | | | | | | | | | | | | | | | |
| *Abudefduf bengalensis* | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 87 |
| *Abudefduf lorenzi* | 0 | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 63 |
| *Abudefduf septemfasciatus* | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 61 |
| *Abudefduf sexfasciatus* | X | X | X | - | - | X | 0 | - | - | - | - | X | 0 | - | - | - | - | 0 | 58, 60, 63, 67, 75, 87 |
| *Abudefduf sparoides* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Abudefduf vaigiensis* | X | X | - | - | - | X | X | - | - | - | - | X | X | - | - | - | - | 0 | 58, 63, 71, 73, 75 |
| *Abudefduf whitleyi* | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 60 |
| *Amblyglyphidodon batunai* | X | - | - | - | - | X | X | - | - | - | - | X | 0 | - | - | - | - | X | 75 |
| *Amblyglyphidodon curacao* | 0 | - | - | X | - | X | 0 | - | - | - | - | X | 0 | - | - | - | - | X | 74, 75 |
| *Amblyglyphidodon leucogaster* | X | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 67, 71, 74 |
| *Amphiprion akallopisos* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 67 |
| *Amphiprion allardi* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Amphiprion bicinctus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Amphiprion ocellaris* | 0 | - | - | - | - | X | 0 | - | - | - | - | X | 0 | - | - | - | - | X | 75 |
| *Amphiprion rubrocinctus* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 81 |
| *Cheiloprion labiatus* | X | - | - | - | - | X | X | - | - | - | - | X | X | - | - | - | - | X | 75 |
| *Chromis atripectoralis* | X | - | - | - | - | X | 0 | - | - | - | - | X | 0 | - | - | - | - | X | 67, 75 |
| *Chromis dimidiata* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Chromis lepidolepis* | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 74 |
| *Chromis margaritifer* | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 74 |
| *Chromis opercularis* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Chromis retrofasciata* | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 74 |
| *Chromis ternatensis* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |

| | | All | | | | | | Juveniles | | | | | | Adults | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **References** |
| | *Chromis viridis* | X | - | X | - | - | - | X | - | X | - | - | - | - | - | - | - | - | - | 60, 65, 67, 71, 73 |
| | *Chrysiptera annulata* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| | *Chrysiptera cyanea* | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | 73 |
| | *Chrysiptera rex* | 0 | - | - | - | - | X | 0 | - | - | - | - | 0 | 0 | - | - | - | - | X | 75 |
| | *Chrysiptera rollandi* | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 74 |
| | *Chrysiptera talboti* | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 74 |
| | *Chrysiptera unimaculata* | X | - | - | 0 | - | - | X | - | - | 0 | - | - | X | - | - | 0 | - | - | 68, 69 |
| | *Dascyllus aruanus* | X | 0 | X | X | - | X | X | 0 | X | X | - | X | X | 0 | - | X | - | X | 58, 60, 62, 64, 65, 70, 71, 73, 75 |
| | *Dascyllus carneus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| | *Dascyllus marginatus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| | *Dascyllus reticulatus* | - | - | X | X | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 65, 74 |
| | *Dascyllus trimaculatus* | X | 0 | - | X | - | - | X | - | - | - | - | - | - | - | - | - | - | - | 58, 71, 73, 74 |
| | *Dischistodus chrysopoecilus* | X | - | - | - | - | X | X | - | - | - | - | X | X | - | - | - | - | X | 75 |
| | *Dischistodus melanotus* | X | - | - | - | - | X | 0 | - | - | - | - | 0 | X | - | - | - | - | X | 75 |
| | *Dischistodus perspicillatus* | X | - | X | - | - | 0 | X | - | X | - | - | 0 | X | - | - | - | - | 0 | 65, 75 |
| | *Dischistodus prosopotaenia* | X | - | X | 0 | - | X | X | - | X | 0 | - | X | X | - | - | 0 | - | X | 65, 68, 69, 75 |
| | *Neoglyphidodon melas* | X | 0 | X | - | - | X | 0 | - | X | - | - | X | 0 | - | - | - | - | X | 58, 65, 71, 75 |
| | *Neoglyphidodon nigroris* | 0 | - | - | - | - | X | 0 | - | - | - | - | 0 | 0 | - | - | - | - | X | 75 |
| | *Neopomacentrus azysron* | 0 | - | - | - | - | X | 0 | - | - | - | - | 0 | 0 | - | - | - | - | X | 75 |
| | *Neopomacentrus cyanomos* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 81 |
| | *Neopomacentrus filamentosus* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 81 |
| | *Neopomacentrus fuliginosus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| | *Neopomacentrus miryae* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| | *Plectroglyphidodon lacrymatus* | X | 0 | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 68, 65, 67 |
| | *Plectroglyphidodon leucozonus* | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | 73 |
| | *Pomacentrus adelus* | X | - | - | - | - | X | 0 | - | - | - | - | X | X | - | - | - | - | X | 75 |
| | *Pomacentrus amboinensis* | X | 0 | - | X | - | X | X | - | - | - | - | X | 0 | - | - | - | - | X | 64, 73, 74, 75 |
| | *Pomacentrus baenschi* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 67 |
| | *Pomacentrus bankanensis* | X | - | - | - | - | X | X | - | - | - | - | 0 | 0 | - | - | - | - | X | 73, 75 |
| | *Pomacentrus burroughi* | X | - | - | - | - | X | 0 | - | - | - | - | X | X | - | - | - | - | X | 75 |

| | All | | | | | | Juveniles | | | | | | Adults | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **References** |
| *Pomacentrus chrysurus* | X | - | - | 0 | - | X | X | - | - | 0 | - | 0 | X | - | - | 0 | - | X | 68, 69, 73, 75 |
| *Pomacentrus coelestis* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 65 |
| *Pomacentrus limosus* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 81 |
| *Pomacentrus milleri* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 81 |
| *Pomacentrus moluccensis* | X | - | X | X | - | X | X | - | X | - | - | X | 0 | - | - | - | - | 0 | 60, 65, 73, 74, 75 |
| *Pomacentrus nigromanus* | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 74 |
| *Pomacentrus philippinus* | 0 | 0 | X | X | - | X | 0 | - | - | - | - | X | 0 | - | - | - | - | X | 60, 64, 75 |
| *Pomacentrus trichrourus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 67, 71 |
| *Pomacentrus trilineatus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 67 |
| *Pomacentrus vaiuli* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 65 |
| *Stegastes nigricans* | X | 0 | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 58, 65 |
| *Stegastes obreptus* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 65 |
| Priacanthidae | | | | | | | | | | | | | | | | | | | |
| *Heteropriacanthus cruentatus* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Priacanthus hamrur* | X | 0 | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 64 |
| Pseudochromidae | | | | | | | | | | | | | | | | | | | |
| *Pseudochromis flavivertex* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Pseudochromis fridmani* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Pseudochromis fuscus* | X | - | X | - | - | 0 | 0 | - | X | - | - | 0 | X | - | - | - | - | 0 | 75, 77, 81 |
| *Pseudochromis olivaceus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Pseudochromis springeri* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| Scarinae | | | | | | | | | | | | | | | | | | | |
| *Bolbometopon muricatum* | X | X | - | - | - | - | X | X | - | - | - | - | - | - | - | - | - | - | 85 |
| *Calotomus carolinus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 66, 67, 82 |
| *Calotomus spinidens* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 73, 82 |
| *Calotomus viridescens* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Chlorurus atrilunula* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 66 |
| *Chlorurus gibbus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Chlorurus microrhinos* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 65 |
| *Chlorurus sordidus* | X | 0 | X | 0 | - | X | X | - | X | - | - | X | 0 | - | - | - | - | X | 58, 65, 66, 67, 71, 72, 75, 81, 82 |

| | All | | | | | | Juveniles | | | | | | Adults | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **References** |
| *Chlorurus strongylocephalus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 82 |
| *Hipposcarus harid* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 66, 82 |
| *Leptoscarus vaigiensis* | X | 0 | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 58, 65, 66, 79, 82 |
| *Scarus dubius* | X | - | - | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 72 |
| *Scarus ferrugineus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Scarus frenatus* | X | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 65, 67, 82 |
| *Scarus ghobban* | X | X | X | X | - | X | X | X | X | 0 | - | X | 0 | X | - | 0 | - | 0 | 58, 60, 61, 62, 64, 66, 67, 68, 69, 71, 75, 81, 82 |
| *Scarus niger* | X | - | - | - | - | X | 0 | - | - | - | - | 0 | 0 | - | - | - | - | X | 71, 75, 82 |
| *Scarus prasiognathos* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 65 |
| *Scarus psittacus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 66, 71, 82 |
| *Scarus quoyi* | 0 | - | - | - | - | X | 0 | - | - | - | - | X | 0 | - | - | - | - | X | 75 |
| *Scarus rivulatus* | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 87 |
| *Scarus russelii* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 66, 82 |
| *Scarus scaber* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 82 |
| *Scarus tricolor* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 67 |
| *Scarus viridifucatus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| Scombridae | | | | | | | | | | | | | | | | | | | |
| *Rastrelliger kanagurta* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| Scorpaenidae | | | | | | | | | | | | | | | | | | | |
| *Caracanthus unipinna* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 77 |
| *Dendrochirus brachypterus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Parascorpaena mossambica* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Pterois antennata* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Pterois miles* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 71 |
| *Pterois radiata* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Pterois volitans* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 63 |
| *Scorpaenopsis venosa* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| Serranidae | | | | | | | | | | | | | | | | | | | |
| *Anyperodon leucogrammicus* | 0 | X | - | - | - | X | 0 | - | - | - | - | X | 0 | - | - | - | - | 0 | 58, 75 |

| | All | | | | | | Juveniles | | | | | | Adults | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **SG** | **MG** | **MA** | **SS** | **E** | **OT** | **References** |
| *Cephalopholis argus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Cephalopholis boenak* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 81 |
| *Cephalopholis cyanostigma* | 0 | - | - | - | - | X | 0 | - | - | - | - | X | 0 | - | - | - | - | 0 | 75 |
| *Cephalopholis miniata* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Epinephelus areolatus* | - | 0 | - | X | - | - | | | | | | | | | | | | | 64 |
| *Epinephelus coeruleopunctatus* | X | X | - | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 61, 64 |
| *Epinephelus coioides* | 0 | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Epinephelus cyanopodus* | - | 0 | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 61, 64 |
| *Epinephelus fasciatus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Epinephelus fuscoguttatus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Epinephelus lanceolatus* | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 61 |
| *Epinephelus maculatus* | - | 0 | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 64 |
| *Epinephelus malabaricus* | 0 | X | - | 0 | - | - | - | X | - | 0 | - | - | - | X | - | 0 | - | - | 58, 61, 62 |
| *Epinephelus merra* | X | 0 | - | - | - | X | 0 | - | - | - | - | X | 0 | - | - | - | - | X | 63, 64, 75 |
| *Epinephelus polyphekadion* | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 61 |
| *Epinephelus rivulatus* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 81 |
| *Epinephelus tauvina* | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 61 |
| *Epinephelus tukula* | 0 | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Grammistes sexlineatus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 67, 71 |
| *Plectropomus leopardus* | - | 0 | - | X | - | - | - | 0 | - | 0 | - | - | - | 0 | - | X | - | - | 62, 64 |
| *Plectropomus maculatus* | - | - | X | - | - | - | - | - | X | - | - | - | - | - | - | - | - | - | 81 |
| *Pseudanthias squamipinnis* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Variola louti* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| Siganidae | | | | | | | | | | | | | | | | | | | |
| *Siganus argenteus* | - | 0 | - | X | - | - | - | 0 | - | X | - | - | - | 0 | - | 0 | - | - | 62 |
| *Siganus canaliculatus* | X | X | - | X | - | - | - | X | - | X | - | - | - | X | - | 0 | - | - | 58, 61, 62, 64 |
| *Siganus doliatus* | X | 0 | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 60, 85 |
| *Siganus fuscescens* | X | X | - | X | - | - | X | - | - | - | - | - | X | - | - | - | - | - | 59, 63, 80, 105 |
| *Siganus guttatus* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 63, 89 |
| *Siganus lineatus* | 0 | X | - | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | 61, 85, 87, 106 |
| *Siganus luridus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 71 |
| *Siganus puellus* | X | 0 | - | X | - | - | X | - | - | - | - | - | X | - | - | - | - | - | 59, 64 |

| Species | All | | | | | | Juveniles | | | | | | Adults | | | | | | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | SG | MG | MA | SS | E | OT | SG | MG | MA | SS | E | OT | SG | MG | MA | SS | E | OT | |
| *Siganus rivulatus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Siganus spinus* | X | X | - | 0 | - | - | X | - | - | 0 | - | - | X | - | - | 0 | - | - | 59, 63, 68, 69, 72 |
| *Siganus stellatus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | | - | - | - | - | 58, 66, 82 |
| *Siganus sutor* | X | X | - | - | - | - | X | 0 | - | - | - | 0 | X | 0 | - | - | - | 0 | 58, 66, 67, 82, 91 |
| *Siganus virgatus* | X | X | X | - | - | X | X | - | X | - | - | X | 0 | - | - | - | - | X | 63, 75, 81 |
| Sillaginidae | | | | | | | | | | | | | | | | | | | |
| *Sillago sihama* | 0 | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| Sphyraenidae | | | | | | | | | | | | | | | | | | | |
| *Sphyraena barracuda* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Sphyraena flavicauda* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 67 |
| *Sphyraena forsteri* | 0 | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Sphyraena jello* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Sphyraena obtusata* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Sphyraena putnamae* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| Synanceiidae | | | | | | | | | | | | | | | | | | | |
| *Synanceia verrucosa* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| Syngnathidae | | | | | | | | | | | | | | | | | | | |
| *Corythoichthys flavofasciatus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 67, 71 |
| *Corythoichthys haematopterus* | X | 0 | - | 0 | - | - | 0 | - | - | 0 | - | - | X | - | - | 0 | - | - | 63, 68, 69 |
| *Corythoichthys intestinalis* | X | - | - | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 72 |
| *Corythoichthys schultzi* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Hippocampus comes* | X | - | X | - | - | - | 0 | - | X | - | - | - | X | - | X | - | - | - | 107 |
| *Hippocampus histrix* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Syngnathoides biaculeatus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| Synodontidae | | | | | | | | | | | | | | | | | | | |
| *Saurida gracilis* | X | 0 | - | X | - | - | X | - | - | 0 | - | - | X | - | - | X | - | 0 | 58, 68, 69, 71, 72 |
| *Saurida nebulosa* | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 61 |
| *Saurida undosquamis* | - | 0 | - | X | - | - | - | 0 | - | X | - | - | - | 0 | - | X | - | - | 62 |
| *Synodus dermatogenys* | 0 | - | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 83 |
| *Synodus variegatus* | X | X | - | X | - | - | 0 | - | - | X | - | - | - | - | - | - | - | - | 58, 70, 71, 72, 83 |

