Lutzenkirchen, Lucas Leo (2024) *Upscaling ecosystem studies on coral reefs.* Masters (Research) Thesis, James Cook University.

https://doi.org/10.25903/1gd4%2Dfb46

Upscaling ecosystem studies on coral reefs

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January 2024

For the degree of Master of Philosophy

College of Science and Engineering

Research Hub for Coral Reef Ecosystem Functions

James Cook University

Acknowledgements

First and foremost, I express my heartfelt appreciation to my supervisor, Professor David Bellwood. Dave, your invaluable guidance, unwavering support, and encouragement throughout this research journey have been deeply appreciated. Even when I struggled to see my own abilities, your trust in me, unconditional availability, and willingness to share wisdom have shaped my critical thinking skills and contributed to both my academic and personal growth. Your mentorship extended beyond encouraging me to develop my own voice, explore new ideas, and take ownership of my research path. Your genuine investment in my success and well-being has had a profound impact on my development as a researcher and an individual, reaching beyond the technical aspects of academia. The countless moments of laughter and wisdom we shared have been truly cherished, and I am immensely grateful for the transformative influence you've had on my journey.

I would also like to thank my co-supervisor, Dr. Stephanie Duce. Steph, your exceptional expertise, dedication, and calm persona have profoundly influenced my academic and personal growth. The nurturing environment you cultivated made me feel welcomed and supported, regardless of the simplicity or complexity of my questions. Your patient guidance and ability to provide clarity in the face of intricate geospatial problems have been instrumental in shaping my research approach. Your meticulous attention to detail and insightful feedback consistently challenged me to refine my work and strive for excellence. Beyond academia, your genuine concern for my well-being and your encouragement to explore new perspectives have instilled in me a profound sense of confidence and self-belief.

I am immensely grateful for the exceptional group of scientists who not only served as my lab mates but also became cherished friends: Casey Bowden, Samantha Crisp, William Collins, Chris Hemingson, Mike Mihalitsis, Juliano Morais, Isabelle Ng, Caitlin Phillips, Pooven Muruga, Ale Siqueira, Sam Swan, and, from my earliest days here at JCU, Orpha Bellwood. I want to express my deepest appreciation to each of you for the unwavering friendship, infectious laughter, and countless memorable experiences we shared. The bonds we forged transcended the confines of our research, fostering a sense of community and support. The invaluable encouragement we provided one another, the countless conversations over shared coffees, and the lively discussions during lunch breaks, where topics other than science took centre stage, enriched my journey in immeasurable ways. I would like to extend a special thank you to James Gahan and Robert Streit for their unwavering presence during both challenging and joyous times, accompanying me on endless walks around campus and offering steadfast support. Additionally, I express my sincere gratitude to Helen Yan and Sterling Tebbett for their incredible patience and shared wisdom, which propelled my career further. To all of you, thank you for playing a vital role in both my academic and personal growth.

This thesis would not have been possible without the invaluable contributions and support of numerous staff members at JCU. My heartfelt gratitude goes to JCU for bestowing upon me a Postgraduate Research Scholarship, in support of the ARC Laureate Fellowship to DRB. This generous support not only made the undertaking of this thesis possible but also enabled me to wholeheartedly focus and dedicate my time to its completion. I am deeply grateful to Greg Suosaari from Boating and Diving, Andrew Norton and the IT-helpdesk staff for their prompt assistance and technical expertise. Special thanks to the Graduate Research School and College of Science and Engineering staff, including Debbie Berry, Tammy Walsh, Jodie Wilson, and others. The unwavering support from the Student Wellbeing and Equity team was invaluable during challenging times. I also extend my deepest appreciation to the International Student team for their exceptional support, especially during the pandemic. Lastly, I am grateful to Dr. Murray Logan for his expertise in statistics. Together, their collective efforts and dedication played a vital role in the successful completion of this thesis.

I am deeply grateful for the connections and friendships I have formed in Townsville, which have enriched my experience in immeasurable ways. To my friends from around the world, your enduring support has transcended time and distance. Special thanks to my incredible housemates and extended family away from home, including William Collins, Ellen Clark, Cara Shelley, Nina Freitas, and Victor Huertas. I also want to express special gratitude to Tori Nunis, Declan Cargill, James Gahan, and all the other remarkable individuals I have had the privilege of meeting. Tori, Deccy, and James, your unwavering presence has been my anchor, grounding me through life's twists and turns, and I'm endlessly grateful for the laughter, understanding, and shared moments that have made the journey richer and more meaningful. Thank you all for warmly embracing me and for your invaluable contributions to the unforgettable connections that have profoundly shaped my journey.

Undoubtedly, I owe an immeasurable debt of gratitude to my family, whose love and lifelong encouragement have paved the way for my academic journey. Mama, Papa, und Lea, I cannot express my appreciation enough for your constant support and unwavering belief in me. You have always encouraged me to explore my interests and follow my passions, even when they led me on unconventional paths. Your optimism and wholehearted involvement in my life, despite the physical distance, have been a constant source of strength and inspiration. Thank you for being an integral part of this incredible journey, for embracing the challenges and triumphs alongside me, and for playing a vital role in shaping the person I have become. Ich liebe euch!

Statement of the Contribution of Others

This thesis was made possible by funds provided by my supervisor David Bellwood from an Australian Research Council Laureate Fellowship (Grant Number: FL190100062). Throughout my degree I was support by a Postgraduate Research Stipend Scholarship via James Cook University.

All chapters in this thesis benefited from conceptual guidance and editorial assistance from my supervisor Prof. David Bellwood. **Chapter 2** and **3** were conducted under the joint supervision of David Bellwood and Dr. Stephanie Duce. In both chapters, Stephanie Duce assisted with conceptual guidance, methodology and data analysis advice, as well as editorial assistance. In **Chapter 4**, Helen Yan and Dr. Sterling Tebbett assisted with the data and covariate collection, provided conceptual guidance, as well as assistance with both statistical analyses and the editorial process.

Abstract

The Anthropocene epoch is marked by unprecedented human influence on natural systems. Coral reefs, in particular, are confronted with mounting threats, including climate change, habitat destruction, pollution, and overexploitation. These challenges underscore the urgent need for a comprehensive understanding of ecological processes and coral reef functioning. To achieve this, research must encompass expansive spatial and temporal dimensions, recognizing our increasing knowledge of the scale of both key coral reef processes and emerging threats. As stressors continue to escalate, resulting in altered and degraded coral reefs in the Anthropocene, there is a growing imperative to assess coral reef functions across broader scales.

In this thesis, therefore, I aimed to explore multiple coral reef functions across broad scales using geospatial and modelling approaches. Throughout the data chapters (2 to 4), I examine our understanding of ecosystem processes among scales to answer the following questions: a) What are the differences between survey methodologies employed in coral reef ecosystems, and what opportunities exist for future improvements in scalability of reef surveys and generalizability of remote sensing surveys?, b) What are the primary drivers of reef growth at global scales? And, c) What are the correlates of herbivorous fish catches and trends in CPUE in coastal small-scale fisheries across the Western Atlantic and Indo-Pacific?

Chapter 2 encapsulates an extensive review of the literature from the past decade in two key coral reef research areas, ecology and remote sensing, revealing that observer-defined scale artefacts may compromise the various approaches. As expected, the two fields differ substantially in their focal questions: most traditional in-water observation-based coral reef ecology studies assess community composition; while remote sensing studies focus on benthic mapping. Ecological studies typically employ direct measurements from detailed observations of small areas; remote sensing studies typically rely on sensors detecting patterns at broader scales. Remarkably, few studies integrated comprehensive *in-situ* observations with broadscale sensing. Bridging these two scientific disciplines poses challenges but holds great promise for upscaling observations to reef-wide scales.

In **chapter 3**, I used the Allen Coral Atlas to sample over 3700 virtual transects across 60 locations in the Caribbean and Indo-Pacific realms in ArcGIS. The goal was to investigate the extent (i.e. width) of shallow reef habitats. Specifically, whether the disparities between these realms, in terms of biogeographical extents, biodiversity patterns, and evolutionary or sea-level histories, impacted the width of shallow-water biogenic coral reef habitats. Considering the vast differences in the diversity of corals and the stability of sea levels during the Holocene, I expected greater widths in shallow reef habitats in the Indo-Pacific. Contrary to expectations, I found that the widths were

strikingly similar across the two realms, indicating a disconnect between coral growth, an ecological process, and reef growth, a geological process. Reef growth, an important coral ecosystem function, appears to be primarily influenced by local hydrodynamic factors rather than coral diversity or coral growth rates.

In **chapter 4,** I assessed the role of herbivorous fishes in global fishery yields across 69 Exclusive Economic Zones (EEZs) in the Indo-Pacific and Western Atlantic using reported and reconstructed global catch data. Specifically, I assessed indirect measures of fishing pressure and ecosystem attributes that could modify herbivorous fish catches. Reef habitat area and human population densities were identified as key factors influencing herbivorous fish yields and catch-per-unit-effort (CPUE). Rabbitfishes were identified as crucial contributors, explaining the higher herbivorous fish yields in the Indo-Pacific compared to the Western Atlantic. However, all herbivorous fish groups showed distinct declines in CPUE over the last 60 years, potentially indicating a global decrease in production potential . This reveals a significant social-ecological scale mismatch: while coastal habitats may be dynamic, herbivorous fish catches at larger scales are declining, along with their ability to sustain coastal communities.

Overall, the findings of this thesis emphasize the value of upscaling our understanding of critical ecosystem processes. In all cases, this broader perspective provides new insights into how these systems function. To effectively address the escalating temporal and spatial scales of human impacts on coral reefs in the Anthropocene, it is imperative to align the scale of scientific investigation, monitoring, and management with the scale of these pressures, minimising current scale mismatches. The suitability and efficacy of coral reef ecosystem management depends on scale-appropriate knowledge and actions.

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Chapter 1. General Introduction

The Anthropocene marks a new geological epoch, defined by the unprecedented influence of human activities on Earth's ecosystems (Lewis and Maslin 2015; Steffen et al. 2015). As a species, humanity and its societies have become a global geophysical force, intricately intertwined with the biosphere (Steffen et al. 2011; Folke et al. 2021). Unfortunately, the most pressing consequence of this impact is climate change, which is fundamentally altering the conditions of life on our planet (Hoegh-Guldberg and Bruno 2010; Diffenbaugh and Field 2013; Steffen et al. 2015; Pecl et al. 2017). Rising temperatures, changing precipitation patterns, and frequent extreme weather events are already taking a toll on the world's ecosystems and their functioning (Grimm et al. 2013; Hughes et al. 2017; Ummenhofer and Meehl 2017; IPCC 2023). This, in turn, has severe repercussions for biodiversity, food security, and human well-being. However, the impacts of climate change are unevenly distributed worldwide, with poorer nations and individuals bearing a disproportionate burden (Allison et al. 2009; Althor et al. 2016; Islam and Winkel 2017; Thomas et al. 2019). This disparity can be attributed to their limited capacity to implement climate protection measures and their tendency to inhabit warmer regions, where further warming could adversely affect both ecosystem productivity and health (IPCC 2023). Consequently, understanding the intricate interactions between human activities and the Earth's ecosystems has become an urgent research priority, with far-reaching implications for the future of our planet. However, the scale and scope of human impact are now believed to have pushed ecosystems, and the ecological processes that support their functioning, beyond their tipping points on a global scale (Kopf et al. 2015; Duarte et al. 2020), potentially rendering the restoration of its prior states impossible.

The relationship between ecological processes and ecosystem functioning is often compared to a performance in the "ecological theatre" that occurs at different spatial and temporal scales (Hutchinson 1965; Wiens 1989). To fully understand this performance and its impact on ecosystems and patterns, studying ecological phenomena at the appropriate level is crucial (Hutchinson 1965; Wiens 1989). Examining these phenomena at the scales most relevant to the underlying processes is necessary to draw causal and holistic inferences about ecosystems and their functioning. Scale generally refers to the spatial, temporal, or organizational dimension of a phenomenon (Wu and Li 2006; Lecours et al. 2015). Generally, time and space are the fundamental axes of scale, whereas organizational scale elements are usually introduced and dictated by the observer (Levin 1992; Wu and Li 2006; Lecours et al. 2015). Resolution, describing the finest detail achievable in space or time within which homogeneity is assumed, and extent, the total spatial or temporal expanse, are the fundamental components of scale (Wiens 1989; Wu and Li 2006; Lecours et al. 2015). Understanding scale and pattern has been a long-standing problem in ecology, as spatial heterogeneity often forms the basis of structure and functioning in diverse landscapes and seascapes, inevitably making processes, ecological phenomena, and their observations across these systems scale-dependent (Levin 1992; Wu 2004). This issue has become even more important in the face of the escalating threats to ecosystem functioning caused by climate change, which is altering and degrading ecosystems on a global scale. In the Anthropocene, assessing the interfacing phenomena and processes at a multitude of highly variable scales across space, time, and levels of organization is a necessary first step in addressing these threats (Levin 1992; Chave 2013; Verburg et al. 2016).

The degradation and transformation of ecosystems at a global level has led to a profound change in ecological research. Scientists have moved away from taxon-based investigations with a narrow focus, towards more comprehensive, functional or "trait-based" approaches. These functional studies aim to identify an organism's contribution to ecological processes, rather than simply quantifying their identity and abundance (McGill et al. 2006; Violle et al. 2007; Bellwood et al. 2019b; Streit and Bellwood 2022). In the Anthropocene, there has been a growing emphasis on ecosystem functioning, which aims to address the crucial question of "What functions, processes, and services must we preserve?" (Bellwood et al. 2019b; Streit and Bellwood 2022). However, it has been noted that we are facing a ‘functionality crisis’, especially in the marine realm, as many functional studies tend to rely on easy-to-measure traits or proxies that are thought to have functional significance, without empirical or causative evaluations (Bellwood et al. 2019b, Streit and Bellwood 2022). Even the term ‘function’ lacked a unified and broadly applicable definition, prohibiting comparability across studies and disciplinary boundaries. This lack of empirical evidence and unified definitions poses a challenge to making informed recommendations for ecosystem management.

Recently, Bellwood et al. (2019b) proposed ‘*the movement or storage of energy or material’* as a broad and unified definitional framework for the term function on coral reefs. While this framework is applicable to all levels of organization (from cellular to global levels), its main purpose is to shift the focus from how ecological functions are delivered to what functions are necessary to sustain ecosystem functioning and desirable services. For example, herbivory represents a key ecosystem function on coral reefs and is facilitated by numerous nominally herbivorous fishes (Bellwood et al. 2004; Adam et al. 2015; Tebbett et al. 2023a). Thus, by employing an approach that focuses on ‘what’ ecosystem functions are of importance, functional redundancies within a system may become apparent, revealing that the loss of certain individuals may not necessarily jeopardize the delivery of ecosystem functions (Bellwood et al. 2019b). Ultimately, prioritizing ecosystem functions, rather than specific taxa that deliver functions, changes perspectives and helps to increase the scale at which we both observe and understand ecosystem processes. Upscaling our understanding of ecological processes, particularly in an era marked by the accelerating transformations of ecosystems, is vital to ensure that our management approaches and responses are commensurate with the scale of anthropogenic threats.

The large-scale impacts of climate change and dire state of our planet is perhaps nowhere more evident than in the ongoing struggle on coral reefs (Hughes et al. 2017; Bellwood et al. 2019a; Sully et al. 2019), which are among the most productive and vulnerable ecosystems on Earth (Odum and Odum 1955; Connell 1978). These large-scale biogenic structures, formed by living creatures, are a powerful reminder of the widespread repercussions of humanity's impact on the environment (Hughes et al. 2017, Bellwood et al. 2019a). Beyond their intrinsic ecological value, coral reefs play a pivotal role by providing crucial ecosystem services such as coastal protection, fisheries, and tourism (Moberg and Folke 1999; Woodhead et al. 2019), often fostering rapid human population growth in their proximity (Wong et al. 2022). Consequently, communities worldwide exhibit varying degrees of reliance on marine ecosystems and coral reefs (Selig et al. 2019; Allison et al. 2009). Yet, changes in the Anthropocene have undermined the ability of coral reefs to sustain key services at historical levels and to uphold their ecological and geological productivity (Hughes et al. 2017; Williams and Graham 2019; Williams et al. 2019; Woodhead et al. 2019; Tebbett et al. 2021). Recent surges in sea-surface temperatures have triggered multiple global coral bleaching events, raising concerns about the future carbonate production on coral reefs (Perry et al. 2018; Perry and Alvarez-Filip 2019; Browne et al. 2021; Cornwall et al. 2021).

Moreover, coral reefs, nestled within tropical seascapes, can harbor a rich diversity of marine life, playing a crucial role in supporting high fish biomass and densities (Sievers et al. 2020). Tropical small-scale fisheries depend heavily on these habitats and constitute approximately half of the global fish catches (FAO 2020). They also provide a livelihood for over 90% of the people who rely on capture fisheries (FAO 2020). Nevertheless, the severe impacts of climate change pose an imminent threat, leading to a global decline in their productivity. The catch per unit effort of coral reef-associated fishes has undergone a decline of over 60% since 1950, presenting significant challenges for millions of people dependent on coral reef ecosystem services for nutrition (Eddy et al. 2021). Unfortunately, the threats to coral reefs have become more extensive and pervasive than ever, and existing management strategies struggle to keep pace with the escalating scale of these challenges (Bellwood et al. 2019a). Addressing these challenges and scaling issues is imperative for the effective management of coral reef ecosystems.

1.1 Thesis outline

Significant disparities exist between the scales examined in ecological studies on coral reefs and the extent to which inferences are being made about the drivers of ecosystem processes. These scale-artefacts hinder our holistic understanding of ecosystem processes, while also undermining our ability to make causal inferences about the drivers of their functioning. This thesis, therefore, aims to explore diverse and vital coral reef functions across different spatial and temporal scales, aiming to shed light on the scale-dependent factors influencing the functioning of coral reef ecosystems. To address the pressure to upscale, it is essential to understand existing methods and assess their application. This analysis will shed light on potential reasons behind current spatial mismatches. Therefore, in **chapter 2**, I investigated and compared the relative contribution and focus of traditional in-water observation-based coral reef ecology and remote sensing-based methods. To identify potential overlap, as well as future blueprints to increase the utility of each, I employed a structured review of the literature spanning all relevant publications in key journals of each field spanning over the last decade. Then in **chapters 3 and 4**, I focused on specific coral reef functions across two major oceanic basins, the Indo-Pacific and Caribbean/Western Atlantic, to identify patterns and explore potential drivers from a functional, large-scale perspective. In **chapter 3** (Lutzenkirchen et al. 2023), I analysed shallow reef width patterns to determine the extent to which the highly divergent evolutionary and biogeographic history, as well as biodiversity gradients, between the two realms impacts coral reef geomorphology. This was achieved by using high-resolution and universally applied satellite-based geomorphic coral reef zonation maps provided by the Allen Coral Atlas and a desktop based geospatial ArcGIS approach. In **chapter 4**, I focused on three nominally herbivorous fish groups to describe their contributions to seascape-associated fisheries across the two realms and their relative levels of exploitation. I also investigated potential correlates of fishery catches. In this project I used reported and reconstructed catch estimates from the Sea Around Us database and modelled the relationship between fishery statistics, such as average total catch and average catch-per-unit-effort, and large-scale social, geomorphic, and biogeographic covariates.

Chapter 2. Exploring benthic habitat assessments on coral reefs: a comparison of direct field measurements vs. remote sensing

Accepted as: Lutzenkirchen, L. L., Duce, S. J., & Bellwood, D. R. (2024). Exploring benthic habitat assessments on coral reefs: a comparison of direct field measurements vs. remote sensing. Coral Reefs

2.1 Abstract

Coral reefs are spatially variable ecosystems that form biogenic structures ranging in size from 10s to 1000s of meters. Their changes in response to anthropogenic stress are occurring across increasingly broad scales, yet our ability to detect, understand and respond to these changes at relevant scales is limited. Traditional in-water observation-based coral reef ecology and remote sensing-based methods both offer valuable insights into benthic change, but their relative scalability and use to-date must be understood to inform optimal future research approaches. We conducted a systematic literature review comparing the approaches used to quantify benthic habitat, through traditional in-water ecological studies and remote sensing studies, with respect to: a) their geographic distribution, b) reef zone selection, and c) their focal questions. Among the 199 studies reviewed, traditional ecological studies primarily concentrated on community composition (89%), using high-detail direct measurements, especially from the reef slope (80%). By contrast, remote sensing studies provided spatially explicit datasets at coarser spatial and thematic resolutions, with a predominant focus on benthic mapping (72%) across entire reef systems. Only 3% of studies integrated both approaches, combining comprehensive in-situ observations with broadscale remote sensing. As anthropogenic stressors continue to increase in scale, bridging these scientific disciplines offers a promising way to upscale observations to entire reef-scape scales. Given the evident limitations in scalability of reef surveys and the constrained generalizability of remote sensing approaches, we identify steps to harness the strengths of both fields and integrate multiple tools at various levels of resolution and scale. Such bridging approaches offer a way forward in understanding and managing coral reef functioning in the Anthropocene.

2.2 Introduction

Ecosystems, both terrestrial and marine, share a degree of hierarchical organization with sublevels operating at distinct temporal and spatial scales, collectively contributing to larger systems (O’Neill et al. 1989). Consequently, each subsystem exhibits varying spatio-temporal heterogeneity and patchy distributions, forming the foundation for ecosystem structure and functioning (O’Neill et al. 1989; Azovsky 2000; Wu 2004). These fundamental characteristics, also found in coral reefs, create scale multiplicity in spatial patterns and ecological processes (O'Neill et al. 1989; Levin 1992). Such that, at smaller scales, ecosystems may be dominated by intricate processes or behaviours of individuals, but their influence becomes negligible at intermediate or broad scales, where environmental, evolutionary, or geomorphological processes shape ecosystems (Wiens 1989; Holling 1992). Therefore, understanding ecosystem structure and functioning necessitates studying ecological phenomena at scales most relevant to the underlying processes. Detecting patterns relies on two scale components: resolution and extent. Extent refers to the overall study area coverage, while resolution describes the size of individual observation units (Wiens 1989; Wu and Li 2006). Combining extent and resolution sets the upper and lower dimensional boundaries of a study, much like the size and mesh of a sieve (Wiens 1989).

In coral reef ecology, addressing processes across various scales is crucial due to the complex interactions within these ecosystems. Reefs, as open systems, are influenced by factors operating at multiple levels, necessitating a comprehensive approach to understand their dynamics and functioning. Scale, pertaining to ecology, can be categorized into three dimensions: spatial, temporal, and thematic (Wu and Li 2006; Lecours et al. 2015). The spatial dimension encompasses the spatial resolution (i.e. level of detail measured) and geographic extent of an object, area, or process. Temporal resolution refers to the frequency of data collection, while temporal extent describes the period of data collection. Thematic scale, refers to the number of classes identified within a chosen domain/s, mainly concerning taxonomic resolution and the level of organization that can be resolved in datasets (Wu and Li 2006; Lecours et al. 2015). As coral reefs face increasing threats, it is becoming more important for research and conservation responses to address changes at broader spatial and temporal scales and in relevant thematic classes. However, there exists a mismatch between the geographic extent of reef stressors (e.g. marine heatwaves which lead to bleaching events) and the extent of scientific investigation, monitoring, and management responses. These challenges and mismatches must be addressed if coral reef ecosystems are to be effectively managed and conserved into the future (Hughes et al. 2017; Bellwood et al. 2019a).

Coral reefs provide crucial functions and ecosystem services, such as coastal protection, fisheries, and tourism (Moberg and Folke 1999; Woodhead et al. 2019). The protection of functionally important groups within coral reef ecosystems is vital for ensuring the continual delivery of these services (Bellwood et al. 2019b; Brandl et al. 2019). However, identifying contributors to ecosystem functioning is challenging, and their identities may change in response to climate change (Bellwood et al. 2019b; Wolfe et al. 2021; Streit and Bellwood 2022). Moreover, coral reefs are dynamic environments where interactions among reef organisms and other ecosystem components occur at various scales and hierarchies (Hatcher 1997; Dietzel et al. 2021; Wolfe et al. 2023). Due to their heterogenous nature, spatial variability, and distribution in clumped patches ranging from 10s to 1000s of metres in extent (Hopley et al. 2007), changes in coral reefs systems are not distributed homogeneously (Morais et al. 2021a; Tebbett et al. 2023b). As a result, most coral reef functions are scale dependent. For instance, the rate and extent of vital functions provided by coral reef fishes, such as herbivory or bioerosion, are often estimated by assuming that fish presence equals function delivery (Bellwood et al. 2003; Graham et al. 2018; Perry et al. 2022). However, the implicit assumption of homogeneity of function across the reef is increasingly being questioned (Streit et al. 2019; Tebbett and Bellwood 2020), particularly in the face of the escalating scale of reef disturbance. The presence-function and scale mismatches present challenges in managing and conserving reef systems in the Anthropocene (Bellwood et al. 2019a; Brandl et al. 2019). Traditional approaches, such as Marine Protected Areas, are no longer sufficient to address the new challenges in coral reef governance, management, and science (Bellwood et al. 2019a).

In coral reef research, benthic metrics like habitat cover, complexity, and diversity are used for evaluating and monitoring reef health and structure. They are commonly assessed using measures such as coral cover, benthic cover, and rugosity (Bellwood et al. 2004; Bruno and Selig 2007; Graham and Nash 2013). Coral cover indicates the percentage of the seafloor occupied by live coral, while benthic cover evaluates the proportion of different substratum types, including coral, algae, sand, and rubble (Bruno and Selig 2007). Rugosity provides a three-dimensional complexity estimate, helping to understand habitat diversity and potential habitat availability for various other reef inhabitants (Graham and Nash 2013; Ferrari et al. 2018). Assessing these metrics has traditionally involved in-water field surveys by skilled scuba divers. However, these labour-intensive surveys are often limited to specific taxa and specific study areas, representing only a small portion of the entire reef ecosystem (Bellwood et al. 2020; Tebbett et al. 2023b). As a result, findings from localized surveys may not fully capture broader patterns and variation at wider spatial scales. Valuable methods and techniques involving the use of remote sensing technologies, both above and below the water, have been emerging over recent decades with the aim of overcoming these challenges. These advances are increasingly employed to map extensive benthic areas for management purposes and to quantify large-scale complexity metrics of the benthos.

Ecology and remote sensing constitute pivotal domains within coral reef research, both characterized by scale awareness and dependence. Their shared objective is to appraise benthic transformations in coral reef systems to improve knowledge and ensure sustainability. While in-situ ecological studies are increasingly addressing coral reef functioning, recent papers have highlighted the constraints placed on our understanding because of the limited spatial extent of study efforts, across both reefs and habitats, as well as the immense associated costs, which constrain our ability to describe dynamic phenomena and processes at broad spatial scales (Hedley et al. 2016; Estes et al. 2018; Bellwood et al. 2020; Kench et al. 2022; Tebbett et al. 2023b). However, the rapid development of in-water remote sensing techniques to derive 3D structural assessments, at unprecedentedly high resolution and across relatively large areas (1ms -100ms), holds the potential to significantly enhance our capacity to monitor these ecosystems (Ferrari et al. 2016, 2022; Calders et al. 2020). Recent advances in aerial and satellite remote sensing technologies offer a promising avenue to upscale the extent of in-situ observations to the reef-scale, of kilometre/hundreds of kilometres, optimizing the efficiency of such studies (Green et al. 2000; Hamylton 2017; Dornelas et al. 2019; D'Urban Jackson et al. 2020) (Figures 2.1 and 2.2). Nevertheless, the potential for scale-dependency raises the question: How can the methods used in traditional coral reef ecology be optimised to accurately assess biological and ecological processes affected by stressors operating at ever-increasing scales? To address this question, this study looked at the relative contribution of two fields (traditional in-situ coral reef ecology and remote sensing), that both assess benthic habitats. This was achieved by conducting a systematic review of relevant literature to compare these two fields of coral reef research and their inherent approaches, in terms of: 1) the geographic distribution of study sites; 2) their inherent approaches; 3) the habitats examined, and 4) their focal questions. Following this evaluation, we outline potential opportunities to create a bridge between these two fields to better address the challenges of scale. Ultimately, by addressing these aims, this study will help identify positive paths towards harnessing the valuable contributions of the two fields, traditional in-water coral reef ecology or remote sensing, in a world that will have to upscale rapidly to meet challenges in the Anthropocene.

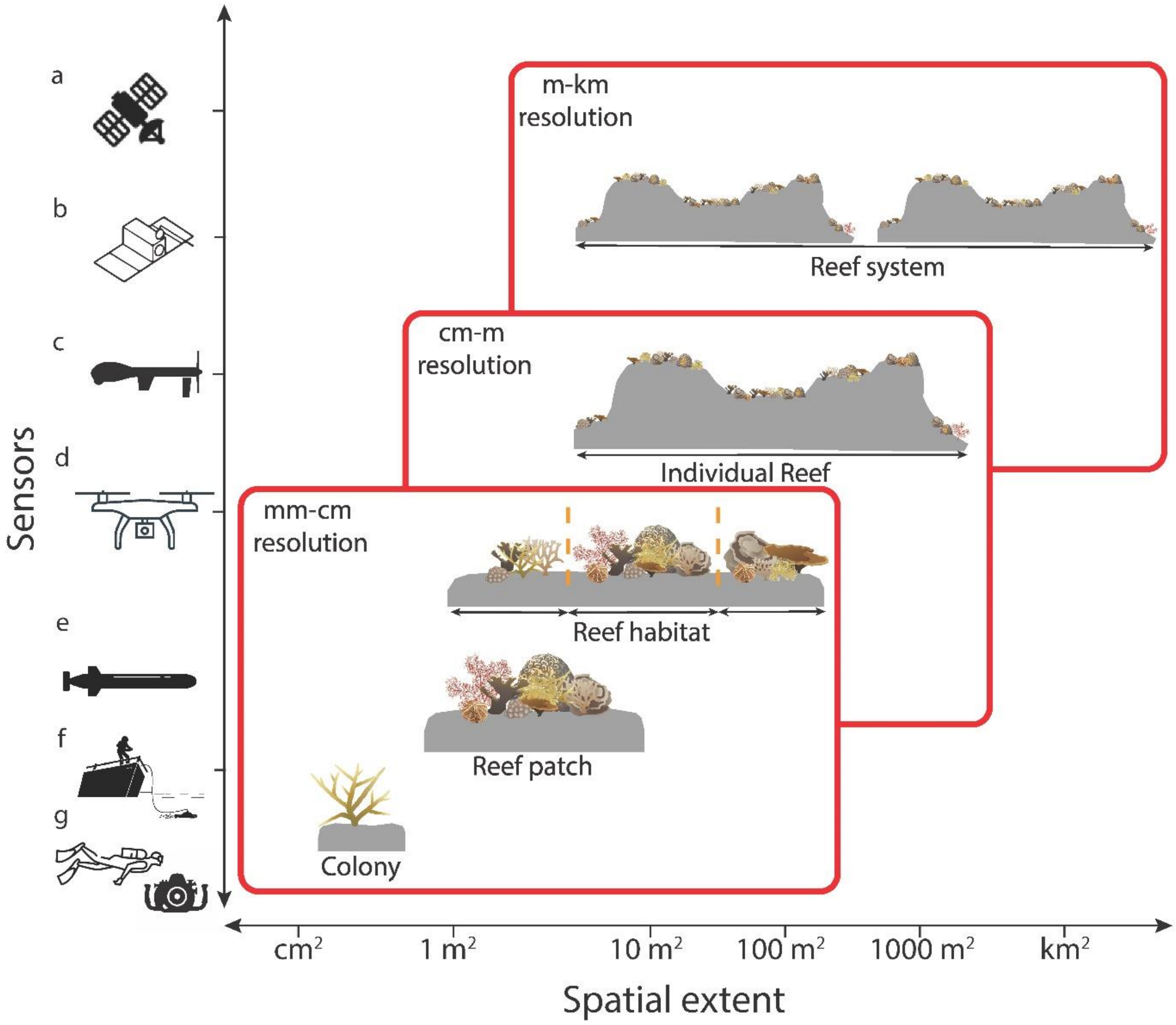

Figure 2.1 Differences in spatial extent and resolution among technologies and approaches employed in coral reef ecosystem research. Specifically, differences among satellite and aerial remote sensing platforms (i.e. a) satellite, b) aeroplane, c) unoccupied aerial vehicles, and **d)** drones); and in-water remote sensing platforms, including **e)** autonomous underwater vehicles, **f)** underwater drones, and **g)** diver-operated camera systems. Figure adapted from Harris et al. (2023) based on the original schematic in Joyce (2004).

Figure 2.2 Examples of the imaging and resolution capabilities of different coral reef remote sensing techniques at Lizard Island Reef in the northern Great Barrier Reef. **a** Satellite imagery (Sentinel-2A imagery. GSD = 10m Courtesy of European Space Agency - ESA), **b** unoccupied aerial vehicles and non-consumer grade drones (UAVs) (GSD ~ 10cm, but cover larger extents), **c** consumer-grade drones (GSD ~ 2cm, cover much smaller extents), **d** and **e** high resolution in-water photography (GSD ~ 5mm).

2.3 Methods

2.3.1 Systematic Review

To address our aims, we surveyed the international journal *Coral Reefs,* one of the world's primary journals for coral reef studies, as a representative sample of coral reef research, similar to the approach of Bellwood et al. (2020). We specifically selected the journal *Coral Reefs* due to its comprehensive coverage of research in the coral reef domain globally. It serves as an ideal choice for our study, with the sole inclusion criterion being scientific quality, provided the papers pertain to coral reefs. Importantly, this journal has no geographical or methodological constraints; including papers from diverse locations and employing various approaches. To ensure we sampled a representative range of relevant remote sensing studies, we surveyed the journals *Frontiers in Marine Science*, *PLoS*

One, *Remote Sensing*, and *Remote Sensing of Environment* as representative journals for remote sensing-based studies on reefs. We used multiple journals as there were fewer relevant articles available when compared to *Coral Reefs*. We acknowledge the potential omission of some studies through this approach, however the attained sample size was robust and representative of the broader body of scientific coral reef literature (cf. Brandl et al. 2019; Sambrook et al. 2019; Bellwood et al. 2020; Crisp et al. 2022).

Studies were downloaded in August 2023 from two databases: 'Scopus' and 'Web of Science'. To facilitate direct comparisons, we included search terms that were broadly overlapping between the two fields (see below). Furthermore, we selected a time slice that ensured both fields had a high chance of appearance and influence, i.e. between 2012 and 2021, inclusive. For the four representative remote sensing journals, the respective search terms were: [Topic sentence (TS) = coral* OR "Coral reef"] AND [TS = Satellite OR UAV OR drone* OR algorithm OR "airborne sensor" OR structure-from-motion OR s-f-m OR "structure from motion" OR photogrammetry OR photomosaic* OR "photo mosaic" OR camera OR "photo-mosaic" OR "remote sensing" OR multispectral OR "imagery" OR "3D" OR "3D mapping" OR "3D modelling" OR "terrain reconstruction" OR "orthomosaic" OR "Large area imaging"]. Hyperspectral sensors hold great promise and are gaining importance in assessing benthic changes on coral reefs by offering imagery data across numerous narrow bands, possibly improving the thematic resolution of outputs (Bajjouk et al. 2019; Dierssen et al. 2021). However, we did not include "hyperspectral" as a search term in this review because, at present, these sensors and the platforms on which they operate, have lower operational efficiency and are not yet as widely available and adopted compared to the majority of methods covered. When a study using hyperspectral imagery was encountered in the review (e.g Joyce et al. 2013) it was included (N =11).

For the Journal *Coral Reefs*, the topic sentence was surveyed for: [benth* OR bathym* OR complexity OR cover OR rugosity OR map*]. Both searches were limited to full articles. After removing duplicates, the initial pool consisted of 747 studies. Among these, 359 were categorized as traditional in-water coral reef ecology (i.e. appearing in *Coral Reefs*), and 363 were classified as remote sensing (i.e. found in the four remote sensing journals). The search in *Coral Reefs* also yielded 25 studies that primarily used remote sensing methods to raise their final metrics (e.g. Doo et al. 2017; Newnham et al. 2020). Consequently, these were included in the remote sensing category, resulting in a total of 388 studies.