| Species | All | | | | | | Juveniles | | | | | | Adults | | | | | | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | SG | MG | MA | SS | E | OT | SG | MG | MA | SS | E | OT | SG | MG | MA | SS | E | OT | |
| *Trachyrhamphus bicoarctatus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| Tetraodontidae | | | | | | | | | | | | | | | | | | | |
| *Arothron diadematus* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Arothron hispidus* | X | X | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 64, 71 |
| *Arothron immaculatus* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Arothron mappa* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Arothron meleagris* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Arothron nigropunctatus* | X | 0 | - | - | - | 0 | 0 | - | - | - | - | 0 | X | - | - | - | - | 0 | 58, 75 |
| *Arothron stellatus* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 71 |
| *Canthigaster bennetti* | X | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 67 |
| *Canthigaster coronata* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Canthigaster margaritata* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 |
| *Canthigaster solandri* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58 |
| *Canthigaster valentini* | X | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 67 |
| Tripterygiidae | | | | | | | | | | | | | | | | | | | |
| *Enneapterygius tutuilae* | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 77 |
| Zanclidae | | | | | | | | | | | | | | | | | | | |
| *Zanclus cornutus* | X | 0 | - | X | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 58, 66, 74 |

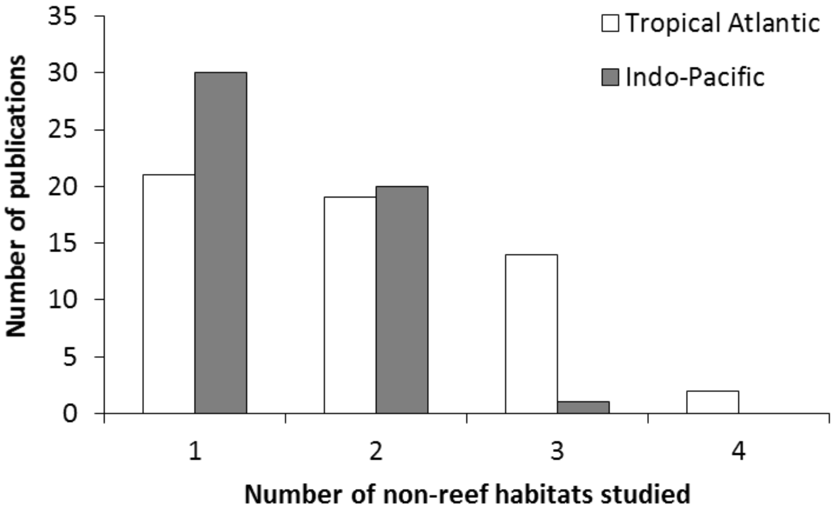


**Figure A2.1.** Number of non-reef habitats surveyed within each of the 107 publications by biogeographic region. In both regions, most studies have examined a single non-reef habitat type. In the Indo-Pacific, far fewer studies have examined three or more non-reef habitats compared to the tropical Atlantic.

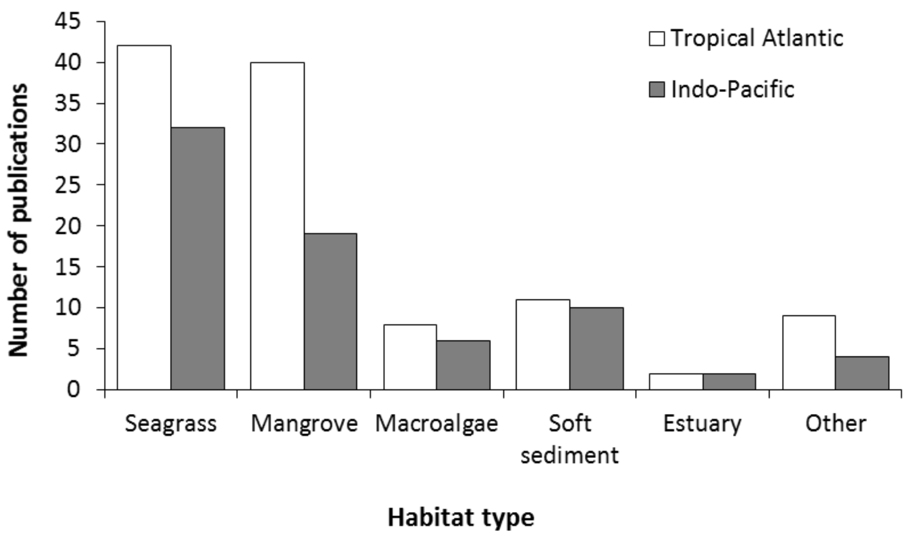


**Figure A2.2.** Habitat types examined within 107 publications that recorded coral reef fishes on coral reefs and in at least one non-reef habitat, by biogeographic region. In the tropical Atlantic, the number of publications collecting data from seagrass and mangrove habitats is almost equal. In contrast, in the Indo-Pacific, the number of studies examining seagrass beds is almost double that examining mangrove habitats. The remaining habitat types have all been studied to a far lesser extent to date.

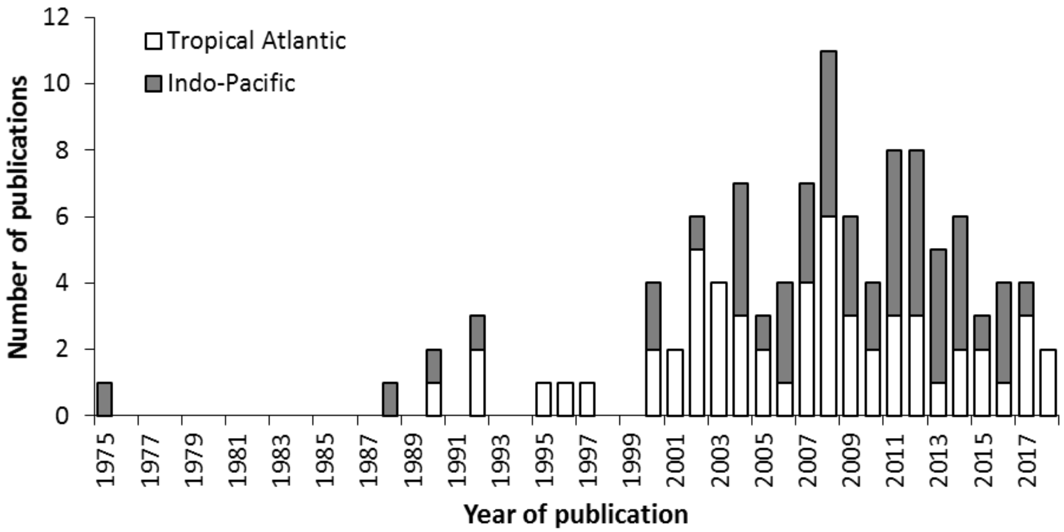


**Figure A2.3.** Number of studies by year (1975-2018) and biogeographic region that surveyed or captured coral reef fishes on coral reefs and in at least one non-reef habitat.

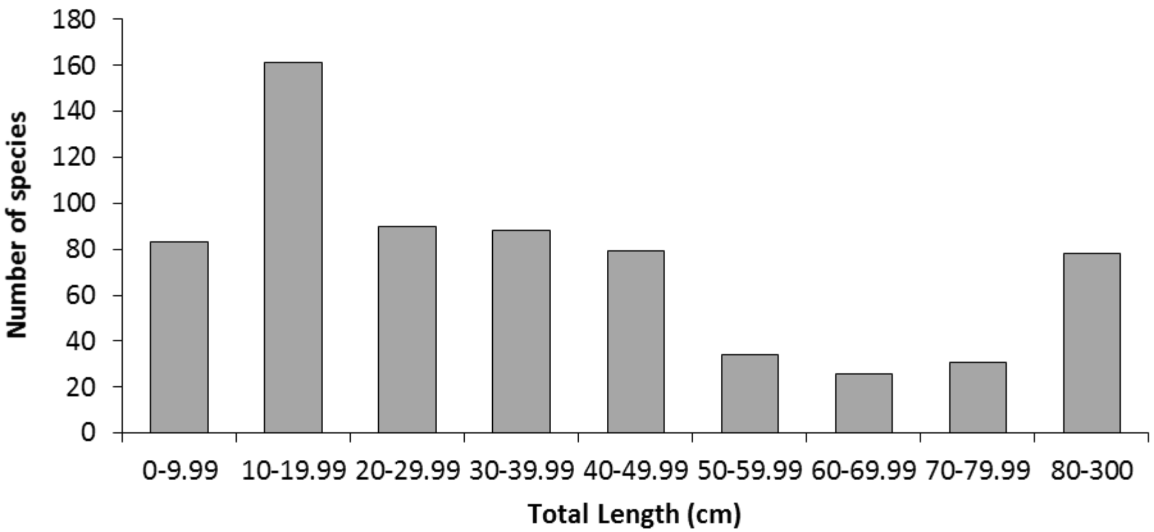


**Figure A2.4.** Maximum total length (cm) of species recorded on coral reefs and in at least one non-reef habitat. Data extracted from *FishBase* (Froese & Pauly 2019).

**References for Supplementary Table A2.1**


1. Adams AJ, Ebersole JP (2002) Use of back-reef and lagoon habitats by coral reef fishes. *Marine Ecology Progress Series* 228: 213-226
2. Aguilar-Perera A, Appeldoorn RS (2008) Spatial distribution of marine fishes along a cross-shelf gradient containing a continuum of mangrove-seagrass-coral reefs off southwestern Puerto Rico. *Estuarine, Coastal and Shelf Science* 76: 378-394
3. Aguilar C, González-Sansón G, Cabrera Y, Ruiz A, Allen Curry R (2014) Inter-habitat variation in density and size composition of reef fishes from the Cuban Northwestern shelf. *Revista de Biología Tropical* 62: 589-602
4. Christensen JD, Jeffrey CFG, Caldow C, Monaco ME, Kendall MS, Appeldoorn RS (2003) Cross-shelf habitat utilization patterns of reef fishes in Southwestern Puerto Rico. *Gulf and Caribbean Research* 14: 9-27
5. Cocheret de la Morinière E, Pollux BJA, Nagelkerken I, van der Velde G (2002) Post-settlement life cycle migration patterns and habitat preference of coral reef fish that use seagrass and mangrove habitats as nurseries. *Estuarine, Coastal and Shelf Science* 55: 309-321
6. Eggertsen L, Ferreira CEL, Fontoura L, Kautsky N, Gullström M, Berkström C (2017) Seaweed beds support more juvenile reef fish than seagrass beds in a south-western Atlantic tropical seascape. *Estuarine, Coastal and Shelf Science* 196: 97-108
7. Eggleston DB, Dahlgren CP, Johnson EG (2004) Fish density, diversity, and size-structure within multiple back reef habitats of Key West National Wildlife Refuge. *Bulletin of Marine Science* 75: 175-204
8. Harborne AR, Mumby PJ, Kappel CV, Dahlgren CP, Micheli F, Holmes KE, Brumbaugh DR (2008) Tropical coastal habitats as surrogates of fish community structure, grazing, and fisheries value. *Ecological Applications* 18: 1689-1701
9. Jaxion-Harm J, Saunders J, Speight MR (2012) Distribution of fish in seagrass, mangroves and coral reefs: life-stage dependent habitat use in Honduras. *Revista de Biología Tropical* 60: 683-698
10. Mateo I, Tobias WJ (2001) Distribution of shallow water coral reef fishes on the northeast coast of St. Croix, USVI. *Caribbean Journal of Science* 37: 210-226
11. Mateo I, Tobias WJ (2004) Survey of nearshore fish communities on tropical backreef lagoons on the southeastern coast of St. Croix. *Caribbean Journal of Science* 40: 327-342
12. Nagelkerken I, van der Velde G (2002) Do non-estuarine mangroves harbour higher densities of juvenile fish than adjacent shallow-water and coral reef habitats in Curaçao (Netherlands Antilles)? *Marine Ecology Progress Series* 245: 191-204
13. Nagelkerken I, van der Velde G (2003) Connectivity between coastal habitats of two oceanic Caribbean islands as inferred from ontogenetic shifts by coral reef fishes. *Gulf and Caribbean Research* 14: 43-59
14. Nagelkerken I, Dorenbosch M, Verberk WCEP, Cocheret de la Morinière E, van der Velde G (2000) Importance of shallow-water biotopes of a Caribbean bay for juvenile coral reef fishes: patterns in biotope association, community structure and spatial distribution. *Marine Ecology Progress Series* 202: 175-192