To ensure a meaningful comparison between the two fields we adopted a filtering protocol to select studies that were broadly comparable. We filtered the initial pool to identify suitable studies from the two fields by specifically looking for studies that assessed a benthic component on coral reefs and were concerned with in-situ measurements by screening the Abstract and Methods. To be included, remote sensing publications had to be undertaken on tropical coral reef systems, involve a benthic component (e.g. studies focusing on water quality were excluded), and had to address an ecological aspect of coral reefs, i.e. they must be concerned with metrics and processes (functions) that contribute to the movement or storage of energy or material on coral reefs. Review-style studies or studies in deep-sea or cold-water environments were excluded. Similarly, ecological papers had to be conducted on tropical reefs, in less than 20 m depth, and be non-experimental (i.e. studies employing terra cotta tiles or collecting specimens for lab experiments were excluded). This screening process resulted in the retention of 111 remote sensing studies and 88 traditional in-water coral reef ecology studies for analysis (see Table A1).

These remaining 199 papers were thoroughly reviewed and for each we recorded: 1) the category of the study (i.e. traditional coral reef ecology or remote sensing), 2) focal question(s) addressed, 3) organisms/parameters investigated, 4) method/approach employed, 5) geographic region(s) each study was conducted in, 6) geomorphic zone(s) surveyed, 7) whether study sites were identified in a reproducible way (i.e. with geographic co-ordinates or shown on a map), and 8) sensor platform(s), 9) spatial resolution, and 10) whether in-water field verification of broad spatial scale remote sensing was undertaken. These variables were chosen to allow for effective and insightful cross-domain comparison (see Table A2 for additional justification). Reporting the "spatial extent" of studies was exceptionally rare, leading us to rely on the geomorphic zone/s of operation as a proxy. Due to the wide range of papers addressing various themes at a range of scales, classifying thematic resolution (e.g. taxonomic resolution or number of benthic classes) consistently and meaningfully proved nearly impossible, necessitating the use of the broader "focal question" category as a substitute. The resulting data were then quantitatively explored to identify the potential overlap and divergences between ecological and remote sensing literature on coral reef systems.

2.3.2 Categorizing studies

Initially, we categorized all studies based on their approach or the type of data they generate. For simplicity and illustrative clarity, we classified studies into two categories: direct ecological observations, primarily utilizing or generating localized in situ data (termed traditional coral reef ecology or CR), and remote sensing (RS), primarily involving the use or creation of spatially explicit map-based data. The focal question(s) addressed in each study were identified and divided into the following categories: benthic mapping, bathymetry, carbonate budget, bleaching detection, disease impact, bioturbation, organism ecology, climate change, or community composition. Benthic mapping was defined as studies concerned with dividing different substrata into respective groups and spatially mapping their location, often producing spatially explicit datasets across large extents (e.g. identifying the benthic communities across the Capricorn Bunker; Hamylton et al. 2017). In contrast, community composition studies assessed and categorized an ecosystem component into high-detail taxonomic categories, quantifying their presence and abundance often in form of localised point-based assessments (e.g. assessing spatial and temporal patterns in hard coral cover; Roelfsema et al. 2021a). When studies addressed multiple focal questions, each of these instances was treated as distinct observations in the dataset. Thus the number of focal questions identified is greater than the number of papers assessed.

2.3.3 Categorizing methods used

We categorized the approaches used in the studies into four main groups: direct quantification, sensor-based, linked studies, and upscaled linked studies. Direct quantification studies involved counting organisms present (e.g. Perry and Morgan 2017). Sensor-based studies utilized various sensors such as satellites or cameras, primarily for mapping or three-dimensional imaging of the benthic environment (e.g. Ferrari et al. 2016). Linked studies combined direct quantification and sensor-based approaches, linking in-situ observations and remote sensing approaches to infer stronger relationships between multiple metrics, such as assessing how coral colony complexity affects fish distributions (e.g. Oakley-Cogan et al. 2020). Upscaled linked studies introduced an additional aspect of aerial remote sensing and ground-truthing to extend ecological observations to entire reef-scape scales such as measuring the biomass of foraminifera in different reef zones and upscaling that to the reef scape scale using classified satellite imagery (e.g. Doo et al. 2017).

2.3.4 Categorizing geographic regions and habitat assessed

To assess how studies from the different fields (CR and RS) were distributed globally and determine if number of studies in a region was related to the area of reef present, we categorized the geographic region/s of each study based on the size of reef areas mapped by the Allen Coral Atlas (2022). For instance, studies conducted in the Great Barrier Reef (GBR) were assigned to the corresponding geographic region “Great Barrier Reef and Torres Strait” mapped area in the Allen Coral Atlas. In cases where a study covered multiple mapped areas, it was classified as surveying 'multiple' reef areas. To calculate the area of reef present in the studied regions the reef areas were extracted from the Allen Coral Atlas in early November 2022 and included the reef's benthic classes such as Coral/Algae, Microalgal Mats, Rock, and Rubble. We excluded Sand and Seagrass as benthic classes to maintain a focus on biogenic reef framework building structures and to prevent an overrepresentation of mapped reef areas, especially in cases with extensive sand banks and seagrass habitats, particularly within the Caribbean context. Data were handled and visualised using ArcGIS Pro (version 2.9) and R (R Core Team 2022), using the *'tidyverse'* package (Wickham et al. 2019).

To assess which coral reef habitats were studied we categorized the habitats investigated within each study into their corresponding geomorphic zones. Our analysis included only those geomorphic zones that were consistently identified, namely back reef, lagoon, reef crest, reef flat, and reef slope/fore reef (as defined in Kennedy et al. 2021). If studies encompassed multiple geomorphic zones, each zone was treated as a separate allocation. Studies that assessed or mapped entire reef-scapes were categorized as 'Entire reef'. To determine the distribution of studies across different zones in relation to the proportional reef area each zone represents, we calculated the average area of each geomorphic zone across all reefs in the Great Barrier Reef and Torres Strait mapped region (Allen Coral Atlas 2022) and derived the relative proportions. It is important to emphasize that our study did not specifically centre on this particular region and we recognise that it may not be representative of reef proportions in all other regions globally. We chose this region to represent the proportional reef area of geomorphic zones because it has received the most extensive scientific attention (Figure 2.3A), making it likely to provide the most reasonable geomorphic zone area estimates due to the substantial mapping efforts (Kennedy et al. 2021; Roelfsema et al. 2021b).

3. Results

A broad and variable geographic spread of studies was identified (Figure 2.3A) with most studies coming from the Great Barrier Reef (GBR) (36 in total, 18% of all studies) with a relatively equal split between traditional in-water ecology and remote sensing (Figure 2.3B). Some regions were dominated by remote sensing studies, for example the SW Pacific, Hawaiian Islands and the Central South Pacific (over 70% of studies) with a paucity of traditional ecological studies (N = 9). There was no obvious relationship between the number of studies conducted in a region and its mapped reef area (Figure 2.3B, Figure A1). For instance, the South-east Asian Archipelago, which had the largest mapped reef area, had only six studies included in the review (Figure 2.3B). In contrast, the Hawaiian Islands, with a relatively small reef extent, contributed 17 studies, almost 90% of which were remote sensing studies (Figure 2.3B). Notably, barely any traditional coral reef ecology studies surveyed more than two regions (N = 2), while remote sensing studies frequently covered multiple regions (N = 13) (Figure 2.3B, number 28 – "Multiple").

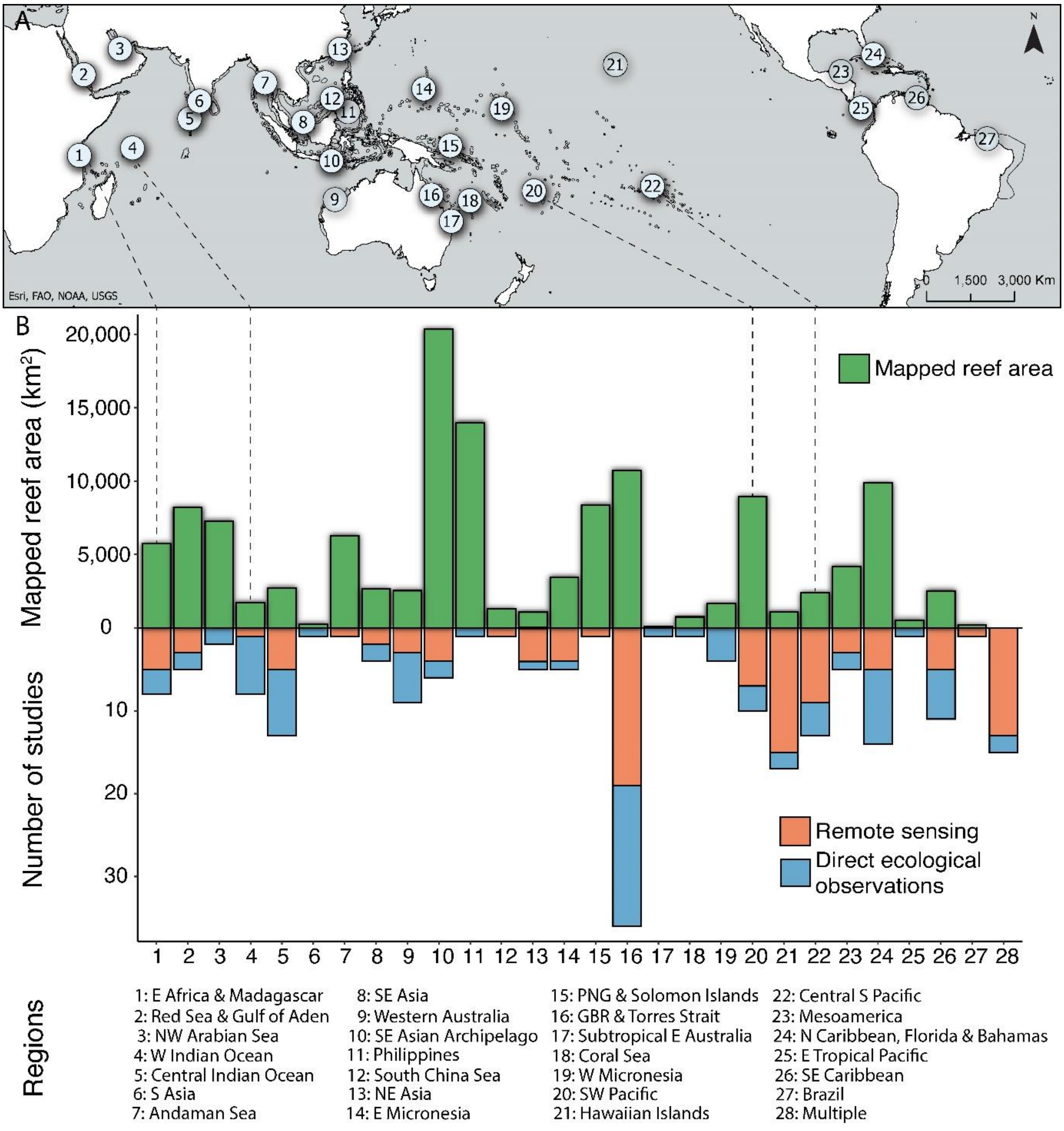

Figure 2.3 A) Map showing the locations of the major reef regions (Allen Coral Atlas 2022). B) Graph comparing the mapped reef area (km^2) (presenting the mapped area of the benthic classes Coral/Algae, Rock, and Rubble; sourced from Allen Coral Atlas 2022) of each region) to the number of studies included in this analysis from each field. The numbers and corresponding name of each major region labelled on the map are displayed at the bottom.

Traditional in-water coral reef ecology studies addressed a wide range of focal questions, but primarily focused on community composition of the benthos, involving a taxonomic level of identification (Figure 2.4A). In contrast, most remote sensing studies (72%) were concerned predominantly with benthic mapping, i.e. the classification of substrata into distinctive groups based on spectral signatures, and/or quantifying bathymetry (18%) (Figure 2.4A). Numerous studies (18%, N = 20) using in-water remote sensing technologies were bridging this gap in focal questions, increasingly investigating community composition with a taxonomic level of identification similar to that of ecological studies (Figure 4A, Figure S2). Unsurprisingly, remote sensing studies predominantly (86%) employed primarily sensor-based approaches ranging from satellite imagery to unoccupied aerial vehicles (UAVs) or underwater photogrammetry approaches (Figure 2.4B). These approaches were mainly passive, gaining data and producing metrics through imagery processing. In-situ field surveys mostly employed methods that directly quantify or count the presence of organisms (95%) (Figure 2.4B). Only 7% (N = 14) of studies used a linked approach combining direct quantification (e.g. counting fish) with, mostly, in-water sensor-based techniques (e.g. photogrammetry), allowing for a more nuanced understanding of processes and higher-order metrics, such as rugosity (e.g. Oakley-Cogan et al. 2020). Notably, only 3% (N = 6) of studies combined multiple approaches (i.e. in water counts, drone imagery and satellite imagery) to upscale observations to an entire reef-scape (Figure 2.4B) (e.g. Doo et al. 2017).

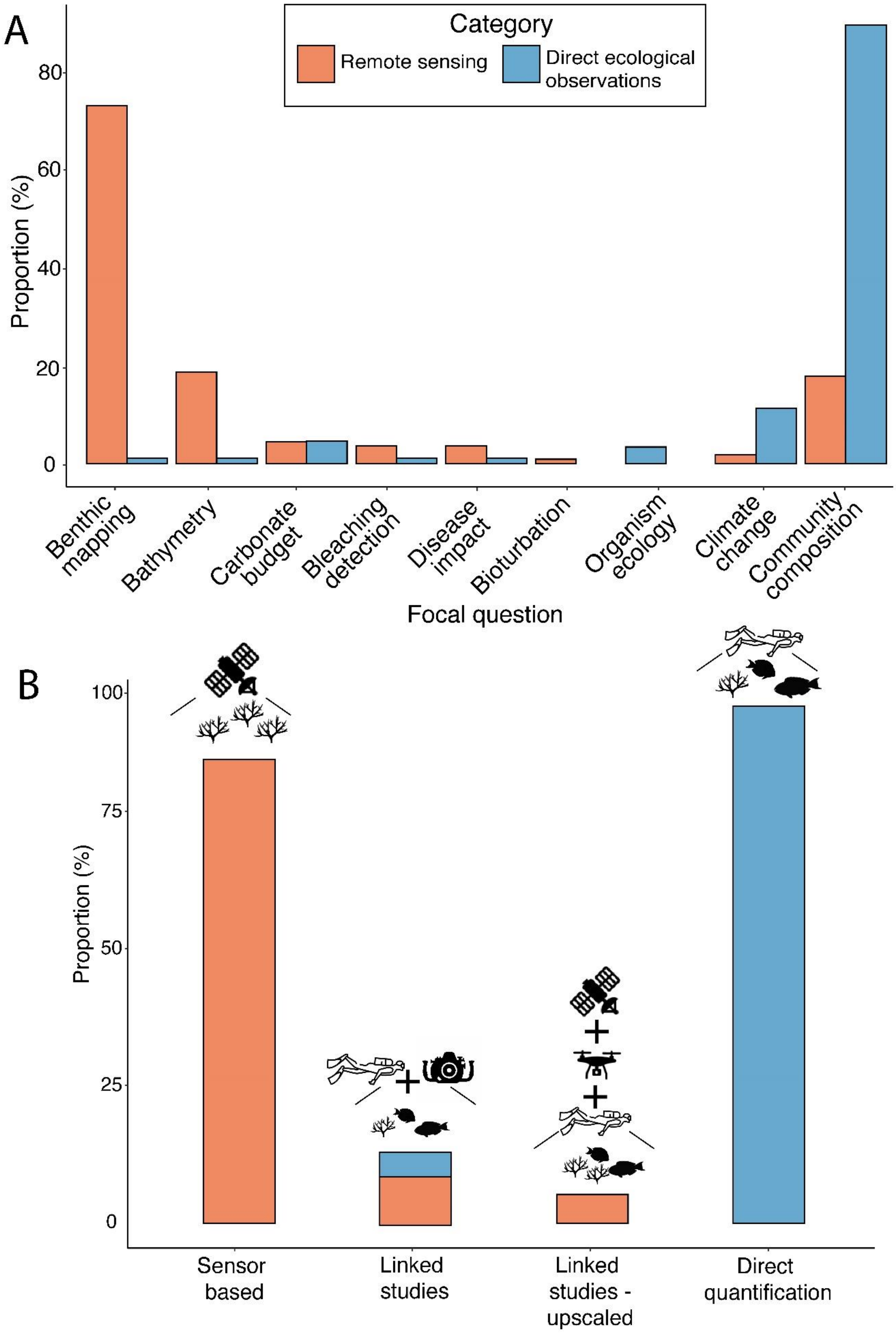
A
Category
Remote sensing
Direct ecological observations
Proportion (%)
0
20
40
60
80
Benthic mapping
Bathymetry
Carbonate budget
Bleaching detection
Disease impact
Bioturbation
Organism ecology
Climate change
Community composition
Focal question
B
Proportion (%)
0
25
50
75
100
Sensor based
Linked studies
Linked studies - upscaled
Direct quantification

Figure 2.4 A) Proportion (%) of focal questions answered by traditional coral reef ecology studies (blue) (N = 100) and remote sensing studies (orange) (N = 139). B) Relative proportion (%) of methodological approaches employed by traditional coral reef ecology studies (blue) (N = 88) and remote sensing studies (orange) (N = 112). Note, when studies addressed multiple focal questions, each of these instances was treated as distinct observations in the dataset.

Most (73%) remote sensing studies accurately reported the location of their study sites in a manner that allowed for reproducibility (i.e. giving coordinates). Just over half (58%) of traditional coral reef ecology studies did likewise (Figure A3). Overall, 45% (N = 40) and 33% (N = 37) of traditional coral reef ecology and remote sensing studies, respectively, did not specify which geomorphic zone (i.e. back reef, lagoon, reef crest, reef flat, and reef slope/fore reef) their study was conducted on. Of those studies that did specify, geomorphic zones examined by each field contrasted markedly (Figure 2.5). The reef slope was the most surveyed habitat (80%) in traditional ecological studies (N = 37), while most remote sensing studies (N = 50) covered entire reef systems (68%) (Figure 2.5). Notably, the reef flat, which often accounts for the largest proportion of a reef by area (Yamano et al. 2001; Lutzenkirchen et al. 2023), received relatively little attention by traditional coral reef ecology, with only 30% of studies specifically mentioning this habitat (Figure 2.5). While only 14% of remote sensing studies explicitly mention this geomorphic zone, it would be encompassed within the 81% of studies operating across entire reef systems (Figure 2.5). In contrast, the smallest of all geomorphic zones on reefs by area, the reef crest (at 3% area), was barely assessed by remote sensing studies (1%) but received moderate attention by coral reef ecologists (26%) (Figure 2.5). There were also temporal scale constraints, with most studies being single, one-off studies (62%). Only 38% of all studies from either field included multiple years.

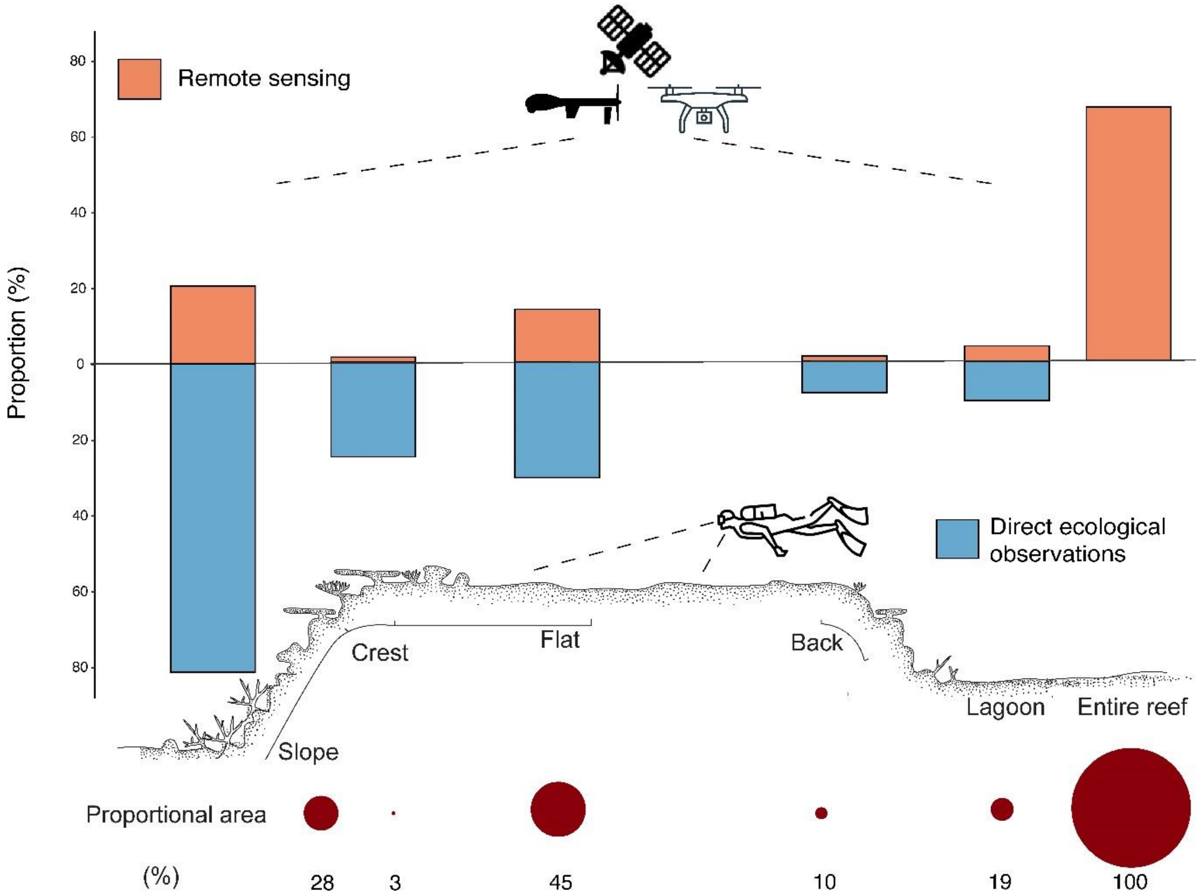

Figure 2.5 Comparing the proportion of studies that allocated specific geomorphic coral reef zones as their area of operation from the fields of traditional coral reef ecology (blue) (N = 48, 45%) and remote sensing (orange) (N = 75, 33%). The size of red circles represents the average proportional area (%) of each reef habitat based on the average mapped area of those zones for all reefs of the GBR and Torres Strait as mapped by the Allen Coral Atlas (2022).

4. Discussion

Unsurprisingly, despite their shared focus on the reef benthos, we found that traditional coral reef ecology and remote sensing studies generally use different approaches and address distinct questions. Integration between the two fields is increasing but to-date there are relatively few studies using a linked approach, that combines in-water and aerial sensor-based methods, to upscale ecological observations to the reef-scape level. While not all coral reef ecosystem functions occur at the reef scale (i.e. across multiple reef habitats), negating the need for wholesale upscaling, this lack of integration to-date shows that our understanding of coral reef systems and their functioning is not easily translatable to larger scales. This is concerning, as threats to these systems are steadily increasing in magnitude. Below, we discuss the limitations of each field and outline a joint approach for future research and development that could enhance the utility of both fields and provide a basis for positive synergies.

4.1 Traditional coral reef ecology

We found that studies in traditional coral reef ecology predominantly employed methods that aim to directly quantify organisms on a very fine taxonomic scale, i.e. genus and species. Such detailed in-situ assessments are valuable to get a high-resolution picture and to make inferences that may help to identify causal relationships and responses to threats (Hughes et al. 2017; Bellwood et al. 2019a). High-detail data enable us to predict the future impact of disturbances on ecosystem functioning in a causal and robust manner, especially at the community and population scale.

However, the greatest problem in upscaling these high-resolution observations is that the delivery of functions by coral reef organisms is not homogenously spread across reef scapes (Streit et al. 2019; Tebbett and Bellwood 2020), emphasising that there is not one unifying scale at which to measure all processes (Holling 1992; Levin 1992; Wu 2004). For example, detritivory delivered by *Ctenochaetus striatus*, a reef surgeonfish, was shown to occur over less than 28% of the entire reef-scape (Tebbett and Bellwood 2020). Thus, *where* we measure shapes *what* we understand. While certain ecosystem functions may occur at smaller scales and provide insights into broader patterns, measuring in high detail everywhere is impossible. Despite coral reef ecologists' substantial effort to broaden their observations' scope and scale, this review identified that study effort is unevenly distributed both at the reef-scape scale and at global levels. Consequently, as researchers, we need to acknowledge that the scale of our research ultimately constrains the scale of our understanding and predictions.

For example, traditional coral reef ecology studies primarily target the reef slope, a structurally complex habitat, which often supports the highest fish densities and coral cover (Wismer et al. 2009; Oakley-Cogan et al. 2020). While covering less than a third of the total reef area (when measured above 20m depth), the reef slope was the focus of 80% of all traditional coral reef ecology studies that specified a habitat. However, relying on a single site or geomorphic zone to represent an entire reef overlooks critical within-reef variability. A long-term study on Heron Island on the GBR spanning 16 years across 31 sites, including 567 sub-sites, revealed significant variation at multiple scales, spanning from the entire reef-scale to smaller subsite divisions (Roelfsema et al. 2021a). Accordingly, recent papers have highlighted the constraints placed on our understanding of coral reef functioning by the limited spatial and temporal distribution of study effort, which often focuses on only a limited subset of available shallow reef habitats (Rocha et al. 2018; Bellwood et al. 2020; Collins et al. 2022; Kench et al. 2022; Tebbett et al. 2023b). For instance, we found that the reef flat, which may play a significant role in reef functioning (i.e. for productivity [Hatcher 1988; Bellwood et al. 2018] and wave energy dissipation [Kench and Brander 2006; Harris et al. 2015]), and is typically the largest reef habitat in terms of area (Bellwood et al. 2018), is often underrepresented in traditional coral reef ecology studies (Bellwood et al. 2020; Tebbett et al. 2023a). In a recent global assessment of coral reef benthic composition change based on 24,000 observations over 22 years, Tebbett et al. (2023a) found that only 7% of the data were derived from reef flat observations. Likewise, less than a quarter of all reef ecology studies included our analysis investigated the reef flat.

Beyond such biases, or selective focus on specific reef habitats, we distinguished regional hotspots of research effort on a global scale. Most coral reef ecology studies took place in a few well-established research areas with existing infrastructure (i.e. research stations), that facilitate effective sampling. These infrastructure patterns may drive local overrepresentation and possibly ecological bias – not because of ecological factors but ease of access (Hedley et al. 2016). In addition, published papers may be biased toward countries and organizations with resources to support publication, potentially overlooking research conducted in nations with more limited financial means. Few ecological studies were able to survey entire reef systems regionally or multiple regions on a global scale.

In sum, these results indicate that traditional coral reef ecology studies are valuable but somewhat limited in their extent and ability to be upscaled, as observations of organisms and their environments are often spatially sparse. They are frequently conducted at scales (spatial, temporal, or thematic) that are chosen subjectively and often dictated by practical factors such as access, time or costs, rather than by the ecosystem processes investigated. These challenges may lead to a considerable mismatch (of an estimated 5.6 orders of magnitude; Estes et al. 2018) between the scales at which ecologists conduct research and the areas their observations are supposed to represent (Wheatley and Johnson 2009; Lecours et al. 2015; Estes et al. 2018). Ecologists acknowledge the disparity between collected samples and the resulting inferences drawn from them. To address this disparity, statistical techniques are frequently employed (e.g Brown et al. 2021; Castro-Sanguino et al. 2021; Edgar et al. 2023). Nonetheless, the efficacy of a model and its transferability heavily depend on the quality of the underlying data it relies upon (Yates et al. 2018). The potential for substantial enhancement in model performance lies in the improved spatial representation of data. Such enhancement becomes even more crucial when considering the inherent spatial heterogeneity, patchiness, and hierarchical structure within ecosystems. Changes in scale can unveil different drivers of patterns and processes (Wiens 1989; Holling 1992; Levin 1992; Wu and Li 2006) . Consequently, the presumption that observations made in a single reef habitat can aptly represent an entire reef-scape can introduce scale-related artefacts. These mismatches between ecological, observational, and analytical scale, ultimately hinder the detection of causal relationships in macroecological patterns (Wheatley and Johnson 2009; Lecours et al. 2015) and the formation of effective management responses (Bellwood et al. 2019a).

If unidentified, such scale artefacts can become widespread and lead to fundamental ecological misinterpretations. We found that most (95%) traditional ecological studies used direct observation techniques which are labour intensive to collect and analyse, whilst also being limited to restricted spatial and temporal scales. These limitations are likely to cause mismatches amongst scales. For instance, recently, discrepancies across both temporal and spatial scales have been found to drive the identified occurrence of coral reef phase shifts (Crisp 2022; Crisp et al. 2022). As a result, the reporting of phase shifts in the coral reef literature may have been overrepresented because most studies detecting phase shift occurrences did not persist long enough to capture reverses (i.e. bidirectional change), thus interpreting short-lived blooms as shifts (Crisp et al. 2022). Spatially, the detectability of phase shifts was highly dependent on the scale of sampling, with a decrease in apparent phase shifts as spatial scale increased (Crisp 2022).

4.2 Remote sensing

Remote sensing approaches may help to address the problem of scale in ecological coral reef studies (Green et al. 2000; Hedley et al. 2016; Kutser et al. 2020). Unlike traditional in-situ studies, our results show that remote sensing studies can assess entire reef systems, even in remote locations, and can encompass multiple geographic regions globally. Over 60% of remote sensing studies in this review assessed entire reef-scapes, rather than specific reef habitats. This offers the opportunity to evaluate benthic changes across diverse spatial, temporal, and thematic scales (Lecours et al. 2015; Hedley et al. 2016; D'Urban Jackson et al. 2020).

Accordingly, our results show that remote sensing studies have made significant progress in upscaling observations to reef-scape scales by combining approaches and linking methodologies. This progress is driven by advances in medium and high-resolution sensors, such as satellites, and UAVs, as well as in-water photogrammetry studies (Ferrari et al. 2016; Bennett et al. 2020; Roelfsema et al. 2021b; Remmers et al. 2023). The Allen Coral Atlas (2022), a global coral reef mapping project, is an example of recent developments. This project used Planet Dove imagery (3 m pixel resolution) and a 'Reef Cover' classification (Kennedy et al. 2021) to map all coral reef systems on Earth. By using uniformly defined algorithms and classification systems, this is the most recent project to create globally consistent benthic and geomorphic reef classes.

Maps are powerful tools for conveying complex spatial information to diverse audiences (Stieb et al. 2019). While a single map can offer a snapshot of a specific reef or marine community, a series of maps can be an effective monitoring tool to track changes in entire coral reef systems across extended temporal and spatial scales (Green et al. 2000; Hedley et al. 2016; Hamylton 2017). However, only a minority (17%) of the remote sensing studies analysed in this review employed multiple time steps. Furthermore, to maximise the utility of time-series analyses, accuracy, i.e. the consistent correct identification of actual features, is key. Ground-truthing fieldwork is commonly used in remote sensing mapping studies to train and validate classification algorithms by conducting georeferenced surveys (Green et al. 2000; Roelfsema and Phinn 2010; Hamylton 2017).

Despite improvements, aerial and satellite remote sensing products are often still limited in their ability to provide an ecological understanding of coral reef systems. Most remote sensing studies are concerned with benthic mapping, but as spatial extents increase, spatial and taxonomic resolution decreases accordingly. Thus, while creating benthic cover maps may be a predominant objective for managing purposes, simply mapping broad benthic classes does not measure the ecological status of the benthos (Hedley et al. 2016). Without empirical ecological in-situ data and multiple time steps, they at best, detect changes, not the cause of change, which is key when developing management responses. Furthermore, mapped benthic classes derived through aerial and satellite remote sensing technology are often based on spectral signatures, restricting accurate datasets to shallow reef zones due to the spectral interference of water. Moreover, the spectral similarity of benthic organisms, such as algae and coral, makes it extremely difficult to separate them (Knudby et al. 2010; Kutser et al. 2020). While not specifically assessed in this review, hyperspectral sensors, with their expanding capabilities and the ability to assess a narrower range of spectral bands, hold the potential to enhance discrimination of benthic components (Bajjouk et al. 2019; Dierssen et al. 2021). Beyond spectral limitations, submergence and light attenuation in the water column also pose significant challenges for aerial and satellite remote sensing (Purkis 2018). Despite improvements in sensor capabilities, including global coverage, higher spatial and temporal resolution (Hedley et al. 2016; Kutser et al. 2020), accurately distinguishing spectrally similar substrata in a heterogeneous environment modulated by variable water depth and quality remains a major challenge (Lucas and Goodman 2015; Purkis 2018). Even moderate-spatial and high-spatial resolution sensors are often unable to reliably differentiate benthic groups, such as algae and hard coral. As a result, aerial and satellite remote sensing studies have difficulty detecting the main ecological transformation on coral reef systems (i.e. algae to/from coral; Tebbett et al. 2023a) (cf. Cornet and Joyce 2021). This predicament is reflected in the distribution of focal questions identified herein. While most traditional in-water ecological studies address community composition, possibly elucidating the response of individual species or groups to environmental variables, most remote sensing studies employing aerial sensors are currently limited to mapping broad benthic classes (i.e. coral and/or algae as one class). Consequently, there is a mismatch between aerial and satellite remote sensing data sets, and the eco-physiologically based demands of potential end users (i.e. ecologists and reef managers) (Kutser et al. 2020).

To establish a functional and mechanistic understanding of coral reef systems and their changes, integrating remote sensing studies with empirical ecological in-situ data (i.e. various underwater visual census methods) is essential. This gap is being effectively bridged using relatively new techniques, particularly in-water photogrammetry, which plays a crucial role in expanding quantitative data on structural complexity (Friedman et al. 2012; Figueira et al. 2015; Ferrari et al. 2016; Pygas et al. 2020; Remmers et al. 2023). These techniques actively leverage in-water remote sensing technology to unite ecological observations with advanced tools, promising a more comprehensive and holistic comprehension of intricate ecosystems like coral reefs. However, comparable links at larger extents afforded by aerial and satellite remote sensing, remain elusive.

4.3 Future directions

As human-induced stressors continue to reshape ecosystems, coral reefs are particularly vulnerable (Hughes et al. 2017; Bellwood et al. 2019a; Woodhead et al. 2019). To understand and manage these fragile ecosystems in the Anthropocene, we may benefit from novel approaches and the integration of scientific disciplines (Dornelas et al. 2019; Williams et al. 2019). Indeed, as threats escalate in scale, it is essential to establish dynamic relations and to upscale observations by combining multiple tools that vary in scale and resolution (Dornelas et al. 2019).

Below we identify approaches that may enable us to harness the best of both traditional coral reef ecology and remote sensing fields, offering the greatest potential to address the scale mismatch between coral reef research and anthropogenic threats by rapidly upscaling observations and inferences. Shallow reef environments (i.e. reef flats and crests) offer the optimal habitats for these upscaled studies as they impose the fewest limitations for aerial and satellite remote sensing (Hedley et al. 2016; Purkis 2018; Kutser et al. 2020). Furthermore, these habitats are ecologically critical (Kench and Brander 2006; Bellwood et al. 2018), yet are often underrepresented in coral reef ecology studies (Bellwood et al. 2020; Kench et al. 2022; Tebbett et al. 2023a). To understand coral reef ecosystem functioning on regional and global scales, in-situ measurements, which provide the finest detail but present multiple trade-offs and a lack of scalability, need to be linked directly (in space and time) with multiple sensors that are less detailed in resolution but offer effective and continuous large spatial coverage (Figure 2.6) (Calders et al. 2020).

For effective cross-scale work, combining ground-truthed remote sensing with high-detail ecological observations in shallow reef settings, like inner and outer reef flats, is crucial. To ensure accurate benthic maps from moderate to high-resolution (< 3m) satellite imagery, georeferenced images could be taken along transects or quadrats, estimating benthic structure and organism abundance in-situ (e.g. Roelfsema et al., 2021b). Several studies have successfully upscaled in-situ ecological measurements via remote-sensed benthic maps (e.g. Doo et al. 2017; Hamylton et al. 2017; Williamson et al. 2021) (Figure 2.6). This approach appears to be particularly promising with the possibilities to expand on these concepts, combining the strengths of both fields for ongoing cross-calibration between sensors and upscaling of ecological observations to large reef-scape scales (Figure 2.6). These methods involve "small-area-high-resolution" in-situ observations and in-water technologies (< 1cm resolution) across shallow reef sites to provide ecological context and ground-truthing, ensuring accurate delineation of key benthic components and data reliability (Figure 2.6A, B), while recent "large-area-lower-resolution" (< 3m) imagery and mapping methods further enhance the reliability of upscaling ecological observations and novel metrics (Figure 2.6C).