15. Nagelkerken I, van der Velde G, Gorissen MW, Meijer GJ, van't Hof T, den Hartog C (2000) Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. *Estuarine, Coastal and Shelf Science* 51: 31-44
16. Pereira PHC, dos Santos MVB, Lippi DL, de Paula Silva PH, Barros B (2017) Difference in the trophic structure of fish communities between artificial and natural habitats in a tropical estuary. *Marine and Freshwater Research* 68: 473-483
17. Pollux BJA, Verberk WCEP, Dorenbosch M, Cocheret de la Morinière E, Nagelkerken I, van der Velde G (2007) Habitat selection during settlement of three Caribbean coral reef fishes: indications for directed settlement to seagrass beds and mangroves. *Limnology and Oceanography* 52: 903-907
18. Seemann J, Yingst A, Stuart-Smith RD, Edgar GJ, Altieri AH (2018) The importance of sponges and mangroves in supporting fish communities on degraded coral reefs in Caribbean Panama. *PeerJ* 6: e4455
19. van der Velde G, Gorissen MW, den Hartog C, van't Hoff T, Meijer GJ (1992) Importance of the Lac-lagoon (Bonaire, Netherlands Antilles) for a selected number of reef fish species. *Hydrobiologia* 247: 139-140
20. Nagelkerken I, Roberts CM, van der Velde G, Dorenbosch M, van Riel MC, Cocheret de la Morinière E, Nienhuis PH (2002) How important are mangroves and seagrass beds for coral-reef fish? The nursery hypothesis tested on an island scale. *Marine Ecology Progress Series* 244: 299-305
21. Acosta A (1997) Use of multi-mesh gillnets and trammel nets to estimate fish species composition in coral reef and mangroves in the southwest coast of Puerto Rico. *Caribbean Journal of Science* 33: 45-57
22. Aguilar-Perera A, Appeldoorn RS (2007) Variation in juvenile fish density along the mangrove-seagrass-coral reef continuum in SW Puerto Rico. *Marine Ecology Progress Series* 348: 139-148
23. Dennis GD (1992) Island mangrove habitats as spawning and nursery areas for commercially important fishes in the Caribbean. *Proceedings of the 41st Gulf and Caribbean Fisheries Institute* 205-225
24. Greenfield DW, Johnson RK (1990) Heterogeneity in habitat choice in Cardinalfish community structure. *Copeia* 4: 1107-1114
25. Rooker JR, Dennis GD, Goulet D (1996) Sampling larval fishes with a nightlight lift-net in tropical inshore waters. *Fisheries Research* 26: 1-15
26. Dorenbosch M, Grol MGG, de Groene A, van der Velde G, Nagelkerken I (2009) Piscivore assemblages and predation pressure affect relative safety of some back-reef habitats for juvenile fish in a Caribbean bay. *Marine Ecology Progress Series* 379: 181-196
27. Harm JH, Kearns E, Speight MR (2008) Differences in coral-reef fish assemblages between mangrove-rich and mangrove-poor islands of Honduras. *Proceedings of the 11th International Coral Reef Symposium* 296-300
28. Jones DL, Walter JF, Brooks EN, Serafy JE (2010) Connectivity through ontogeny: fish population linkages among mangrove and coral reef habitats. *Marine Ecology Progress Series* 401: 245-258

29. Appeldoorn RS, Friedlander A, Sladek Nowlis J, Usseglio P, Mitchell-Chui A (2003) Habitat connectivity in reef fish communities and marine reserve design in Old Providence-Santa Catalina, Colombia. *Gulf and Caribbean Research* 14: 61-77
30. JS, Kenworthy WJ, Wood LL (2009) Ontogenetic patterns of concentration indicate lagoon nurseries are essential to common grunt stocks in a Puerto Rican bay. *Estuarine, Coastal and Shelf Science* 81: 533-543
31. Chittaro PM, Usseglio P, Sale PF (2005) Variation in fish density, assemblage composition and relative rates of predation among mangrove, seagrass and coral reef habitats. *Environmental Biology of Fishes* 72: 175-187
32. Grol MGG, Rypel AL, Nagelkerken I (2014) Growth potential and predation risk drive ontogenetic shifts among nursery habitats in a coral reef fish. *Marine Ecology Progress Series* 502: 229-244
33. Huijbers CM, Grol MGG, Nagelkerken I (2008) Shallow patch reefs as alternative habitats for early juveniles of some mangrove/seagrass-associated fish species in Bermuda. *Revista de Biologia Tropical* 56: 161-169
34. Huijbers CM, Nagelkerken I, Govers LL, van de Kerk M, Oldenburger JJ, de Brouwer JHF (2011) Habitat type and schooling interactively determine refuge-seeking behaviour in a coral reef fish throughout ontogeny. *Marine Ecology Progress Series* 437: 241-251
35. Nagelkerken I, Bothwell J, Nemeth RS, Pitt JM, van der Velde G (2008) Interlinkage between Caribbean coral reefs and seagrass beds through feeding migrations by grunts (Haemulidae) depends on habitat accessibility. *Marine Ecology Progress Series* 368: 155-164
36. Beets J, Muehistein L, Haught K, Schmitges H (2003) Habitat connectivity in coastal environments: patterns and movements of Caribbean coral reef fishes with emphasis on bluestriped grunt, *Haemulon sciurus*. *Gulf and Caribbean Research* 14: 29-42
37. Rooker JR, Dance MA, Wells RJD, Quigg A, Hill RL, Appeldoorn RS, Padovani Ferreira B, Boswell KM, Sanchez PJ, Moulton DL, Kitchens LL, Rooker GJ, Aschenbrenner A (2018) Seascape connectivity and the influence of predation risk on the movement of fishes inhabiting a back-reef ecosystem. *Ecosphere* 9: e02200
38. Hitt S, Pittman SJ, Nemeth RS (2011) Diel movements of fishes linked to benthic seascape structure in a Caribbean coral reef ecosystem. *Marine Ecology Progress Series* 427: 275-291
39. Mumby PJ, Edwards AJ, Arias-González JE, Lindeman KC, Blackwell PG, Gall A, Gorczynska MI, Harborne AR, Pescod CL, Renken H, Wabnitz CCC, Llewellyn G (2004) Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* 427: 533-536
40. Bullard SG, Hay ME (2002) Plankton tethering to assess spatial patterns of predation risk over a coral reef and seagrass bed. *Marine Ecology Progress Series* 225: 17-28
41. Nagelkerken I, van der Velde G, Cocheret de la Morinière E (2001) Fish feeding guilds along a gradient of bay biotopes and coral reef depth zones. *Aquatic Ecology* 35: 73-86
42. Aschenbrenner A, Hackradt CW, Ferreira BP (2016) Spatial variation in density and size structure indicate habitat selection throughout life stages of two Southwestern Atlantic snappers. *Marine Environmental Research* 113: 49-55

43. Feitosa JLL, Chaves LD, Pereira PH, Moraes RL, Ferreira BP (2012) Behavioral and ontogenetic colour changes of a poorly known lutjanid. *Marine Biology Research* 8: 906-911
44. Rooker JR (1995) Feeding ecology of the schoolmaster snapper, *Lutjanus apodus* (Walbaum), from southwestern Puerto Rico. *Bulletin of Marine Science* 56: 881-894
45. Verweij MC, Nagelkerken I, Hol KEM, van den Beld AHJB, van der Velde G (2007) Space use of *Lutjanus apodus* including movement between a putative nursery and a coral reef. *Bulletin of Marine Science* 81: 127-138
46. Luo J, Serafy JE, Sponaugle S, Teare PB, Kieckbusch D (2009) Movement of gray snapper *Lutjanus griseus* among subtropical seagrass, mangrove, and coral reef habitats. *Marine Ecology Progress Series* 380: 255-269
47. Moura RL, Francini-Filho RB, Chaves EM, Minte-Vera CV, Lindeman KC (2011) Use of riverine through reef habitat systems by dog snapper (*Lutjanus jocu*) in eastern Brazil. *Estuarine, Coastal and Shelf Science* 95: 274-278
48. Huijbers CM, Nagelkerken I, Debrot AO, Jongejans E (2013) Geographic coupling of juvenile and adult habitat shapes spatial population dynamics of a coral reef fish. *Ecology* 94: 1859-1870
49. Ben-David J, Kritzer JP (2005) Early life history and settlement of the slender filefish, *Monacanthus tuckeri* (Monacanthidae), at Calabash Caye, Turneffe Atoll, Belize. *Environmental Biology of Fishes* 73: 275-282
50. Mumby PJ, Broad K, Brumbaugh DR, Dahlgren CP, Harborne AR, Hastings A, Holmes KE, Kappel CV, Micheli F, Sanchirico JN (2008) Coral reef habitats as surrogates of species, ecological functions, and ecosystem services. *Conservation Biology* 22: 941-951
51. Dorenbosch M, Grol MGG, Nagelkerken I, van der Velde G (2006a) Seagrass beds and mangroves as potential nurseries for the threatened Indo-Pacific humphead wrasse, *Cheilinus undulatus* and Caribbean rainbow parrotfish, *Scarus guacamaia*. *Biological Conservation* 129: 277-282
52. Feitosa JLL, Ferreira BP (2015) Distribution and feeding patterns of juvenile parrotfish on algal-dominated coral reefs. *Marine Ecology* 36: 462-474
53. Barbour AB, Montgomery ML, Adamson AA, Díaz-Ferguson E, Silliman BR (2010) Mangrove use by the invasive lionfish *Pterois volitans*. *Marine Ecology Progress Series* 401: 291-294
54. Claydon JAB, Calosso MC, Traiger SB (2012) Progression of invasive lionfish in seagrass, mangrove and reef habitats. *Marine Ecology Progress Series* 448: 119-129
55. de la Guardia E, Rojas DC, Espinosa L, Hernández Z, García L, González JEA (2017) Distribution and abundance of the lionfish *Pterois volitans* (Scorpaeniformes: Scorpaenidae) and associated native species in Parque Marino Cayos de San Felipe, Cuba. *Revista de Biologia Tropical* 65: 117-125
56. Pimiento C, Nifong JC, Hunter ME, Monaco E, Silliman BR (2015) Habitat use patterns of the invasive red lionfish *Pterois volitans*: a comparison between mangrove and reef systems in San Salvador, Bahamas. *Marine Ecology* 36: 28-37
57. Claydon JAB, Kroetz AM (2007) The distribution of early juvenile groupers around South Caicos, Turks and Caicos Islands. *Proceedings of the 60th Gulf and Caribbean Fisheries Institute* 345-350

58. Berkström C, Gullström M, Lindborg R, Mwandya AW, Yahya SAS, Kautsky N, Nyström M (2012) Exploring 'knowns' and 'unknowns' in tropical seascape connectivity with insights from East African coral reefs. *Estuarine, Coastal and Shelf Science* 107: 1-21
59. Nakamura Y, Tsuchiya M (2008) Spatial and temporal patterns of seagrass habitat use by fishes at the Ryukyu Islands, Japan. *Estuarine, Coastal and Shelf Science* 76: 345-356
60. Rossier O, Kulbicki M (2000) A comparison of fish assemblages from two types of algal beds and coral reefs in the south-west lagoon of New Caledonia. *Cybium* 24: 3-26
61. Thollot P (1992) Importance of mangroves for Pacific reef fish species, myth or reality? *Proceedings of the Seventh International Coral Reef Symposium* 2: 934-941
62. Thollot P, Kulbicki M, Wantiez L (1990) Temporal patterns of fish populations in three habitats of the St Vincent Bay area (New Caledonia): coral reefs, soft bottoms and mangroves. *Proceedings ISRS Congress* 127-136
63. Honda K, Nakamura Y, Nakaoka M, Uy WH, Fortes MD (2013) Habitat use by fishes in coral reefs, seagrass beds and mangrove habitats in the Philippines. *PLoS ONE* 8: e65735
64. Thollot P, Kulbicki M (1988) Overlap between the fish fauna inventories of coral reefs, soft bottoms and mangroves in Saint-Vincent Bay (New Caledonia). *Proceedings of the 6$^{th}$ International Coral Reef Symposium* 2: 613-618
65. Wilson SK, Depczynski M, Fisher R, Holmes TH, O'Leary RA, Tinkler P (2010) Habitat associations of juvenile fish at Ningaloo Reef, Western Australia: the importance of coral and algae. *PLoS ONE* 5: e15185
66. Dorenbosch M, Grol MGG, Nagelkerken I, van der Velde G (2005) Distribution of coral reef fishes along a coral reef-seagrass gradient: edge effects and habitat segregation. *Marine Ecology Progress Series* 299, 277-288
67. Kruse M, Taylor M, Muhando CA, Reuter H (2016) Lunar, diel, and tidal changes in fish assemblages in an East African marine reserve. *Regional Studies in Marine Science* 3: 49-57
68. Nakamura Y, Sano M (2004) Comparison between community structures of fishes in *Enhalus acoroides*- and *Thalassia hemprichii*-dominated seagrass beds on fringing coral reefs in the Ryukyu Islands, Japan. *Ichthyological Research* 51: 38-45
69. Nakamura Y, Sano M (2004) Overlaps in habitat use of fishes between a seagrass bed and adjacent coral and sand areas at Amitori Bay, Iriomote Island, Japan: importance of the seagrass bed as juvenile habitat. *Fisheries Science* 70: 788-803
70. Ashworth JS, Bruce OE, El Hellw M (2006) Fish assemblages of Red Sea backreef biotopes. *Aquatic Conservation: Marine and Freshwater Ecosystems* 16: 593-609
71. Khalaf MA, Kochzius M (2002) Community structure and biogeography of shore fishes in the Gulf of Aqaba, Red Sea. *Helgoland Marine Research* 55: 252-284
72. Jones RS, Chase JA (1975) Community structure and distribution of fishes in an enclosed high island lagoon in Guam. *Micronesica* 11: 127-148
73. Nakamura Y, Shibuno T, Lecchini D, Kawamura T, Watanabe Y (2009) Spatial variability in habitat associations of pre- and post-settlement stages of coral reef fishes at Ishigaki Island, Japan. *Marine Biology* 156: 2413-2419
74. Sambrook K, Jones GP, Bonin MC (2016) Life on the edge: coral reef fishes exhibit strong responses to a habitat boundary. *Marine Ecology Progress Series* 561: 203-215