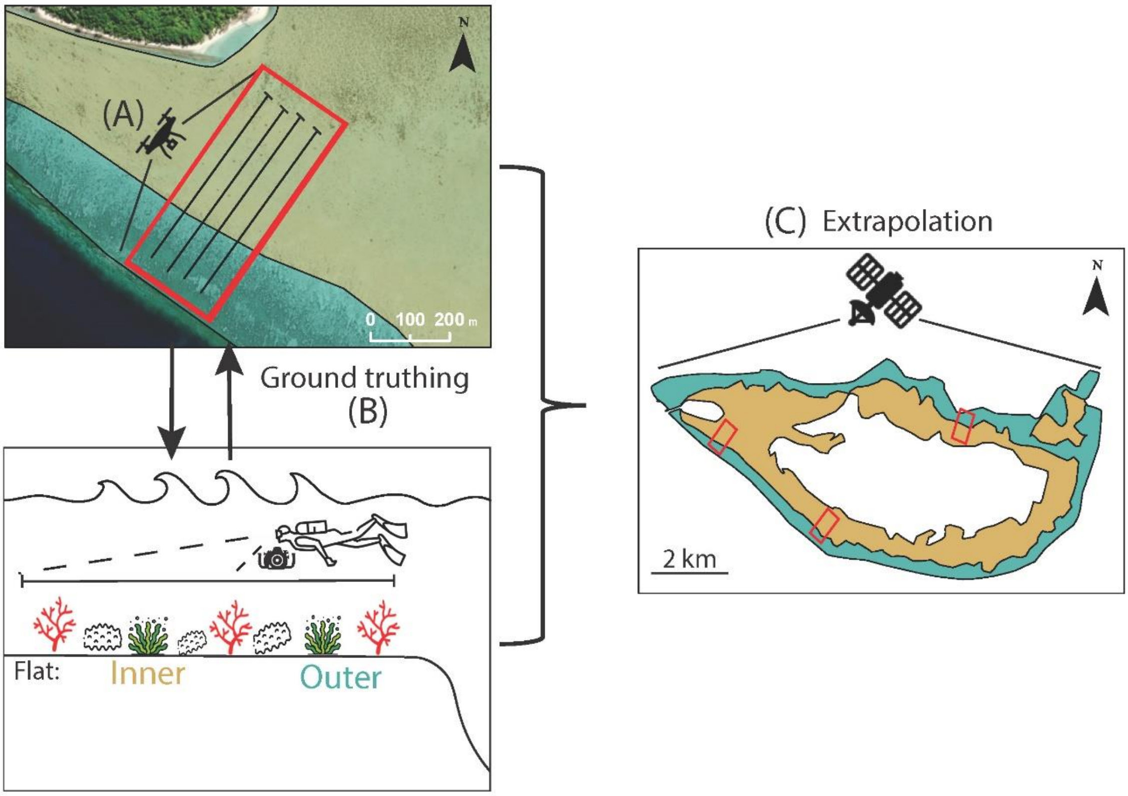

Figure 2.6 Schematic summary outlining a potential approach using in-situ assessments, as well as multiple layers of sensors of varying resolution, to bridge scientific disciplines and upscale observations onto reef-scape scales. After multiple shallow reef areas are surveyed using a 'small-area-high resolution' sensor (A) and ground-truthed using in-situ assessments and sub-cm resolution in-water remote sensing technology (B), observations can be extrapolated and upscaled using a 'large-area-lower-resolution' sensor (C). Geomorphic map in (C) taken from (Phinn et al. 2012).

While combining these approaches will ensure more empirically linked upscaling onto larger reef-wide scales, the utility of each approach may be enhanced by:

1) Standardizing procedures in coral reef ecology to enhance data reproducibility, facilitating robust comparisons across scales and disciplines. While local and regional ecological monitoring protocols may be standardized, global standardization will improve comparability. The MERMAID project (https://datamermaid.org/), an open-source application that gathers and manages real-time coral reef health data, provides an example of this approach. However, existing long-term benthic databases such as Caribbean Coastal Marine Productivity or National Oceanic and Atmospheric Administration lack uniformity, hindering cross-validation, particularly for finer-resolution benthos categorization (Tebbett et al. 2023b, 2023c). Consolidating these datasets under a common protocol would increase the value of data for training and validation of remote sensing mapping algorithms (Lyons et al. 2020).

2) The reliable recording and reporting of survey sites is crucial to data sharing and study replication. Therefore, including the survey start location using global positioning system (GPS) and indicating the direction of the surveys would significantly improve the spatial accuracy and reproducibility of ecological studies.

3) Technological advances, especially in the field of remote sensing, have opened numerous new frontiers in the marine realm. However, moving forwards, we need to ensure that new techniques are responding to critical questions. Despite increasing spatial resolution, current methodological advances are largely used for the same applications. To fully harness the capacity of recent technological innovations and advance our understanding of coral reef functioning in the Anthropocene, we must ensure that critical questions are being addressed and that technology is being developed to address these key questions, rather than retrofitting questions to new tools. We need to move beyond traditional studies that describe patterns to a deeper understanding of the functional and mechanistic basis of change. Integrating remote sensing and coral ecology studies may not directly yield causal insights. However, it has the potential to enhance our comprehension of complex

relationships (Wedding et al. 2019). This integration, particularly when spatially explicit, can offer insights into seascape dynamics.

4) Just as certain parameters of coral biology, such as coral respiration, can only be accurately measured in controlled laboratory experiments, with specialized equipment, there are certain parameters of coral reef processes that cannot be reliably measured using broad-scale remote sensing methods, no matter how advanced the technology becomes. For instance, discerning fine-scale rugosity (<1 m) of coral colonies or distinguishing between live corals and dead corals coated in filamentous algae can be challenging using aerial and satellite remote sensing data, often necessitating optimal conditions. Therefore, it is crucial for coral reef ecologists, biologists, and remote sensing scientists to collaborate and develop new and meaningful indicators or proxies for coral reef processes that are applicable to both remote sensing and ecological methods and that operate at shared scales. Recent success has been shown in employing high-resolution (< 1m) airborne sensors such as LiDAR to accurately describe broadscale coral habitat complexity (Asner et al. 2020; Harris et al. 2023). Furthermore, the utilization of automated image annotation for coral reef monitoring, which demonstrates accurate estimations of benthic abundance with a high agreement of 97%, significantly expedites data analysis by over 200 times and reduces costs by 99% (González-Rivero et al. 2020). Approaches like these enable the translation of detailed in-water measurements to broadscale remotely sensed methods with increased accuracy and relevance.

5) To advance our understanding of ecosystems and their vulnerability in the Anthropocene, increased public availability of datasets is crucial (Calders et al. 2020). However, despite the benefits of open science, data sharing lacks incentivisation and it is often perceived to have potential negative ramifications (Perrier et al. 2020; Gomes et al. 2022). To promote public availability of datasets, data source citations in perpetuity, a growing component in the field of remote sensing, as well as open-source databases such as MERMAID, could provide incentives that would ensure collaboration, promotion, recognition, and reward. Without these incentives, the collection of new data is likely to be impeded.

Overall, our review of studies investigating the benthic habitat of shallow water tropical reefs suggests that a gap exists between traditional coral reef ecology and remote sensing studies. Although advances have been made, especially through in-water photogrammetry, drones, and high-resolution satellite mapping, a more concentrated approach is recommended to effectively bridge this gap, especially at large scales. Coral reef ecologists rely on detailed observations that may not match the spatial scale needed for robust, broadly applicable inferences about complex and dynamic relationships within seascapes. Bound by logistical challenges and resource-intensive high-detail data, they often focus on a subset of habitats, inevitably creating scale artefacts. Remote sensing studies can supply continuous datasets across a range of scales and broader extents, offering a potential way to assess and study the scale of changes in the Anthropocene. However, they need ongoing spatially and temporally matched ecological data to ground-truth observations, ensure accuracy, and start the process of exploring mechanistic explanations for change. As anthropogenically caused stressors continue to escalate in scale, our study suggests that bridging these two scientific disciplines will be challenging but offers promising ways to upscale observations to entire reef-scape scales. We identify potential avenues for increasing the utility of each field, recognizing limitations and emphasizing collaborative approaches. In a world characterized by intensifying global change, such bridged approaches, integrating multiple tools at varying levels of resolution and scale, will be crucial to advance our understanding and management of coral reef functioning in the Anthropocene.

Chapter 3. The global biogeography of reef morphology

Published as: Lutzenkirchen, L. L., Duce, S. J., & Bellwood, D. R. (2023). The global biogeography of reef morphology. Global Ecology and Biogeography, 32, 1353–1364. (flow of paper has been slightly altered to fit the thesis format)

3.1 Abstract

The Caribbean and Indo-Pacific are separate biogeographical realms with distinct biogeographical and evolutionary histories, a 10-fold difference in coral biodiversity, and highly disparate sea-level histories. Since reef morphology often reflects interactions between biological activity and biogeographical history, including sea levels, the widths of shallow coral reef habitats are likely to differ markedly between realms, with ramifications for numerous ecosystem functions. Our goal was to assess the impact of global-scale biogeographical and evolutionary histories on coral reef habitats, specifically investigating if Indo-Pacific reefs are wider than their Caribbean counterparts. We used the Allen Coral Atlas, a global reef mapping system (3 m pixel resolution), to examine 3765 transects, 3 km long and 1 km apart, on 60 reefs across the two realms, quantifying shallow reef habitat widths (Inner and Outer Reef Flat, and Reef Crest) using ArcGIS. Shallow reef habitat widths demonstrated remarkable similarity between the Caribbean and Indo-Pacific. Estimated modal widths diverged by only 37 m; means by just 122 m. Although shallow reef zones appeared wider in the Indo-Pacific, habitat widths on atolls were nearly identical across realms (means varying by less than 8 m). Our remote sensing approach provides a global description of the biogeography of coral reefs as biogenic structures. Furthermore, we can assess the relative importance of realm-wide differences in coral diversity and sea-level history on reef growth. The striking similarity of reef widths across realms suggests that reef growth (net reef accretion) is largely independent of coral diversity, or sea-level history, and that other factors may have played a major role in constraining shallow reef widths. These factors may include geomorphology (e.g. antecedent topography and historical accommodation space) and, once at sea level, self-limiting local hydrodynamics.

3.2 Introduction

Coral reef ecosystems are exceptional in their ability to create broadscale (10s-100s of km) biogenic structures and their own substratum. Coral reefs represent the ultimate expression of an interaction between the biology of organisms and their environment (Smith and Buddemeier 1992). Their morphology and configuration, including shape and size, reflects the relationship between biological activity and biogeographic history, as well as physical hydrodynamic drivers. While coral reefs are incredibly diverse systems globally, they share basic, fundamental, habitat structures and zonation patterns (Goreau et al. 1979). Thus, all coral reefs can be broadly divided into distinct omnipresent habitat zones, including the reef slope, crest, and flat, each with its own distinct community composition and structure (Goreau 1959; Stoddart 1969; Chappell 1980; Done 1983; Bellwood et al. 2018). The relative size of these habitat zones can vary, and help to characterize different coral reef systems around the globe (Adey 1978; Done 1983; Dullo 2005) .

Reef flats are arguably the most conspicuous of all shallow water reef zones (Yamano et al. 2001; Bellwood et al. 2018). They are defined by coral reef growth having reached modern sea-level (Thornborough and Davies 2011) and are often the largest zone of a coral reef by area (Bellwood et al. 2018). Due to their shallow nature, reef flats are highly variable but productive habitats (Hatcher 1988; Bellwood et al. 2018) and are also important dissipators of wave energy (Kench and Brander 2006; Harris et al. 2015). Thus, the extent (i.e. width) of reef flats is an important proxy for reef productivity and coastal buffering. Assessing the global distribution of reef widths may also have implications for understanding how reefs, as broadscale biogenic structures, form and evolve over time and which factors are most important in determining their growth.

The Caribbean and Indo-Pacific are highly divergent biogeographic realms in terms of their evolutionary history, biogeography and biodiversity (Cowman and Bellwood 2013a; Bellwood et al. 2017; Siqueira et al. 2019a) (Figure 3.1A). They also differ markedly in their sea-level history, and timing of reef initiation (Montaggioni and Braithwaite 2009; Gischler 2010, 2015; Woodroffe and Webster 2014) (Figure 3.1B).

Geologically, the long-term biogeographic and evolutionary differences between the Caribbean and the Indo-Pacific coincide with more recent disparities in sea-level history (Figure 3.1B). The Holocene period (ca. 11,500 YBP – present), for example, has been characterized by widespread environmental change, including extensive global sea-level rise (Fairbanks 1989; Bard et al. 1996). In the Caribbean, sea-level history can be described by a transgressive curve, where sea-levels rose rapidly during the Mid-Holocene, but decelerated afterwards, never exceeding modern sea-levels (Gischler 2015). By contrast, in the Indo-Pacific, after a steep initial rise, reef systems experienced relatively static sea-levels (1-2 m above modern levels) for the past 6000 years, with a fall towards modern levels at the end of the Holocene (Gischler 2010) (Figure 3.1B).

Sea-level is a major controlling factor, determining both the onset of coral reef growth, as well as the extent and progradation of shallow reef zones. This control is manifest through its impact on available vertical accommodation space (Kennedy and Woodroffe 2002), which is a function of sea-level changes and antecedent (basement) topography, primarily Pleistocene reef substrata, that may play a pivotal role in the initiation and development of modern coral reefs (Camoin and Webster 2015; Gischler 2015). Reefs are thus commonly categorised as ‘keep-up’, ‘catch-up’ or ‘give up’ according to their response to sea-level rises increasing the available accommodation space (Davies and Montaggioni 1985; Neumann and Macintyre 1985).

Given that Indo-Pacific reefs had sea-levels at or above present for approximately 6 ka longer than Caribbean reefs they have had considerably more time to accrete laterally regardless of whether they were ‘keep-up’ or ‘catch-up’ reefs. A review of Indo-Pacific reefs found lateral accretion rates ranged from 8 to 330 m/ka with a mean of 84 m/ka (Yamano et al. 2003). Given these rates, one may expect Indo-Pacific shallow reef habitats to be about 500m wider than their Caribbean counterparts. This sustained growth could be expected to be further facilitated by the higher diversity of corals in the Indo-Pacific as discussed below.

Ecologically, the evolutionary history, and the subsequently highly disparate coral species richness and composition of the Caribbean and Indo-Pacific, was primarily driven by tectonic activity during the Miocene, which resulted in the formation of hard geological barriers that isolated the Atlantic and Caribbean from the Indo-Pacific (O’Dea et al. 2007; Lessios 2008; Cowman and Bellwood 2013b) and by intensifying extinctions of coral lineages in the Caribbean during the Plio-Pleistocene (Budd et al. 2011; van Woesik et al. 2012). Coral reefs in the Caribbean (Tropical Western Atlantic) show a much more depauperate coral and fish fauna, compared to reefs in the Indo-Pacific (Spalding et al. 2001; Bellwood et al. 2004; Cowman and Bellwood 2013b; Siqueira et al. 2019b) (Figure 3.1A). Coral species richness in the Indo-Pacific is an order of magnitude higher than in the Caribbean, with only 51 species of corals present in the Caribbean compared to almost 700 species in the Indo-Pacific (Roff 2021). Furthermore, many coral lineages found in the Atlantic (including most Caribbean species) are evolutionary distinct (Fukami et al. 2004), emphasising a long evolutionary history driven by isolation (Bellwood and Wainwright 2002; Floeter et al. 2008). If coral biodiversity does indeed promote reef growth, or ecosystem stability, one may therefore expect greater and/or more sustained growth of reefs in the Indo-Pacific.

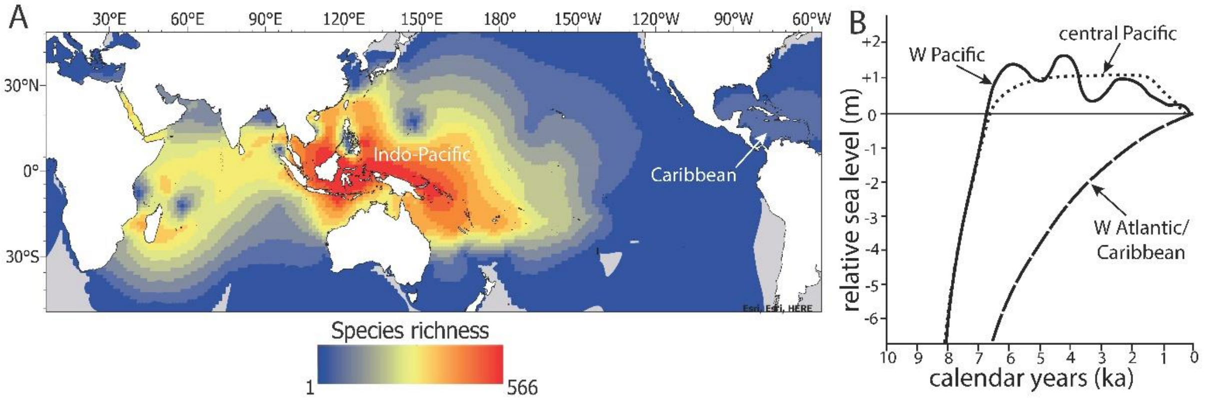

Figure 3.1. A) Coral species richness across the tropics of the world (Ecoregions based on Spalding et al. [2007] and coral species richness data: www.coralsoftheworld.org, see Veron et al. [2015], B) Holocene relative sea-level curves for the Western Atlantic/Caribbean and Pacific from Gischler [2010], modified).

The impact of these potential drivers of regional reef development may have significant implications for reef habitat widths, the functionality of shallow reef systems, and their response to climate change. As some of the most productive reef habitats (Bellwood et al. 2018; Kench et al. 2022), with a major influence on wave attenuation (Harris et al. 2015), and sediment retention (Schlaefer et al. 2022), any differences in reef habitat widths could have far reaching implications for the sustainability of reefs and their ability to deliver ecosystem services to humans in the future (Morais et al. 2021b; Tebbett et al. 2022). Thus, globally, reefs may differ markedly in their ability to deliver key functions. However, there has been no quantification of global differences in the widths of shallow reef habitats.

Historically, the spatial quantification of reefs has been restricted by the available data. However, advances in remote sensing now permits the assessment of reefs at global scales and in increasingly high detail (Hedley et al. 2016; Kutser et al. 2020). The Allen Coral Atlas enables us to undertake the first standardised worldwide assessment of benthic cover and geomorphic zonation of coral reefs using fine-scale (3 m) resolution imagery and maps (Allen Coral Atlas 2022). The present study utilises this cutting-edge dataset to investigate how the contrasting biogeographic and regional evolutionary histories of the Caribbean and Indo-Pacific may have shaped shallow reef width patterns at 60 reefs in 20 reef locations within these two realms. Specifically, transects spaced at 1 km intervals were used to: 1) quantify shallow reef habitat widths between the Caribbean and Indo-Pacific, and 2) explore potential geological, ecological and biogeographical drivers of any differences. The key question is: Are Indo-Pacific shallow reef habitats broader than their Caribbean counterparts, and, if so, what are the potential implications for reefs given escalating climate change?

3.3 Methods

3.3.1 Data acquisition

Biogeographic variation in the width of shallow coral reef ecosystems was evaluated using the Allen Coral Atlas, a global mapping project aiming to combine conventional ecological-biophysical perspectives of coral reef ecosystems with an earth observation systems view of reefs, provided through remote sensors (Kennedy et al. 2021). The Coral Allen Atlas uses PlanetScope (Dove) imagery (Allen Coral Atlas 2022) and the 'Reef Cover' classification described by Kennedy et al. (2021), which combines machine-based learning algorithms and Object-Based-Analysis (Lyons et al. 2020) to create a coral reef classification system consisting of 17 geomorphic class descriptors. Our study used this new and freely available data resource to investigate the width of shallow water reef zones across 3,765 transects on 60 reefs across the Indo-Pacific (n = 30) and Caribbean (n = 30) (Figure 3.2) (accessed: March 2022). While the total geographic extents of the two realms may differ (Figure 3.2), we ensured that the reef extent (i.e. the area of mapped reef chosen per location as indicated by the Allen Coral Atlas) was comparable. Shallow water reef zones were defined as the inner, outer and reef crest zones of the Allen Coral Atlas' geomorphic map (accessed: March 2022). To facilitate between-realm comparisons, sample reefs were chosen to ensure a balanced sample in both realms based on reef types, individual reef area, and location (oceanic vs continental) (see Text B1 for further information). Major reef types were classified as: Barrier reefs (n = 11), Atolls (n = 10), Low Islands (n = 2) and High Islands (sensu Nunn et al. 2016) (n = 37). In our analyses, we purposefully did not include reefs close to, or attached to, mainland shores that could be classified as 'fringing reefs'. The term is very broad and lacks consistent definition, as fringing reef types vary markedly on a global reef scale (Kennedy et al. 2021). Therefore, 'fringing reefs' were only included if located adjacent to isolated islands. In these cases, the topography of the adjacent island was used to differentiate such reef systems, following Nunn et al. (2016) (categorising islands with elevations above 30m as high islands). Furthermore, to minimise the potential for variation in terrestrial influences and coastal effects, including turbidity, compromising image classification accuracy, we excluded the 'Terrestrial Reef Flat' class (as defined by Kennedy et al. 2021) from our analyses. Our approach, as applied to both realms, therefore, focusses solely on shallow reef habitat width estimates from geomorphic zones (Inner Reef Flat, Outer Reef Flat and Reef Crest) that are interrelated in the classification scheme, widely supported in the geological and ecological literature, and in locations where terrestrial influences are likely to be limited or non-existent. Therefore, we specifically look at reefs in shallow, clear water situations (up to 15 meters depth). Outer reef flats are defined by the Allen Coral Atlas as shallow, strictly horizontal habitats, characterized by increased coral cover and relatively high wave energy gradients. Inner reef flats, on the other hand, are deeper, gently sloping habitats, dominated by the presence of sand-covered substrata. Reef crests are defined as the narrow zones experiencing the greatest wave exposure, dominated by hard-bottom substrata with little structural complexity (Kennedy et al. 2021). These classifications use interzonal relationships as part of their class description, meaning that Inner Reef Flat, Outer Reef Flat, and Reef Crest must be adjacent to one another, and in that order, increasing accuracy within these class descriptors. Map accuracies partially depend on the availability of reference data, as well as potential obstructions that may vary across locations. The Appendix (Table B1) includes a comprehensive list of further potential limitations inherent to the mapping process.

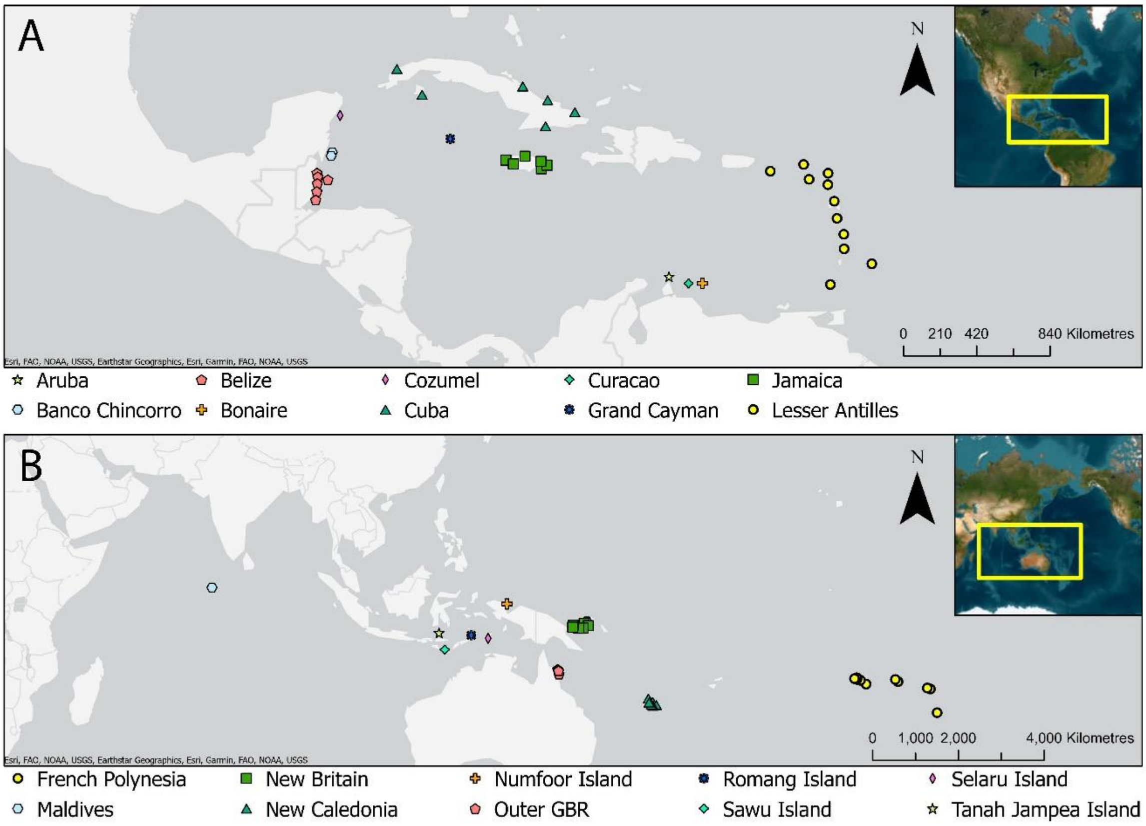

Figure 3.2 Map of the geographic position of the 20 sites containing the 60 reefs used in this study in the Caribbean (A) and Indo-Pacific (B).

3.3.2 Geospatial analysis

The geomorphic zones for the study reefs were downloaded from Allen Coral Atlas (Allen Coral Atlas 2022). The desired reef zones (Inner Reef Flat, Outer Reef Flat, and Reef Crest) were then selected (Figure 3.3B). A polyline was created along the outline of each reef, roughly following the crest (Figure

3.3C). Along this outline of each reef, three kilometre long cross-reef transects were generated every kilometre (Figure 3.3D). Reef width transects were also divided by exposure status, according to the prevailing wind in the region (e.g. leeward or windward) accessed through a simulated and modelled weather dataset created by meteoblue (Meteoblue 2022). Hereby, modelled wind roses for each location, quantifying the predominant wind direction and speed, were used as estimates of prevailing wind directions to assign each transect an exposure status (exposed, sheltered). Exposure status was assigned according to the typical wind direction of the transect (indicated as hours per year), not the intensity. Potential limitations and caveats of the dataset used are described in Table B1 of the supplementary material. Lastly, we measured the width of the reef zones intersected by each transect. All geospatial analyses were performed in the software ArcGIS Pro 2.7.0 (Esri Inc. 2022).

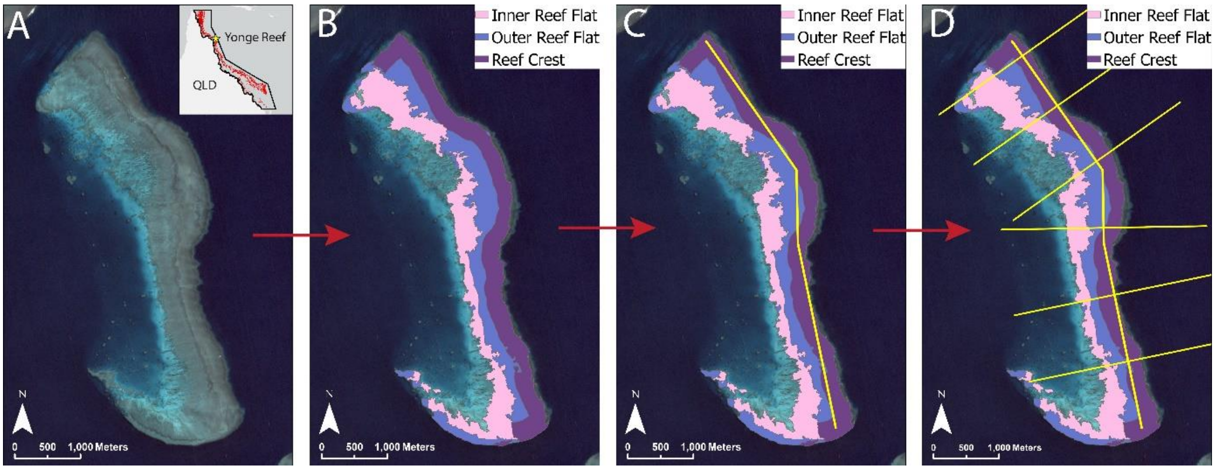

Figure 3.3 Process and methodology of shallow reef habitat width estimation. A) Access high-resolution PlanetDove imagery through the Coral Allen Atlas (Yonge Reef, Northern GBR, AUS), B) filter for desired reef zones, C) create polyline (yellow) along the crest of the reef and D) create equally spaced cross-reef transects every kilometre along the polyline.

3.3.3 Data exploration

Measurements of the Inner Reef Flat, Outer Reef Flat, and Reef Crest width on each transect were summed to calculate the total shallow reef habitat width on that transect. Transects with a shallow reef extent of 0 were excluded from further analysis. All statistical analyses were conducted in the software R (R Core Team 2022), 'tidyverse' (Wickham et al. 2019), 'moments' (Komsta and Novomestky 2022), 'glmmTMB' (Brooks et al. 2017), 'DHARMa' (Hartig 2022) and 'vegan' (Oksanen et al. 2022) packages. Relationships between the various reef zone widths and independent variables, including realm (Caribbean vs. Indo-Pacific), exposure status (leeward vs. windward) and reef type (atoll, barrier, low or high island), were assessed using a Principal Component Analysis (PCA). The PCA was performed on a correlation matrix. Kernel densities were estimated using the *density* function to visualize and compare mean, as well as modal, shallow reef habitat width patterns. We used a generalized linear mixed model (GLMM) to assess the nature of the relationship between the shallow reef habitat width and realm. Realm was used as a fixed effect, while reef and transect ID were fitted as nested random effects. The most parsimonious model was chosen based on Akaike Information Criterion (AIC) and was fitted using a tweedie distribution with log link. Model assumptions were assessed using residual diagnostics and post-hoc pairwise means comparisons were conducted employing a Tukey's adjustment. While the relationship of shallow reef habitat width between realms was statistically insignificant (Appendix B Table B2), we strongly caution against using this model as the extensive spatial autocorrelation in the dataset precluded detailed statistical comparisons (violating the assumptions of ANOVA and GLM or GLMM, as well as not meeting residual diagnostic standards) (Appendix B Table B3). We therefore provide descriptive statistics and a multivariate analysis which can accommodate non-independent data. Further spatial autocorrelation and cluster analyses were conducted in the statistical analyses package GeoDa 1.4.1 (Anseling et al. 2006). See Appendix B for details.

3.4 Results

The widths of shallow reef habitat (inner and outer reef flat and crest combined) in the Caribbean and Indo-Pacific ranged from 0 m to over 3000 m, although the vast majority are less than 500m wide (Figure 3.4). Interestingly, modal shallow reef widths between the two realms differed by only approximately 37 m (estimated by kernel density estimates; 117.35 m Indo-Pacific, 80 m Caribbean). Averages likewise differ by just 122 m (486.9 m ± 9.45m Indo-Pacific, 365.1 m ± 9.92 m Caribbean) (Figure 3.4). In both cases, Indo-Pacific reefs were marginally wider than those in the Caribbean (Figure 3.4). Both realms exhibit right skewed distributions, with a greater prevalence of narrow width values, however, the Caribbean exhibits a stronger skew and relatively higher kurtosis than the Indo-Pacific (Figure 3.4) (see Appendix B Table B4).

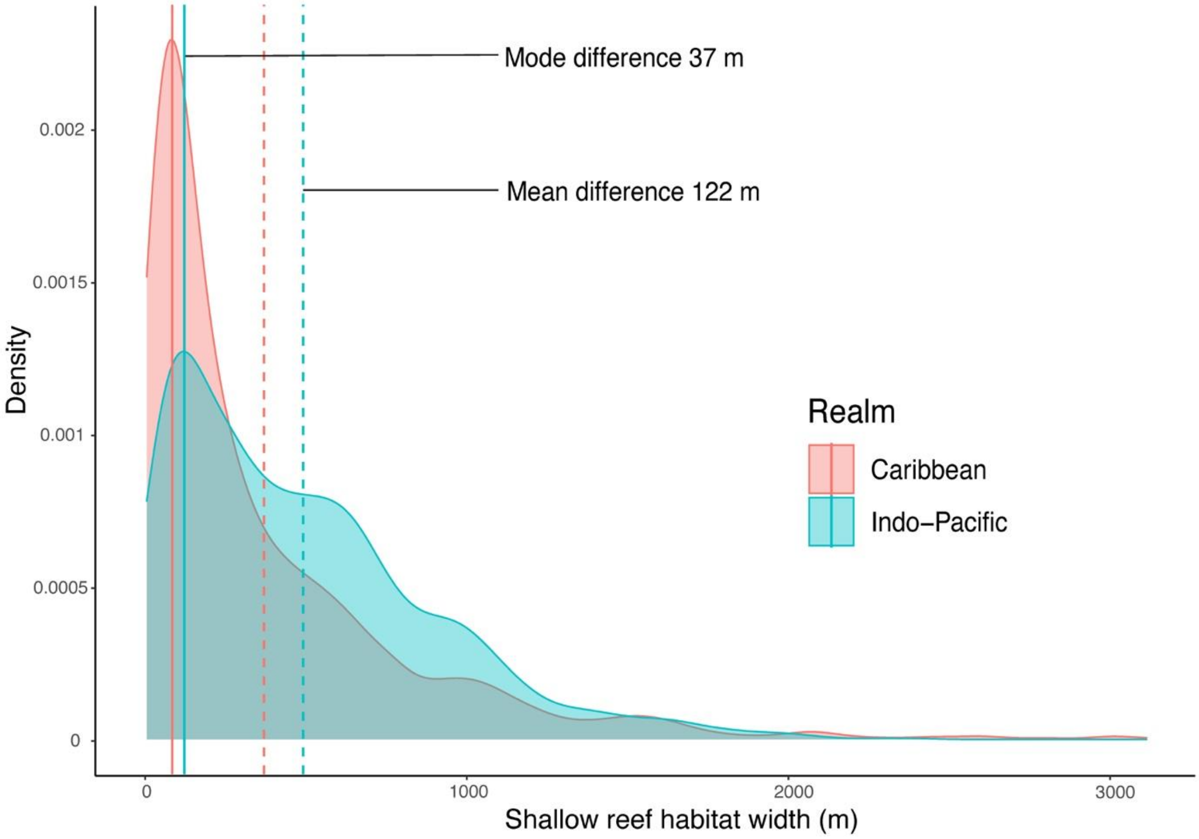

Figure 3.4 Kernel Density Estimates of shallow reef widths (m) in the Caribbean (red) (n = 1945 transects) and Indo-Pacific (blue) (n = 1820 transects). Dashed lines represent the means and solid lines the modes of the shallow reef widths in the Caribbean and Indo-Pacific (shallow reef widths = inner reef flat + outer reef flat + reef crest).

Generally, shallow reef systems in the Indo-Pacific were wider than their Caribbean counterparts. This holds true for total shallow reef width (Figure 3.4), and individual zone widths (Reef flat and Crest) (Figure 3.5). Reef flats (inner + outer reef flat) across both realms showed similar mean widths, ranging roughly between 350 m and 475 m regardless of their exposure status (Figure 3.5). Crests were by far the narrowest zone and again were wider in the Indo-Pacific and wider at windward sites in both realms (Figure 3.5). While windward sites seem to be marginally wider, total shallow reef habitat widths at windward versus leeward transects differed by just 29 m on average (windward 436.9 +/- 9.8 m, leeward 408.1 +/- 9.8 m) (Appendix B Table B5).