75. Campbell SJ, Kartawijaya T, Sabarini EK (2011) Connectivity in reef fish assemblages between seagrass and coral reef habitats. *Aquatic Biology* 13: 65-77
76. Vagelli AA (2004) Ontogenetic shift in habitat preference by *Pterapogon kauderni*, a shallow water coral reef apogonid, with direct development. *Copeia* 2: 364-369
77. Ahmadia GN, Sheard LJ, Pezold FL, Smith DJ (2012) Cryptobenthic fish assemblages across the coral reef-seagrass continuum in SE Sulawesi, Indonesia. *Marine Ecology Progress Series* 16: 125-135
78. Wetherbee BM, Holland KN, Meyer CG, Lowe CG (2004) Use of a marine reserve in Kaneohe Bay, Hawaii by the giant trevally, *Caranx ignobilis*. *Fisheries Research* 67: 253-263
79. Unsworth RKF, Bell JJ, Smith DJ (2007) Tidal fish connectivity of reef and sea grass habitats in the Indo-Pacific. J*ournal of the Marine Biological Association of the United Kingdom* 87: 1287-1296
80. Travers MJ, Potter IC, Clarke KR, Newman SJ, Hutchins JB (2010) The inshore fish faunas over soft substrates and reefs on the tropical west coast of Australia differ and change with latitude and bioregion. *Journal of Biogeography* 37: 148-169
81. Evans RD, Wilson SK, Field SN, Moore JAY (2014) Importance of macroalgal fields as coral reef fish nursery habitat in north-west Australia. *Marine Biology* 161: 599-607
82. Dorenbosch M, Grol MGG, Nagelkerken I, van der Velde G (2006b) Different surrounding landscapes may result in different fish assemblages in East African seagrass beds. *Hydrobiologia* 563: 45-60
83. Shibuno TM, Nakamura Y, Horinouchi M, Sano M (2008) Habitat use patterns of fishes across the mangrove-seagrass-coral reef seascape at Ishigaki Island, southern Japan. *Ichthyological Research* 55: 218-237
84. Hernaman V, Probert PK (2008) Spatial and temporal patterns of abundance of coral reef gobies (Teleostei: Gobiidae). *Journal of Fish Biology* 72: 1589-1606
85. Olds AD, Connolly RM, Pitt KA, Maxwell PS, Aswani S, Albert S (2014) Incorporating surrogate species and seascape connectivity to improve marine conservation outcomes. *Conservation Biology* 28: 982-991
86. Tupper M (2007) Identification of nursery habitats for commercially valuable humphead wrasse *Cheilinus undulatus* and large groups (Pisces: Serranidae) in Palau. *Marine Ecology Progress Series* 332: 189-199
87. Barnes L, Bellwood DR, Sheaves M, Tanner JK (2012) The use of clear-water non-estuarine mangroves by reef fishes on the Great Barrier Reef. *Marine Biology* 159: 211-220
88. Fairclough DV, Clarke KR, Valesini FJ, Potter IC (2008) Habitat partitioning by five congeneric and abundant *Choerodon* species (Labridae) in a large subtropical marine embayment. *Estuarine, Coastal and Shelf Science* 77: 446-456
89. Honda K, Uy WH, Baslot DI, Pantallano ADS, Nakamura Y, Nakaoka M (2016) Diel habitat-use patterns of commercially important fishes in a marine protected area in the Philippines. *Aquatic Biology* 24,:153-174
90. Wilson SK, Depczynski M, Holmes TH, Noble MM, Radford BT, Tinkler P, Fulton CJ (2017) Climatic conditions and nursery habitat quality provide indicators of reef fish recruitment strength. *Limnology and Oceanography* 10.1002/lno.10540

91. Kimirei IA, Nagelkerken I, Griffioen B, Wagner C, Mgaya YD (2011) Ontogenetic habitat use by mangrove/seagrass-associated coral reef fishes shows flexibility in time and space. *Estuarine, Coastal and Shelf Science* 92: 47-58
92. Kimirei IA, Nagelkerken I, Mgaya YD, Huijbers CM (2013b) The mangrove nursery paradigm revisited: otolith stable isotopes support nursery-to-reef movements by Indo-Pacific fishes. *PLoS ONE* 8: e66320
93. Kimirei IA, Nagelkerken I, Trommelen M, Blankers P, van Hoytema N, Hoejmakers D, Huijbers CM, Mgaya YD, Rypel AL (2013a) What drives ontogenetic niche shifts of fishes in coral reef ecosystems? *Ecosystems* 16: 783-796
94. Lee C, Lin H (2015) Ontogenetic habitat utilization patterns of juvenile reef fish in low-predation habitats. *Marine Biology* 162: 1799-1811
95. Nanami A, Yamada H (2009) Site fidelity, size, and spatial arrangement of daytime home range of thumbprint emperor *Lethrinus harak* (Lethrinidae). *Fisheries Science* 75: 1109-1116
96. Unsworth RKF, De León PS, Garrard SL, Smith DJ, Bell JJ (2009) Habitat usage of the thumbprint emperor *Lethrinus harak* (Forsskål, 1775) in an Indo-Pacific coastal seascape. *The Open Marine Biology Journal* 3: 16-20
97. Pillans RD, Bearham D, Boomer A, Downie R, Patterson TA, Thomson DP, Babcock RC (2014) Multi year observations reveal variability in residence of a tropical demersal fish, *Lethrinus nebulosus*: implications for spatial management. *PLoS ONE* 9: e105507
98. Berkström C, Jörgensen TL, Hellström M (2013) Ecological connectivity and niche differentiation between two closely related fish species in the mangrove-seagrass-coral reef continuum. *Marine Ecology Progress Series* 477: 201-215
99. McMahon KW, Berumen ML, Mateo I, Elsdon TS, Thorrold SR (2011) Carbon isotopes in otolith amino acids identify residency of juvenile snapper (Family: Lutjanidae) in coastal nurseries. *Coral Reefs* 30: 1135-1145
100. McMahon KW, Fogel ML, Johnson BJ, Houghton LA, Thorrold SR (2011) A new method to reconstruct fish diet and movement patterns from $\delta^{13}C$ values in otolith amino acids. *Canadian Journal of Fisheries and Aquatic Sciences* 68: 1330-1340
101. Paillon C, Wantiez L, Kulbicki M, Labonne M, Vigliola L (2014) Extent of mangrove nursery habitats determines the geographic distribution of a coral reef fish in a South-Pacific archipelago. *PLoS ONE* 9: e105158
102. Nakamura Y, Horinouchi M, Shibuno T, Tanaka Y, Miyajima T, Koike I, Kurokura H, Sano M (2008) Evidence of ontogenetic migration from mangroves to coral reefs by black-tail snapper *Lutjanus fulvus*: stable isotope approach. *Marine Ecology Progress Series* 355: 257-266
103. Vignon M (2012) Ontogenetic trajectories of otolith shape during shift in habitat use: interaction between otolith growth and environment. *Journal of Experimental Marine Biology and Ecology* 420-421: 26-32
104. Meyer CG, Holland KN, Wetherbee BM, Lowe CG (2000) Movement patterns, habitat utilization, home range size and side fidelity of whitesaddle goatfish, *Parupeneus porphyreus,* in a marine reserve. *Environmental Biology of Fishes* 59: 235-242
105. Olds AD, Connolly RM, Pitt KA, Maxwell PS (2012) Habitat connectivity improves reserve performance. *Conservation Letters* 5: 56-63

106. Fox RJ, Bellwood DR (2011) Unconstrained by the clock? Plasticity of diel activity rhythm in a tropical reef fish, *Siganus lineatus*. *Functional Ecology* 25: 1096-1105
107. Morgan SK, Vincent ACJ (2007) The ontogeny of habitat associations in the tropical tiger tail seahorse *Hippocampus comes* Cantor, 1850. *Journal of Fish Biology* 71: 701-724

## Appendix B: Supplementary materials for Chapter 3

# *Broadening our horizons: seascape use by coral reef-associated fishes in Kavieng, Papua New Guinea, is common and diverse*

**Table A3.1:** Frequency of occurrence (%) of coral reef-associated fishes occurring in non-reef habitats. RS = Reef slopes, RF = Reef flat, MA = Macroalgae, MG = Mangrove, SG = Seagrass.

| | RS | RF | MA | MG | SG |
|---|---|---|---|---|---|
| **Acanthuridae** | | | | | |
| *Acanthurus spp.* | 19.8 | 12.0 | 2.4 | 1.7 | 0 |
| *Acanthurus auranticavus* | 2.3 | 0 | 0 | 5.2 | 0 |
| *Acanthurus triostegus* | 1.7 | 41.3 | 12.2 | 0 | 3 |
| *Ctenochaetus spp.* | 0 | 0 | 0 | 1.7 | 0 |
| *Ctenochaetus striatus* | 84.9 | 70.7 | 7.3 | 0 | 0 |
| **Apogonidae** | | | | | |
| *Apogonidae spp.* | 0 | 0 | 0 | 17.2 | 0 |
| *Cheilodipterus spp.* | 0 | 2.7 | 0 | 1.7 | 0 |
| *Sphaeramia orbicularis* | 0 | 0 | 0 | 37.9 | 0 |
| **Balistidae** | | | | | |
| *Rhinecanthus aculeatus* | 0 | 0 | 22 | 1.7 | 0 |
| *Rhinecanthus verrucosus* | 2.3 | 30.7 | 29.3 | 0 | 4 |
| **Carangidae** | | | | | |
| *Carangidae spp.* | 8.1 | 0 | 0 | 8.6 | 0 |
| *Caranx ignobilis* | 0 | 2.7 | 7.3 | 1.7 | 0 |
| *Caranx papuensis* | 1.2 | 0 | 0 | 0 | 1 |
| *Caranx sexfasciatus* | 0 | 0 | 0 | 12.1 | 1 |
| *Caranx spp.* | 4.7 | 5.3 | 4.9 | 1.7 | 3 |
| *Gnathanodon speciosus* | 1.2 | 0 | 0 | 0 | 1 |
| **Carcharhinidae** | | | | | |
| *Carcharhinus melanopterus* | 18.6 | 6.7 | 12.2 | 0 | 4 |
| **Chaetodontidae** | | | | | |
| *Chaetodon lunula* | 11.6 | 2.7 | 0 | 6.9 | 0 |
| *Chaetodon rafflesii* | 18.6 | 21.3 | 4.9 | 0 | 0 |
| *Chaetodon vagabundus* | 37.2 | 36 | 24.4 | 22.4 | 3 |
| **Gerreidae** | | | | | |
| *Gerres longirostris* | 0 | 0 | 0 | 0 | 3 |
| *Gerres oyena* | 1.2 | 0 | 0 | 51.7 | 12 |
| **Haemulidae** | | | | | |
| *Plectorhinchus albovittatus* | 0 | 0 | 0 | 1.7 | 0 |
| *Plectorhinchus gibbosus* | 0 | 0 | 0 | 5.2 | 0 |
| *Plectorhinchus spp.* | 0 | 0 | 0 | 1.7 | 0 |
| **Kyphosidae** | | | | | |
| *Kyphosus cinerascens* | 14 | 0 | 0 | 1.7 | 0 |
| **Labridae** | | | | | |
| *Cheilinus chlorourus* | 2.3 | 0 | 9.8 | 0 | 0 |
| *Cheilinus spp.* | 0 | 2.7 | 0 | 1.7 | 0 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | *Cheilinus trilobatus* | 27.9 | 28 | 2.4 | 3.4 | 3 |
| | *Cheilio inermis* | 15.1 | 21.3 | 24.4 | 0 | 19 |
| | *Choerodon anchorago* | 32.6 | 66.7 | 63.4 | 15.5 | 30 |
| | *Coris spp.* | 0 | 0 | 2.4 | 0 | 0 |
| | *Halichoeres argus* | 0 | 18.7 | 36.6 | 3.4 | 33 |
| | *Halichoeres chloropterus* | 5.8 | 22.7 | 2.4 | 0 | 1 |
| | *Halichoeres margaritaceus* | 0 | 4 | 7.3 | 0 | 0 |
| | *Halichoeres marginatus* | 27.9 | 22.7 | 2.4 | 0 | 0 |
| | *Halichoeres melanurus* | 54.7 | 25.3 | 2.4 | 0 | 1 |
| | *Halichoeres miniatus* | 0 | 5.3 | 19.5 | 0 | 0 |
| | *Halichoeres nebulosus* | 3.5 | 14.7 | 46.3 | 0 | 0 |
| | *Halichoeres nigrescens* | 2.3 | 18.7 | 41.5 | 5.2 | 1 |
| | *Halichoeres papilionaceus* | 0 | 4 | 26.8 | 1.7 | 2 |
| | *Halichoeres scapularis* | 15.1 | 58.7 | 73.2 | 6.9 | 16 |
| | *Halichoeres spp.* | 11.6 | 45.3 | 80.5 | 1.7 | 36 |
| | *Halichoeres trimaculatus* | 12.8 | 38.7 | 53.7 | 5.2 | 4 |
| | *Stethojulis bandanensis* | 16.3 | 13.3 | 14.6 | 0 | 0 |
| | *Stethojulis interrupta* | 4.7 | 9.3 | 24.4 | 1.7 | 5 |
| | *Stethojulis spp.* | 1.2 | 2.7 | 4.9 | 0 | 2 |
| | *Stethojulis strigiventer* | 8.1 | 30.7 | 43.9 | 5.2 | 28 |
| | *Stethojulis trilineata* | 64 | 66.7 | 24.4 | 5.2 | 0 |
| | *Thalassoma amblycephalum* | 4.7 | 1.3 | 0 | 0 | 1 |
| | *Thalassoma hardwicke* | 65.1 | 66.7 | 12.2 | 0 | 1 |
| **Latidae** | | | | | | |
| | *Psammoperca waigiensis* | 0 | 0 | 0 | 6.9 | 0 |
| **Lethrinidae** | | | | | | |
| | *Lethrinid* early stage juvenile | 1.2 | 0 | 7.3 | 0 | 21 |
| | *Lethrinus erythropterus* | 14 | 1.3 | 2.4 | 0 | 0 |
| | *Lethrinus harak* | 12.8 | 50.7 | 73.2 | 36.2 | 53 |
| | *Lethrinus obsoletus* | 0 | 4 | 9.8 | 0 | 1 |
| | *Lethrinus spp.* | 24.4 | 4 | 9.8 | 10.3 | 10 |
| **Lutjanidae** | | | | | | |
| | *Lutjanus argentimaculatus* | 0 | 0 | 0 | 13.8 | 0 |
| | *Lutjanus carponotatus* | 24.4 | 20 | 0 | 0 | 5 |
| | *Lutjanus ehrenbergii* | 0 | 0 | 0 | 50 | 1 |
| | *Lutjanus fulviflamma* | 12.8 | 12 | 7.3 | 36.2 | 17 |
| | *Lutjanus fulvus* | 10.5 | 4 | 0 | 17.2 | 0 |
| | *Lutjanus gibbus* | 18.6 | 6.7 | 4.9 | 0 | 1 |
| | *Lutjanus monostigma* | 4.7 | 1.3 | 0 | 3.4 | 0 |
| | *Lutjanus russellii* | 8.1 | 0 | 0 | 13.8 | 0 |
| | *Lutjanus semicinctus* | 39.5 | 44 | 31.7 | 0 | 1 |
| **Monacanthidae** | | | | | | |
| | *Acreichthys tomentosus* | 0 | 0 | 0 | 0 | 19 |
| **Mugilidae** | | | | | | |
| | *Ellochelon vaigiensis* | 0 | 0 | 0 | 1.7 | 3 |
| | *Mugilidae spp.* | 0 | 0 | 0 | 3.4 | 2 |
| **Mullidae** | | | | | | |
| | *Mullidae spp.* | 0 | 0 | 0 | 1.7 | 0 |
| | *Mulloidichthys flavolineatus* | 14 | 6.7 | 2.4 | 3.4 | 5 |

| | | | | | |
|---|---|---|---|---|---|
| *Parupeneus barberinus* | 37.2 | 54.7 | 22 | 8.6 | 29 |
| *Parupeneus crassilabris* | 33.7 | 38.7 | 9.8 | 0 | 0 |
| *Parupeneus cyclostomus* | 11.6 | 4 | 2.4 | 0 | 0 |
| *Parupeneus indicus* | 1.2 | 5.3 | 19.5 | 3.4 | 3 |
| *Upeneus tragula* | 2.3 | 0 | 0 | 1.7 | 4 |
| **Muraenidae** | | | | | |
| *Muraenidae spp.* | 0 | 0 | 0 | 0 | 1 |
| **Nemipteridae** | | | | | |
| *Pentapodus trivittatus* | 61.6 | 61.3 | 61 | 22.4 | 31 |
| *Scolopsis bilineata* | 19.8 | 6.7 | 2.4 | 0 | 0 |
| *Scolopsis ciliata* | 10.5 | 4 | 0 | 1.7 | 2 |
| *Scolopsis lineata* | 7 | 34.7 | 43.9 | 19 | 7 |
| *Scolopsis margaritifer* | 48.8 | 33.3 | 14.6 | 0 | 0 |
| *Scolopsis trilineata* | 0 | 0 | 9.8 | 0 | 0 |
| **Pomacentridae** | | | | | |
| *Abudefduf lorenzi* | 0 | 0 | 0 | 22.4 | 1 |
| *Abudefduf sexfasciatus* | 26.7 | 20 | 7.3 | 1.7 | 0 |
| *Abudefduf sordidus* | 0 | 0 | 0 | 1.7 | 0 |
| *Abudefduf vaigiensis* | 5.8 | 5.3 | 0 | 5.2 | 0 |
| *Chrysiptera biocellata* | 0 | 0 | 2.4 | 1.7 | 0 |
| *Chrysiptera unimaculata* | 0 | 1.3 | 2.4 | 0 | 0 |
| *Dischistodus chrysopoecilus* | 0 | 30.7 | 65.9 | 0 | 3 |
| *Dischistodus melanotus* | 23.3 | 62.7 | 4.9 | 0 | 0 |
| *Dischistodus perspicillatus* | 4.7 | 16 | 7.3 | 0 | 1 |
| *Dischistodus prosopotaenia* | 0 | 2.7 | 0 | 0 | 1 |
| *Pomacentridae spp.* | 33.7 | 33.3 | 9.8 | 0 | 0 |
| *Pomacentrus adelus* | 18.6 | 14.7 | 2.4 | 1.7 | 0 |
| *Pomacentrus bankanensis* | 17.4 | 17.3 | 4.9 | 0 | 0 |
| *Pomacentrus simsiang* | 0 | 8 | 0 | 0 | 1 |
| *Pomacentrus tripunctatus* | 0 | 1.3 | 0 | 3.4 | 0 |
| *Stegastes albifasciatus* | 1.2 | 12 | 17.1 | 0 | 0 |
| **Scaridae** | | | | | |
| *Chlorurus sordidus* | 32.6 | 13.3 | 0 | 0 | 1 |
| *Hipposcarus longiceps* | 40.7 | 8 | 0 | 0 | 3 |
| *Scarus globiceps* | 1.2 | 1.3 | 2.4 | 0 | 0 |
| *Scarus psittacus* | 9.3 | 0 | 2.4 | 0 | 0 |
| *Scarus spinus* | 3.5 | 5.3 | 2.4 | 0 | 0 |
| *Scarus spp.* | 89.5 | 86.7 | 17.1 | 1.7 | 8 |
| **Scatophagidae** | | | | | |
| *Scatophagus argus* | 0 | 0 | 0 | 8.6 | 0 |
| **Serranidae** | | | | | |
| *Cephalopholis spiloparaea* | 0 | 0 | 2.4 | 0 | 0 |
| *Epinephelus corallicola* | 0 | 0 | 0 | 1.7 | 0 |
| **Siganidae** | | | | | |
| *Siganus argenteus* | 12.8 | 6.7 | 0 | 0 | 1 |
| *Siganus canaliculatus* | 12.8 | 22.7 | 12.2 | 3.4 | 34 |
| *Siganus doliatus* | 25.6 | 32 | 0 | 1.7 | 2 |
| *Siganus lineatus* | 47.7 | 8 | 9.8 | 43.1 | 16 |
| *Siganus spinus* | 1.2 | 16 | 56.1 | 5.2 | 11 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | *Siganus spp.* | 1.2 | 1.3 | 0 | 0 | 5 |
| | *Siganus vermiculatus* | 0 | 0 | 0 | 5.2 | 2 |
| **Sphyraenidae** | | | | | | |
| | *Sphyraena barracuda* | 0 | 0 | 0 | 0 | 3 |
| | *Sphyraenidae spp.* | 0 | 0 | 0 | 0 | 2 |
| **Tetraodontidae** | | | | | | |
| | *Arothron hispidus* | 0 | 0 | 0 | 1.7 | 0 |
| **Toxotidae** | | | | | | |
| | *Toxotes jaculatrix* | 0 | 0 | 0 | 17.2 | 0 |

**Table A3.2.** Frequency of occurrence (%) and mean Max*N* (± SE) for the eighteen coral reef-associated fish species observed in all five habitat types. Bold indicates habitat most frequently observed in.

| Family | Species | Reef slope (*n*=86) | | Reef flat (*n*=75) | | Macroalgae (*n*=41) | | Mangrove (*n*=58) | | Seagrass (*n*=100) | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Freq (%) | Mean Max*N* ± SE | Freq (%) | Mean Max*N* ± SE | Freq (%) | Mean Max*N* ± SE | Freq (%) | Mean Max*N* ± SE | Freq (%) | Mean Max*N* ± SE |
| Chaetodontidae | *Chaetodon vagabundus* | **37.2** | 0.5 ± 0.1 | 36.0 | 0.6 ± 0.1 | 24.4 | 0.2 ± 0.1 | 22.4 | 0.3 ± 0.1 | 3.0 | 0.0 ± 0.0 |
| Labridae | *Cheilinus trilobatus* | 27.9 | 0.3 ± 0.1 | **28.0** | 0.3 ± 0.1 | 2.4 | 0.0 ± 0.0 | 3.4 | 0.1 ± 0.0 | 3.0 | 0.0 ± 0.0 |
| Labridae | *Choerodon anchorago* | 32.6 | 0.4 ± 0.1 | **66.7** | 0.9 ± 0.1 | 63.4 | 1.0 ± 0.2 | 15.5 | 0.2 ± 0.0 | 30.0 | 0.4 ± 0.1 |
| Labridae | *Halichoeres nigrescens* | 2.3 | 0.0 ± 0.0 | 18.7 | 0.3 ± 0.1 | **41.5** | 0.8 ± 0.2 | 5.2 | 0.1 ± 0.0 | 1.0 | 0.0 ± 0.0 |
| Labridae | *Halichoeres scapularis* | 15.1 | 0.2 ± 0.1 | 58.7 | 1.2 ± 0.2 | **73.2** | 1.9 ± 0.3 | 6.9 | 0.1 ± 0.1 | 16.0 | 0.2 ± 0.1 |
| Labridae | *Halichoeres trimaculatus* | 12.8 | 0.2 ± 0.0 | 38.7 | 0.5 ± 0.1 | **53.7** | 0.7 ± 0.1 | 5.2 | 0.1 ± 0.1 | 4.0 | 0.0 ± 0.0 |
| Labridae | *Stethojulis interrupta* | 4.7 | 0.1 ± 0.1 | 9.3 | 0.1 ± 0.1 | **24.4** | 0.6 ± 0.2 | 1.7 | 0.0 ± 0.0 | 5.0 | 0.1 ± 0.1 |
| Labridae | *Stethojulis strigiventer* | 8.1 | 0.1 ± 0.0 | 30.7 | 0.5 ± 0.1 | **43.9** | 0.8 ± 0.2 | 5.2 | 0.1 ± 0.1 | 28.0 | 1.2 ± 0.4 |
| Lethrinidae | *Lethrinus harak* | 12.8 | 0.2 ± 0.1 | 50.7 | 1.8 ± 0.3 | **73.2** | 3.0 ± 0.4 | 36.2 | 0.5 ± 0.1 | 53.0 | 1.7 ± 0.3 |
| Lutjanidae | *Lutjanus fulviflamma* | 12.8 | 1.0 ± 0.4 | 12.0 | 0.3 ± 0.1 | 7.3 | 0.3 ± 0.2 | **36.2** | 1.6 ± 0.4 | 17.0 | 0.3 ± 0.1 |
| Mullidae | *Mulloidichthys flavolineatus* | **14.0** | 0.8 ± 0.4 | 6.7 | 0.2 ± 0.1 | 2.4 | 0.0 ± 0.0 | 3.4 | 0.0 ± 0.0 | 5.0 | 0.1 ± 0.0 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Mullidae | *Parupeneus barberinus* | 37.2 | 0.4 ± 0.1 | **54.7** | 0.9 ± 0.1 | 22.0 | 0.5 ± 0.2 | 8.6 | 0.1 ± 0.1 | 29.0 | 0.8 ± 0.2 |
| Mullidae | *Parupeneus indicus* | 1.2 | 0.0 ± 0.0 | 5.3 | 0.1 ± 0.0 | **19.5** | 0.3 ± 0.1 | 3.4 | 0.0 ± 0.0 | 3.0 | 0.0 ± 0.0 |
| Nemipteridae | *Pentapodus trivittatus* | **61.6** | 0.8 ± 0.1 | 61.3 | 0.8 ± 0.1 | 61.0 | 0.9 ± 0.1 | 22.4 | 0.2 ± 0.1 | 31.0 | 0.5 ± 0.1 |
| Nemipteridae | *Scolopsis lineata* | 7.0 | 0.2 ± 0.1 | 34.7 | 1.8 ± 0.5 | **43.9** | 2.5 ± 0.9 | 19.0 | 0.7 ± 0.3 | 7.0 | 0.3 ± 0.1 |
| Siganidae | *Siganus canaliculatus* | 12.8 | 0.8 ± 0.5 | 22.7 | 1.5 ± 0.5 | 12.2 | 0.6 ± 0.4 | 3.4 | 0.1 ± 0.1 | **34.0** | 1.7 ± 0.4 |
| Siganidae | *Siganus lineatus* | **47.7** | 6.5 ± 1.5 | 8.0 | 0.8 ± 0.7 | 9.8 | 0.4 ± 0.2 | 43.1 | 1.8 ± 0.5 | 16.0 | 0.7 ± 0.2 |
| Siganidae | *Siganus spinus* | 1.2 | 0.0 ± 0.0 | 16.0 | 0.7 ± 0.3 | **56.1** | 4.3 ± 1.0 | 5.2 | 0.5 ± 0.3 | 11.0 | 0.8 ± 0.3 |

## *Relative importance of seascape versus within-habitat variables on the distribution of fishes in tropical seagrass beds*