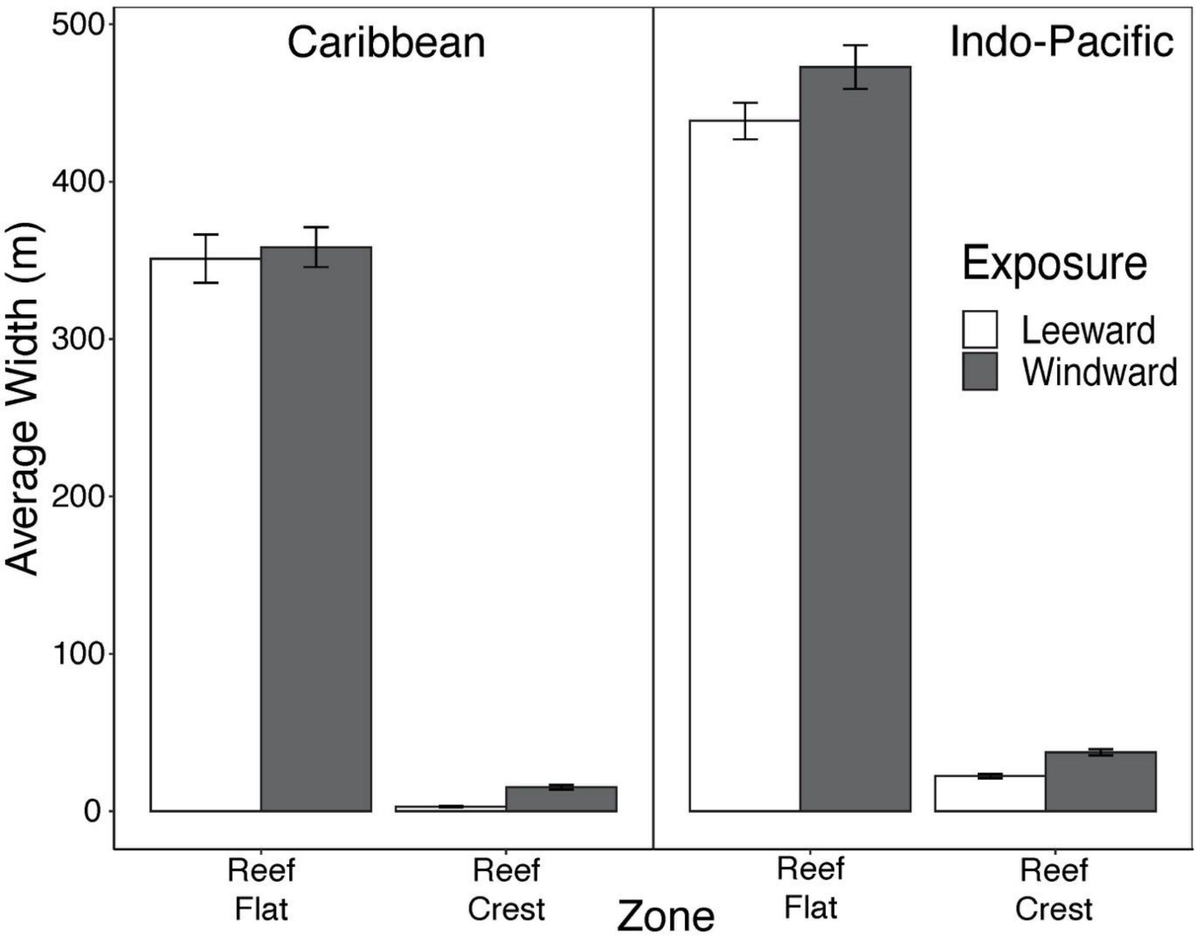

Figure 3.5 Average width (m) (+/- SE) of each geomorphic zone grouped by exposure to prevailing winds (white = leeward, grey = windward) across the Caribbean and Indo-Pacific realms Reef flats represent the combined data of Inner and Outer flat. Note: see Appendix B Figure B1 for Average width (m) (+/- SD).

The patterns described above were strongly supported by the PCA, which explained over 90% of the total variance along its first two axes (Figure 3.6). The two realms showed substantial overlap, further emphasising the overall trend of similarity in shallow reef habitat widths (Figure 3.6). However, the Indo-Pacific demonstrates larger variation along the PC2 axis, primarily driven by wider reef crests on the GBR, and generally wider shallow reef habitat zones (Figure 3.6). Notably the loading vectors all orient in the same direction, signifying a shared increase in all habitats, i.e., wider reefs have consistently wider individual zones (Figure 3.6). These patterns were also strongly supported by the geospatial analyses conducted in GeoDa which showed positive spatial autocorrelation (Moran's I = 0.694 in the Caribbean and 0.674 in the Indo-Pacific) with narrow reef zones clustered together and wide zones clustered near other wide zones (Appendix B Figures B2 and B3).

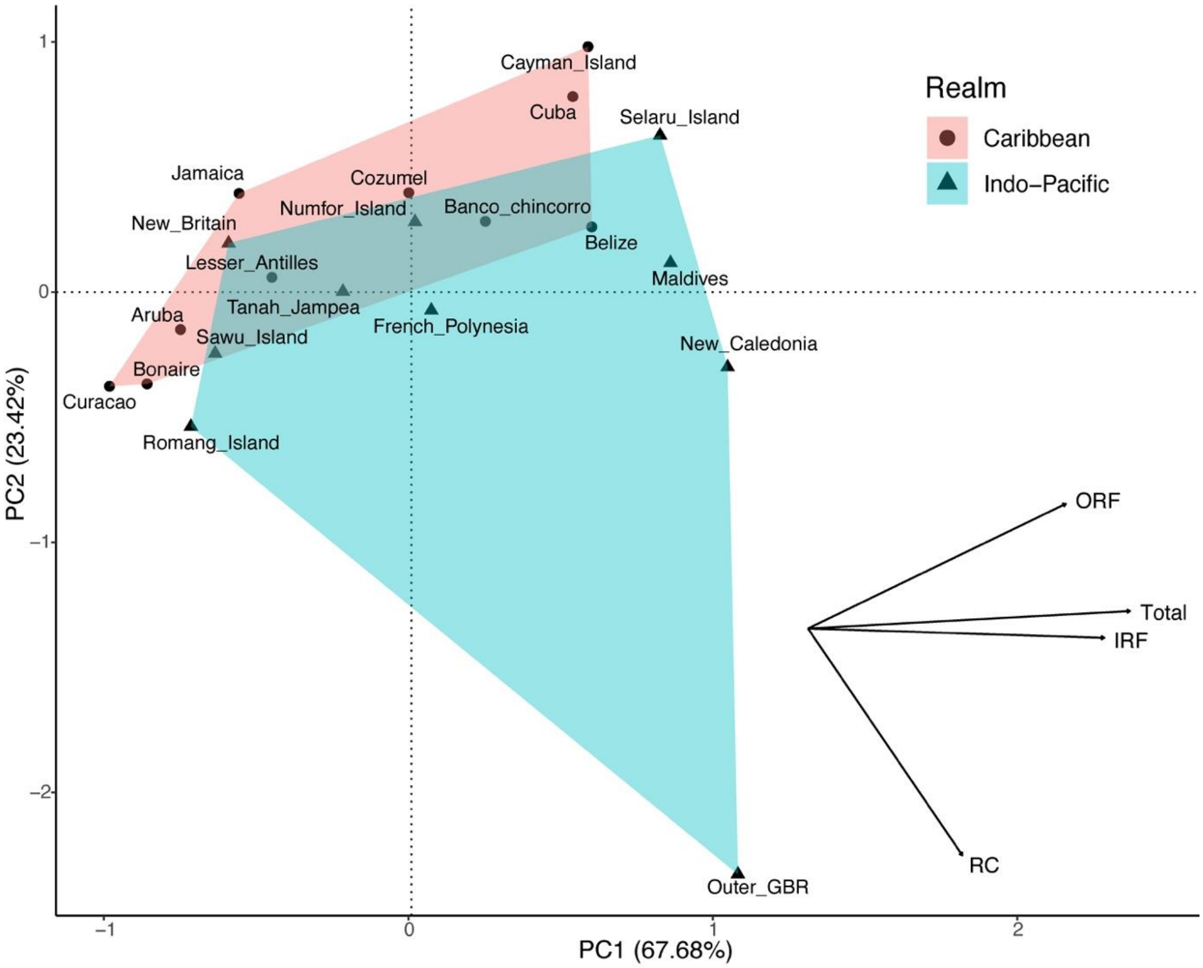

Figure 3.6 Principal Component Analysis (PCA) of the average widths of shallow reef habitat zones (vectors - IRF = Inner Reef Flat, ORF = Outer Reef Flat, RC = Reef Crest, Total = total shallow reef width) and their associated reefs based on their location. Circles and red hull: Caribbean, triangles and blue hull: Indo-Pacific.

The average width also varied across the different reef types (Figure 3.7, Appendix B Figures B4 and B5). Within reef types, shallow reef width averages and distributions show notable similarities, especially atolls (Figure 3.7A). Remarkably, mean shallow reef habitat widths of transects across atolls in the Indo-Pacific (n = 710) and Caribbean (n = 261) vary by just 8 m, averaging 503.73 m (+/- 14.31 m) and 511.75 m (+/- 19.89 m), respectively (Figure 3.7A). Furthermore, the Kernel Density estimates are very similar, showing slightly different modes but with substantial overlap in the distributions (Figure 3.7A). By contrast, the kernel density estimate distributions of shallow reef habitat widths of barrier reef systems in the Caribbean differ markedly from the Indo-Pacific (Figure 3.7B). Although average widths across barrier reef systems in the Indo-Pacific (n = 63) and Caribbean (n = 151) vary by less than 33 m (Figure 3.7B, the Indo-Pacific barrier reefs show a narrower range, averaging 682.6 m (+/- 21.5 m), while their counterparts in the Caribbean show a broader range and average 649.9 m (+/-

37.7 m) (Figure 3.7B). By contrast, reefs around high islands show a broader distribution in the Indo-Pacific (n = 1047), averaging 463.7 m (+/- 13.1 m) (Figure 3.7C) when compared to their counterparts in the Caribbean (n = 1356) which have a mean shallow reef habitat width of 286.7 m (+/- 10.9 m); their modal classes vary by just 48 m (Figure 3.7C). Lastly, low islands are absent from our Indo-Pacific data set and average 507.4 m (+/- 45.4 m) in the Caribbean (n = 177) (Figure 3.7D). Overall, while there is some variation in the shape of kernel distributions, and in the biogeographic location of the reefs with the largest modes or means, the overall pattern is one of remarkably similar sizes, especially in atolls.

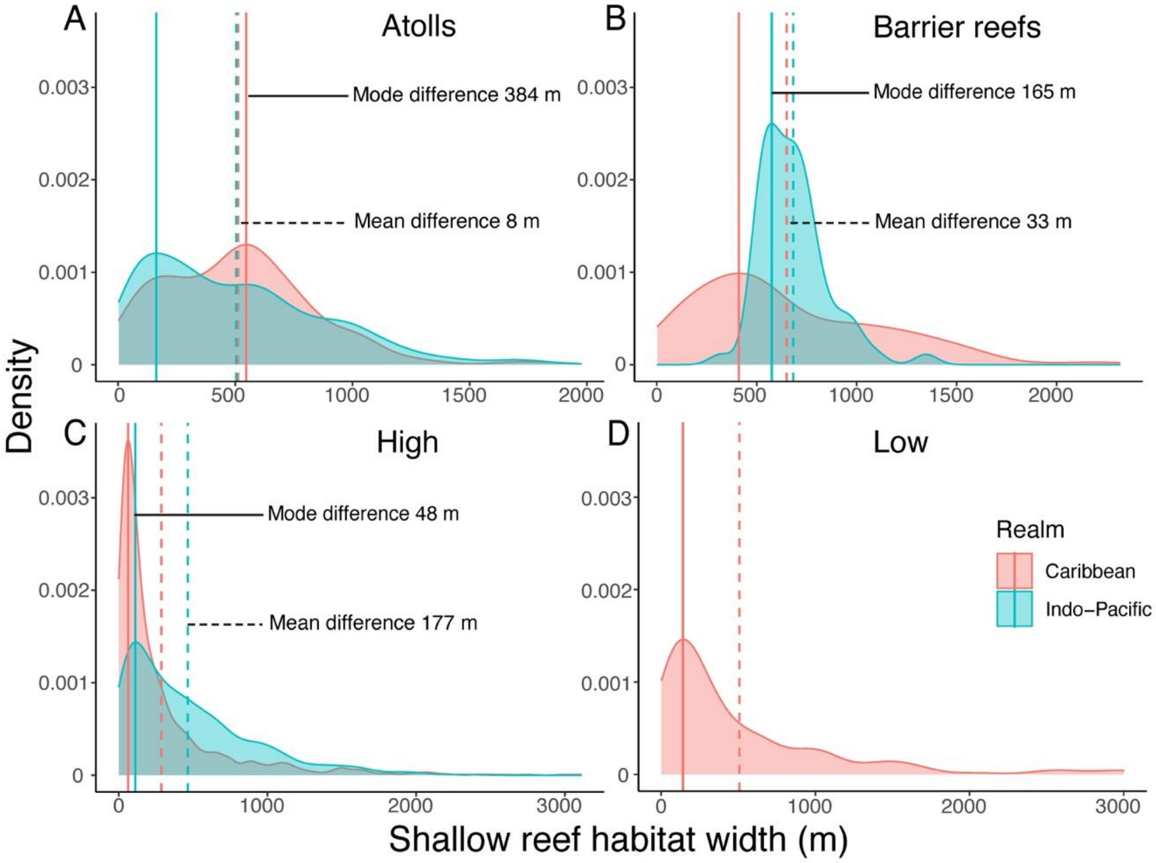

Figure 3.7 Kernel Density Estimates of shallow reefs widths (m) for A) atolls, B) barrier reefs, C) high islands and D) low islands within the Caribbean (red) and Indo-Pacific (blue). Dashed lines represent the means and solid lines the modes of the shallow reef widths in the Caribbean (red) and Indo-Pacific (blue). Note the x-axes scales differ between upper and lower panels.

3.5 Discussion

This study represents a preliminary description of the biogeography of coral reefs as biogenic structures. Using novel remotely sensed data, we revealed that, in general, shallow reef habitats in the Indo-Pacific were only marginally wider than in the Caribbean, with the modal widths between the two realms diverging by just 37 m and means by a mere 122 m. This pattern is consistent with our expectations, in direction, but not in extent. As described in the introduction, we hypothesised shallow reef habitats of the Indo-Pacific should be considerably wider than those in the Caribbean (at least 500 m wider). The unexpected similarity in widths between the two realms suggests that species richness, sea-level regime and biogeographic history potentially have a limited impact on reef accretion, and that other drivers may be more important in constraining the size of biogenic coral reef structures. These other factors that may drive the homogenous distributions of shallow water habitat widths between these two vastly different biogeographic realms may include: (1) antecedent topography of the Pleistocene substratum, (2) non-coral components as drivers of reef growth, or (3) local hydrodynamics. Below, we discuss these factors and their implications for our understanding of reef accretion, herein used as a term to describe both lateral and/or vertical reef growth, and the future of coral reefs.

3.5.1 Antecedent topography

Today, it is widely understood that during the Holocene many reefs initiated their accretion and reef formation on Pleistocene reef substrata (Hopley et al. 2007; Montaggioni and Braithwaite 2009). Thus, it has been hypothesised that the extent and nature of these Pleistocene foundations may govern the physiography of Holocene and modern coral reef structures (Purdy 1974; Grigg et al. 2002; Gischler and Hudson 2004; Barrett and Webster 2012). More specifically, the literature suggests that the unique morphology, size, and shape of both atolls and barrier reef systems is predominantly produced by the subaerial exposure of relic Pleistocene substrata (Montaggioni and Braithwaite 2009; Davies 2011; Droxler and Jorry 2021). For instance, Pirazzoli and Montaggioni (1986) found that the reticulated lagoon at Mataiva Atoll in the central Pacific, which is divided into a series of central basins, is a result of extensive sub-aerial exposure of the antecedent Pleistocene platform. Consequently, the similarity in average shallow reef widths in both atoll and barrier reefs systems across both realms in this study could potentially be a result of similar sub-aerial exposure regimes during the Pleistocene. However, on more local scales, Holocene reef growth can occur independently, without the restrictions of antecedent topography (Montaggioni and Braithwaite 2009; Salas-Saavedra et al. 2018). In his study on John Brewer Reef in the central GBR, Walbran (1994) found that modern morphologies of coral reef structures may result from the interactions between Holocene sea-level rise, prevalent hydrodynamics, and the biological activity of organisms in response to these other factors. Thus, modern coral reef structures appear to be the result of a complex suite of interactions between the biology and diversity of reef dwelling organisms within the context of prevailing hydrodynamic or environmental drivers. This may be influenced, but is not necessarily constrained, by the underlying Pleistocene substratum (Adey 1978; Walbran 1994).

3.5.2 Coral growth driving reef accretion (vertical and lateral)

Corals throughout the world share the ability to create three-dimensional, biogenic structures through the accumulation of calcium carbonate. Given the markedly different coral lineages and 14-fold difference in coral species richness between the two realms, reefs in the Indo-Pacific were expected to exhibit much more extensive reef growth, both vertically and laterally once at sea-level. However, our results reveal that the difference in shallow reef habitat widths between Caribbean and Indo-Pacific reefs was not as pronounced as anticipated. Furthermore, throughout the Holocene, both realms showed similar historical rates of carbonate production and reef growth. While Caribbean reefs accreted between 3 mm – 4 mm/year (Hubbard 2009), reef accretion rates in the Indo-Pacific were only slightly below that average (Dullo 2005). However, Holocene reef development models assume that reef accretion is directly controlled by the accretion rates of the local dominant coral species, implying that reefs dominated by branching species would accrete faster than reef systems dominated by slow-growing massive coral species (Adey 1978; Chappell 1980; Gischler 2008). Recently, Roff (2020) used cores from two opposing reef slopes at an inshore reef on the central GBR to explore reef accretion patterns of late-Holocene reef frameworks. While the two sites were dominated by different coral species, namely *Goniopora* and *Acropora*, that show a ten-fold difference in potential growth capacity, core data revealed that vertical reef accretion rates were strikingly similar over the last 750 years (Roff 2020). Similarly, in the Caribbean, there was no significant difference in reef accretion rates between reefs dominated by fast-growing and slow-growing coral species (Gischler 2008; Hubbard 2009). Moreover, using new and previously published fossil data, Johnson et al. (2008) showed that Caribbean reef development remained unaffected by an extinction event in the late Pliocene that decreased coral diversity by 50%. Thus, coral reef functioning, defined as the movement or storage of energy or material (sensu Bellwood et al. 2019) and pertaining herein to reef growth, appears to remain largely unaffected by variation in biodiversity. Reef growth appears to be primarily driven by abiotic and biotic interactions with the environment (Johnson et al. 2008).

At Holocene time scales, coral growth and reef accretion may be decoupled processes; challenging the common assumption that the life-history and growth capabilities of corals dictate reef accretion rates (cf. Roff 2020; Hammerman et al. 2022). Consequently, it has been suggested that past research may have overestimated the role of in-situ coral growth in reef building processes (Hubbard et al. 1990; Perry et al. 2012; Blanchon et al. 2017; Hammerman et al. 2022). Although our study provides valuable insights, it has certain limitations. It is a snapshot in time and does not include an analysis of existing geological core data or the timing of sea-level rise and reef initiation. Nonetheless, the striking similarities in shallow reef widths in the Caribbean and Indo-Pacific, despite highly disparate coral assemblages, may support this emerging perspective. Based on our findings, it appears that reef accretion (both vertical and lateral) and coral diversity may not be linked. This may indicate a potential separation between biodiversity and a key reef function (i.e., reef growth). Indeed, the accumulation of stressors on coral reefs in the Anthropocene may cause further decoupling of the processes that support reef accretion from the more visible ecological coral-based processes that appear to drive carbonate production on the reef surface (Morais et al. 2022).

Coral reef accretion, herein the function of both vertical and lateral reef expansion, can be facilitated through a multitude of other, non-coral growth processes and by other non-coral organisms, such as crustose coralline algae, foraminifera, molluscs, or *Halimeda*. Recently, Hammermann et al. (2022) showed that a large percentage of investigated reef slopes in the Red Sea were not constructed solely by in-situ coral growth, with a considerable contribution from unconsolidated coral rubble. Similarly, in St. Croix, US Virgin Islands, Hubbard et al. (1990) described the local reef framework as a ‘garbage pile’ of carbonate reef detritus rather than an array of in-situ coral framework assemblages. Montaggioni (2005) likewise identified coral and skeletal rubble facies as the most prominent features of reef cores in the Indo-Pacific, occupying up to 60% of the total core volume, while Morais et al. (2022) showed that dead coral skeletons may have a negligible contribution to local, in-situ, reef accretion.

If corals do not contribute to reef accretion as much as previously assumed, other organisms may underpin reef accretion. Crustose coraline algae (CCA), for example, have been shown to be key secondary reef builders, able to consolidate and cement reef framework (Littler and Littler 2013), thus playing an important role in reef accretion (Nash et al. 2013). Kench et al. (2022) showed that vertical reef accretion in the low coral cover wave breaking zone (reef crest) was maintained, even shortly after periods of elevated sea-surface temperatures, by CCA calcification. Within two years of a major bleaching event, the outer rim of the reef flat and reef crest maintained positive accretion rates that, averaging up to 6.6 mm/year vertical growth, match pre-bleaching values (Kench et al. 2022). Reef accretion may therefore still occur in disturbed areas lacking live coral cover. Accretion rates appear to be predominantly influenced by local environmental factors, rather than by the abundance or diversity of corals. Clearly the future of coral reefs will also depend on the response of these non-coral taxa to climate change. However, our understanding and knowledge regarding the potential responses of these non-coral organisms to climate change, and ultimately, their capacity to facilitate reef growth in the future, remain limited (Short et al. 2015). Addressing the knowledge gaps surrounding the non-coral components of reef vertical and lateral accretion will be vital to predicting the impacts of climate change on these biogenic coral reef structures.

3.5.3 Local hydrodynamics as common factor

While limited in number, studies investigating mid-late Holocene coral assemblages and their living counterparts across reefs in the Indo-Pacific and Red Sea have found little variation in overall composition and diversity (Pandolfi and Minchin 1996; Roche et al. 2011; Hallmann et al. 2020). This suggests that over the course of the Holocene, environmental parameters - such as light conditions or nutrient levels, have changed relatively little, except within the context of sea-level driven hydrodynamic regimes (Hallmann et al. 2020). The importance of hydrodynamics has been established for other reefal structures, such as reticulate ridges in reef systems (Schlager and Purkis 2015) and sand aprons (Isaack and Gischler 2017). However, the degree to which modern reef morphology can be attributed to prevalent hydrodynamics remains relatively poorly understood (Woodroffe and Webster 2014; Camoin and Webster 2015; Salas-Saavedra et al. 2018). While reef structures on the GBR show vast differences in their timing of initiation and rate of accretion during the early phases of reef development, once sea-level was reached, they appear to be strikingly similar (Dechnik et al. 2015, 2017; Salas-Saavedra et al. 2018). This concept is underlined by the results in the present study where isolated carbonate platforms, such as atolls and barrier reef systems, showed remarkably similar average widths between biogeographic realms. This emphasises the potential role of local hydrodynamics in shaping, and potentially homogenising, modern reef structures and their morphology. It also suggests that the influence of hydrodynamics on reef accretion at sea-level may be a common factor shaping and constraining reef growth (Dechnik et al. 2016, 2017; Salas-Saavedra et al. 2018), independent of biogeographic location.

Recently, Rankey (2021) investigated the interactions between geomorphology and hydrodynamic setting to assess reef progradation patterns on isolated carbonate platforms and atolls. He identified that sand aprons on the windward side are generally wider due to the higher energy across these locations. This is consistent with the existing literature (Yamano et al. 2003; Hongo and Kayanne 2009) and the findings herein, which showed consistently wider shallow reef habitats along exposed, windward, margins. However, sand apron development and more generally reef progradation, has been shown to be self-limiting (Ortiz and Ashton 2019; Rankey 2021; Vila-Concejo et al. 2022). As reef flat and sand apron width increases, shear stress decreases to a point where no sediment can be moved by hydrodynamic forces (Rankey 2021). Early work also suggested that the reefs' ability to prograde lagoonward would be limited by extreme levels of temperature, turbidity and salinity in lagoons which may exceed coral reef growth thresholds (Neumann and Macintyre 1985). Therefore, the shallow reef habitats of atolls and other isolated carbonate platforms may reach a width that ultimately halts leeward accretion. Seaward accretion is also likely to be limited by the steepness of the reef slope (Maxwell 1968; Kan et al. 1995; Duce et al. 2020). These factors potentially explain the homogenous distribution of shallow reef habitat widths documented herein for atoll systems in the Caribbean and Indo-Pacific. Prevailing hydrodynamics may be the primary driving force underpinning the similarity of widths of biogenic coral reef structures in the Caribbean and Indo-Pacific. Hydrodynamics may be a universal factor that overrides the biogeographic, historic and evolutionary contingencies between these two distinct realms.

3.6 Conclusion

This study demonstrates that the widths of shallow-water biogenic coral reef habitats in the Caribbean and Indo-Pacific are strikingly similar. Although these two realms, have highly disparate biogeographic extents, biodiversity patterns, evolutionary and sea-level histories, their modal shallow reef zone widths differed by just 37 m. This suggests that there are other, non-historical, drivers underpinning this remarkable similarity; drivers that can override the influence of biogeography and sea-level history. Furthermore, the results of this study may lend support to the perspective that reef accretion, a geological process, is largely decoupled from coral growth an ecological process; with the corollary that coral diversity does not determine reef accretion rates. Once biogenic coral reef structures reach sea-level, hydrodynamic forcing appears to be the major force in a self-limiting system that constrains reef accretion. While climate change is driving the global loss of corals, the results of this study emphasise the need for a more thorough understanding of the contribution of non-coral components to coral reef functioning and growth including further examination of historical reef development trajectories, for example by coring and dating studies.

Chapter 4: Correlates of tropical marine herbivorous fish catches across the Indo-Pacific and Western Atlantic

Submitted as: Lutzenkirchen, L. L., Tebbett, S.B., Yan, H.F. & Bellwood, D. R. (*Under revision*). Drivers of tropical marine herbivorous fish catches across the Indo-Pacific and Western Atlantic. Cell Reports Sustainability (flow of paper has been slightly altered to fit the thesis format)

4.1 Abstract

Ensuring food security in the Anthropocene presents a significant socio-ecological challenge, especially in the rapidly changing coastal seascapes that sustain critical fisheries. Herbivorous fishes support human communities by providing food and financial security via fisheries, however, their contribution to realm-wide catches is not well understood. By analysing reported and reconstructed large-scale catch data across 69 Exclusive Economic Zones, we identify shallow reef area and human coastal population density as significant predictors of between-realm herbivorous fish catches, with rabbitfishes making a disproportionately large contribution to herbivorous fishery catches. While rabbitfishes have the potential to support productive fisheries, due to their life history traits, a 60% decline in catch per unit effort suggests that their production potential, along with parrotfishes and surgeonfishes, may be decreasing globally. Our study highlights a concerning social-ecological mismatch between rising human population levels and declines in area-dependent fisheries which are vital for sustaining coastal human communities.

4.2 Introduction

Sustaining food security in an era of global change represents a critical socio-ecological challenge (Willett et al. 2019; FAO et al. 2020). This challenge is multifaceted as an ever-growing human population places an increasing demand on the world’s ecosystems to supply nutritional resources, while human activities are also rapidly altering the world’s ecosystems and reducing their capacities to deliver critical ecosystem services (Steffen et al. 2011; Folke et al. 2021). These issues are epitomised in the world’s coastal seascapes, especially on coral reefs (Hughes et al. 2017; Fulton et al. 2019; He and Silliman 2019). Globally, the connection between humanity and near-shore seascapes has intensified, particularly among coastal communities that rely on these ecosystems to secure livelihoods through subsistence and artisanal fisheries (Cinner et al. 2012; Hoegh-Guldberg et al. 2019; Wong et al. 2022). Coastal seascape-associated fisheries are critical for human development through the supply of high-quality protein and micronutrients (Tacon and Metian 2013; Hicks et al. 2019).

However, coastal seascapes are also among the most threatened ecosystems on the planet, as a range of stressors, especially global climate change, are re-shaping the composition of these systems (Hughes et al. 2017; He and Silliman 2019; Tebbett et al. 2023b). Ultimately, as the condition of coastal seascapes declines, their capacity to sustain fisheries yields is expected to follow (Bell et al. 2013; Eddy et al. 2021).

Coastal seascape habitats display highly heterogeneous and patchy distributions, resulting in scale-dependent characteristics for associated fish assemblages and fisheries (Taylor et al. 2015; Heenan et al. 2016; Sambrook et al. 2019; Wilson et al. 2022). The influence of bottom-up effects (e.g. habitat quality and availability) and top-down effects (e.g. fishing pressure) can vary across local, regional, and biogeographic scales (Williams et al. 2015; Harborne et al. 2018; Samoilys et al. 2019; McClure et al. 2021). Given the limited availability of comprehensive small-scale fishery-dependent data across larger scales (Zeller et al. 2015; Grafeld et al. 2017), fish biomass often serves as a valuable fishery-independent indicator of potential yield (Harborne et al. 2018; McClure et al. 2021; Zamborain-Mason et al. 2023).

Fish biomass is used to track changes in fish stock volume over time and facilitates cross-stock comparisons, particularly in multi-species coral reef fisheries (Nash and Graham 2016; Birkeland 2017). Recent research has linked fishery-independent data, including coral reef fish biomass, with environmental and socioeconomic time-series data (e.g. Samoilys et al. 2019; McClure et al. 2021; Morais et al. 2023). Such studies often highlight that coral reef fish biomass is driven by bottom-up factors, such as habitat quality, primary productivity, and reef geomorphology, which can lead to increased catch volumes (Samoilys et al. 2019; McClure et al. 2021). However, in large-scale studies, habitat availability (i.e. the accessible habitat area for fishers) may be omitted (Williams et al. 2015), potentially due to its seemingly self-obvious relationship. This omission means that relationships between fisheries catch and habitat area are not fully explored, and might lead to an underestimation of the importance of habitat area in supporting fish biomass. On more local scales, fishing has also been found to exert a pronounced top-down influence, leading to a significant reduction in reef fish biomass (Jennings and Polunin 1996b; Taylor et al. 2015). Notably, in small-scale coral reef fisheries, which are characterized by diverse species, habitats, and gear types, there are a limited number of species that often dominate a significant portion of the total catch (Jennings and Polunin 1996a; Samoilys et al. 2017; Rassweiler et al. 2020).

Herbivorous fishes represent a key group of organisms that lay at the junction of coastal ecosystem decline and small-scale fisheries yields (Robinson et al. 2023). Herbivory is widely viewed as a critical ecosystem function on coral reefs (Bellwood et al. 2004; Adam et al. 2015) as it has been suggested that herbivory may limit the dominance of algae via top-down control, potentially facilitating recovery of corals after disturbance (Bellwood et al. 2004; Hughes et al. 2007). This, in turn, has led to calls for the protection of herbivorous fishes in coastal seascapes via ecosystem- and stock-based management approaches (Rogers et al. 2015; Williams et al. 2016; Chung et al. 2019). Yet, herbivorous fishes are also a key component of coastal fisheries (Bejarano et al. 2013; Edwards et al. 2014; Humphries et al. 2019; Fulton et al. 2020), and are typically targeted once higher-trophic level fish stocks have been overfished (Pauly et al. 1998; Mumby et al. 2012). Indeed, Robinson et al. (2023) concluded that herbivorous fishes are now the primary contributors to fisheries services across varying reef habitats.

Despite the attention herbivorous fishes have received from an ecological perspective (e.g. Bellwood et al. 2004; Adam et al. 2015; Bruno et al. 2019), we have a limited understanding of the biogeographical, geomorphological, and socioeconomical factors influencing between-realm catches (i.e. between the Western Atlantic and Indo-Pacific). Fishery-independent data suggests that herbivorous fish biomass patterns tend to align with general drivers, where habitat effects take precedence at larger scales, potentially overshadowing more local fishing-related impacts on biomass reduction (Taylor et al. 2015; Heenan et al. 2016). However, assessments of fishery-dependent datasets, specifically total catch data, predominantly pertain to localized studies. Indeed, at the local scale, herbivorous fishes can contribute over 50% of the total catch to coral reef fisheries (Houk et al. 2012; Bejarano et al. 2013; Samoilys et al. 2017). This substantial contribution is influenced by various factors affecting catch success, including environmental conditions, exposure regimes, dominant gear types, and behavioural traits. Moreover, herbivorous fishes are captured using diverse gear types, including hook and lines, traps, spears, and nets, rendering them susceptible to a wide array of accessible fishing methods (Bejarano et al. 2013; Campbell et al. 2014; Samoilys et al. 2017; Humphries et al. 2019).

Given the ecological importance of herbivorous fishes in coastal seascapes (Bellwood et al. 2004; Hughes et al. 2007; Adam et al. 2015), and their potential to be a productive nutritional resource to people (Robinson et al. 2019, 2023; Hamilton et al. 2022), a better understanding of their fishery, at large scales, is clearly important. Previously, this endeavour has been constrained by the scarcity of large-scale fishery-dependent datasets. However, the Sea Around Us project has been pivotal in overcoming this limitation, with this project now providing global time series data on reported and reconstructed fisheries catches (Pauly et al. 2020). This project conducts taxon and fishery-specific catch data reconstructions by analysing additional fisheries, socio-economic, and population data sources, offering both total catch (in tonnes) and fishing effort (kW) estimates for various fishing sectors at the country/territory level. These large-scale fishery-dependent data have previously been instrumental in identifying the data-poor and underreported nature of small-scale fisheries across Pacific islands (Zeller et al. 2015) and the possible global decline in the production potential of coral reef fisheries (Eddy et al. 2021).

Here, we utilized large-scale catch estimates of three archetypical tropical fish groups that are predominantly considered nominal herbivores (i.e. surgeonfishes, parrotfishes, and rabbitfishes; Figure 4.1), to examine how yields are related to potential biogeographic, geomorphic, and social correlates and ecosystem attributes. Our analysis involved fishery-dependent data, including total catches (in tonnes), and indirect measures of fishing pressure, namely catch-per-unit effort (CPUE), from the Exclusive Economic Zones (EEZs) of 69 nations (i.e. countries and territories), spanning the period from 1950 to 2019, with an emphasis on the most recent decade from 2009 to 2019. Moreover, we evaluate how these fishery estimates change over time and consider how the specific life histories of herbivorous fishes may enhance their ability to withstand exploitation and adapt to future changes.

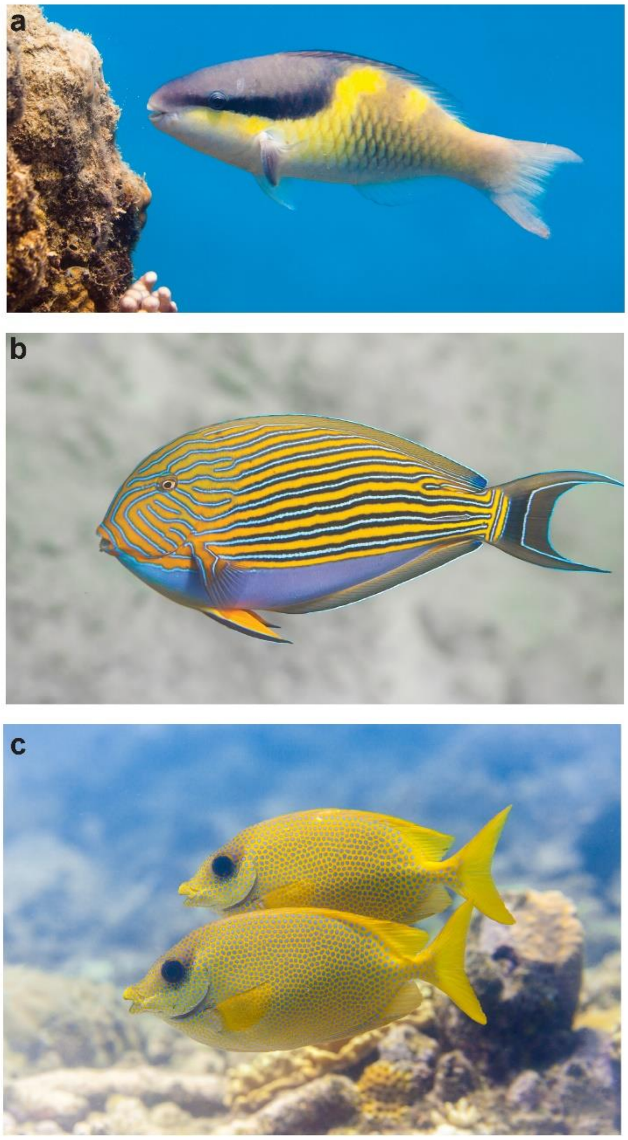

Figure 4.1 Species from the three focal herbivorous fish groups. The a) parrotfish (Scarus oviceps), b) surgeonfish (Acanthurus lineatus), and c) rabbitfish (Siganus corallinus) (images V. Huertas).