**Table A4.1.** Final BRT models for each response variable following model optimisation, optimal number of trees and % deviance explained.

| Response variable | Metric | Distribution | Tree complexity | Learning rate | Bag fraction | Number of trees | Deviance explained |
|---|---|---|---|---|---|---|---|
| **Families** | | | | | | | |
| Labridae (exc. Scarinae) | Abundance | Poisson | 3 | 0.001 | 0.8 | 5800 | 0.83 |
| Lethrinidae | Presence | Bernoulli | 1 | 0.001 | 0.7 | 7050 | 0.53 |
| Lutjanidae | Abundance | Poisson | 1 | 0.001 | 0.5 | 5850 | 0.78 |
| Mullidae | Presence | Bernoulli | 5 | 0.0001 | 0.5 | 8150 | 0.20 |
| Nemipteridae | Presence | Bernoulli | 1 | 0.001 | 0.7 | 7400 | 0.48 |
| Pomacentridae | Abundance | Poisson | 1 | 0.001 | 0.8 | 2850 | 0.44 |
| Scarinae | Abundance | Poisson | 2 | 0.001 | 0.7 | 4900 | 0.77 |
| Siganidae | Abundance | Poisson | 3 | 0.001 | 0.7 | 4550 | 0.88 |
| **Adults vs juveniles** | | | | | | | |
| Lethrinid Adult | Presence | Bernoulli | 5 | 0.001 | 0.7 | 2300 | 0.54 |
| Lethrinid Juvenile | Presence | Bernoulli | 5 | 0.001 | 0.7 | 2200 | 0.56 |
| Scarinae TP/IP | Presence | Bernoulli | 4 | 0.001 | 0.8 | 1650 | 0.56 |
| Scarinae Juvenile | Presence | Bernoulli | 1 | 0.001 | 0.5 | 6900 | 0.42 |
| **Species / genera** | | | | | | | |
| *Lethrinus harak* (Lethrinidae) | Presence | Bernoulli | 3 | 0.001 | 0.5 | 4250 | 0.59 |
| *Lutjanus fulviflamma* (Lutjanidae) | Presence | Bernoulli | 3 | 0.001 | 0.7 | 5900 | 0.89 |
| *Halichoeres scapularis* (Labridae) | Abundance | Poisson | 5 | 0.001 | 0.5 | 1500 | 0.49 |
| *Halichoeres trimaculatus* (Labridae) | Abundance | Poisson | 2 | 0.001 | 0.7 | 2650 | 0.75 |
| *Other Halichoeres spp.* (Labridae) | Abundance | Poisson | 2 | 0.001 | 0.7 | 7350 | 0.81 |
| *Stethojulis strigiventer* (Labridae) | Abundance | Poisson | 1 | 0.001 | 0.8 | 2550 | 0.57 |
| *Siganus canaliculatus* (Siganidae) | Presence | Bernoulli | 2 | 0.001 | 0.7 | 1850 | 0.40 |
| *Siganus lineatus* (Siganidae) | Presence | Bernoulli | 2 | 0.001 | 0.7 | 2400 | 0.56 |
| *Siganus spinus* (Siganidae) | Presence | Bernoulli | 5 | 0.001 | 0.8 | 6700 | 0.94 |

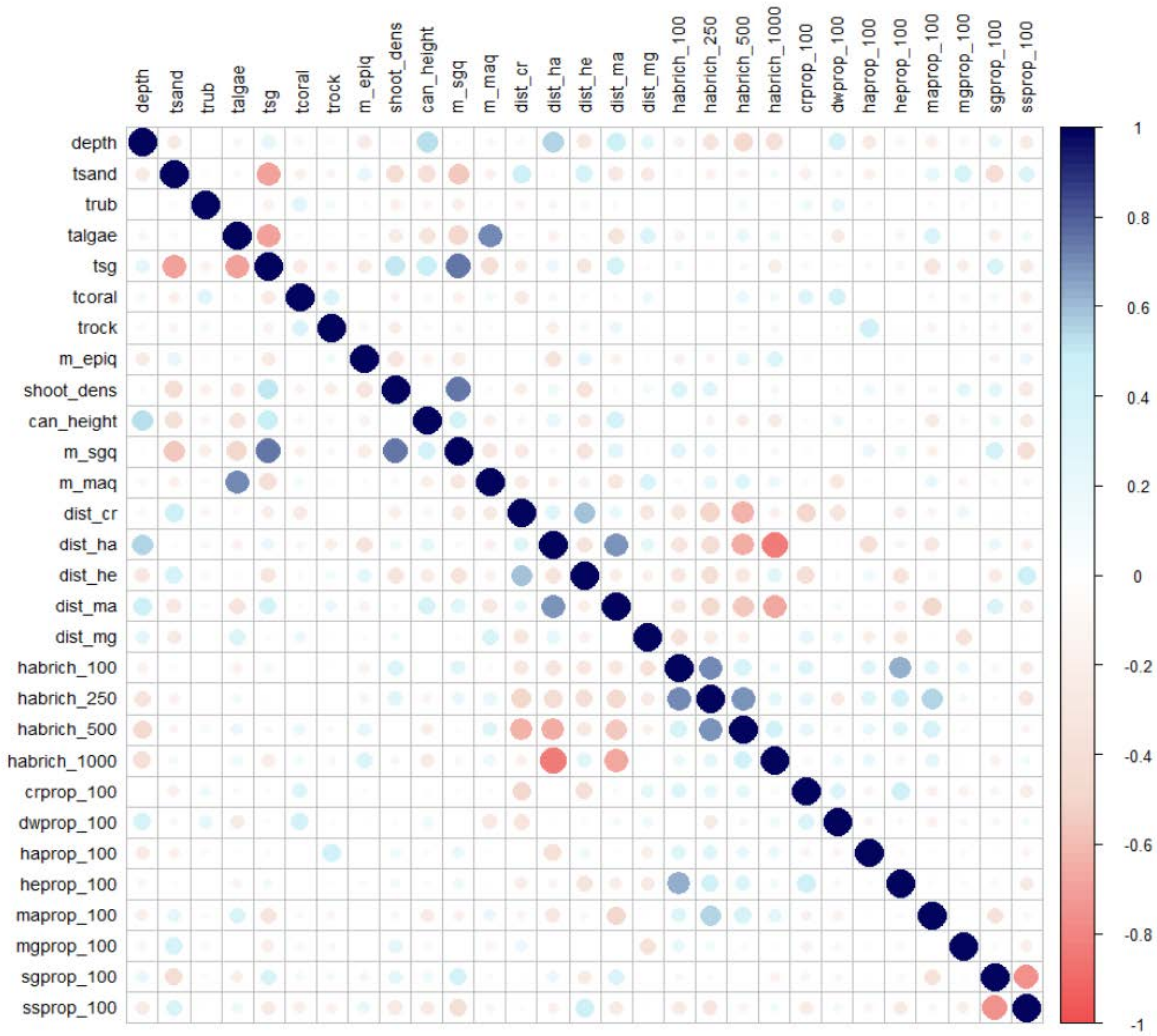


**Figure A4.1.** Multi-collinearity matrices between within-habitat and seascape predictor variables. Only includes area metrics at 100 m radius.

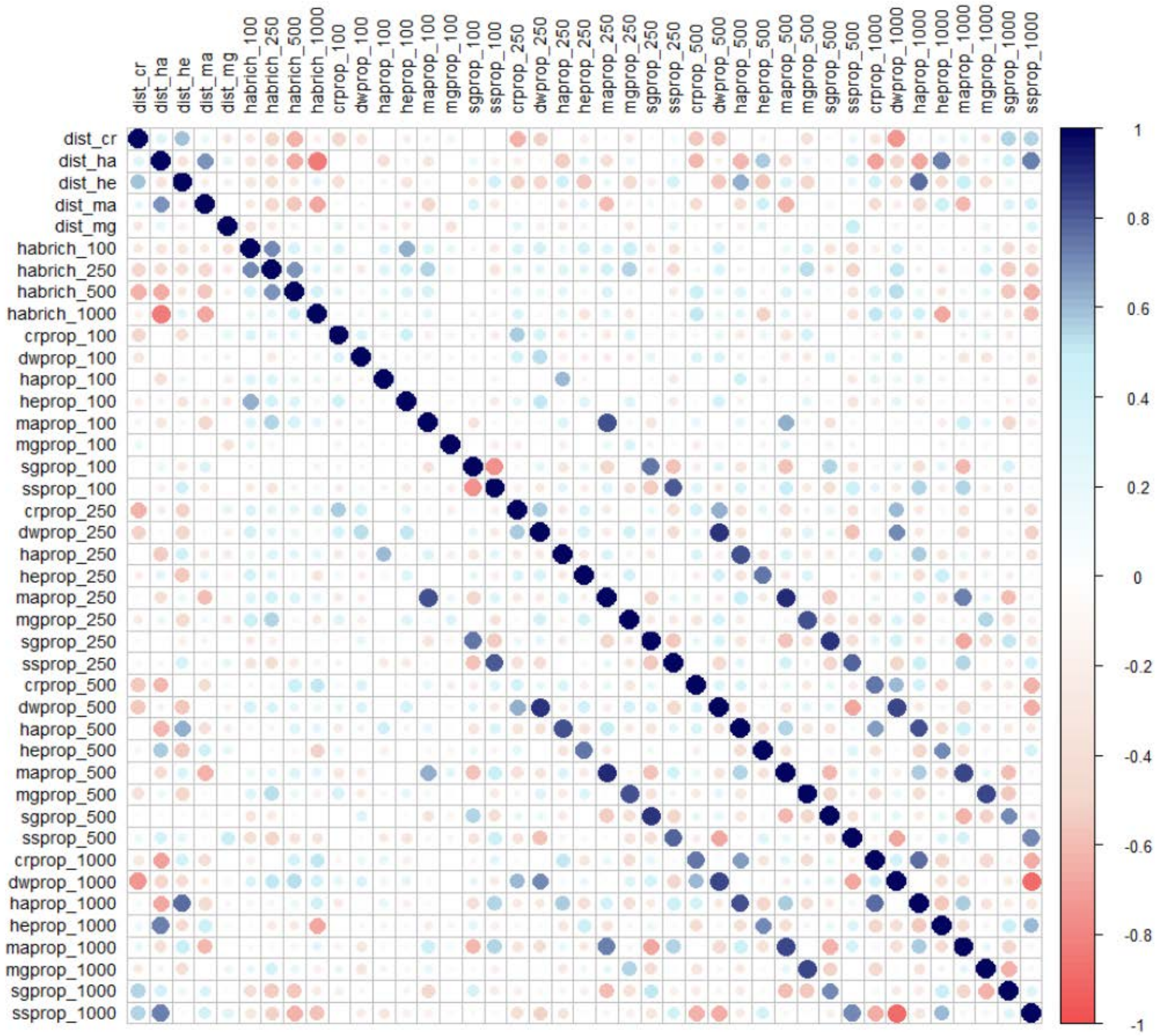


**Figure A4.2.** Multi-collinearity matrices between all seascape predictor variables examined across the four spatial scales (100 m, 250 m, 500 m and 1000 m radii).

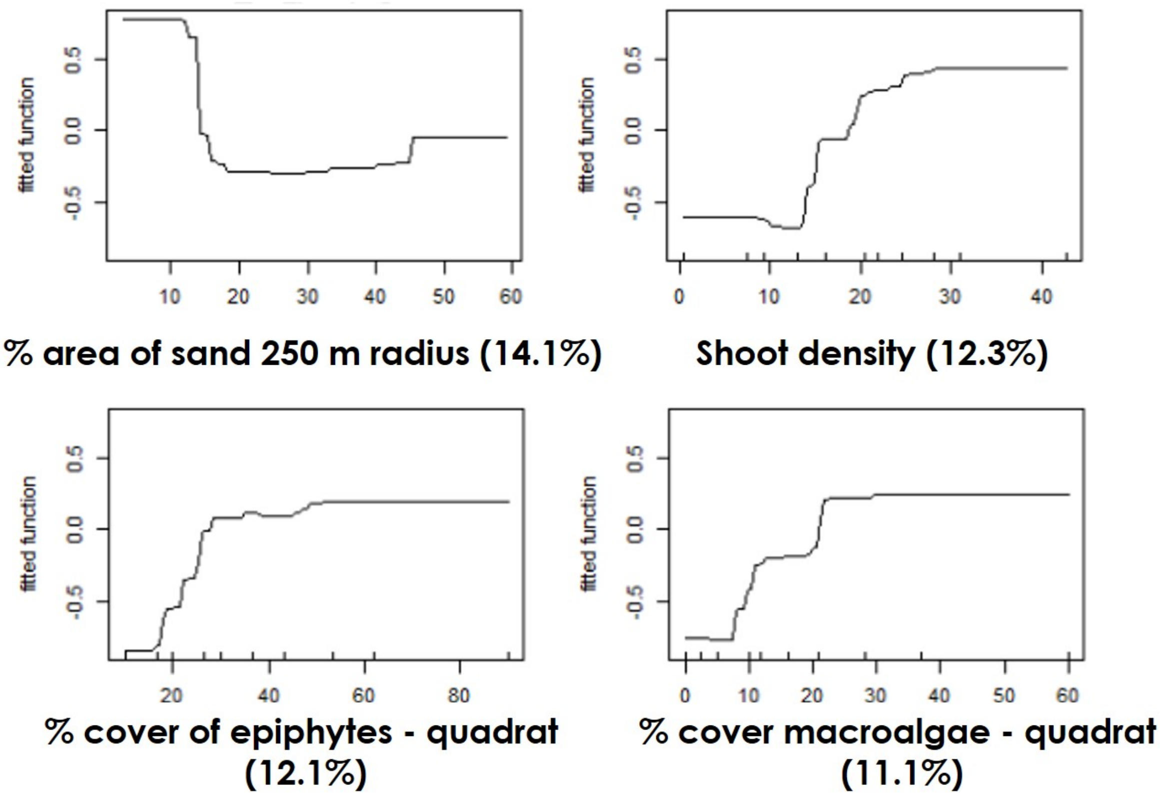


**Figure A4.3.** Partial dependency plots for the four most influential predictor variables explaining the presence of juvenile parrotfishes (subfamily: Scarinae) in seagrass beds.

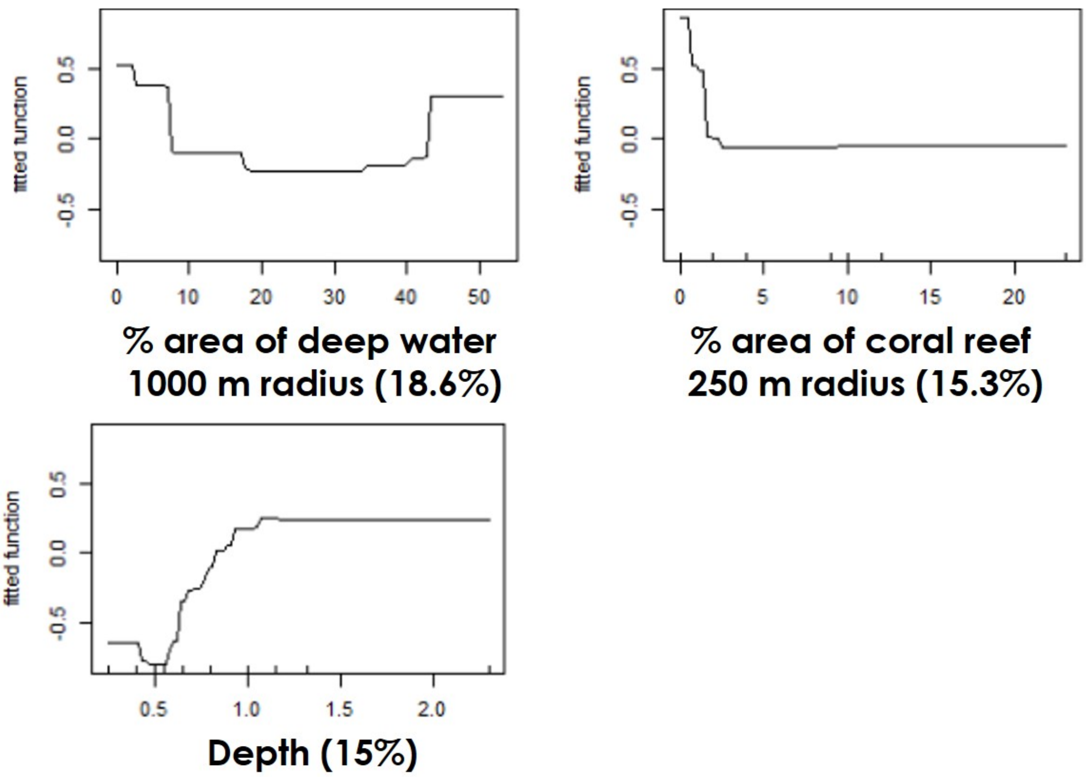

**Figure A4.4.** Partial dependency plots for four most influential predictor variables explaining the presence of juvenile emperors (family: Lethrinidae) in seagrass beds.

**Table A4.2**. Moran's I spatial autocorrelation for all response and predictor variables based on the average distance from each site (n = 32 sites) to its eight nearest neighbours. Following Hamylton & Barnes (2018), variables with a Moran's I value > 0.4 are considered spatially autocorrelated (denoted with *).

| **Variable** | **Type** | **Description** | **IDW-Threshold-1394m-Standardised** | | |
|---|---|---|---|---|---|
| | | | ***Moran's*** | ***z*** | ***p-value*** |
| Labridae | Response | Taxa abundance/ presence | 0.105 | 1.663 | 0.096 |
| Lethrinidae | | | 0.116 | 1.569 | 0.117 |
| Lutjanidae | | | 0.010 | 1.701 | 0.089 |
| Mullidae | | | 0.021 | 0.558 | 0.577 |
| Nemipteridae | | | 0.158 | 1.987 | 0.047 |
| Pomacentridae | | | -0.109 | -0.894 | 0.372 |
| Scarinae | | | -0.064 | -0.526 | 0.599 |
| Siganidae | | | 0.097 | 1.477 | 0.140 |
| Scarinae adult | | | 0.182 | 2.987 | 0.003 |
| Scarinae juvenile | | | -0.055 | -0.387 | 0.698 |
| Lethrinidae adult | | | 0.026 | 0.808 | 0.419 |
| Lethrinidae juvenile | | | 0.128 | 1.699 | 0.089 |
| *Lutjanus fulviflamma* | | | -0.016 | 1.346 | 0.178 |
| *Lethrinus harak* | | | 0.026 | 0.808 | 0.419 |
| *Parupeneus barberinus* | | | 0.035 | 0.709 | 0.478 |
| *Siganus canaliculatus* | | | -0.073 | -0.462 | 0.644 |
| *Siganus lineatus* | | | -0.013 | 1.623 | 0.104 |
| *Siganus spinus* | | | 0.251 | 3.474 | 0.001 |
| *Stethojulis strigiventer* | | | 0.165 | 3.567 | 0.000 |
| *Halichoeres spp.* | | | 0.066 | 1.036 | 0.300 |
| *Halichoeres scapularis* | | | -0.050 | -0.202 | 0.840 |
| *Halichoeres trimaculatus* | | | -0.020 | 0.120 | 0.905 |
| Depth | Predictor | Measured at 25 m transect | 0.097 | 1.278 | 0.201 |
| % cover sand | | | 0.290 | 3.376 | 0.001 |
| % cover rubble | | | 0.002 | 0.677 | 0.498 |
| % cover macroalgae | | | -0.019 | 0.113 | 0.910 |
| % cover seagrass | | | 0.032 | 0.626 | 0.531 |
| % cover hard coral | | | -0.025 | 0.163 | 0.870 |
| % cover rock | | | 0.042 | 1.057 | 0.290 |
| Shoot density | Predictor | Measured by $0.25m^2$ quadrats | 0.113 | 1.445 | 0.149 |
| Canopy height | | | 0.296 | 3.311 | 0.001 |
| % cover epiphytes | | | 0.145 | 1.799 | 0.072 |

| | | | | | |
|---|---|---|---|---|---|
| % cover seagrass | | | -0.038 | -0.079 | 0.937 |
| % cover macroalgae | | | -0.120 | -0.917 | 0.359 |
| Distance to coral reef | Predictor | Seascape metrics | 0.201 | 2.413 | 0.016 |
| Distance to hardground | | | 0.105 | 1.355 | 0.175 |
| Distance to heterogeneous | | | 0.217 | 2.572 | 0.010 |
| Distance to macroalgae | | | -0.026 | 0.044 | 0.965 |
| Distance to mangrove | | | 0.065 | 0.980 | 0.327 |
| Habitat richness (100 m radius) | | | -0.051 | -0.212 | 0.832 |
| Habitat richness (250 m radius) | Predictor | | 0.031 | 0.617 | 0.537 |
| Habitat richness (500 m radius) | | | -0.018 | 0.121 | 0.904 |
| Habitat richness (1000 m radius) | | | 0.114 | 1.449 | 0.147 |
| Area of coral reef (100 m radius) | | | -0.042 | -0.131 | 0.895 |
| Area of deep water (100 m radius) | | | 0.326 | 3.943 | 0.001 |
| Area of hardground (100 m radius) | | | -0.079 | -0.556 | 0.579 |
| Area of heterogeneous (100 m radius) | | | Only 1 site has heterogeneous habitat within 100 m | | |
| Area of macroalgae (100 m radius) | | | -0.010 | 0.234 | 0.815 |
| Area of mangrove (100 m radius) | | | -0.044 | -0.163 | 0.870 |
| Area of seagrass (100 m radius) | | | 0.115 | 1.481 | 0.139 |
| Area of sand (100 m radius) | | | 0.064 | 0.941 | 0.347 |
| Area of coral reef (1000 m radius) | | | 0.572* | 6.045 | 0.000 |
| Area of deep water (1000 m radius) | | | 0.364 | 3.922 | 0.000 |
| Area of hardground (1000 m radius) | | | 0.190 | 2.235 | 0.025 |
| Area of heterogeneous (1000 m radius) | | | 0.132 | 1.644 | 0.100 |
| Area of macroalgae (1000 m radius) | | | 0.316 | 3.490 | 0.000 |
| Area of mangrove (1000 m radius) | | | 0.606* | 6.481 | 0.000 |
| Area of seagrass (1000 m radius) | | | 0.185 | 2.157 | 0.031 |
| Area of sand (1000 m radius) | | | 0.302 | 3.322 | 0.001 |

## Appendix D: Supplementary materials for Chapter 5

# *Influence of seascape and within-reef variables on a key ecosystem process, macroalgal browsing, on coral reefs in Papua New Guinea*

**Table A5.1.** Predictor variables used to examine the influence of seascape structure and within-reef benthic variables on browsing activity on coral reefs.

| Seascape variable | Within-reef benthic variables | |
|---|---|---|
| Distance to oceanic environment | *Acropora* tabular | Other massive corals |
| ***Area of habitat in 250 m radii*** | *Acropora* staghorn | Other encrusting corals |
| Hard & soft coral | *Acropora* bottlebrush | Soft coral |
| Hardground | *Acropora* digitate | Epilithic algal matrix (EAM) |
| Macroalgae | Other *Acropora* | Crustose coralline algae (CCA) |
| Sand | *Pocillopora* | Sand |
| Seagrass | Massive *Porites* | Rubble |
| | Branching *Porites* | Macroalgae |

**Table A5.2**. Moran's I spatial autocorrelation for response and predictor variables based on the average distance from each site (n = 24 sites) to its four nearest neighbours. Following Hamylton & Barnes (2018), variables with a Moran's I value >0.4 are considered spatially autocorrelated (denoted with *).

| Variable | Type | IDW-Threshold-3459m-Standardised | | |
|---|---|---|---|---|
| | | ***Moran's*** | ***z*** | ***p-value*** |
| Max*N* browsers (>99% of bites spp. only) | Response | 0.109 | 0.992 | 0.321 |
| *Kyphosus cinerascens* Max*N* | | -0.025 | 0.317 | 0.751 |
| *Kyphosus vaigiensis* Max*N* | | -0.093 | -0.449 | 0.653 |
| *Naso lituratus* Max*N* | | 0.208 | 1.710 | 0.087 |
| *Naso unicornis* Max*N* | | 0.087 | 0.880 | 0.379 |
| *Siganus canaliculatus* Max*N* | | 0.021 | 0.550 | 0.582 |
| *Siganus doliatus* Max*N* | | -0.056 | -0.080 | 0.937 |
| Total mass standardised bites (>99% of bites spp. only) | | **0.626*** | 4.387 | 0.000 |
| *Kyphosus cinerascens* ms bites | | -0.036 | 0.252 | 0.801 |
| *Kyphosus vaigiensis* ms bites | | -0.193 | -1.044 | 0.297 |
| *Naso lituratus* ms bites | | **0.598*** | 4.428 | 0.000 |
| *Naso unicornis* ms bites | | 0.208 | 1.747 | 0.080 |

| | | | | |
|---|---|---|---|---|
| *Siganus canaliculatus* ms bites | | 0.030 | 0.533 | 0.594 |
| *Siganus doliatus* ms bites | | -0.138 | -0.800 | 0.424 |
| Mean macroalgae consumed (%) per site | | **0.686*** | 4.563 | 0.000 |
| Area of hard & soft coral habitat (250 m radius) | Predictor | 0.221 | 1.875 | 0.061 |
| Area of hardground/heterogeneous habitat (250 m radius) | | 0.178 | 1.228 | 0.119 |
| Area of macroalgal beds (250 m radius) | | 0.362 | 2.748 | 0.006 |
| Area of seagrass beds (250 m radius) | | 0.367 | 2.990 | 0.003 |
| Area of sand (250 m radius) | | **0.479*** | 3.252 | 0.001 |

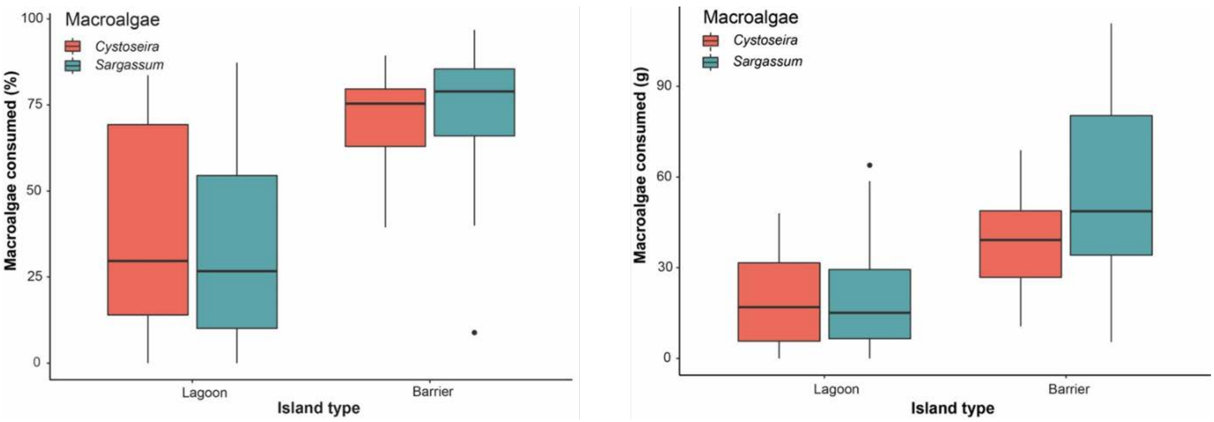


**Figure A5.1.** Comparison of macroalgae assays consumed between reef positions for each genera of macroalgae. Left figure shows percent consumed, right figure shows removal in grams (g).