4.3 Materials and Methods

4.3.1 Catch data collation

Our study focused on three groups of fishes: parrotfishes, surgeonfishes, and rabbitfishes, which are widely recognized as the primary tropical nominal herbivorous fish groups (Tebbett et al. 2023a). These three groups are ecologically important (Bellwood et al. 2004; Adam et al. 2015) and contribute to numerous artisanal and subsistence fisheries (Robinson et al. 2011; Hicks and McClanahan 2012; Bejarano et al. 2013; Samoilys et al. 2017; Fulton et al. 2020). To examine how the catch of these three nominal tropical herbivorous reef fish groups varied between realms, we compiled a dataset using reported and reconstructed catch data from the Sea Around Us Project (Pauly et al. 2020) which reports landings data (in tonnes) for each taxonomic group (from 1950 onwards) from a nation’s Exclusive Economic Zones (EEZ). Here, we included both countries’ and territories’ EEZs that reported individual landings data; for example, although the Andaman and Nicobar Islands are not an independent state, their landings data were reported separately from those of India and were thus treated as an individual nation in our analyses. It is crucial to highlight that global catch data are limited by what nation’s actually report annually to the Food and Agriculture Organization of the United Nations, which can be improved with reconstructions (as done by the Sea Around Us Project; Pauly and Zeller 2014). Although small-scale artisanal and subsistence fisheries are typically underreported (Sale 2008; Teh et al. 2013), such as those targeting herbivorous fishes, non-commercial fisheries can contribute up to 80% of the total production in coastal fisheries in certain countries (Dalzell et al. 1996; Grafeld et al. 2017). Consequently, the use of catch data here, particularly the analyses of average total catch across herbivorous fish groups and average catch-per-unit-effort, are likely to be conservative estimates as true catch values are likely much higher.

We generated a list of species and genera for each herbivorous fish group from Acanthuridae, ‘Scaridae’, and Siganidae from Fish Base (Froese and Pauly 2022). Note, although parrotfishes are taxonomically within the family Labridae, they are still often reported as ‘Scaridae’ (cf. Bellwood 1994). We then extracted all available taxon-specific catch data for each at the species, genus, and family level to avoid incomplete catch data due to the variation of taxonomic resolution of reported and reconstructed catches. In addition, Sea Around Us provides catch data categorized by ‘functional groups’, with one of these groups being all reef-associated fishes. Therefore, following the same approach as above, we also extracted catch estimates for all reef-associated fishes from the same EEZs, as well as overall catch by each EEZ per year.

We applied the methods outlined by Eddy et al. (2021) to calculate catch per unit effort (CPUE) for each group (i.e. surgeonfishes, parrotfishes, and rabbitfishes) from 1950 to 2010. We first determined the proportion of herbivore catch for each group from the total catch of all reef-associated fishes in each EEZ from 1950 to 2010. We then multiplied each EEZ's total fishing effort, which we extracted from the Sea Around Us database (Greer 2014), by that proportion. Lastly, we divided the total herbivorous fish catch by the estimate previously calculated (i.e. effort multiplied by the proportion) (Text C2). To ensure comparability in effort and associated CPUE calculations, we focused solely on effort expended in the subsistence and artisanal sectors, excluding gear types not commonly used for harvesting herbivorous fishes (i.e. Drifting Longlines, Driftnets, Gleaning, Lampara, Longline Not Specified, Midwater Shrimp Trawl, Pelagic Longline, Set Longline, and Trolling). This produced a comparable relative estimate of CPUE for each herbivorous group per EEZ per year. Fishing effort data was only available for 1950-2010, limiting CPUE analyses to that period.

Both total catch and CPUE offer crucial insights for understanding fisheries dynamics. Total catch provides a comprehensive view of harvesting scale, aiding in the evaluation of fishing's overall influence on aquatic resources (Pauly et al. 2013). In contrast, CPUE assists in assessing the effectiveness and impact of fishing efforts. It may reveal trends that arise from the interplay between harvested biomass and fishing effort expenditure, acting as an indicator of relative biomass (Eddy et al. 2021). By analysing both metrics, our objective is to disentangle trends within small-scale seascape-associated fisheries in a more comprehensive manner, allowing for more informed inferences regarding large-scale correlates. Temporal trends in total catch, fishing effort, and CPUE for each herbivorous fish group were plotted across the entire dataset, which spans from 1950 to 2020 (1950-2010 for fishing effort). It is important to note that these trends serve as an overview of the dataset and were not subjected to formal analysis, as the primary focus of this study was placed on the most recent decade which has the most robust data.

4.3.2 Environmental and socioeconomic variable collation

We used large-scale geomorphic and social variables to assess how potential correlates and ecosystem attributes could modify herbivore catches. To explore potential biogeographic differences, we assigned each EEZ a biogeographic location following the general delineation of realms by Kulbicki et al. (2013). Namely, we separated EEZs into the Indo-Pacific and the Western Atlantic. We focused on the Indo-Pacific and Western Atlantic as these areas incorporate the majority of countries bordering coral reefs (Wong et al. 2022), as well as major marine biodiversity hotspots (Roberts et al. 2002). We found that in the Tropical Eastern Pacific (TEP), only Nicaragua and Colombia had available data for reconstructed or reported herbivorous fish catch. However, due to the nature of our covariates, which are primarily country-based, and considering the complexity of differentiating catch estimates between the Pacific and Caribbean sides of these countries, we chose to categorize both Nicaragua and Colombia as part of the Western Atlantic region. This decision was influenced by the fact that a significant portion of their EEZ and shelf area is located in the Caribbean, the inherent evolutionary link between the TEP and Western Atlantic, the comparatively depauperate fish fauna, and the absence of rabbitfishes in both biogeographic realms (Kulbicki et al. 2013; Siqueira et al. 2019a, 2019b).

Area estimates of each EEZ, as well as a spatial layer of their global distribution, were accessed via the Flanders Maritime Institute (Flanders Marine Institute 2019). Using a global coral reef distribution layer (UNEP-WCMC et al. 2021) and global bathymetry layer (GEBCO Compilation Group 2023), we estimated the area of reef habitat and shallow coastal habitat (0-30 m depth) area within each EEZ using ArcGIS Pro 2.9.0. The global reef distribution layer was derived from the Millenium Coral Reef Mapping Project that mapped geomorphic reef classes globally at a 30 m resolution using Landsat 7 satellite imagery (Andréfouët et al. 2006). The global bathymetry layer was derived from a 30 m resolution global terrain model for ocean and land, closely matching the reef area resolution (GEBCO Compilation Group 2023). We limited shallow coastal habitats to the tropics (i.e. between 30 degrees North and South) as we were examining tropical herbivorous fish groups. We intersected global reef and shallow water habitat distributions with the EEZ spatial layer, after projecting each to the Equal Earth projection (EPSG 1078), to calculate both coral reef area and shallow water habitat area per EEZ. Importantly, shallow coastal habitat area and reef area were highly correlated (Pearson's r = 0.84; Figure C6). Thus, in our statistical analyses, we solely included reef area as a predictor to avoid collinearity.

A range of social correlates were included and assigned to each EEZ to determine the potential relationship between socio-economic factors affecting herbivorous fish catches. Social variables included coastal population density levels, Marine Dependency Score (MDS), and Ocean Health Index (OHI), which were chosen because of their availability at an EEZ level, and their contribution to varying aspects of human dependence on marine resources. The coastal population density for each EEZ was estimated using a 100 km buffer along the coastline of each EEZ and a population density raster from 2010 and 2020 (Center for International Earth Science Information 2022). We then calculated population density per reef area by dividing coastal population density by the estimated reef area for each EEZ for both time periods (following Houk et al. 2012; Brewer et al. 2013; Campbell et al. 2014; Samoilys et al. 2019). For modelling purposes, in cases where the population density per reef area was zero (such as isolated island states like Wake Island), we assigned a low value (0.1), which corresponds to 10% of the lowest value found in the dataset.

We also used the Marine Dependency Score (MDS) as a standardised measure of the importance of marine-derived services as it encompasses the nutritional, economic, and coastal protection dependency of each nation (Selig et al. 2019). This relatively novel conceptual framework represents a detailed quantitative assessment of the level of human dependence on marine ecosystems based on the value of the benefit, vulnerability to loss, and availability of substitutes (Selig et al. 2019). Although published in 2019, the MDI calculations primarily relied on datasets from 2011, thus reducing temporal disparities between response and explanatory variables in our statistical analyses. Because the Ocean Health Index (OHI) is a framework for assessing the health of marine ecosystems based on ten broad ecological, social, and economic goals (Halpern et al. 2012), it was also included in our analyses. OHI values were available from 2012 onwards. Other social variables like the Human Development Index or Gross Domestic Product (GDP) are only available at a sovereignty (i.e. country) level, whereas OHI and MDS are available for countries and territories. By using both indices in our analyses, we can comprehensively account for both the state of the surrounding marine environment as well as the usage of marine resources.

4.3.3 Statistical analyses

To explore the relationship between our fishery estimates (average total catch and average CPUE) and large-scale environmental and socioeconomic covariates, we employed Generalized Linear Models (GLMs). Renowned for their versatility and effectiveness across various applications (Zuur et al. 2009), GLMs possess a key feature—proficiency in fitting predictors, enabling us to compare the effects of predictor variables on the response variable (Bolker et al. 2009; Harrison et al. 2018). In addition, we centred and scaled all continuous predictors (via *z*-score transformations), a process aimed at enhancing the relative interpretability of regression coefficients across multiple predictors (Schielzeth 2010).

To generate a single estimate of catch for each herbivorous group per EEZ for analysis, we used the average total catch (i.e the average summed/total catch across reported years) for each group over the most recent decade available (i.e. from 2009-2019). To examine the relationship between average total herbivore catches between 2009 and 2019 and the set of explanatory variables, we used GLMs with a Gamma distribution and a log-link from the *glmmTMB* package (Brooks et al. 2017) as the average total catch was never zero. Specifically, we assessed if reef area (km^2), realm (i.e. Indo-Pacific and Western Atlantic), and social correlates (i.e. OHI, MDS, and/or coastal population per unit reef area), were related to average total fishery catches of each herbivorous fish group. We used the average OHI from 2012 to 2019 and population density data from 2020 to ensure close temporal alignment. For all GLMs, average total catch for each group from each EEZ was treated as the response variable, while realm was treated as a categorical fixed effect and all other variables as continuous fixed effects. All continuous fixed effects were centred and scaled by subtracting the mean and dividing by the standard deviation, while reef area and coastal population per reef area were also logged. We specified models with an interaction between realm and reef area, and additive effects between all social covariates (i.e. no interactions). Subsequently, when models were indistinguishable based on Akaike Information Criterion corrected for small sample sizes (i.e. Δ AICc < 2), we chose the most parsimonious model (Table C1).

We also used GLMs with a Gamma distribution and a log-link to assess the relationship between CPUE of all herbivorous fishes and the same set of explanatory variables. Since effort data was only available until 2010 and only for 62 of the EEZs included in this analysis, we used the average CPUE of all nominal herbivorous groups over the five most recent years available (2005-2010). Although this analysis represents only a subset of those used to assess average total catches, these 62 nations still accounted for 84% of the total catches. Using the average CPUE between 2005-2010 of all herbivorous groups, we generated a single, positive estimate of CPUE per EEZ and treated this as the response variable. To ensure consistency in the temporal scales of our explanatory variables, we utilized the OHI from 2012 and coastal population density data from 2010, while keeping the other explanatory variables constant. Furthermore, to investigate whether the significant interaction between reef area and realm, as well as the impact of OHI on the average CPUE, was driven by a single outlier (Niue), we used the same GLM structure on a dataset that excluded Niue (Table C2). However, we had no biological or socio-economic reason to remove the outlier, so we show the complete analyses and results for full transparency. All model assumptions and fit were assessed using simulated residuals, which were satisfactory in all cases (package: '*DHARMa'*; Hartig 2022). All statistical analyses and data manipulations were performed using the software R 4.2.2 (R Core Team 2022) and '*tidyverse'* package (Wickham et al. 2019).

4.4 Results

4.4.1 Herbivorous fish catches – an overview

Between 1950 and 2019, a total of 69 EEZs in the Sea Around Us database harvested parrotfishes, rabbitfishes, and/or surgeonfishes (Figure 4.2a). During this period, total catch (i.e. the sum of all herbivorous fish catches in each of the 69 EEZs across years) per km^2 of reef area increased for all groups. Notably, the catch of rabbitfishes increased the most, from 0.16 tonnes per km^2 to 0.73 tonnes per km^2 between 1950 and 2019, while the catch of parrotfishes and surgeonfishes increased from 0.12 tonnes per km^2 to 0.15 tonnes per km^2 and 0.1 tonnes per km^2 to 0.17 tonnes per km^2, respectively (Figure 4.2b). Importantly, the notable increase in total rabbitfish catches from 1950-2019 (Figure 4.2b) can, at least partially, be attributed to a substantial increase in fishing effort for this group, which, in 2010, was almost 8-fold higher than parrotfishes and surgeonfishes combined (Figure 4.2c). Furthermore, rabbitfishes consistently contributed the most to the total catch of all herbivorous fishes (Figure 4.2b). This pattern remains consistent when considering the families relative to catch of all reef-associated fishes (Figure C1). Nonetheless, the contribution of rabbitfishes to total reef-associated fisheries has declined from 7% to 4.6%, with similar declines in the contribution of parrotfishes and surgeonfishes over the same period (Figure C1).

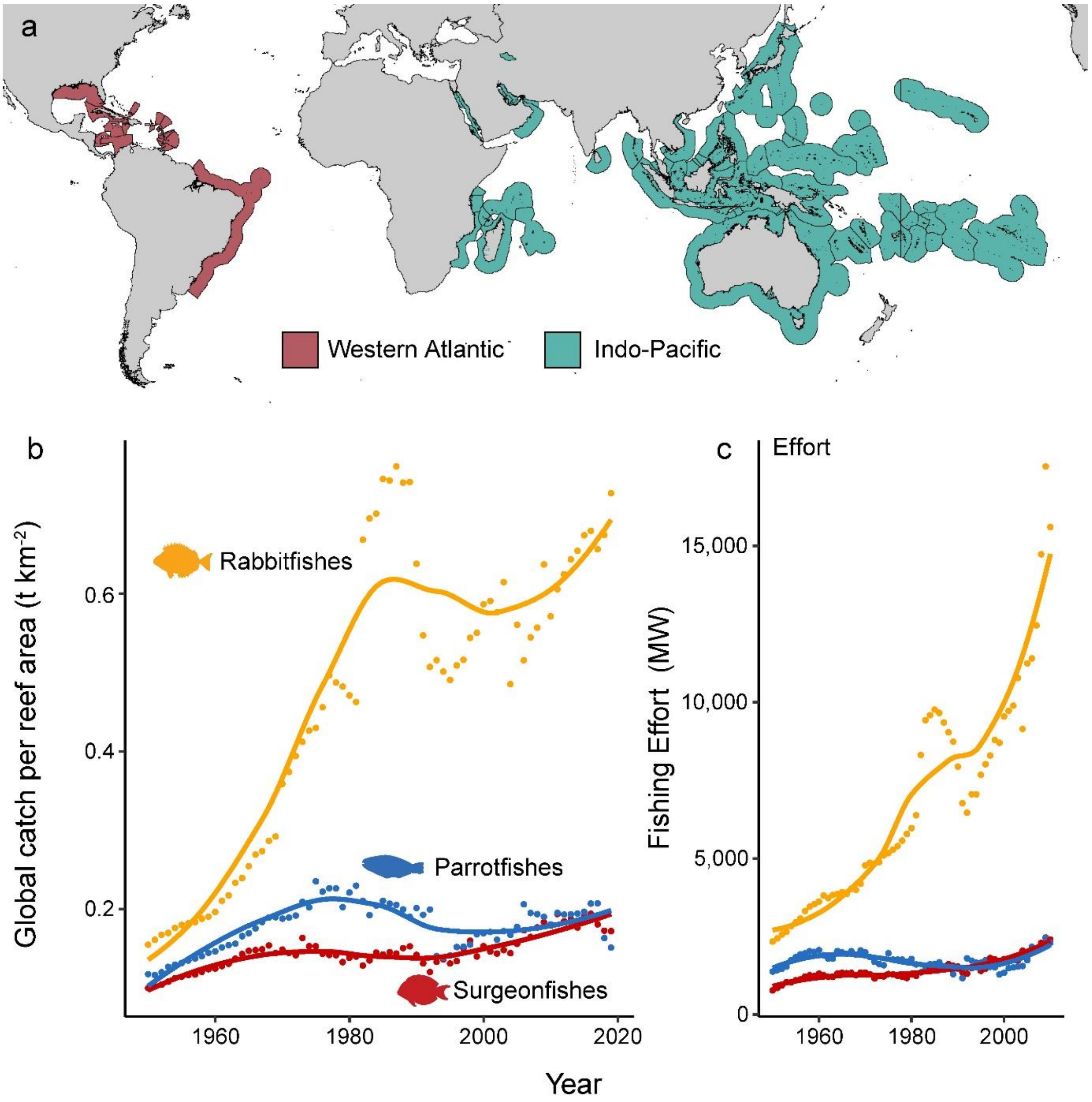

Figure 4.2 Temporal patterns of tropical herbivorous fish catch data. a) Location of the 69 Exclusive Economic Zones (EEZs) included in the analysis, b) total catches of herbivorous fishes, standardised by reef area, across all EEZs per year between 1950-2019, and c) the total fishing effort (Mega Watts) for each herbivorous fish group across all EEZs per year. In all panels, points are the raw data points (i.e. sums of annual estimates across all EEZs) while the lines were produced by the loess function of the '*stats'* package (R Core Team 2022) and are used for illustration purposes only.

4.4.2 Spatial distribution of herbivorous fish catches

Based on the initial exploration of the data, rabbitfishes appear to disproportionately contribute to large-scale catch patterns. But, this initial overview did not consider the inherent spatial variability in the data, nor the potential drivers of this variability. To explore how average total herbivorous fish catches (in tonnes) were spatially distributed, and how this variability related to key correlates, we focused on the most recent 10 years of data (2009-2019) available. These data are likely to be the most robust as they consist of fewer reconstructed catch estimates and allow the most reliable comparison with recent estimates of both geomorphic and social covariates. During this ten-year period, the average total catches of herbivores (i.e. the average annual total catch of herbivorous fishes within each of the 69 EEZs between 2009-2019, calculated by summing the yearly catches per EEZ and then averaging them over the decade) was spatially heterogenous, ranging from 0.01 tonnes in Eritrea to 22,572 tonnes in the Philippines (Figure 4.3a-c). In addition, as expected based on the biogeographic distribution of rabbitfishes (i.e. they are absent from the Western Atlantic; Siqueira et al. 2019a), the data also shows that rabbitfishes were only a major contributor to the herbivore catch in the Indo-Pacific, while both surgeonfishes and parrotfishes were harvested across both realms (Figure 4.3a-c).

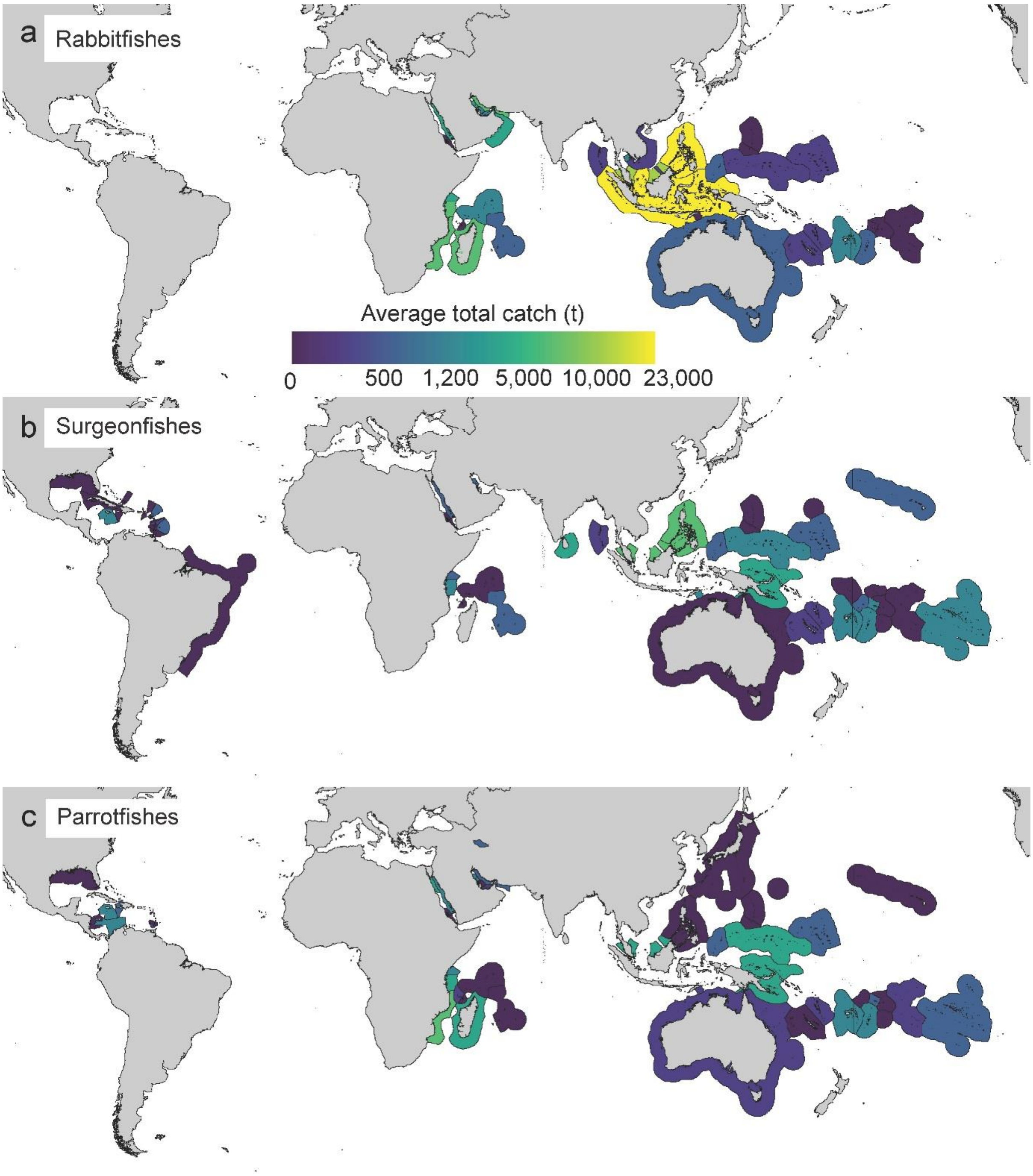

Figure 4.3 Spatial distribution of tropical herbivorous fish catches. The average total catches (i.e. the average annual total catch of herbivorous fishes within each of the 69 EEZs between 2009-2019, calculated by summing the yearly catches per EEZ and then averaging them over the decade; in tonnes; t) of a) rabbitfishes, b) surgeonfishes, and c) parrotfishes across Exclusive Economic Zones (EEZs) between 2009 and 2019.

4.3.3 Potential correlates of herbivorous fish catches

Given the heterogenous distribution of average total herbivorous fish catches over the most recent decade, we formally tested their variability and correlation to potential covariates using generalised linear models (GLMs) for each herbivorous fish group. The unequal distribution of catches around the globe (Figure 4.3a-c) follows previous suggestions that consumption is often highest in developing nations with extensive coastal populations (Allison et al. 2009; Hicks et al. 2021), where social drivers often have strong relationships with fishery yields (e.g. Brewer et al. 2013; Cinner et al. 2016; Seguin et al. 2023). We therefore explored how a range of large-scale biogeographic, geomorphic, and social factors, previously linked to fishery yields, were related to herbivore catch. Specifically, we considered reef area, the Marine Dependency Score (MDS; Selig et al. 2019), Ocean Health Index (OHI; Halpern et al. 2012), and coastal population standardised per km^2 of reef area (Houk et al. 2012; Brewer et al. 2013; Campbell et al. 2014; Samoilys et al. 2019).

Across all herbivorous fish groups, we found that reef area stood out as the sole consistently significant covariate (Figure 4.4a-c; Table C2; see Figure C2 for raw data points). Generally, the GLMs employed to evaluate the relationship between the average total catch (in tonnes) of each herbivorous fish group over the last decade and our large-scale covariates indicated an increase in average total catch across all herbivorous fish groups with greater habitat availability. Rabbitfishes, in particular, displayed the highest average catch for any given reef area (Figure 4.4a-c). Furthermore, for rabbitfishes, reef area (*$p < 0.001$*; Figure 4.4a; Table C2), coastal human population per km^2 of reef area (*$p < 0.001$*; Figure C3a; Table S2), and OHI (*$p = 0.03$*; Table C2) were able to explain over 67% of the variability in average total catches across EEZs between 2009 and 2019. Average total catch of surgeonfishes differed between realms (*$p = 0.01$*; Figure 4.4b; Table C2) and was positively correlated to reef area *($p < 0.01$*; Figure 4.4b; Table C2), coastal population per km^2 of reef area (*$p < 0.001$*; Figure C3b; Table C2), and MDS (*$p = 0.04$*; Table C2). Lastly, reef area alone (*$p < 0.001$*; Figure 4.4c; Table C2) explained over 54% of the variability in parrotfish catch. Overall, these results highlight that, at a large scale, EEZs that contain larger areas of shallow reef habitat and higher coastal human population densities, landed higher catches of herbivorous fishes.

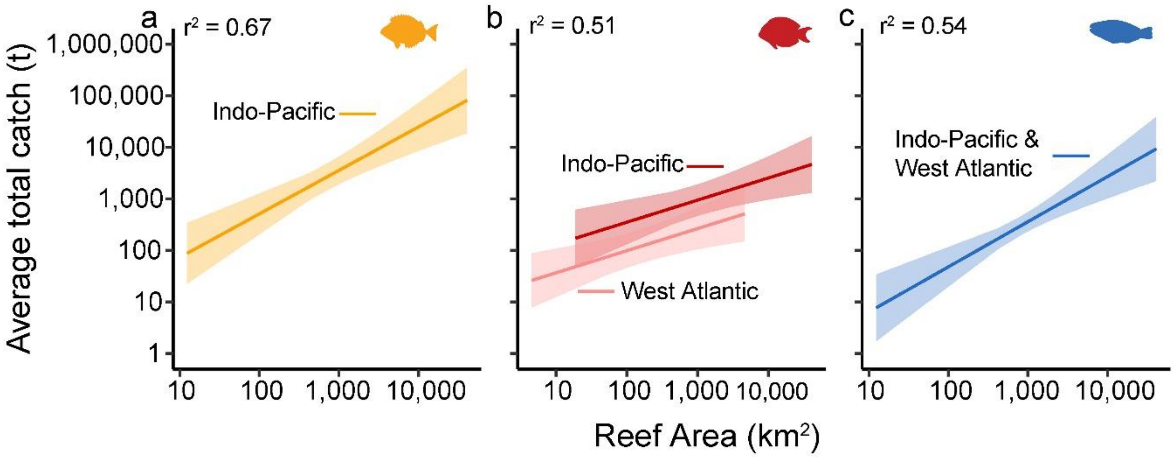

Figure 4.4 Herbivorous fish catches among major realms. The relationship between the average total catch (2009-2019) of a) rabbitfishes (r^2 = 0.67), b) surgeonfishes (r^2 = 0.5), and c) parrotfishes (r^2 = 0.54) and the corresponding reef area (km^2) across the Indo-Pacific (darker colours) and Western Atlantic (lighter colour in panel b). Lines show the mean predicted fits from generalised linear models, shaded ribbons are the 95% confidence intervals. Note the y- and x-axes are on the $\log_{10}$ scale in both cases and the r^2 value refers to the fit of the entire model. For a version of this figure with raw data points refer to Figure C1 in the supplemental material.

4.4.4 Herbivorous fishes as fisheries resources

While the analyses above provide insights into geomorphic and socio-economic correlates of average total catches across each herbivorous fish group, it is obvious that fishing effort is likely a determining force as well (Figure 4.2c). When we examined catch-per-unit-effort (CPUE) for rabbitfishes, surgeonfishes, and parrotfishes, effectively standardizing total catch by fishing effort, clear declines were apparent between 1950 and 2010 (Figure 4.5a). These declines in CPUE were greatest for rabbitfishes with a 60% decrease compared to a 42% and 52% decrease in surgeonfishes and parrotfishes, respectively (Figure 4.5a). We used GLMs to assess how the factors (i.e. the same covariates as above) were linked to variability of the average CPUE (tonnes per kW) for all herbivorous fish groups combined for the most recent five years available (2005-2010). In doing so, we revealed a significant negative relationship between coastal population density and average herbivorous fish CPUE ($p < 0.001$; Figure 4.5b; Table C2). Furthermore, average CPUE between 2005 and 2010 was significantly positively correlated with reef area in the Western Atlantic ($p < 0.001$, Table C2), but not the Indo-Pacific, and was significantly positively correlated with the Ocean Health Index ($p < 0.01$, Table C2).

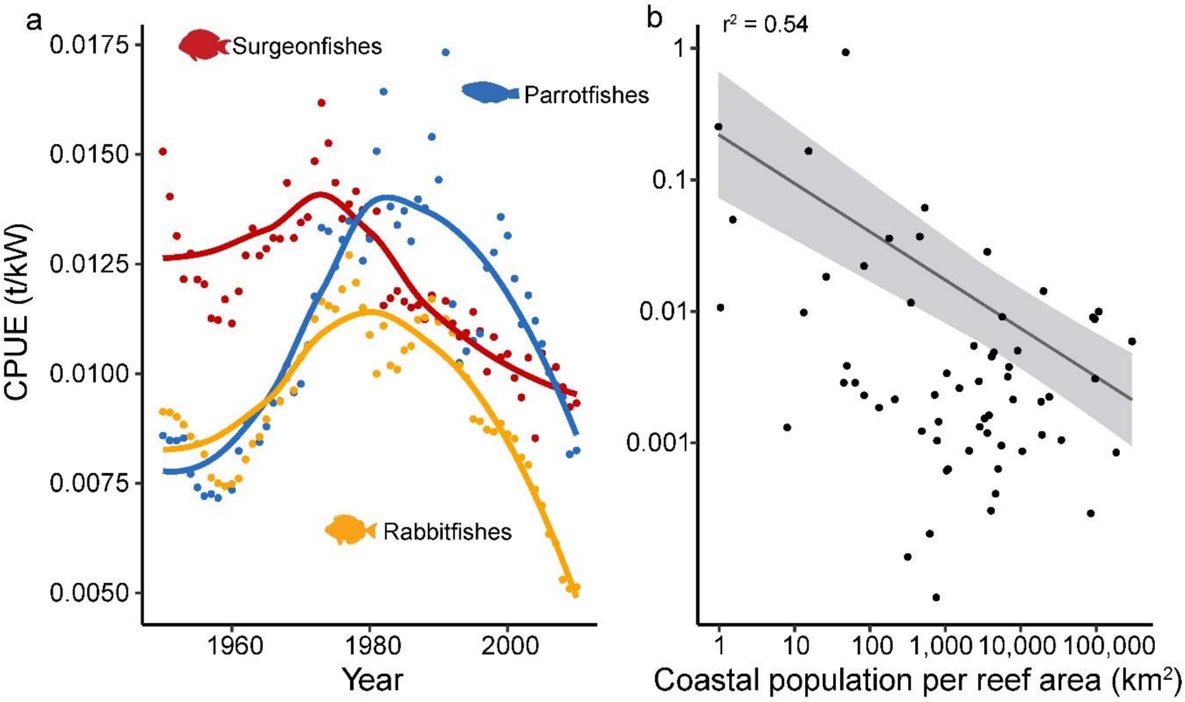

Figure 4.5 Tropical herbivorous fish catch-per-unit-effort. A) Catch-per-unit-effort (CPUE) of each herbivorous fish group across all EEZs between 1950-2010, and b) the relationship between average CPUE (tonnes per kW) of all herbivorous fish groups between 2005-2010 vs. coastal human population per km^2 of reef area ($r^2 = 0.54$). In panel a), points are the raw data points (i.e. sums of CPUE annual estimates) and the lines were produced by the loess function of the '*stats'* package (R Core Team 2022) and are used for illustration purposes only. In panel b) the points represent the raw data points (i.e. the average CPUE of all herbivorous fish groups between 2005-2010) and the lines show the mean predicted fits from generalised linear models, shaded ribbons are the 95% confidence intervals. Note the y- and x-axes are on the $\log_{10}$ scale (which is why the majority of points appear to fall below the fitted line) and the r^2 value refers to the fit of the entire model.

4.5 Discussion

Our study explored 70 years of large-scale herbivore catch data from the Exclusive Economic Zones (EEZs) of 69 nations to examine the contributions of parrotfishes, rabbitfishes, and surgeonfishes to fishery catches. As expected, we found that reef area and coastal human population density were the strongest predictors of average herbivore catch. However, we also revealed that rabbitfishes yielded the highest contribution to catches across all herbivorous fish groups. Furthermore, despite increasing average total catches, our study reports a concerning decline in the CPUE for all three herbivorous groups over the same period. Our findings indicate potential global decrease in production potential of these functionally important herbivorous fish groups from coastal seascapes in recent years. This has clear implications for the critical ecosystem functions that these fishes deliver across coastal seascapes, as well as for the ongoing sustainability of current fishery yields.

We observed that average herbivore catches increased with higher human population density and reef area. However, when standardised for fishing effort, we revealed a negative relationship between CPUE of herbivorous fish groups and coastal population density, indicating that higher human densities may contribute to the decrease in production potential of herbivorous fishes through increased fishing effort. These results suggest that: a) there may be an area-dependent baseline level of catch that is consistent across large-scales, irrespective of social drivers, b) that coastal fishers in tropical seascapes catch the fishes available to them in accessible habitats (Samoilys et al. 2017; Robinson et al. 2020), and c) that more people lead to higher herbivorous fish catches, but as human density increases CPUE declines dramatically, which is likely due to a reduction in fishable biomass (Edwards et al. 2014; Heenan et al. 2016). Consequently, nations with larger areas of shallow reef habitats may be better positioned to extract more resources, in terms of herbivorous fishes, while smaller nations with limited access to such habitats may face challenges in meeting their resource needs, particularly as human populations grow (Robinson 2020).

While it is well established that human activities have a significant impact on coastal habitats and their capacity to provide ecosystem services at smaller scales (Brewer et al. 2013; Cinner et al. 2016; Seguin et al. 2023), our results indicate that social correlates, other than human population density, had a limited relationship with large-scale herbivore catch patterns. This finding is consistent with previous studies in the Indo-Pacific region that also found distinct relationships between human density and reef fish trophic structure, but limited relationships with other social variables (Ruppert et al. 2018). However, it is important to note that the manner in which links between fisheries catches, social correlates, and habitat area manifest in the data could be dependent on the scale examined. For example, a study in Timor-Leste found that the availability and distribution of shallow reef habitat can play a critical role in determining the success of livelihood strategies that rely on them (Grantham et al. 2021). Human engagement with ecosystems can, therefore, be influenced by the constraints and resources arising from the type and extent of shallow reef habitat (Grantham et al. 2021). Hence, at smaller scales, an interconnection between reef area and social correlates could dictate the nature and extent of human-nature interactions in coastal areas. However, at a regional or national scale, the availability of habitat and the density of humans that can exploit that habitat appear to be the primary correlates that account for most of the variability in herbivore catch data. In this respect, at a between-realm scale, it is also important to consider the types of fishes available to fishers in different areas.

Fish communities across tropical seascapes in the Atlantic and Indo-Pacific differ fundamentally in composition and diversity (Kulbicki et al. 2013), with significant implications for what is available to people. In terms of herbivorous fishes, the Western Atlantic has a far less diverse fish fauna than the Indo-Pacific, exemplified by the complete absence of rabbitfishes in the Atlantic (Siqueira et al. 2019b). Interestingly, the high contribution of rabbitfishes to herbivorous fish catch in the Indo-Pacific aligns with evidence from smaller scale studies, which show that rabbitfishes can account for up to 60% of total fisheries catch (by weight) in some areas (Hicks and McClanahan 2012; Muallil et al. 2014; FAO 2023). Moreover, previous studies in the Indo-Pacific have highlighted the ability of rabbitfishes to maintain coastal fishery yields even in the face of ecosystem change (McClanahan et al. 2008; Rogers et al. 2018; Robinson et al. 2019; Hamilton et al. 2022). For example, Robinson et al. (2019) found that despite extensive coral reef change caused by a mass coral mortality event and persistent macroalgal regime shifts, fishery yields in the Seychelles were maintained; driven primarily by a 2-fold increase in the CPUE of rabbitfishes. Together, these lines of evidence suggest that rabbitfishes may have traits that make them more capable of withstanding both ongoing fishing pressure and environmental change.

The life history characteristics of fishes that can help withstand fishing pressure include shorter generation times and higher somatic growth rates (Jennings et al. 1998; Denney et al. 2002; Zhou et al. 2012; Abesamis et al. 2014). Both traits bolster population growth rates and fishable biomass production, potentially enhancing resistance to overfishing through rapid population turnover (Jennings et al. 1998; Denney et al. 2002; Zhou et al. 2012; Abesamis et al. 2014). Rabbitfishes possess both exceptional life history traits, reaching their asymptotic size twice as fast as parrotfishes and surgeonfishes (Text C1; Figure C5), and demonstrating an ability to reproduce and recruit to fishery sizes within one year (Grandcourt 2002). These faster life history strategies may be coupled with their remarkable habitat versatility, which enables them to thrive in a diverse range of environments, including clear-water, coral-dominated reefs, and mangrove-dominated turbid estuaries (Sambrook et al. 2019, 2020). With over 50% of rabbitfish species exhibiting this versatility (Sambrook et al. 2019, 2020), and some species having wide home/occupancy ranges (Kaunda-Arara and Rose 2004; Ebrahim et al. 2020), their adaptability to various habitats is evident. The combination of key life history traits and a capacity to occupy a range of habitats may, therefore, underpin the high contribution of rabbitfishes to fisheries catches.

However, the sustainability of rabbitfish catches, as well as those of parrotfishes and surgeonfishes, within their native range remains uncertain. A recent study revealed a significant decline of 63% in CPUE of reef-associated fishes since the 1990s, compromising the production potential of coral reef fisheries (Eddy et al. 2021) and potentially affecting the coastal communities reliant on these fishes (Cinner et al. 2012; Hicks et al. 2021). Our analysis, employing similar methods, indicates that the decline in CPUE for parrotfishes, surgeonfishes, and rabbitfishes is less than the global average decline for reef-associated fisheries. However, rabbitfishes, in particular, have experienced an alarming decrease (over 60%) in CPUE from 1950 to 2010, raising concerns over potential over-exploitation. Whilst rabbitfishes exhibit life-history traits that may increase resilience, their unique reproductive biology, characterized by benthic spawning (Woodland 1990) and the vulnerability of large spawning aggregations to fishing (Grandcourt et al. 2007; Robinson et al. 2011; Samoilys et al. 2013), may contribute to their susceptibility to overexploitation.

Although high somatic growth rates can potentially support higher catch rates in rabbitfishes, exploitation before sexual maturity and the targeting of both adult and juvenile specimens have led to growth and recruitment overfishing of rabbitfishes in certain regions (Grandcourt et al. 2007; Hicks and McClanahan 2012). Furthermore, rabbitfishes seem to be more susceptible to specific gear types than other herbivorous fishes; notably nets and traps which account for approximately 27% and 22% of all artisanal rabbitfish catches (Figure C6). These findings align with previous local studies that have emphasized the vulnerability of rabbitfishes to various gear types, with nets and traps frequently being the primary contributors to the overall catch (McClanahan and Mangi 2004; Soliman et al. 2009; Hicks and McClanahan 2012; Samoilys et al. 2017). For instance, McClanahan and Mangi (2004) observed that while *Siganus sutor* contributed around 16% to the total catch across all gear types, it displayed the highest susceptibility to gill nets (32% of the total catch) and large traps (21% of the total catch). To ensure the sustainability of rabbitfish fisheries, effective management measures, such as size-based catch restrictions, seasonal fisheries, and gear modifications, could be effective (Hicks and McClanahan 2012; Gomes et al. 2014; Condy et al. 2015; Carvalho and Humphries 2022). These management strategies may be essential to safeguard the potential of rabbitfishes as a resilient and sustainable component of coastal seascape fisheries.

Coastal fisheries are crucial for sustaining food security in the Anthropocene, and herbivorous fishes, which play key ecosystem roles, are part of this equation. By revealing that habitat extent and coastal human population densities are large-scale factors that relate to herbivorous fish catches and CPUE, we highlight the potential for a growing mismatch between increasing population levels and area-dependent fisheries productivity. This mismatch has particularly large ramifications for developing countries, such as island nations, which are limited by small available habitat areas. Moreover, given the distinct declines of CPUE across all herbivorous fish groups, as well as reef fishes more generally (Eddy et al. 2021), the data suggests that these ecologically important fishes may already be exhibiting decreased production potential (overexploitation?) at large-scales. To ensure the sustainability and resilience of coastal seascape fisheries, it is crucial to advance our understanding of herbivorous fish fisheries, and to implement effective management of diverse tropical seascapes in a changing world.

Chapter 5. General Discussion

In the year 2023, during which much of this thesis' research took place, humanity found itself navigating uncharted territory in the climate crisis, marked by unprecedented extremes (IPCC 2023; Ripple et al. 2023). With numerous days surpassing the global average temperature by 1.5 degrees Celsius, the year held significant implications for coastal seascapes, particularly coral reefs (Ripple et al. 2023). Consequently, 2023 became another record-breaking year, marked by an escalating scale of anthropogenic stressors on coral reefs, leading to a reconfiguration of their benthic composition and functionality. However, I discovered that current methodologies for assessing such large-scale transformations on coral reef ecosystems face serious scale-related limitations. Current approaches have not yet effectively incorporated the increasing scale of threats and they may thus inadequately assess large-scale transformations. To illustrate how upscaling coral reef studies can provide novel insights into drivers of ecosystem functioning I provide two examples of vital coral reef ecosystem functions (reef development [Chapter 3] and fisheries yield [Chapter 4] at large scales. Firstly, coral growth and reef development were shown to be distinct processes. Reef development and growth, a geological phenomenon, doesn't appear to be shaped by region (i.e. by ocean basin), but rather a local-scale phenomena, where local hydrodynamics appear to override large-scale biogeographic and evolutionary histories. In contrast, herbivorous fisheries exhibit a markedly different pattern, with national variations in catches influenced primarily by social correlates. However, at the global scale, I observed a pronounced negative trend in catch-per-unit-effort, indicating the potential for a global decrease in production potential of these fishes. Furthermore, total fisheries catches at a regional scale appear to be area-dependent, carrying significant ramifications, particularly for nations characterized by limited coastal shallow water habitat and high population growth.

Importantly, to comprehensively grasp the benthic dynamics and associated shifts in fish and coral fauna within the context of extensive coral reef transformations, it is imperative to use long-term monitoring datasets with standardized protocols (Edgar and Stuart-Smith 2014; Obura et al. 2019; Tebbett et al. 2023b; Yan and Bellwood 2023). However, in **chapter 2** I revealed that, while direct field measurements provide crucial, high-detail data, they are both restricted spatially (i.e. to subsets of coral reef habitat) and temporally (i.e. to single studies), making them hard to upscale without creating scale-artefacts. Remote sensing technologies are rapidly advancing, placing emphasis on ecosystem assessment, which is accurately evaluated through an ecological lens, may help upscale observations (Hedley et al. 2016; Calders et al. 2020; Roelfsema et al. 2021b; Purkis and Chirayath 2022; Remmers et al. 2023). **Chapter 2** identified that the most promising approach involves integrating multiple tools and products, combining broader coverage with higher-resolution data and *in-situ* information

(Dornelas et al. 2019; Bakker et al. 2023). This integration can bridge the gap between point-based ecology and macroecology, enabling a more effective evaluation of environmental change and its drivers across various scales – while reducing scale artifacts.

Beyond the synergies and ways to improve the utility of joint approaches I identify in **chapter 2**, novel emerging technologies that address the trade-off between extent and resolution, as well as spectral signature similarity of algae and coral, may pave the way forward. In particular, LiDAR and fluid lensing may effectively bridge scale-related issues, drawing traditional high-detail *in-situ* observations and remote sensing measurements closer together. Airborne Light Detection and Ranging (LiDAR) utilizes laser light to generate precise three-dimensional information about objects or landscapes (Purkis and Brock 2013). The high-resolution of airborne LiDAR-derived Digital Elevation Models (DEMs), with grid cells often less than 1 meter, allows mapping of fine-scale features and provides information on broad-scale elevation changes across entire coral reef systems (Brock and Purkis 2009; Hostetler et al. 2018; Asner et al. 2020; Harris et al. 2023; Li and Asner 2023). Furthermore, NASA recently introduced an innovative remote sensing technique, airborne fluid lensing using the FluidCam instrument, designed to robustly image underwater objects by overcoming refractive distortions caused by surface waves (Chirayath and Li 2019; Purkis and Chirayath 2022). This technique can create cm-scale 3D images of coral reefs at depths up to ~15m, demonstrating its effectiveness in resolving both sessile benthic ecosystems and mobile targets within the water column (Chirayath and Earle 2016; Chirayath and Instrella 2019; Chirayath 2021). Taken together, the inclusion and integration of diverse approaches spanning multiple disciplines with varying extents and resolutions holds the potential to enhance the effectiveness of upscaling observations and studies, particularly in ecosystems like coral reefs. Generally, these mixed approaches may enable us to overcome the inherent issue of heterogeneity in these systems by aligning with the second law of geography, where "everything is related to everything else, but things observed at a coarser resolution are more related than things observed at a finer scale" (Arbia et al. 1996). Essentially, by upscaling coral reef studies, we have the potential to minimize noise arising from minute relationships, allowing for identification of major, large-scale drivers influencing these processes.

Indeed, applying the theory of integration at scale can amend prior understandings of reef functionality. For instance, reef growth models often presume that the life-history traits and growth capabilities of dominant coral taxa determine a reef's growth rate, both vertically and laterally (e.g. Perry et al. 2018; but see Roff 2020). According to this assumption, a reef dominated by fast-growing branching species should exhibit faster accretion than one dominated by slow-growing massive coral formations. Nevertheless, the findings in **chapter 3** (Lutzenkirchen et al. 2023), coupled with recent research (Roff 2020; Hammerman et al. 2022), challenge this assumption. By upscaling reef size measurements, albeit presenting a single snapshot in time, I found that environmental local-scale drivers, such as hydrodynamics, may homogenise reef width patterns, overwhelming large-scale biogeographical or evolutionary factors. While variations in reef growth rates may exist on local or regional scales, the remarkable consistency in reef widths globally suggests that coral growth as an ecological process and reef growth as a geological process should be treated as distinct entities (a concept that appears to be more clearly understood in geological rather than ecological studies; Toth et al. 2018, 2022). Moreover, it emphasizes the importance of inclusion of other calcifying non-coral reef components in terms of reef growth, a function that is crucial for coastal protection under future sea-level rise scenarios.

In terms of wave dissipation and the wave buffering role of coral reefs, the crucial factor lies in the direct alteration of reef crest/flat elevation, emphasizing the significance of the absolute elevation change rather than particular aspects of change (e.g. loss of fine-scale coral-derived structural complexity) (Ferrario et al. 2014; Kench et al. 2022). Given the decoupling between coral growth and reef growth discovered in **chapter 3**, the significance of non-coral calcifying components in constructing and maintaining coral reef carbonate structures is expected to grow in importance in a future dominated by structurally less complex, turf-algae dominated states (Cornwall et al. 2021, 2023; Tebbett et al. 2023b). Recent research indicates that some crustose coralline algae maintain stable calcification rates under heat treatments, suggesting their ability to sustain vital ecological roles, such as reef accretion, in a warming ocean (Krieger et al. 2023). Therefore, these findings offer some hope that anthropogenic coral reefs, even those without a coral-dominated benthos, can uphold critical ecosystem functions and services, such as reef growth and coastal protection.

Similarly, recent efforts show that despite coral reefs shifting towards high algal turf cover and lower coral cover (Tebbett et al. 2023b), effective management can maintain fisheries productivity to a certain extent. Changes in the structure of fish assemblages, including the increasing abundance of plant material, may result in a rise in abundance/biomass of herbivorous fishes (Pratchett et al. 2018; Robinson et al. 2019; Morais et al. 2020). The findings in **Chapter 4**, strongly support previous work in the Indo-Pacific (Hicks and McClanahan 2012; Muallil et al. 2014; Robinson et al. 2019; Hamilton et al. 2022), and identifies herbivorous fishes, particularly rabbitfishes, as significant contributors to total catches in small-scale (i.e. artisanal and subsistence) fisheries. However, fisheries depend on a constant flux of resource production (Morais and Bellwood 2020). Therefore, elucidating the rates at which biomass is produced and stored as standing biomass (i.e. biomass turnover) is crucial for understanding the long-term stability of fisheries yield (Morais et al. 2020). Recent efforts focusing on ecosystem processes directly revealed a decoupling of standing fish biomass and productivity or fishery yields in coral reef ecosystems (Rogers et al. 2018; Morais and Bellwood 2019, 2020; Robinson et al.

2019; Morais et al. 2021b, 2023). Coral reef fish communities exhibit a level of buffering capacity. This means that the productivity of a given community is less sensitive to fishing-induced biomass or size-structure alterations, therefore exhibiting potential resistance to increased fishing (Morais et al. 2020, 2023). These buffering responses could be particularly influenced by highly productive species that prosper in post-bleaching and altered coral reef habitats, such as herbivores-detritivores (Morais et al. 2020; Hamilton et al. 2022). Indeed, in **chapter 4** I found that rabbitfishes, in particular, may be one such group as they reach their asymptotic size twice as fast as parrotfishes or surgeonfishes. Thus, due to their high productivity, as well as life history characteristics and recent range extensions, they may, if managed correctly, be a vital part of these buffering responses, as well as an integral component of resilient and sustainable coastal seascape fisheries.

These findings underscore the adaptive capacity of coral reef ecosystems, suggesting the potential for sustaining coral reef fisheries in the Anthropocene, especially by prioritizing lower trophic level species and offshore resources (Bell et al. 2018; Hamilton et al. 2022; Robinson et al. 2023). However, **chapter 4** also revealed that the growing catch of herbivorous fishes is likely a result of increasing coastal population density and fishing effort. Although total catches may rise with higher coastal population density, CPUE shows a significant decline, likely attributed to a reduction in fishable biomass. Therefore, vigilance is essential regarding the challenges brought to light by the decline in herbivorous fish CPUE **(chapter 4)** and coral reef fisheries more broadly (Eddy et al. 2021). To reliably assess the longevity and temporal stability of these buffering responses, particularly of herbivores, it is important to ensure that the apparent stability of catches is not the result of catch diversification or fishing ground expansion (Robinson et al. 2020). Modelled relationships need empirical assessment through quantifying *in-situ* catches and fishing effort (Morais et al. 2023), at appropriate scales.

Given that anthropogenic influences are driving fundamental changes to the foundational ecology of coral reefs, the central theme of this thesis was to explore whether adopting a more expansive perspective, through upscaling, offers fresh insights into the functioning of these systems. My research delved into the potential of upscaling ecosystem studies on coral reefs, revealing intriguing results. For instance, reef growth, a geological process, may be primarily dictated by local hydrodynamics. By contrast, patterns in herbivore catches may vary at local scales, potentially distracting attention from large-scale correlates and trends. These findings underscore the advantages of upscaling functional and spatial ecology studies by leveraging basic geographical concepts, where processes at a coarser resolution exhibit stronger correlations than at finer resolutions. Effectively addressing the escalating temporal and spatial impacts of human activity on coral reefs in the Anthropocene will benefit from the alignment of scientific inquiry, monitoring, and management with the scale of pressures faced by these ecosystems. The challenges confronting these vital but delicate ecosystems have never been more pervasive and continue to intensify across space and time. Adopting a more macroscopic approach may rectify existing scale mismatches, ensuring more appropriate application and effectiveness of future coral reef ecosystem management.

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Appendix A: Supporting information for chapter 2

Table A1. List of all studies included in the review.

Authors	Title	Source title	Year
Reverter M., Jackson M., Daraghmeh N., von Mach C., Milton N.	11-yr of coral community dynamics in reefs around Dahab (Gulf of Aqaba, Red Sea): the collapse of urchins and rise of macroalgae and cyanobacterial mats	CORAL REEFS	2020
Meiling, S; Muller, EM; Smith, TB; Brandt, ME	3D Photogrammetry Reveals Dynamics of Stony Coral Tissue Loss Disease (SCTLD) Lesion Progression Across a Thermal Stress Event	FRONTIERS IN MARINE SCIENCE	2020
de Bakker D.M., van Duyl F.C., Bak R.P.M., Nugues M.M., Nieuwland G., Meesters E.H.	40 Years of benthic community change on the Caribbean reefs of Curaçao and Bonaire: the rise of slimy cyanobacterial mats	CORAL REEFS	2017
Richards, Z.T.	A comparison of proxy performance in coral biodiversity monitoring	CORAL REEFS	2013
Burns John H. R., Weyenberg Grady, Mandel Travis, Ferreira Sofia B., Gotshalk Drew, KiNoshita Chad K., Marshall Micah J., Del Moral Nicholas A. V., Murphy Shane J., Pascoe Kailey H., Runyan Alexandra, Spengler Alexander J., Wells Brittany D., Wilde Danielle K., Pelayo Roberto	A Comparison of the DiagNostic Accuracy of in-situ and Digital Image-Based Assessments of Coral Health and Disease	FRONTIERS IN MARINE SCIENCE	2020
Hamylton, S.; East, H.	A Geospatial Appraisal of Ecological and Geomorphic Change on Diego Garcia Atoll, Chagos Islands (British Indian Ocean Territory)	REMOTE SENSING	2012
Hamylton, S.M., Pescud, A., Leon, J.X. et al.	A geospatial assessment of the relationship between reef flat community calcium carbonate production and wave energy	CORAL REEFS	2013

Li J., Knapp D.E., Fabina N.S., Kennedy E.V., Larsen K., Lyons M.B., Murray N.J., Phinn S.R., Roelfsema C.M., Asner G.P.	A global coral reef probability map generated using convolutional neural networks	CORAL REEFS	2020
Edmunds P.J., Zimmermann S.A., Bramanti L.	A spatially aggressive peyssonnelid algal crust (PAC) threatens shallow coral reefs in St. John, US Virgin Islands	CORAL REEFS	2019
Robinson J.P.W., Wilson S.K., Graham N.A.J.	Abiotic and biotic controls on coral recovery 16 years after mass bleaching	CORAL REEFS	2019
Januchowski-Hartley F.A., Bauman A.G., Morgan K.M., Seah J.C.L., Huang D., Todd P.A.	Accreting coral reefs in a highly urbanized environment	CORAL REEFS	2020
Hatcher, GA; Warrick, JA; Ritchie, AC; Dailey, ET; Zawada, DG; Kranenburg, C; Yates, KK	Accurate Bathymetric Maps From Underwater Digital Imagery Without Ground Control	FRONTIERS IN MARINE SCIENCE	2020
Li, JW; Knapp, DE; Schill, SR; Roelfsema, C; Phinn, S; Silman, M; Mascaro, J; Asner, GP	Adaptive bathymetry estimation for shallow coastal waters using Planet Dove satellites	REMOTE SENSING OF ENVIRONMENT	2019
Thompson, DR; Hochberg, EJ; Asner, GP; Green, RO; Knapp, DE; Gao, BC; Garcia, R; Gierach, M; Lee, Z; Maritorena, S; Fick, R	Airborne mapping of benthic reflectance spectra with Bayesian linear mixtures	REMOTE SENSING OF ENVIRONMENT	2017
Kerr, JM; Purkis, S	An algorithm for optically-deriving water depth from multispectral imagery in coral reef landscapes in the absence of ground-truth data	REMOTE SENSING OF ENVIRONMENT	2018

Ma, YH; Zhang, HG; Li, XR; Wang, J; Cao, WT; Li, DL; Lou, XL; Fan, KG	An Exponential Algorithm for Bottom Reflectance Retrieval in Clear Optically Shallow Waters from Multispectral Imagery without Ground Data	REMOTE SENSING	2021
Comeros-Raynal, M.T., Lawrence, A., Sudek, M. et al	Applying a ridge-to-reef framework to support watershed, water quality, and community-based fisheries management in American Samoa	CORAL REEFS	2019
Levy J., Hunter C., Lukacazyk T., Franklin E.C.	Assessing the spatial distribution of coral bleaching using small unmanned aerial systems	CORAL REEFS	2018
Mohamed, H; Nadaoka, K; Nakamura, T	Assessment of Machine Learning Algorithms for Automatic Benthic Cover Monitoring and Mapping Using Towed Underwater Video Camera and High-Resolution Satellite Images	REMOTE SENSING	2018
Fukunaga, A; Burns, JHR; Pascoe, KH; Kosaki, RK	Associations between Benthic Cover and Habitat Complexity Metrics Obtained from 3D Reconstruction of Coral Reefs at Different Resolutions	REMOTE SENSING	2020
Hopkinson BM, King AC, Owen DP, Johnson-Roberson M, Long MH, Bhandarkar SM	Automated classification of three-dimensional reconstructions of coral reefs using convolutional neural networks	PLOS ONE	2020
Li, JW; Knapp, DE; Lyons, M; Roelfsema, C; Phinn, S; Schill, SR; Asner, GP	Automated Global Shallow Water Bathymetry Mapping Using Google Earth Engine	REMOTE SENSING	2021
Ackleson, SG; Smith, JP; Rodriguez, LM; Moses, WJ; Russell, BJ	AutoNomous Coral Reef Survey in Support of Remote Sensing	FRONTIERS IN MARINE SCIENCE	2017
Harrison H.B., Álvarez-Noriega M., Baird A.H., Heron S.F., MacDonald C., Hughes T.P.	Back-to-back coral bleaching events on isolated atolls in the Coral Sea	CORAL REEFS	2019
Huang, RY; Yu, KF; Wang, YH; Wang, JK; Mu, L; Wang, WH	Bathymetry of the Coral Reefs of Weizhou Island Based on Multispectral Satellite Images	REMOTE SENSING	2017

Garcia, RA; Lee, Z; Barnes, BB; Hu, CM; Dierssen, HM; Hochberg, EJ	Benthic classification and IOP retrievals in shallow water environments using MERIS imagery	REMOTE SENSING OF ENVIRONMENT	2020
WicaksoNo, P; Aryaguna, PA; Lazuardi, W	Benthic Habitat Mapping Model and Cross Validation Using Machine-Learning Classification Algorithms	REMOTE SENSING	2019
Lange I.D., Perry C.T.	Bleaching impacts on carbonate production in the Chagos Archipelago: influence of functional coral groups on carbonate budget trajectories	CORAL REEFS	2019
Depczynski, M., Gilmour, J.P., Ridgway, T. et al.	Bleaching, coral mortality and subsequent survivorship on a West Australian fringing reef	CORAL REEFS	2013
Wilson S.K., Robinson J.P.W., Chong-Seng K., Robinson J., Graham N.A.J.	Boom and bust of keystone structure on coral reefs	CORAL REEFS	2019
Collin, A.; Archambault, P.; Planes, S.	Bridging ridge-to-reef patches: Seamless classification of the coast using very high resolution satellite	REMOTE SENSING	2013
Sambrook K., Bonin M.C., Bradley M., Cumming G.S., Duce S., Andréfouët S., Hoey A.S.	Broadening our horizons: seascape use by coral reef-associated fishes in Kavieng, Papua New Guinea, is common and diverse	CORAL REEFS	2020
Burt J.A., Paparella F., Al-Mansoori N., Al-Mansoori A., Al-Jailani H.	Causes and consequences of the 2017 coral bleaching event in the southern Persian/Arabian Gulf	CORAL REEFS	2019
Carter A.L., Edwards C.B., Fox M.D., Amir C.G., Eynaud Y., Johnson M.D., Lewis L.S., Sandin S.A., Smith J.E.	Changes in benthic community composition associated with the outbreak of the corallimorph, Rhodactis howesii, at Palmyra Atoll	CORAL REEFS	2019
Bargahi H.R., Shokri M.R., Kaymaram F., Fatemi M.R.	Changes in reef fish assemblages following multiple bleaching events in the world’s warmest sea (Kish Island, the Persian Gulf)	CORAL REEFS	2020
Thompson C.A., Matthews S., Hoey A.S., Pratchett M.S.	Changes in sociality of butterflyfishes linked to population declines and coral loss	CORAL REEFS	2019

Yadav, S., Rathod, P., Alcoverro, T. et al.	Choice and destiny: the substrate composition and mechanical stability of settlement structures can mediate coral recruit fate in post-bleached reefs	CORAL REEFS	2016
Colella, M.A., Ruzicka, R.R., Kidney, J.A. et al.	Cold-water event of January 2010 results in catastrophic benthic mortality on patch reefs in the Florida Keys	CORAL REEFS	2012
Carlot J., Rovère A., Casella E., Harris D., Grellet-Muñoz C., Chancerelle Y., Dormy E., Hedouin L., Parravicini V.	Community composition predicts photogrammetry-based structural complexity on coral reefs	CORAL REEFS	2020
Barrera-Falcon, E; Rioja-Nieto, R; Hernandez-Landa, RC; Torres-Irineo, E	Comparison of Standard Caribbean Coral Reef Monitoring Protocols and Underwater Digital Photogrammetry to Characterize Hard Coral Species Composition, Abundance and Cover	FRONTIERS IN MARINE SCIENCE	2021
Teixeira, L.; Hedley, J.; Shapiro, A.; Barker, K.	Comparison of two independent mapping exercises in the Primeiras and Segundas archipelago, Mozambique	REMOTE SENSING	2016
Rodríguez-Martínez, R.E., Jordán-Garza, A.G., Baker, D.M. et al.	Competitive interactions between corals and Trididemnum solidum on Mexican Caribbean reefs	CORAL REEFS	2012
Lee Y.-L., Lam S.Q.Y., Tay T.S., Kikuzawa Y.P., Tan K.S.	Composition and structure of tropical intertidal hard coral communities on natural and man-made habitats	CORAL REEFS	2021
Goodman, JA; Lay, M; Ramirez, L; Ustin, SL; Haverkamp, PJ	Confidence Levels, Sensitivity, and the Role of Bathymetry in Coral Reef Remote Sensing	REMOTE SENSING	2020
Burkepile, D.E.	Context-dependent corallivory by parrotfishes in a Caribbean reef ecosystem	CORAL REEFS	2012
Hédouin L., Rouzé H., Berthe C., Perez-Rosales G., Martinez E., Chancerelle Y., Galand P.E., Lerouvreur F., Nugues M.M., Pochon X., Siu G., Steneck R., Planes S.	Contrasting patterns of mortality in Polynesian coral reefs following the third global coral bleaching event in 2016	CORAL REEFS	2020
Johns, K.A., Osborne, K.O. & Logan, M.	Contrasting rates of coral recovery and reassembly in coral communities on the Great Barrier Reef	CORAL REEFS	2014

Xu, YP; Vaughn, NR; Knapp, DE; Martin, RE; Balzotti, C; Li, JW; Foo, SA; Asner, GP	Coral Bleaching Detection in the Hawaiian Islands Using Spatio-Temporal Standardized Bottom Reflectance and Planet Dove Satellites	REMOTE SENSING	2020
Head, C.E.I., Bayley, D.T.I., Rowlands, G. et al.	Coral bleaching impacts from back-to-back 2015-2016 thermal anomalies in the remote central Indian Ocean	CORAL REEFS	2019
Thompson, A., Schroeder, T., Brando, V.E. et al.	Coral community responses to declining water quality: Whitsunday Islands, Great Barrier Reef, Australia	CORAL REEFS	2014
Figueroa-Pico J., Tortosa F.S., Carpio A.J.	Coral fracture by derelict fishing gear affects the sustainability of the marginal reefs of Ecuador	CORAL REEFS	2020
Eckrich, C.E., Engel, M.S.	Coral overgrowth by an encrusting red alga (Ramicrusta sp.): a threat to Caribbean reefs?	CORAL REEFS	2013
Hedley, JD; Roelfsema, C; Brando, V; GiardiNo, C; Kutser, T; Phinn, S; Mumby, PJ; Barrilero, O; Laporte, J; Koetz, B	Coral reef applications of Sentinel-2: Coverage, characteristics, bathymetry and benthic mapping with comparison to Landsat 8	REMOTE SENSING OF ENVIRONMENT	2018
Gapper, JJ; El-Askary, H; Linstead, E; Piechota, T	Coral Reef Change Detection in Remote Pacific Islands Using Support Vector Machine Classifiers	REMOTE SENSING	2019
Roelfsema, C; Kovacs, E; Ortiz, JC; Wolff, NH; Callaghan, D; Wettle, M; Ronane, M; Hamylton, SM; Mumby, PJ; Phinn, S	Coral reef habitat mapping: A combination of object-based image analysis and ecological modelling	REMOTE SENSING OF ENVIRONMENT	2018
da Silveira, CBL; Strenzel, GMR; Maida, M; Gaspar, ALB; Ferreira, BP	Coral Reef Mapping with Remote Sensing and Machine Learning: A Nurture and Nature Analysis in Marine Protected Areas	REMOTE SENSING	2021
NoceriNo, E; Menna, F; Gruen, A; Troyer, M; Capra, A; Castagnetti, C; Rossi, P; Brooks, AJ; Schmitt, RJ; Holbrook, SJ	Coral Reef Monitoring by Scuba Divers Using Underwater Photogrammetry and Geodetic Surveying	REMOTE SENSING	2020

Raj K.D., Aeby G.S., Mathews G., Williams G.J., Caldwell J.M., Laju R.L., Bharath M.S., Kumar P.D., Arasamuthu A., Asir N.G.G., Wedding L.M., Davies A.J., Moritsch M.M., Edward J.K.P.	Coral reef resilience differs among islands within the Gulf of Mannar, southeast India, following successive coral bleaching events	CORAL REEFS	2021
Yadav S., Alcoverro T., Arthur R.	Coral reefs respond to repeated ENSO events with increasing resistance but reduced recovery capacities in the Lakshadweep archipelago	CORAL REEFS	2018
Young GC, Dey S, Rogers AD, Exton D	Cost and time-effective method for multiscale measures of rugosity, fractal dimension, and vector dispersion from coral reef 3D models	PLOS ONE	2017
Casey, J.M., Choat, J.H. & Connolly, S.R.	Coupled dynamics of territorial damselfishes and juvenile corals on the reef crest	CORAL REEFS	2015
McClanahan, T.R.	Decadal coral community reassembly on an African fringing reef	CORAL REEFS	2014
McClanahan T.R.	Decadal turnover of thermally stressed coral taxa support a risk-spreading approach to marine reserve design	CORAL REEFS	2020
Russ, G.R., Bergseth, B.J., Rizzari, J.R. et al.	Decadal-scale effects of benthic habitat and marine reserve protection on Philippine goatfish (F: Mullidae)	CORAL REEFS	2015
Tang S., Graba-Landry A., Hoey A.S.	Density and height of Sargassum influence rabbitfish (f. Siganidae) settlement on inshore reef flats of the Great Barrier Reef	CO RAL REEFS	020
Bramanti, L., Edmunds, P.J.	Density-associated recruitment mediates coral population dynamics on a coral reef	CORAL REEFS	2016
Hamylton, S.M.; Hedley, J.D.; Beaman, R.J.	Derivation of high-resolution bathymetry from multispectral satellite imagery: A comparison of empirical and optimisation methods through geographical error analysis	REMOTE SENSING	2015

Maina, J.M.; Jones, K.R.; Hicks, C.C.; McClanahan, T.R.; Watson, J.E.M.; Tuda, A.O.; Andréfouët, S	Designing climate-resilient marine protected area networks by combining remotely sensed coral reef habitat with coastal multi-use maps	REMOTE SENSING	2015
Liu, BL; Guan, L; Chen, H	Detecting 2020 Coral Bleaching Event in the Northwest Hainan Island Using CoralTemp SST and Sentinel-2B MSI Imagery	REMOTE SENSING	2021
Dadhich, A.P., Nadaoka, K., Yamamoto, T. et al.	Detecting coral bleaching using high-resolution satellite data analysis and 2-dimensional thermal model simulation in the Ishigaki fringing reef, Japan	CORAL REEFS	2012
Xu, JP; Zhao, JH; Wang, F; Chen, YL; Lee, ZP	Detection of Coral Reef Bleaching Based on Sentinel-2 Multi-Temporal Imagery: Simulation and Case Study	FRONTIERS IN MARINE SCIENCE	2021
Singh, AA; Maharaj, A; Kumar, M; Singh, P; Singh, S; Muller-Karger, FE; Mccarthy, M; Joseph, L; Damlamian, H; Begg, Z	Developing High Resolution Baseline Coast Resource Maps Using World View 2 Imagery for a Coastal Village in Fiji	FRONTIERS IN MARINE SCIENCE	2019
Ebrahim A., Martin T.S.H., Mumby P.J., Olds A.D., Tibbetts I.R.	Differences in diet and foraging behaviour of commercially important rabbitfish species on coral reefs in the Indian Ocean	CORAL REEFS	2020
Dustan P, Doherty O, Pardede S	Digital Reef Rugosity Estimates Coral Reef Habitat Complexity	PLOS ONE	2013
Haapkylä, J., Melbourne-Thomas, J., Flavell, M. et al.	Disease outbreaks, bleaching and a cyclone drive changes in coral assemblages on an inshore reef of the Great Barrier Reef	CORAL REEFS	2013
Done, T., Gilmour, J. & Fisher, R.	Distance decay among coral assemblages during a cycle of disturbance and recovery	CORAL REEFS	2015
Dean, A.J., Steneck, R.S., Tager, D. et al.	Distribution, abundance and diversity of crustose coralline algae on the Great Barrier Reef	CORAL REEFS	2015

Toth, L.T., van Woesik, R., Murdoch, T.J.T. et al	Do no-take reserves benefit Florida's corals? 14 years of change and stasis in the Florida Keys National Marine Sanctuary	CORAL REEFS	2014
Sato Y., Bell S.C., Nichols C., Fry K., Menéndez P., Bourne D.G.	Early-phase dynamics in coral recovery following cyclone disturbance on the inshore Great Barrier Reef, Australia	CORAL REEFS	2018
Heres M.M., Farmer B.H., Elmer F., Hertler H.	Ecological consequences of Stony Coral Tissue Loss Disease in the Turks and Caicos Islands	CORAL REEFS	2021
Jupiter, S.D., Weeks, R., Jenkins, A.P. et al.	Effects of a single intensive harvest event on fish populations inside a customary marine closure	CORAL REEFS	2012
Mumby, P.J., Bejarano, S., Golbuu, Y. et al.	Empirical relationships among resilience indicators on Micronesian reefs	CORAL REEFS	2013
Storlazzi, C.D., Dartnell, P., Hatcher, G.A. et al.	End of the chain? Rugosity and fine-scale bathymetry from existing underwater digital imagery using structure-from-motion (SfM) technology	CORAL REEFS	2016
Gutierrez-Heredia L, Benzoni F, Murphy E, Reynaud EG	End to End Digitisation and Analysis of Three-Dimensional Coral Models, from Communities to Corallites	PLOS ONE	2016
Collin, A.; Planes, S.	Enhancing coral health detection using spectral diversity indices from worldview-2 imagery and machine learners	REMOTE SENSING	2012
Robinson J.P.W., Williams I.D., Yeager L.A., McPherson J.M., Clark J., Oliver T.A., Baum J.K.	Environmental conditions and herbivore biomass determine coral reef benthic community composition: implications for quantitative baselines	CORAL REEFS	2018
Rowley S.J.	Environmental gradients structure gorgonian assemblages on coral reefs in SE Sulawesi, Indonesia	CORAL REEFS	2018
Perry, C.T., Edinger, E.N., Kench, P.S. et al.	Estimating rates of biologically driven coral reef framework production and erosion: a new census-based carbonate budget methodology and applications to the reefs of Bonaire	CORAL REEFS	2012