**Table A5.3**. Pairwise PERMANOVA tests comparing macroalgal removal rates around each island.

| **Islands** | **t** | **P(perm)** | **Unique permutations** |
|---|---|---|---|
| Enuk, Kabotteron | 1.4022 | 0.130 | 9947 |
| Enuk, Ungan | 0.4816 | 0.832 | 9942 |
| Enuk, Nusalik | 2.5547 | 0.002 | 9942 |
| Enuk, Nusalomon | 4.1847 | 0.000 | 9934 |
| Enuk, Ral | 4.0519 | 0.000 | 9937 |
| Kabotteron, Ungan | 1.6298 | 0.074 | 9951 |
| Kabotteron, Nusalik | 4.4622 | 0.000 | 9954 |
| Kabotteron, Nusalomon | 6.6043 | 0.000 | 9936 |
| Kabotteron, Ral | 6.5076 | 0.000 | 9956 |
| Ungan, Nusalik | 2.4369 | 0.006 | 9941 |
| Ungan, Nusalomon | 3.6854 | 0.000 | 9956 |
| Ungan, Ral | 3.5993 | 0.000 | 9948 |

| | | | |
|---|---|---|---|
| Nusalik, Nusalomon | 4.3651 | 0.000 | 9916 |
| Nusalik, Ral | 3.5295 | 0.000 | 9937 |
| Nusalomon, Ral | 2.0799 | 0.043 | 9918 |

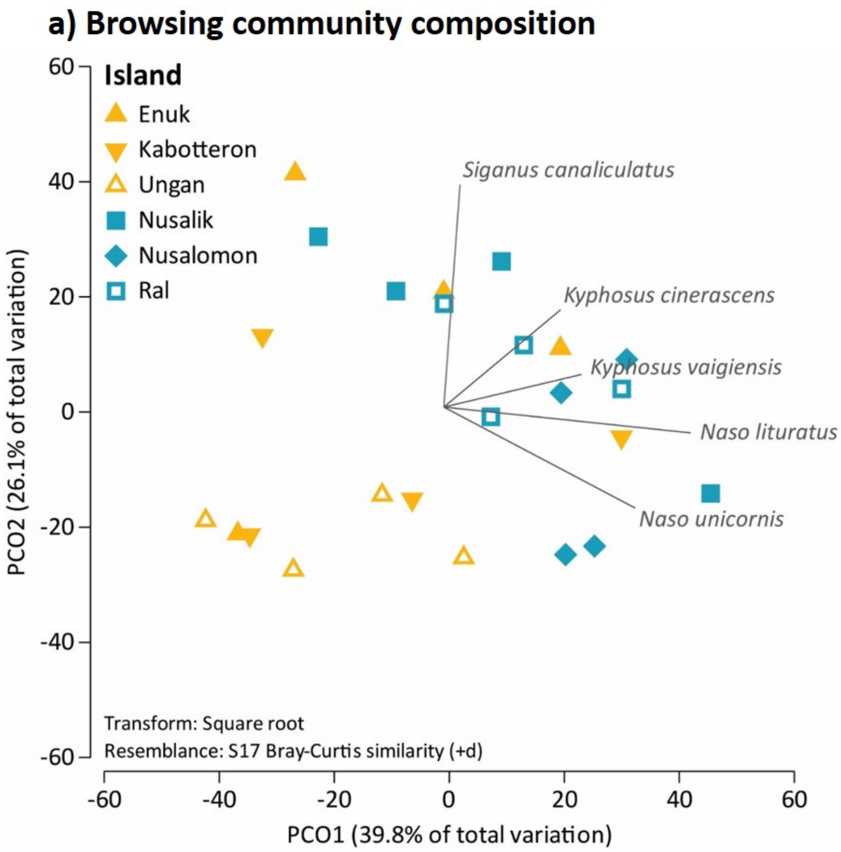


**Figure A5.2.** PCO of relative abundance (Max*N*) of browsing community for the six browsing species accounting for 99% of mass standardised bites. Vectors show species contributing to community patterns. Yellow = lagoon island reefs, blue = barrier island reefs.

### *Characterising the within-reef benthic community composition and seascape structure*

We characterised the assay sites at two different spatial scales: within-reef benthic community composition, and the seascape composition within 250 m radius. Differences in the benthic community along transects and the seascape composition surrounding a site were explored using a two-factor nested permutational analysis of variance (PERMANOVA) with reef position (i.e. barrier vs lagoon) as a fixed factor, and island as a random factor nested within reef position. For the benthic community analysis, transect data were averaged by site and square-root transformed. Seascape data were log transformed. Resemblance matrices were constructed based on Bray-Curtis for the benthic community data and Euclidean distances for the seascape data. Patterns were visualised using principal component analysis (PCA).

***Within-reef benthic community composition***

Mean live hard coral cover was variable among sites ranging from 8% ± 3.7 SE to 62% ± 2.6 SE (overall mean 37.9% ± 3.1 SE) (Figure A5.3). Macroalgae cover was generally low across all sites (7.9% ± 1.4 SE; Figure A5.3), with *Halimeda* spp. dominating the algal assemblage. There was no significant difference in benthic community composition between the barrier and lagoon sites (pseudo-*F* = 1.41, df = 1, p(mc) = 0.24) (Figure A5.4a, Table A5.4). However, there was a significant difference between islands nested in reef position (pseudo-*F* = 1.92, df = 4, p = 0.006) (Table A5.4). Pairwise comparisons revealed that the difference was attributable to one barrier reef island, Nusalik, which had a different benthic community to the other two barrier reef islands (p(mc) <0.05). SIMPER analysis identified that this was driven by higher amounts of epilithic algae matrix (EAM) and *Porites* spp. at Nusalik, compared to higher amounts of crustose coralline algae (CCA) at the other two barrier reef islands (i.e., Nusalomon and Ral).

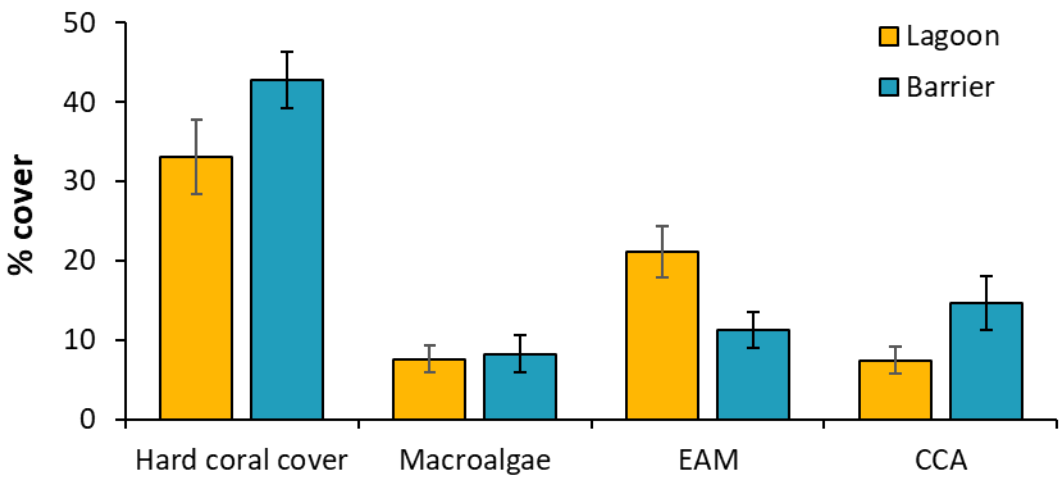


**Figure A5.3.** Comparison of four ecologically relevant benthic habitat categories between lagoon and barrier reef sites.

***Seascape structure***

The composition of the seascape within a 250 m radius of each site was also significantly different between islands nested in reef position (df = 4, pseudo-*F* = 2.81, p = 0.005) but not between the lagoon and barrier reef sites (pseudo-*F* = 1.99, df = 1, p(mc) = 0.168) (Figure A5.4b, Table A5.4). Pairwise comparisons showed that the barrier reef island, Nusalik, had a different seascape composition to the other two barrier reef islands, Nusalomon and Ral (p(mc) <0.01). SIMPER analysis identified that this was driven by the higher areal coverage of seagrass around the Nusalik sites compared to the other two barrier reef islands.

**Table A5.4.** PERMANOVA results for comparing differences between reef position (fixed) and islands (random nested within reef position) for the benthic community and seascape composition. *ECV denotes percent estimated components of variation.

| | df | SS | MS | Pseudo-*F* | P(perm) | ECV* |
|---|---|---|---|---|---|---|
| **Benthic community** | | | | | | |
| Reef position | 1 | 14.874 | 14.874 | 1.4091 | 0.2322 | 5.1% |
| Island(Reef position) | 4 | 42.224 | 10.556 | 1.9226 | **0.0041** | 17.8% |
| Residual | 18 | 98.825 | 5.4903 | | | |
| Total | 23 | 155.92 | | | | |
| **Seascape composition** | | | | | | |
| Reef position | 1 | 20.413 | 20.413 | 1.9938 | 0.168 | 13.8% |
| Island(Reef position) | 4 | 40.953 | 10.238 | 2.8146 | **0.005** | 26.9% |
| Residual | 18 | 65.475 | 3.6375 | | | |
| Total | 23 | 126.84 | | | | |

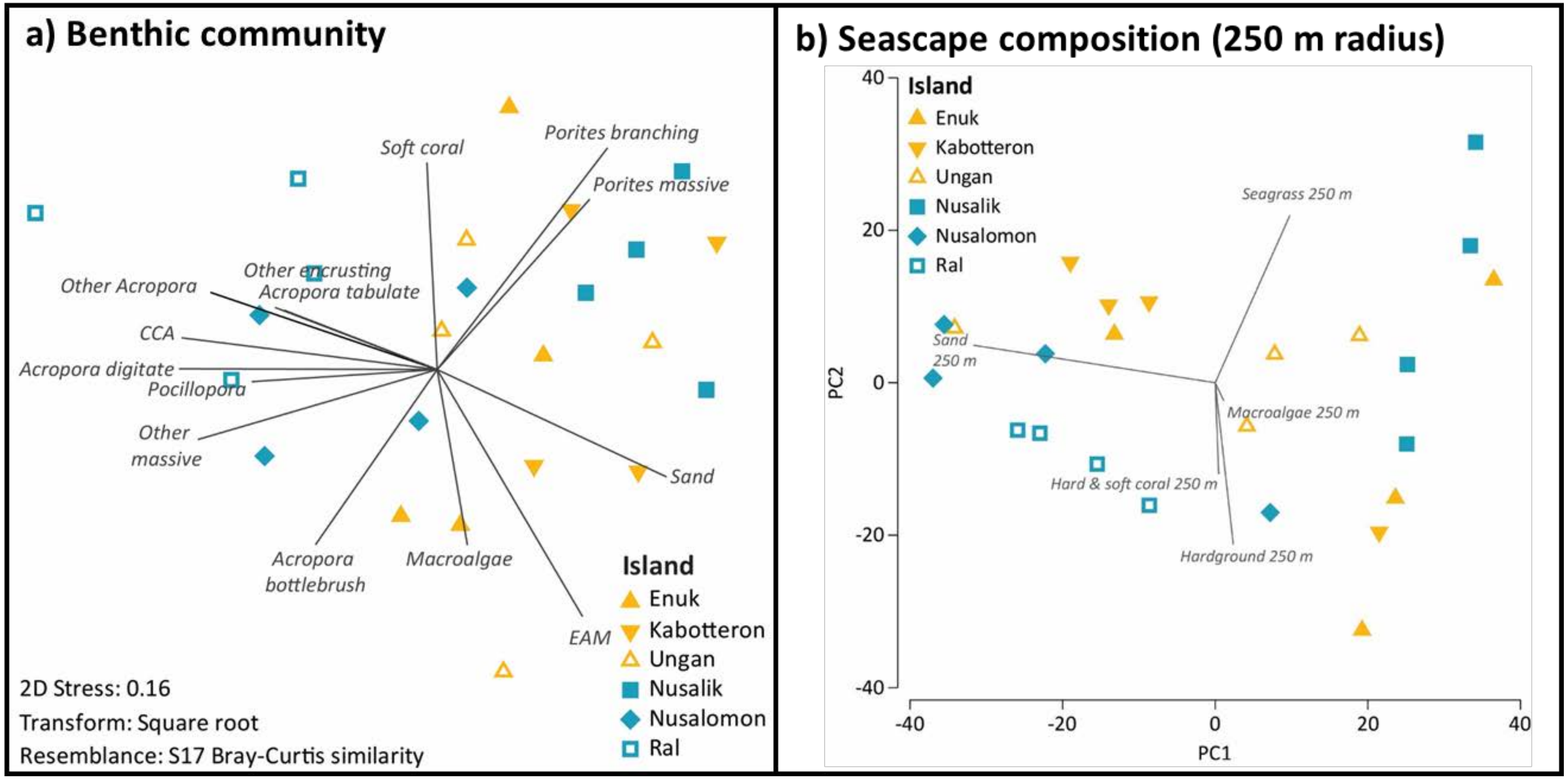


**Figure A5.4.** a) nMDS plot of benthic community, and b) PCA plot of the seascape composition to visualise differences between sites, islands and reef positions. Vectors show variables contributing to benthic and seascape patterns. Yellow = lagoon islands, blue = barrier reef islands.