Hamylton, SM; Duce, S; Vila-Concejo, A; Roelfsema, CM; Phinn, SR; Carvalho, RC; Shaw, EC; Joyce, KE	Estimating regional coral reef calcium carbonate production from remotely sensed seafloor maps	REMOTE SENSING OF ENVIRONMENT	2017
Gapper, JJ; El-Askary, H; Linstead, E; Piechota, T	Evaluation of Spatial Generalization Characteristics of a Robust Classifier as Applied to Coral Reef Habitats in Remote Islands of the Pacific Ocean	REMOTE SENSING	2018
Shedrawi, G., Harvey, E.S., McLean, D.L. et al.	Evaluation of the effect of closed areas on a unique and shallow water coral reef fish assemblage reveals complex responses	CORAL REEFS	2014
Roff, G., Chollett, I., Doropoulos, C. et al.	Exposure-driven macroalgal phase shift following catastrophic disturbance on coral reefs	CORAL REEFS	2015
Andréfouët, S., Guillaume, M.M.M., Delval, A. et al.	Fifty years of changes in reef flat habitats of the Grand R,cif of Toliara (SW Madagascar) and the impact of gleaning	CORAL REEFS	2013
Collings, S.; Martin, T.J.; Hernandez, E.; Edwards, S.; Filisetti, A.; Catt, G.; Marouchos, A.; Boyd, M.; Embry, C.	Findings from a Combined Subsea LiDAR and Multibeam Survey at Kingston Reef, Western Australia.	REMOTE SENSING	2020
Roelfsema C., Kovacs E.M., Vercelloni J., Markey K., Rodriguez-Ramirez A., Lopez-Marcano S., Gonzalez-Rivero M., Hoegh-Guldberg O., Phinn S.R.	Fine-scale time series surveys reveal new insights into spatio-temporal trends in coral cover (2002–2018), of a coral reef on the Southern Great Barrier Reef	CORAL REEFS	2021
Chirayath, V; Instrella, R	Fluid lensing and machine learning for centimeter-resolution airborne assessment of coral reefs in American Samoa	REMOTE SENSING OF ENVIRONMENT	2019
Caras, T.; Karnieli, A.	Ground-level classification of a coral reef using a hyperspectral camera	REMOTE SENSING	2015

Caras, T., Karnieli, A.	Ground-level spectroscopy analyses and classification of coral reefs using a hyperspectral camera	CORAL REEFS	2013
Roelfsema C.M., Kovacs E.M., Ortiz J.C., Callaghan D.P., Hock K., Mongin M., Johansen K., Mumby P.J., Wettle M., Ronan M., Lundgren P., Kennedy E.V., Phinn S.R.	Habitat maps to enhance monitoring and management of the Great Barrier Reef	CORAL REEFS	2020
Oakley-Cogan A, Tebbett SB, Bellwood DR	Habitat zonation on coral reefs: Structural complexity, nutritional resources and herbivorous fish distributions	PLOS ONE	2020
an Wynsberge S, Andréfouët S, Hamel MA, Kulbicki M	Habitats as surrogates of taxonomic and functional fish assemblages in coral reef ecosystems: A critical analysis of factors driving effectiveness	PLOS ONE	2012
Palma, M; Casado, MR; Pantaleo, U; CerraNo, C	High Resolution Orthomosaics of African Coral Reefs: A Tool for Wide-Scale Benthic Monitoring	REMOTE SENSING	2017
Collin, A; Hench, JL; Pastol, Y; Planes, S; Thiault, L; Schmitt, RJ; Holbrook, SJ; Davies, N; Troyer, M	High resolution topobathymetry using a Pleiades-1 triplet: Moorea Island in 3D	REMOTE SENSING OF ENVIRONMENT	2018
Purkis S.J., Gleason A.C.R., Purkis C.R., Dempsey A.C., Renaud P.G., Faisal M., Saul S., Kerr J.M.	High-resolution habitat and bathymetry maps for 65,000 sq. km of Earth's remotest coral reefs	CORAL REEFS	2019
Asner, GP; Vaughn, NR; Balzotti, C; Brodrick, PG; Heckler, J	High-Resolution Reef Bathymetry and Coral Habitat Complexity from Airborne Imaging Spectroscopy	REMOTE SENSING	2020
Brisset, M; Van Wynsberge, S; Andrefouet, S; Payri, C; Soulard, B; Bourassin, E; Le Gendre, R; Coutures, E	Hindcast and Near Real-Time Monitoring of Green Macroalgae Blooms in Shallow Coral Reef Lagoons Using Sentinel-2: A New-Caledonia Case Study	REMOTE SENSING	2021
Elliott, J., Patterson, M., Summers, N. et al.	How does the proliferation of the coral-killing sponge Terpios hoshinota affect benthic community structure on coral reefs?	CORAL REEFS	2016

Roelfsema, CM; Lyons, MB; Castro-SanguiNo, C; Kovacs, EM; Callaghan, D; Wettle, M; Markey, K; Borrego-Acevedo, R; Tudman, P; Roe, M; Kennedy, EV; Gonzalez-Rivero, M; Murray, N; Phinn, SR	How Much Shallow Coral Habitat Is There on the Great Barrier Reef?	REMOTE SENSING	2021
Raoult, V; Reid-Anderson, S; Ferri, A; Williamson, JE	How Reliable Is Structure from Motion (SfM) over Time and between Observers? A Case Study Using Coral Reef Bommies	REMOTE SENSING	2017
Petit, T; Bajjouk, T; Mouquet, P; Rochette, S; Vozel, B; Delacourt, C	Hyperspectral remote sensing of coral reefs by semi-analytical model inversion - Comparison of different inversion setups	REMOTE SENSING OF ENVIRONMENT	2017
Garcia, RA; Lee, Z; Hochberg, EJ	Hyperspectral Shallow-Water Remote Sensing with an Enhanced Benthic Classifier	REMOTE SENSING	2018
Bel, TW; Okin, GS; Cavanaugh, KC; Hochberg, EJ	Impact of water characteristics on the discrimination of benthic cover in and around coral reefs from imaging spectrometer data	REMOTE SENSING OF ENVIRONMENT	2020
Kolodziej, G; Studivan, MS; Gleason, ACR; Langdon, C; ENochs, IC; Manzello, DP	Impacts of Stony Coral Tissue Loss Disease (SCTLD) on Coral Community Structure at an Inshore Patch Reef of the Upper Florida Keys Using Photomosaics	FRONTIERS IN MARINE SCIENCE	2021
Cerutti J.M.B., Burt A.J., Haupt P., Bunbury N., Mumby P.J., Schaepman-Strub G.	Impacts of the 2014–2017 global bleaching event on a protected remote atoll in the Western Indian Ocean	CORAL REEFS	2020
Kornder N.A., Cappelletto J., Mueller B., Zalm M.J.L., Martinez S.J., Vermeij M.J.A., Huisman J., de Goeij J.M.	Implications of 2D versus 3D surveys to measure the abundance and composition of benthic coral reef communities	CORAL REEFS	2021

Shaw, E.C., Hamylton, S.M. & Phinn, S.R.	Incorporating benthic community changes into hydrochemical-based projections of coral reef calcium carbonate production under ocean acidification	CORAL REEFS	2016
Pratchett, M.S., Blowes, S.A., Coker, D. et al.	Indirect benefits of high coral cover for non-corallivorous butterflyfishes	CORAL REEFS	2015
O'Leary, J.K., Potts, D.C., Braga, J.C. et al.	Indirect consequences of fishing: reduction of coralline algae suppresses juvenile coral abundance	CORAL REEFS	2012
Edwards C.B., Eynaud Y., Williams G.J., Pedersen N.E., Zgliczynski B.J., Gleason A.C.R., Smith J.E., Sandin S.A.	Large-area imaging reveals biologically driven non-random spatial patterns of corals at a remote reef	CORAL REEFS	2017
Williams Ivor D., Couch Courtney S., Beijbom Oscar, Oliver Thomas A., Vargas-Angel Bernardo, Schumacher Brett D., Brainard Russell E.	Leveraging automated image analysis tools to transform our capacity to assess status and trends on coral reefs	FRONTIERS IN MARINE SCIENCE	2019
Fox M.D., Carter A.L., Edwards C.B., Takeshita Y., Johnson M.D., Petrovic V., Amir C.G., Sala E., Sandin S.A., Smith J.E.	Limited coral mortality following acute thermal stress and widespread bleaching on Palmyra Atoll, central Pacific	CORAL REEFS	2019
Joyce, K.E.; Phinn, S.R.; Roelfsema, C.M.	Live coral cover index testing and application with hyperspectral airborne image data	REMOTE SENSING	2013
Brooker, R.M., Munday, P.L., Brandl, S.J. et al.	Local extinction of a coral reef fish explained by inflexible prey choice	CORAL REEFS	2014
Shedrawi G., Falter J.L., Friedman K.J., Lowe R.J., Pratchett M.S., Simpson C.J., Speed C.W., Wilson S.K., Zhang Z.	Localised hydrodynamics influence vulnerability of coral communities to environmental disturbances	CORAL REEFS	2017
Karkarey, R., Kelkar, N., Lobo, A.S. et al.	Long-lived groupers require structurally stable reefs in the face of repeated climate change disturbances	CORAL REEFS	2014
Newnham T.J., Browne N.K., Bumbak J., Loudon L., Wellington H., Shedrawi G., Hacker J., O'Leary M.	Long-term (70-year) monitoring of reef structure through high-resolution multidecadal aerial imagery	CORAL REEFS	2020

Golbuu, Y., Gouezo, M., Kurihara, H. et al.	Long-term isolation and local adaptation in Palau's Nikko Bay help corals thrive in acidic waters	CORAL REEFS	2016
Lenz, E.A., Bramanti, L., Lasker, H.R. et al.	Long-term variation of octocoral populations in St. John, US Virgin Islands	CORAL REEFS	2015
Leiper, I.A.; Phinn, S.R.; Roelfsema, C.M.; Joyce, K.E.; Dekker, A.G.	Mapping coral reef benthos, substrates, and bathymetry, using compact airborne Spectrographic Imager (CASI) data	REMOTE SENSING	2014
Knudby, A.; Jupiter, S.; Roelfsema, C.; Lyons, M.; Phinn, S.	Mapping coral reef resilience indicators using field and remotely sensed data	REMOTE SENSING	2013
Casella E., Collin A., Harris D., Ferse S., Bejarano S., Parravicini V., Hench J.L., Rovere A.	Mapping coral reefs using consumer-grade drones and structure from motion photogrammetry techniques	CORAL REEFS	2017
Giardino, C.; Bresciani, M.; Fava, F.; Matta, E.; Brando, V.E.; Colombo, R.	Mapping submerged habitats and mangroves of Lampi Island Marine National Park (Myanmar) from in situ and satellite observations	REMOTE SENSING	2016
Couch CS, Burns JHR, Liu G, Steward K, Gutlay TN, Kenyon J, et al	Mass coral bleaching due to unprecedented marine heatwave in Papahānaumokuākea Marine National Monument (Northwestern Hawaiian Islands)	PLOS ONE	2017
Fukunaga, A; Burns, JHR	Metrics of Coral Reef Structural Complexity Extracted from 3D Mesh Models and Digital Elevation Models	REMOTE SENSING	2020
Whittey K.E., Dunkley K., Young G.C., Cable J., Perkins S.E.	Microhabitats of sharknose goby (Elacatinus evelynae) cleaning stations and their links with cleaning behaviour	CORAL REEFS	2021
Brandl, S.J., Hoey, A.S. & Bellwood, D.R.	Micro-topography mediates interactions between corals, algae, and herbivorous fishes on coral reefs	CORAL REEFS	2014
Gonzalez-Rivero, M; Beijbom, O; Rodriguez-Ramirez, A; Bryant, DEP; Ganase, A; Gonzalez-Marrero, Y; Herrera-Reveles, A; Kennedy, EV; Kim, CJS; Lopez-MarcaNo, S; Markey, K; Neal, BP; Osborne, K; Reyes-Nivia, C;	Monitoring of Coral Reefs Using Artificial Intelligence: A Feasible and Cost-Effective Approach	REMOTE SENSING	2020

Sampayo, EM; Stolberg, K; Taylor, A; Vercelloni, J; Wyatt, M; Hoegh-Guldberg, O			
Tanner J.E.	Multi-decadal analysis reveals contrasting patterns of resilience and decline in coral assemblages	CORAL REEFS	2017
Fallati, L; Saponari, L; Savini, A; Marchese, F; Corselli, C; Galli, P	Multi-Temporal UAV Data and Object-Based Image Analysis (OBIA) for Estimation of Substrate Changes in a Post-Bleaching Scenario on a Maldivian Reef	REMOTE SENSING	2020
Murphy, G.N., Perry, C.T., Chin, P. et al.	New approaches to quantifying bioerosion by endolithic sponge populations: applications to the coral reefs of Grand Cayman	CORAL REEFS	2016
McNeil, M.A., Webster, J.M., Beaman, R.J. et al.	New constraints on the spatial distribution and morphology of the Halimeda bioherms of the Great Barrier Reef, Australia	CORAL REEFS	2016
Kobryn HT, Wouters K, Beckley LE, Heege T	Ningaloo Reef: Shallow Marine Habitats Mapped Using a Hyperspectral Sensor	PLOS ONE	2013
Mizerek T.L., Madin J.S., Benzoni F., Huang D., Luiz O.J., Mera H., Schmidt-Roach S., Smith S.D.A., Sommer B., Baird A.H.	No evidence for tropicalization of coral assemblages in a subtropical climate change hot spot	CORAL REEFS	2021
Altman-Kurosaki N.T., Smith C.M., Franklin E.C.	Oahu's marine protected areas have limited success in protecting coral reef herbivores	CORAL REEFS	2021
Li, JW; Schill, SR; Knapp, DE; Asner, GP	Object-Based Mapping of Coral Reef Habitats Using Planet Dove Satellites	REMOTE SENSING	2019
McClanahan T.R., Muthiga N.A.	Oceanic patterns of thermal stress and coral community degradation on the island of Mauritius	CORAL REEFS	2021
Pavoni, G; Corsini, M; Callieri, M; Fiameni, G; Edwards, C; CigNoni, P	On Improving the Training of Models for the Semantic Segmentation of Benthic Communities from Orthographic Imagery	REMOTE SENSING	2020

Lechene, MAA; Haberstroh, AJ; Byrne, M; Figueira, W; Ferrari, R	Optimising Sampling Strategies in Coral Reefs Using Large-Area Mosaics	REMOTE SENSING	2019
Perry C.T., Morgan K.M.	Post-bleaching coral community change on southern Maldivian reefs: is there potential for rapid recovery?	CORAL REEFS	2017
Bruckner A.W., Coward G., Bimson K., Rattanawongwan T.	Predation by feeding aggregations of Drupella spp. inhibits the recovery of reefs damaged by a mass bleaching event	CORAL REEFS	2017
Williamson J.E., Duce S., Joyce K.E., Raoult V.	Putting sea cucumbers on the map: projected holothurian bioturbation rates on a coral reef scale	CORAL REEFS	2021
Palma, M; Magliozzi, C; Casado, MR; Pantaleo, U; Fernandes, J; Coro, G; CerraNo, C; Leinster, P	Quantifying Coral Reef Composition of Recreational Diving Sites: A Structure from Motion Approach at Seascape Scale	REMOTE SENSING	2019
Combs IR, Studivan MS, Eckert RJ, Voss JD	Quantifying impacts of stony coral tissue loss disease on corals in Southeast Florida through surveys and 3D photogrammetry	PLOS ONE	2021
Ferrari, R.; McKinnon, D.; He, H.; Smith, R.N.; Corke, P.; González-Rivero, M.; Mumby, P.J.; Upcroft, B	Quantifying multiscale habitat structural complexity: A cost-effective framework for underwater 3D modelling	REMOTE SENSING	2016
Archer-Rand, S; Whomersley, P; O'ConNor, J; Dosell, A	Rapid Assessment of Seabed Habitats Around Pitcairn Island in Aid of Activity Management During the COVID-19 Global Pandemic	FRONTIERS IN MARINE SCIENCE	2021
Shlesinger, T., Loya, Y.	Recruitment, mortality, and resilience potential of scleractinian corals at Eilat, Red Sea	CORAL REEFS	2016
Perry, CT; Morgan, KM; Yarlett, RT	Reef Habitat Type and Spatial Extent as Interacting Controls on Platform-Scale Carbonate Budgets	FRONTIERS IN MARINE SCIENCE	2017
Schill, SR; McNulty, VP; Pollock, FJ; Luethje, F; Li, JW; Knapp, DE; Kington, JD; McDonald, T; Raber, GT; Escovar-Fadul, X; Asner, GP	Regional High-Resolution Benthic Habitat Data from Planet Dove Imagery for Conservation Decision-Making and Marine Planning	REMOTE SENSING	2021

Asner, GP; Vaughn, N; Grady, BW; Foo, SA; Anand, H; Carlson, RR; Shafron, E; Teague, C; Martin, RE	Regional Reef Fish Survey Design and Scaling Using High-Resolution Mapping and Analysis	FRONTIERS IN MARINE SCIENCE	2021
Darling E.S., Graham N.A.J., Januchowski-Hartley F.A., Nash K.L., Pratchett M.S., Wilson S.K.	Relationships between structural complexity, coral traits, and reef fish assemblages	CORAL REEFS	2017
Yuval, M; Alonso, I; Eyal, G; TcherNov, D; Loya, Y; Murillo, AC; Treibitz, T	Repeatable Semantic Reef-Mapping through Photogrammetry and Label-Augmentation	REMOTE SENSING	2021
Han, X., Adam, T.C., Schmitt, R.J. et al.	Response of herbivore functional groups to sequential perturbations in Moorea, French Polynesia	CORAL REEFS	2016
Price B.A., Harvey E.S., Mangubhai S., Saunders B.J., Puotinen M., Goetze J.S.	Responses of benthic habitat and fish to severe tropical cyclone Winston in Fiji	CORAL REEFS	2021
Collin Antoine, Archambault Philippe, Planes Serge	Revealing the regime of shallow coral reefs at patch scale by continuous spatial modeling	FRONTIERS IN MARINE SCIENCE	2014
Ma, Y; Xu, N; Liu, Z; Yang, BS; Yang, FL; Wang, XH; Li, S	Satellite-derived bathymetry using the ICESat-2 lidar and Sentinel-2 imagery datasets	REMOTE SENSING OF ENVIRONMENT	2020
González-Rivero, M.; Beijbom, O.; Rodriguez-Ramirez, A.; Holtrop, T.; González-Marrero, Y.; Ganase, A.; Roelfsema, C.; Phinn, S.; Hoegh-Guldberg, O.	Scaling up ecological measurements of coral reefs using semi-automated field image collection and analysis	REMOTE SENSING	2016
Nozawa Y., Lin C.-H., Meng P.-J.	Sea urchins (diadematids) promote coral recovery via recruitment on Taiwanese reefs	CORAL REEFS	2020
Mohamed, H.; Nadaoka, K.; Nakamura, T.	Semiautomated Mapping of Benthic Habitats and Seagrass Species Using a Convolutional Neural Network Framework in Shallow Water Environments	REMOTE SENSING	2020

Saul, S.; Purkis, S.	Semi-automated object-based classification of coral reef habitat using discrete choice models	REMOTE SENSING	2015
Amrari, S; Bourassin, E; Andrefouet, S; Soulard, B; Lemonnier, H; Le Gendre, R	Shallow Water Bathymetry Retrieval Using a Band-Optimization Iterative Approach: Application to New Caledonia Coral Reef Lagoons Using Sentinel-2 Data	REMOTE SENSING	2021
Wei, JW; Wang, MH; Lee, ZP; BriceNo, HO; Yu, XL; Jiang, LD; Garcia, R; Wang, JW; Luis, K	Shallow water bathymetry with multi-spectral satellite ocean color sensors: Leveraging temporal variation in image data	REMOTE SENSING OF ENVIRONMENT	2020
Nababan, B; Mastu, LK; Idris, NH; Panjaitan, JP	Shallow-Water Benthic Habitat Mapping Using Drone with Object Based Image Analyses	REMOTE SENSING	2021
Manessa, M.D.M.; Kanno, A.; Sekine, M.; Ampou, E.E.; Widagti, N.; As-syakur, A.R.	Shallow-water benthic identification using multispectral satellite imagery: Investigation on the effects of improving noise correction method and spectral cover	REMOTE SENSING	2014
Walker, B.K., Larson, E.A., Moulding, A.L.	Small-scale mapping of indeterminate arborescent acroporid coral (Acropora cervicornis) patches	CORAL REEFS	2012
Couch, C.S., Garriques, J.D., Barnett, C. et al.	Spatial and temporal patterns of coral health and disease along leeward Hawai'i Island	CORAL REEFS	2014
Doo S.S., Hamylton S., Finfer J., Byrne M.	Spatial and temporal variation in reef-scale carbonate storage of large benthic foraminifera: a case study on One Tree Reef	CORAL REEFS	2017
Zuo, XL; Su, FZ; Yu, KF; Wang, YH; Wang, Q; Wu, HS	Spatially Modeling the Synergistic Impacts of Global Warming and Sea-Level Rise on Coral Reefs in the South China Sea	REMOTE SENSING	2021
Richards, Z.T., Juszkiewicz, D.J. & Hoggett	Spatio-temporal persistence of scleractinian coral species at Lizard Island, Great Barrier Reef	CORAL REEFS	2021
Burkepile D.E., Adam T.C., Roycroft M., Ladd M.C., Munsterman K.S., Ruttenberg B.I.	Species-specific patterns in corallivory and spongivory among Caribbean parrotfishes	CORAL REEFS	2019

Agudo-Adriani, EA; Cappelletto, J; Cavada-Blanco, F; Croquer, A	Structural Complexity and Benthic Cover Explain Reef-Scale Variability of Fish Assemblages in Los Rogues National Park, Venezuela	FRONTIERS IN MARINE SCIENCE	2019
David C.G., Kohl N., Casella E., Rovere A., Ballesteros P., Schlurmann T.	Structure-from-Motion on shallow reefs and beaches: potential and limitations of consumer-grade drones to reconstruct topography and bathymetry	CORAL REEFS	2021
Raymundo L.J., Burdick D., Hoot W.C., Miller R.M., Brown V., Reynolds T., Gault J., Idechong J., Fifer J., Williams A.	Successive bleaching events cause mass coral mortality in Guam, Micronesia	CORAL REEFS	2019
Dee S., Cuttler M., O'Leary M., Hacker J., Browne N.	The complexity of calculating an accurate carbonate budget	CORAL REEFS	2020
Miller S., Yadav S., Madin J.S.	The contribution of corals to reef structural complexity in Kāneʻohe Bay	CORAL REEFS	2021
Weiler B.A., Van Leeuwen T.E., Stump K.L.	The extent of coral bleaching, disease and mortality for data-deficient reefs in Eleuthera, The Bahamas after the 2014–2017 global bleaching event	CORAL REEFS	2019
Butler, I.R., Sommer, B., Zann, M. et al.	The impacts of flooding on the high-latitude, terrigenoclastic influenced coral reefs of Hervey Bay, Queensland, Australia	CORAL REEFS	2013
Fidler R.Y., Andradi-Brown D.A., Awaludinnoer, Pada D., Purwanto, Hidayat N.I., Ahmadia G.N., Harborne A.R.	The importance of biophysical context in understanding marine protected area outcomes for coral reef fish populations	CORAL REEFS	2021
Gleason, ACR; Smith, R; Purkis, SJ; Goodrich, K; Dempsey, A; Mantero, A	The Prospect of Global Coral Reef Bathymetry by Combining Ice, Cloud, and Land Elevation Satellite-2 Altimetry With Multispectral Satellite Imagery	FRONTIERS IN MARINE SCIENCE	2021
Li, JW; Fabina, NS; Knapp, DE; Asner, GP	The Sensitivity of Multi-spectral Satellite Sensors to Benthic Habitat Change	REMOTE SENSING	2020

Gilmour J.P., Cook K.L., Ryan N.M., Puotinen M.L., Green R.H., Shedrawi G., Hobbs J.-P.A., Thomson D.P., Babcock R.C., Buckee J., Foster T., Richards Z.T., Wilson S.K., Barnes P.B., Coutts T.B., Radford B.T., Piggott C.H., Depczynski M., Evans S.N., Schoepf V., Evans R.D., Halford A.R., Nutt C.D., Bancroft K.P., Heyward A.J., Oades D.	The state of Western Australia's coral reefs	CORAL REEFS	2019
Jones N.P., Figueiredo J., Gilliam D.S.	Thermal stress-related spatiotemporal variations in high-latitude coral reef benthic communities	CORAL REEFS	2020
Lamy, T., Galzin, R., Kulbicki, M. et al. Three decades of recurrent declines and recoveries in corals belie ongoing change in fish assemblages	Three decades of recurrent declines and recoveries in corals belie ongoing change in fish assemblages	CORAL REEFS	2016
Beijbom O, Edmunds PJ, Roelfsema C, Smith J, Kline DI, Neal BP, et al.	Towards automated annotation of benthic survey images: Variability of human experts and operational modes of automation	PLOS ONE	2015
Mohamed, H; Nadaoka, K; Nakamura, T	Towards Benthic Habitat 3D Mapping Using Machine Learning Algorithms and Structures from Motion Photogrammetry	REMOTE SENSING	2020
Dajka J.-C., Wilson S.K., Robinson J.P.W., Chong-Seng K.M., Harris A., Graham N.A.J.	Uncovering drivers of juvenile coral density following mass bleaching	CORAL REEFS	2019
Brodnicke O.B., Bourne D.G., Heron S.F., Pears R.J., Stella J.S., Smith H.A., Willis B.L.	Unravelling the links between heat stress, bleaching and disease: fate of tabular corals following a combined disease and bleaching event	CORAL REEFS	2019
Bodmer, M.D.V., Rogers, A.D., Speight, M.R. et al.	Using an isolated population boom to explore barriers to recovery in the keystone Caribbean coral reef herbivore Diadema antillarum	CORAL REEFS	2015

Candela, A; Edelson, K; Gierach, MM; Thompson, DR; Woodward, G; Wettergreen, D	Using Remote Sensing and in situ Measurements for Efficient Mapping and Optimal Sampling of Coral Reefs	FRONTIERS IN MARINE SCIENCE	2021
Lange I.D., Benkwitt C.E., McDevitt-Irwin J.M., Tietjen K.L., Taylor B., Chinkin M., Gunn R.L., Palmisciano M., Steyaert M., Wilson B., East H.K., Turner J., Graham N.A.J., Perry C.T.	Wave exposure shapes reef community composition and recovery trajectories at a remote coral atoll	CORAL REEFS	2021

Table A2. Explanation of the rationale behind each assessed variable across all studies.

Variable	Rationale
Category of the study	Based on the premise of this review, to compare synergies, overlap, and scalability, all studies need to be first assigned a category (i.e. remote sensing studies or coral reef ecology studies).
Focal question	To facilitate a comprehensive comparison of the primary focus of each study and to delineate the specific facets they explored, we implemented a filtering process where studies were required to incorporate a benthic component and address ecological aspects of coral reef systems. Subsequently, each study was allocated one or multiple focal questions. This approach was employed to enable a thorough analysis and visual representation of disparities between these two domains concerning their overarching thematic interests within coral reef benthic communities.
Organisms/parameters investigated	We included both the organisms and parameters investigated by each study to get a representation of what each field commonly is used to assess.
Methodology/ approach employed	We incorporated the methodology section to glean insights into the prevailing approaches within each domain. This also afforded us the opportunity to evaluate approaches or subdisciplines that notably contribute to benthic assessments, such as the generation of high-detail structural metrics or comprehensive analyses of benthic community composition. Furthermore, this methodology section provided the means to connect the previously assigned focal questions, representing the overarching interests of each study, with the methodologies employed. This linkage enabled us to identify common practices concerning specific metrics or assessments.
Location of the study	We integrated the study locations, based on the coral reef realms mapped by the Allen Coral Atlas, to facilitate a comparison of the distribution of scientific studies across various coral reef-associated regions globally. By aligning these studies with the mapped areas delineated by the Allen Coral Atlas, we could directly compare the number of studies against the actual coral reef area within each

	mapped location. This approach aimed to highlight potential biases within each scientific domain.
Habitats investigated	Since a direct comparison of spatial extent between these distinct scientific domains is challenging, our focus shifted to comparing their extent and focus at the reef scape scale. It is acknowledged in the literature that both coral reef ecology and remote sensing studies could exhibit biases towards specific habitats, whether driven by observer bias or sensor limitations in surveying certain environments. Moreover, this approach enabled us to evaluate the actual mention of reef habitats in studies, rather than merely a depth gradient, ensuring the reproducibility of findings.
Identification of study sites	We observed whether each study provided a dependable and consistent identification of their study site. This comparison aimed to identify shared practices or mismatches within each scientific domain that enhance transparency and reproducibility in scientific studies.
sensor platform(s), spatial resolution, and ground truthing of remote sensing	These criteria were specific to remote sensing studies and were evaluated to provide further differentiation among approaches within that domain. Sensor platforms were examined to understand the range of platforms or technologies utilized, with the notation varying based on the methodology employed. When mentioned, spatial resolution was assessed to compare the sensitivity across different sensor platforms and methodologies. Additionally, we documented whether and how studies underwent ground truthing, a practice primarily relevant to mapping and bathymetry studies, aimed at ensuring a consistent protocol.

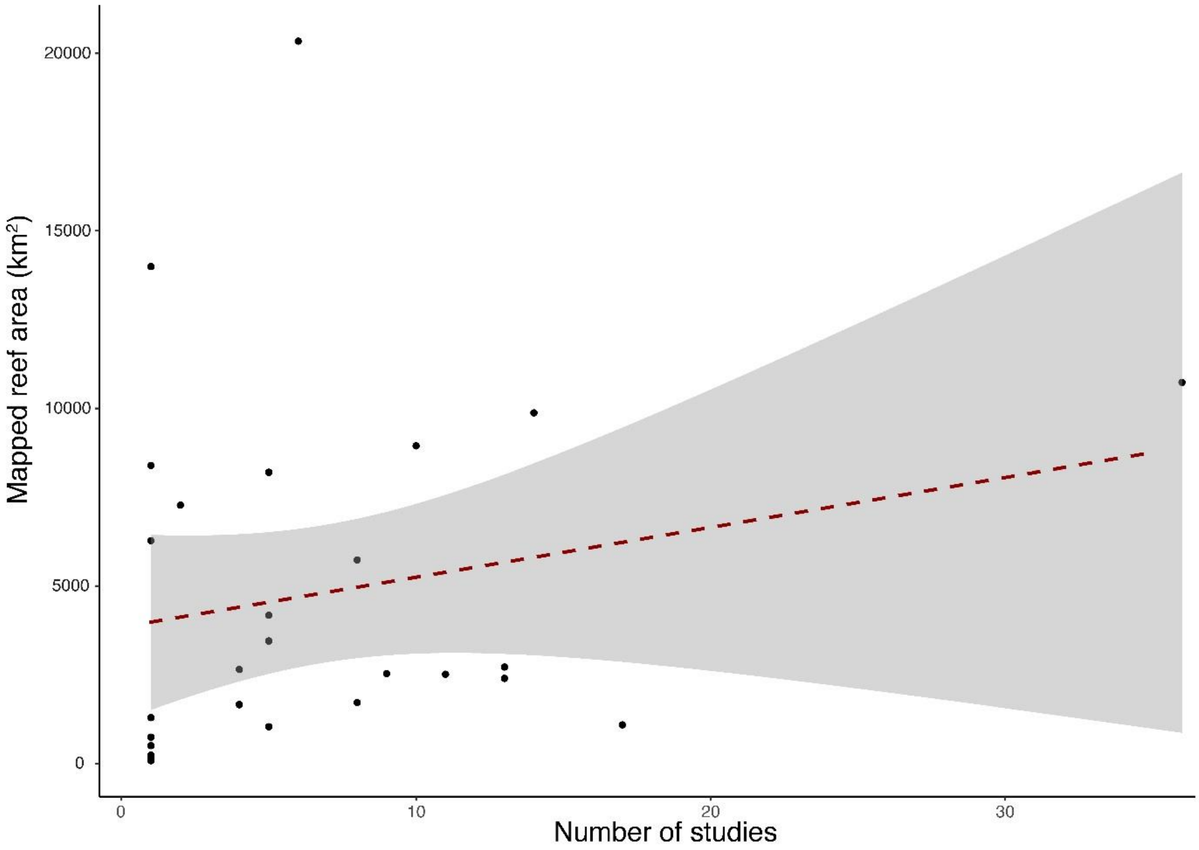

Figure A1. Relationship between number of studies and mapped reef area (km^2) within each mapped region.

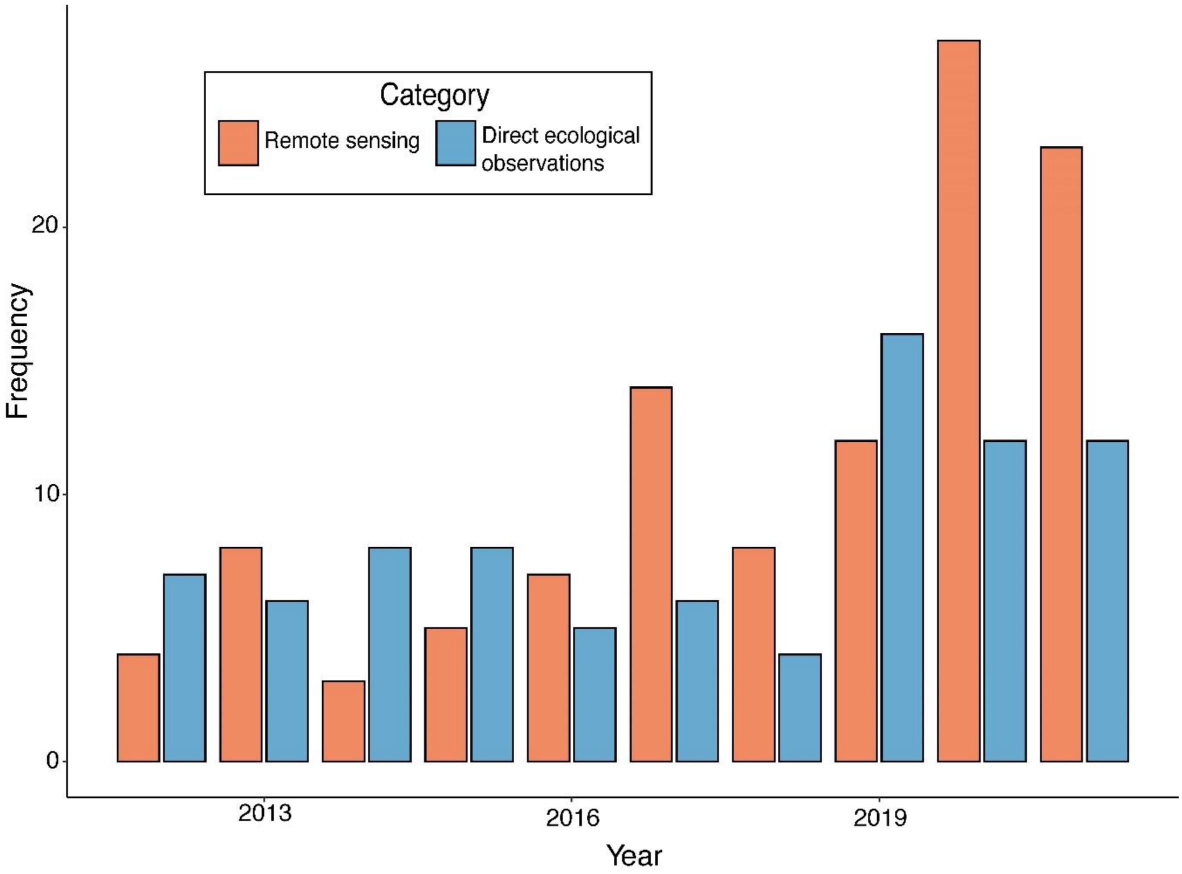

Figure A2. Number of studies across the fields coral reef ecology and remote sensing through time.

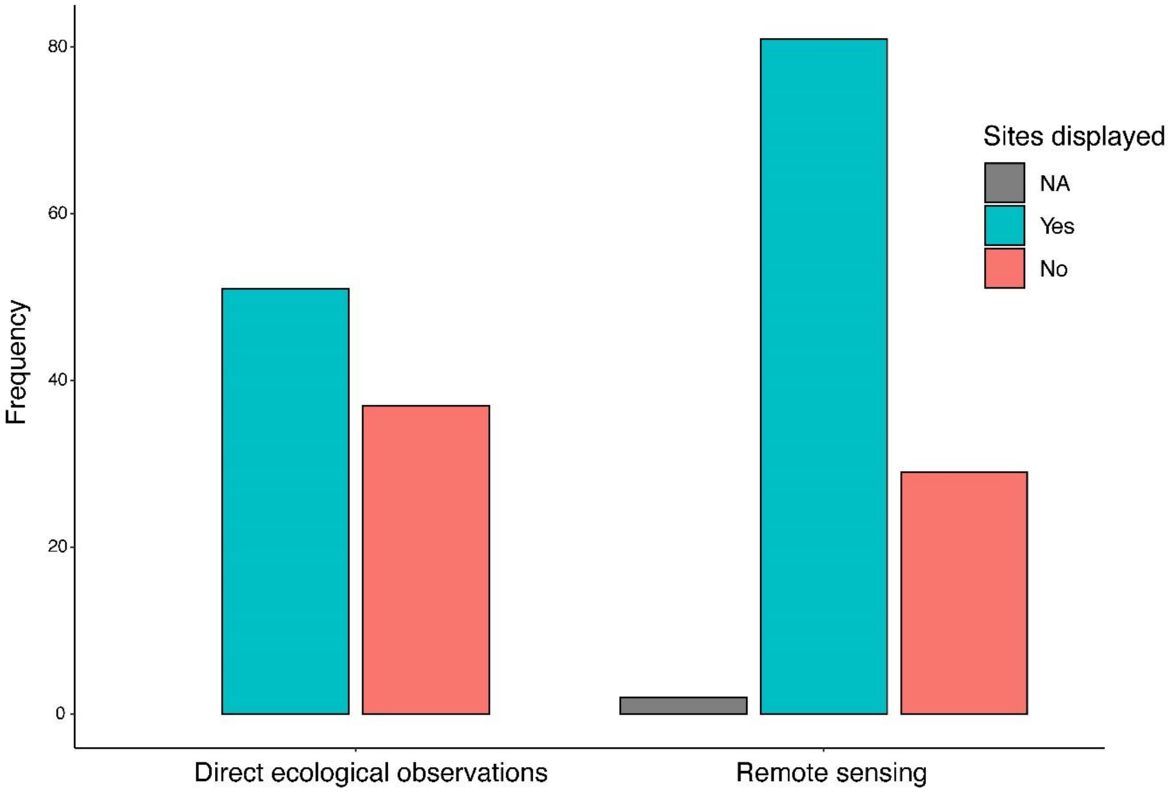

Figure A3. Number of studies across the fields coral reef ecology and remote sensing specifically locating their survey sites (blue) versus those with limited/no details (red).

Appendix B: Supporting information for chapter 3

Text B1. Explanation and justification of the selection process of reefs within the two biogeographic realms.

To facilitate comparison across the Caribbean and the Indo-Pacific, sites were chosen based on location (oceanic vs. continental), reef type, relative reef area, and data accuracy. Sites were chosen based on a paired comparison scheme (Figure 2) to increase robustness of the analysis. For example, the Belizean Barrier Reef and Great Barrier Reef were included as counterparts, both representing barrier reef morphologies. Pairing was firstly driven by similar locations, i.e. ensuring that the locations treated as analogues were positioned in similar oceanic or continental settings. Then, using the Allen Coral Atlas, the initial sites were compared according to their mapped reef area to ensure all were fully developed reef systems (excluding exceptionally small or incomplete reefs, e.g. plug reefs or isolated mounts). Reefs were then evaluated in an initial accuracy assessment (conducted by the authors) to ensure correct classifications in the algorithms employed by the Allen Atlas. In this data checking stage, mapped reef areas, as provided by the Atlas, were investigated and compared to independent estimates to ensure that the algorithms presented reef area within the specific location correctly. Accuracy was visually determined by assessing the high-resolution imagery of shallow reef zones using expert knowledge and visual cues (i.e., colour or texture) to distinguish geomorphic zones, and then comparing our estimates against the classification by the Atlas. Preference was given to sites that showed higher accuracies for the shallow reef habitat zones of interest, i.e., Inner Reef Flat, Outer Reef Flat and Reef Crest. We endeavoured to compare sites that were not only similar in their geographic setting and reef type, but also balancing mapping accuracy. Finding analogues in the two highly disparate realms was challenging. For example, few atolls occur in the Caribbean. Banco Chincorro atoll was selected in the Caribbean because mapping accuracy is likely to be much higher than other atolls in the Caribbean region as it has been more intensively surveyed due to its closeness to Belize and Mexico.

It must be noted that sites within the Caribbean are entirely in the Northern hemisphere and sites in the Indo-Pacific mostly in the Southern Hemisphere since the majority of reef area in each realm is encompassed within these longitudes. Furthermore, research effort is highly concentrated in specific locations within each realm, meaning that mapping accuracies in these regions are much higher due to the existence of long-term in-situ training datasets. However, these differences are an inherent part of the between-realm variation and there is no *a priori* reason to believe that hemisphere will influence shallow reef extents.

Table B1. Potential limitations and caveats pertaining to the data set of geomorphic reef classes classified by Kennedy et al. (2021) accessed through the Allen Coral Atlas (2022).

Potential Limitation	Reasoning
Environmental	Characteristics of the natural environment could potentially limit or decrease the scope and accuracy of generated maps. Cloud cover, turbidity, and breaking waves could hinder the automated image processing, ultimately affecting classifications. Geomorphic maps will be limited to a maximum depth of 15m due to the varying ability of satellite imagery to penetrate the water column and potentially restrained by the lack of accurate training bathymetry data. Furthermore, reliability of accurate bathymetry data will decrease with turbidity and high-energy wave climates. Source imagery was generally taken between January 2018 and December 2020, allowing for a broad series of images meaning that poor visibility conditions could be avoided thus increasing the accuracy of class assessments.
Algorithm training process	Maps are created with a semi-automated machine learning algorithm and cleaned up with an object-based analysis approach. Therefore, the accuracy is highly dependent on the abundance, availability and quality of the data and imagery utilized during the training and classification process, as well as the availability of local reference data. Generally, the maps are created and validated for broad-scale assessments and class description and not focused on small reef-scale (e.g., 10 – 100 meters) areas. Additionally, reference data availability varies between regions and is sometimes dependent on expert interpretation only (rather than in-situ field data), thus limiting the scope of training for the algorithm. Therefore, accuracy varies between 60-90% (Allen Coral Atlas 2022). While maps that are very localised, generated in correspondence with in-situ observations, might be more accurate, the methodology of the Allen Coral Atlas does allow for mapping on a much broader scale and globally consistent basis.
Classification - Exposure	Classes assigned ‘sheltered’ status within the ‘Reef Cover’ classification scheme are any geomorphic classes more protected from strong directional prevailing wind or current, either by land or by opposing reef structures (Kennedy et al. 2020). Classes that are

	nominated as ‘sheltered’ are heavily context dependent. However, within the class descriptors, no thresholds for what constitutes “exposed” in terms of wind speeds, current velocities or wave energy are established. Therefore, sheltered reef classes may appear on both windward and leeward sides of reef systems. Similarly, in their provided case studies, *Back Reef Slope* was identified with the lowest confidence (5.9 +/- 1.7 SD) by experts. (NB the sheltered and exposed classifications within the present study used a different set of criteria based on predominant wind directions; in this case it must be acknowledged that intense winds and waves can be periodically experienced in ‘sheltered’ locations).
Classification – reef categorization	The Allen Coral Atlas allows for the first unified and standardised assessment of large-scale patterns of benthic, as well as geomorphic zonation patterns of the world’s coral reefs. However, it does not provide any categorization of general reef types (e.g. Barrier Reef). Categorizing reef type will, therefore, be open to interpretation by the end users of the Atlas. The end products will depend on their expert knowledge or the literature.

References

Allen Coral Atlas (2022) Imagery, maps and monitoring of the world’s tropical coral reefs.

Kennedy E, Roelfsema C, Kovacs E, Lyons M, Borrego-Acevedo R, Roe M, Yuwono D, Wolff J, Tudman P, Murray N, Phinn S (2020) Reef Cover Classification: Coral reef internal class descriptors for global habitat mapping.

Kennedy EV, Roelfsema CM, Lyons MB, Kovacs EM, Borrego-Acevedo R, Roe M, Phinn SR, Larsen K, Murray NJ, Yuwono D, Wolff J, Tudman P (2021) Reef Cover, a coral reef classification for global habitat mapping from remote sensing. Sci Data 8:1–20

Table B2. Summary of the generalised linear mixed effect model assessing the shallow reef habitat width patterns between the Caribbean and Indo-Pacific. Model outputs are presented on the log-scale.

Response variable	Model used	Predictor variable	Estimate	SE	*statistic*	*p* value
Shallow reef habitat width	tweedie GLMM	Intercept	5.4931	0.2288	24.011	<0.001
		LocationIndo-Pacific	0.3937	0.3233	1.218	0.223

Table B3. Summary of the DHARMa Moran's I test results for distance-based autocorrelation.

observed	expected	SD	*p* value
0.26118197	-0.00027473	0.00384216	<0.001

Text B2. Spatial autocorrelation and cluster analysis in GeoDa

A univariate Local Moran's I with spatial weighting based on six K-nearest neighbours was used as a local indicator of spatial association to identify local clusters and local spatial outliers (Anselin 1995). Clustering was assessed using 99,999 permutations and a False Discovery Rate (Benjamini and Hochberg 1995) creating a significance level cut-off of p = 0.0143 (designated by the program).

References

Anselin L (1995) Local Indicators of Spatial Association—LISA. Geogr Anal 27:93–115

Benjamini Y, Hochberg Y (1995) Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing. Journal of the Royal Statistical Society: Series B 57:289–300

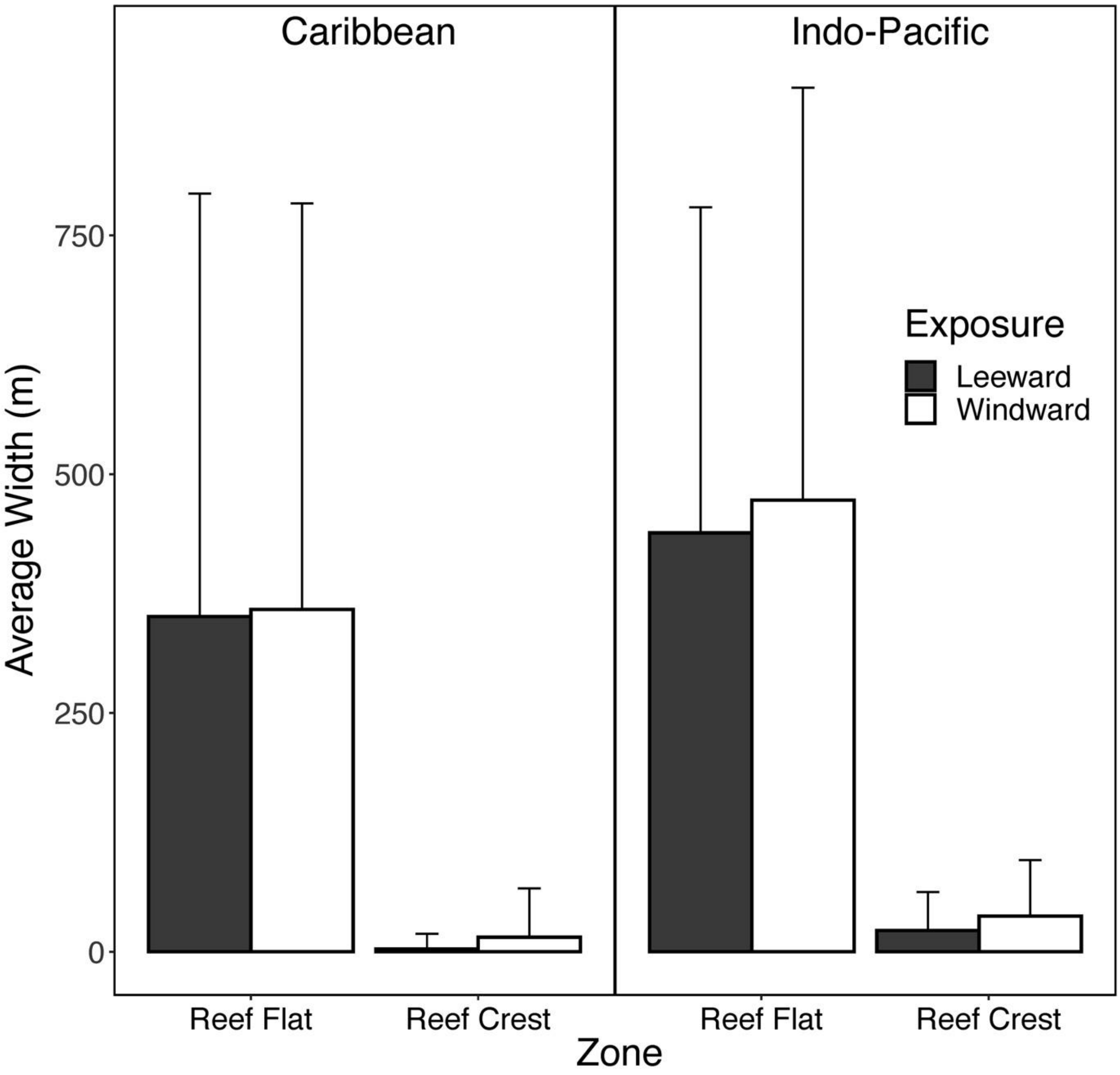

Figure B1. Average width (m) (+/- SE) of each geomorphic zone grouped by exposure to prevailing winds (white = leeward, grey = windward) across the Caribbean and Indo-Pacific realms Reef flats represent the combined data of Inner and Outer flat.

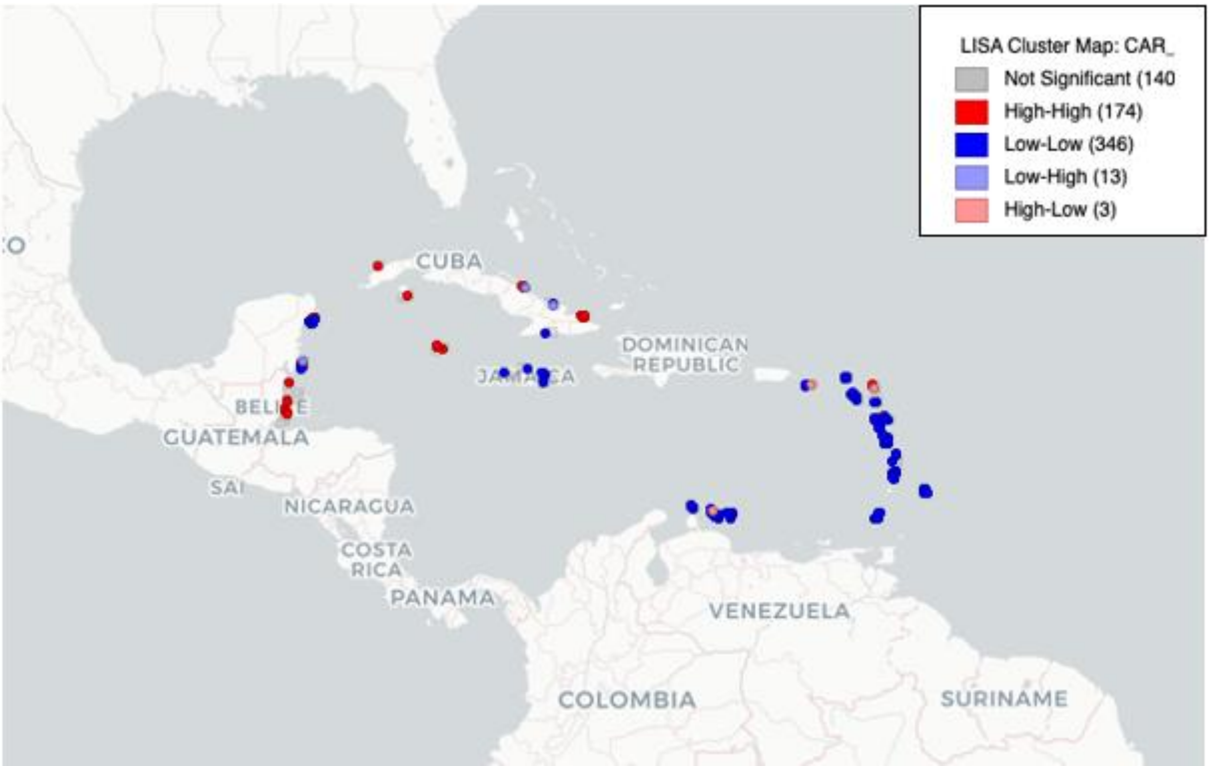

Figure B2. GeoDa LISA (Local Indicators of Spatial Association) cluster map for shallow reef habitat widths across the Caribbean. Data showed a Moran’s I of 0.694.

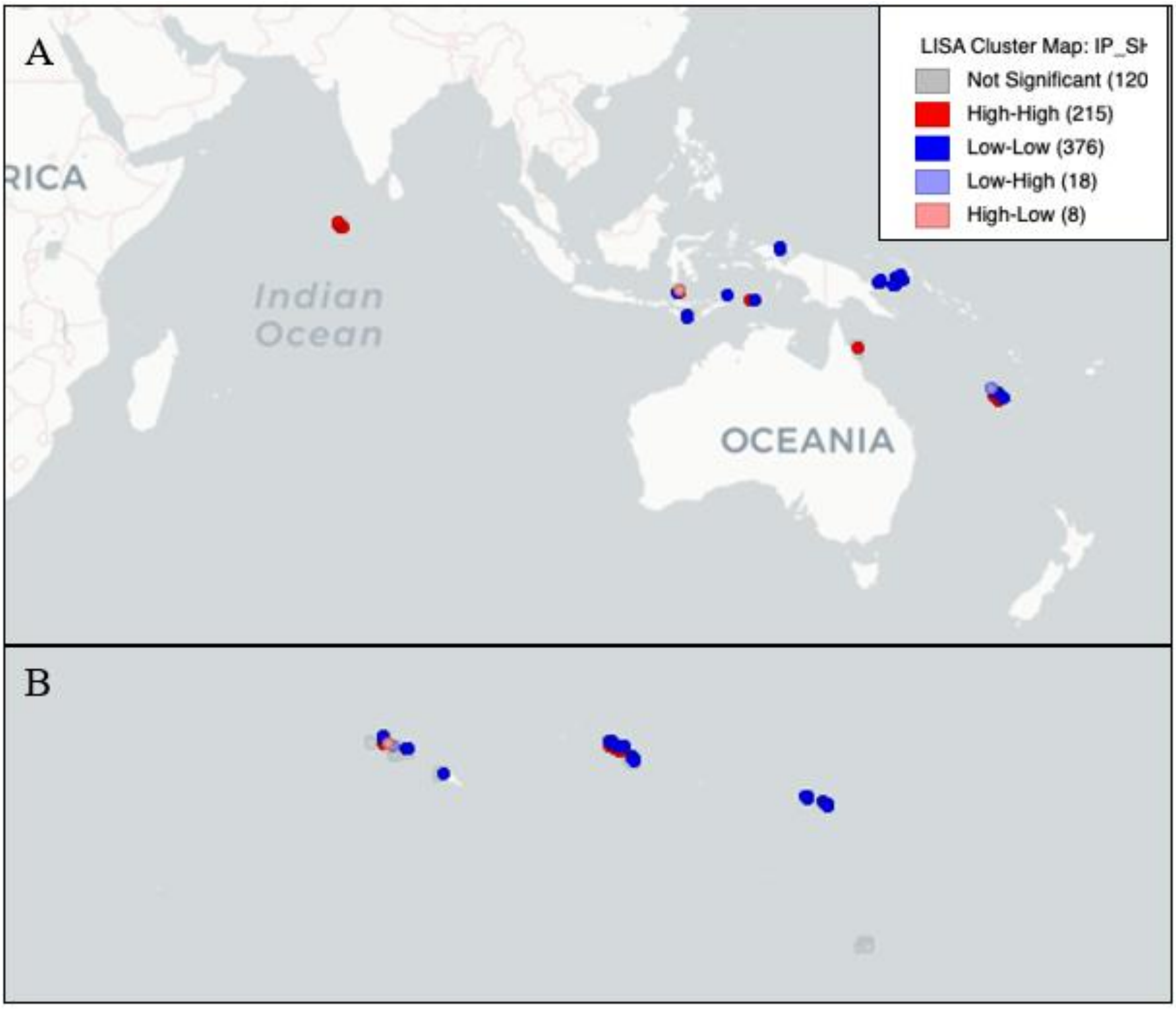

Figure B3. GeoDa LISA (Local Indicators of Spatial Association) cluster map for shallow reef habitat widths across the Indo-Pacific (A = ranging from the Maledives to New Caledonia, and B = French Polynesia). Data showed a Moran's I of 0.674.

Table S4. Measurements of the shape of the distribution of shallow reef habitat margins across biogeographic realms.

Location	Skewness	Kurtosis
Caribbean	2.287673	9.840317
Indo-Pacific	1.144568	4.289006

Table S5. Comparison of the average widths (m) (+/- SE) for windward and leeward shallow reef habitat margins between biogeographic realms, as well as globally.

Location	Leeward		Windward	
Caribbean	353.93 ± 15.36	N = 833	373.54 ± 12.99	N = 1112
Indo-Pacific	460.77 ± 11.86	N = 856	510.03 ± 14.36	N = 964
Global	408.1 ± 9.76	N = 1689	436.92 ± 9.75	N = 2076

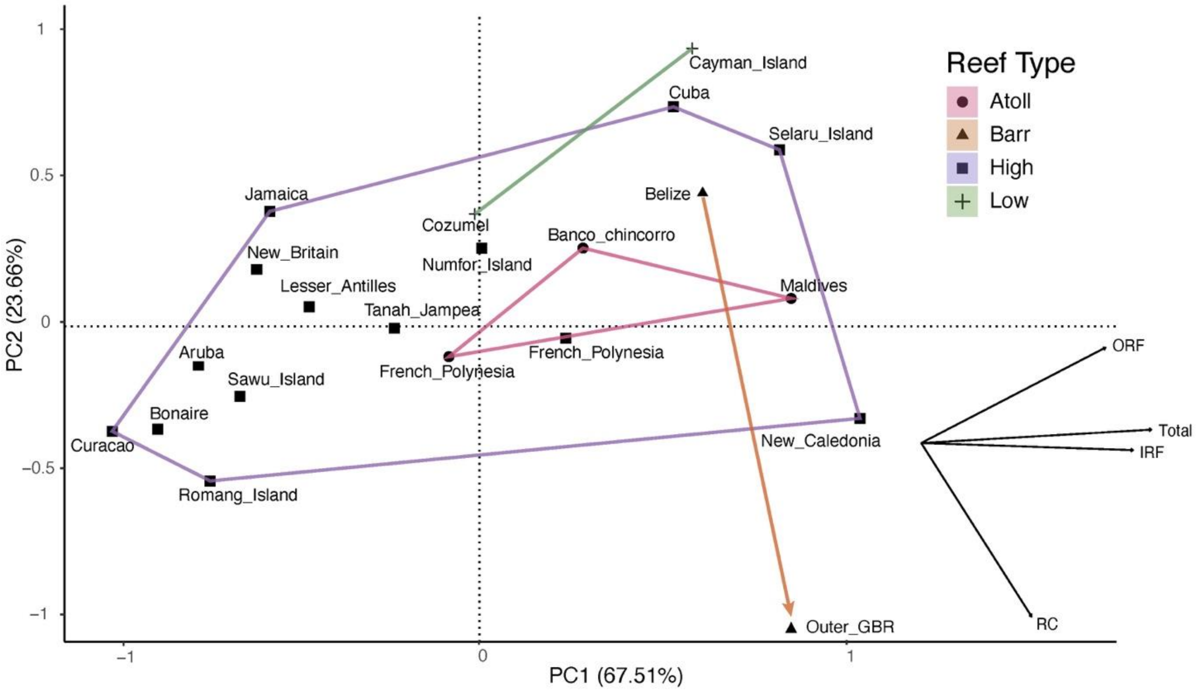

Figure B4. Principal Component Analysis (PCA) of the average widths of shallow reef habitat zones (IRF = Inner Reef Flat, ORF = Outer Reef Flat, RC = Reef Crest, Total = total shallow reef width) and their associated reefs based on the reef types (Circles and red hull = atolls, triangles and orange hull = barrier reef systems, squares and purple hull = high islands, and crosses and green hull = low islands). Closed symbols are reefs in the Indo-Pacific, open symbols reefs in the Caribbean. For position of Outer_GBR, see Figure 3.6.

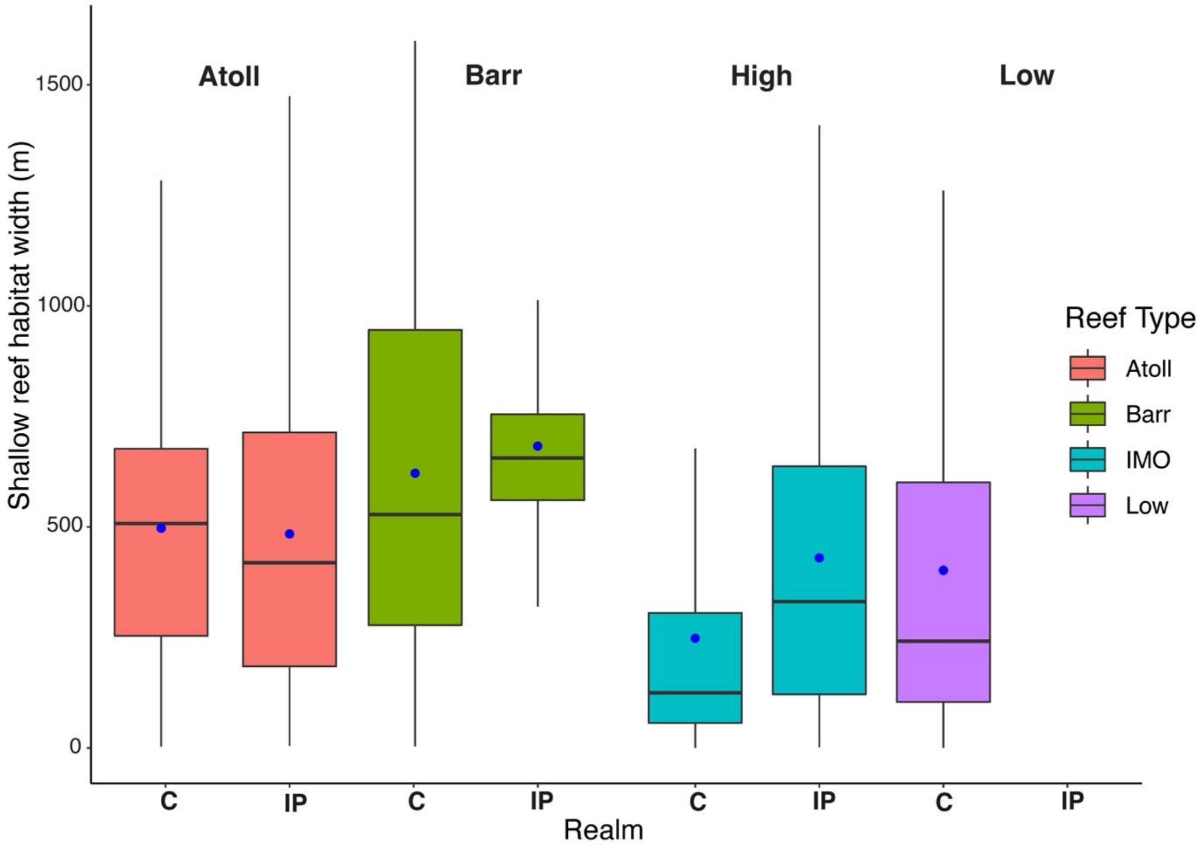

Figure B5. Shallow reef habitat widths (m) of different reef types (Atoll = Atoll reefs, Barr = barrier reefs, High = high islands, and Low = low lying islands) across the Caribbean (C) and Indo-Pacific (IP). Blue dots represent the mean for each morphology, the bar shows the median, box the inter-quartile range (IQR) and lines the 1.5 IQR values. Outliers were removed from the figure for visual appeal.

Appendix C: Supporting information for chapter 4

Text C1. Trends in growth rates across tropical herbivorous fishes.

Given the overwhelming contribution of rabbitfishes to herbivore catches, we explored other factors that may be driving the disproportionately high catch of rabbitfishes. Specifically, we hypothesised that the overwhelming contribution of rabbitfishes to fisheries may stem, at least partially, from life history characteristics that can be correlated with faster population growth rates (Denney et al. 2002). To assess this hypothesis, we utilised a derived parameter from the Von Bertalanffy growth equation, K_{max} (*sensu* Morais and Bellwood 2018), across species of parrotfishes, surgeonfishes, and rabbitfishes. In short, K_{max} is the rate at which a population with specific Von Bertalanffy growth parameters would reach its asymptotic size, $L\infty$, if it grew to the maximum size reported for that species (Morais and Bellwood 2018). This standardisation allows for cross-species comparisons of growth rates (Morais and Bellwood 2018, 2020). Data were available for 31 parrotfish species, 30 surgeonfish species, and eight rabbitfish species (R package *'rfishprod'*; Morais and Bellwood 2020), representing approximately 37%, 30%, and 28% of described species, respectively.

Using a generalized linear mixed effect model (GLMM), we compared growth rates across the three herbivorous fish groups. For the GLMM, we used group as a categorical fixed effect (three levels: parrotfishes, surgeonfishes, and rabbitfishes) to explain variation in K_{max} and specified random intercepts for each species to account for repeated observations at the species level. Models with different distributions were compared using AICc, with the best-fit model being a Gamma distribution with a log link. Pairwise comparisons with Tukey's adjustment between herbivorous groups (Table C3) were conducted using *'emmeans'* (Lenth et al. 2020). All model assumptions and fit were assessed using simulated residuals, which were satisfactory in all cases (package: '*DHARMa'*; Hartig 2022). All statistical analyses and data manipulations were performed using the software R 4.2.2 (R Core Team 2022) and '*tidyverse'* package (Wickham et al. 2019).

Based on the GLMM, the average K_{max} of rabbitfishes was significantly higher than both parrotfishes and surgeonfishes by roughly two-fold ($p < 0.01$; Figure C4; Table C2, C3). There was no difference between parrotfishes and surgeonfishes (Figure C4; Table C2, C3). This suggests that rabbitfishes grow twice as quickly as the other herbivorous fish groups and, therefore, could potentially sustain higher fishing pressure than the other groups.

Text C2. Catch-per-unit-effort calculations.

The equation used to calculate catch-per-unit effort from the Sea Around Us catch data as in Eddy et al. (2021).

$$CPUE\ (EEZ) = \frac{total\ herbivore\ catch\ (t)}{\left(\left(\frac{total\ herbivore\ catch\ (t)}{total\ catch\ (t)}\right) * fishing\ effort\ \left(\frac{kW}{day}\right)\right)}$$

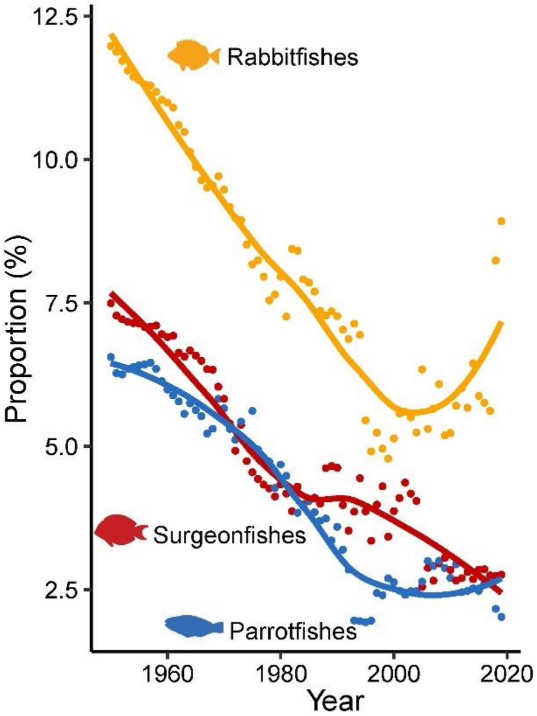

Figure C1. The relative contribution of each herbivorous fish group to overall reef-associated fish catches across all EEZs per year. The points are the raw data points (i.e. sums of global annual estimates) while the lines are produced by the loess function of the 'stats' package [6] and are used for illustration purposes only.

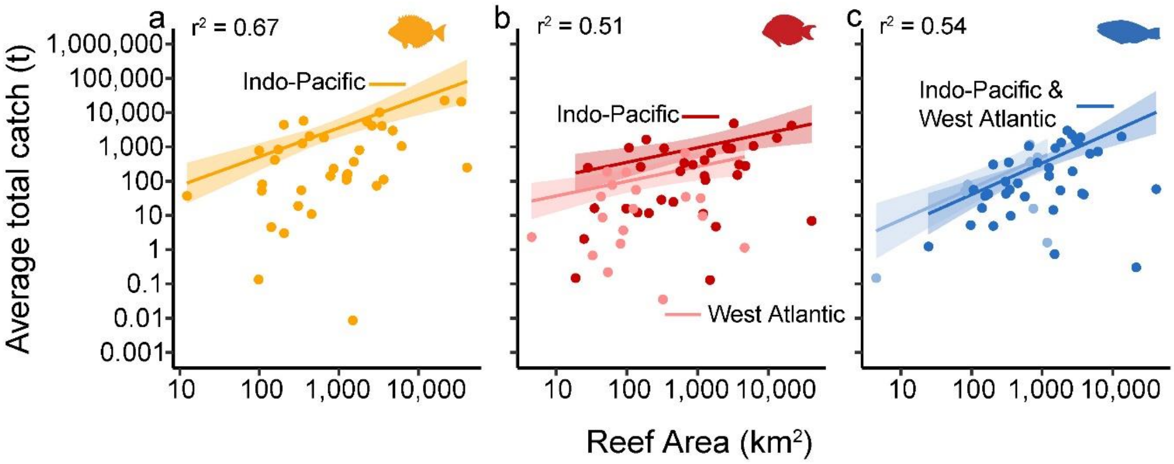

Figure C2. The relationship between the average total catch (2009-2019) of a) rabbitfishes ($r^2 = 0.67$), b) surgeonfishes ($r^2 = 0.51$), and c) parrotfishes ($r^2 = 0.54$) and the corresponding reef area (km^2) across the Indo-Pacific (darker colours) and Western Atlantic (lighter colours). Lines show the mean predicted fits from generalised linear models, shaded ribbons are the 95% confidence intervals, and points represent the raw data (i.e. the average total herbivore catch for each group between 2009-2019 for each EEZ). Note the y- and x-axes are on the $\log_{10}$ scale in all cases (which is why the majority of points appear to fall below the fitted line) and the r^2 value refers to the fit of the entire model.

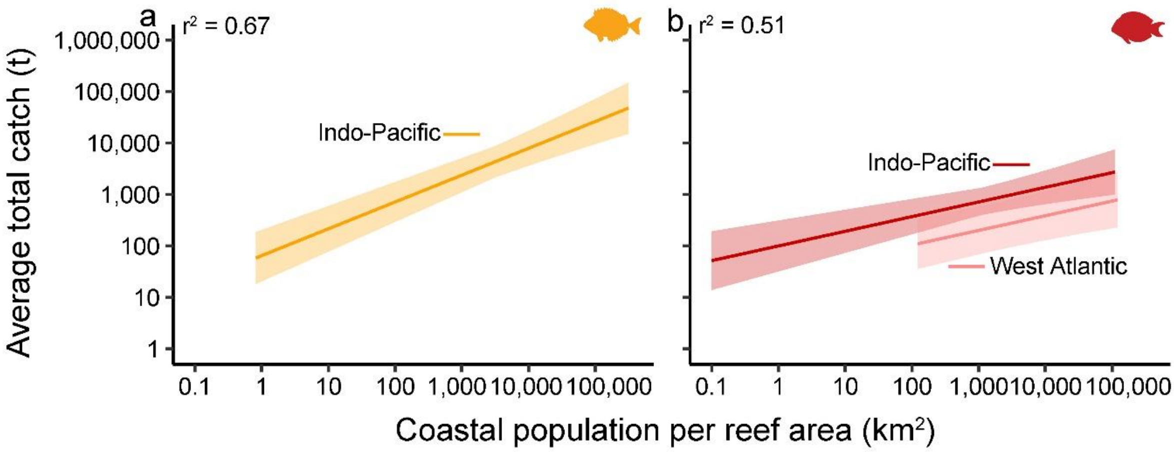

Figure C3. The relationship between average total herbivore catches (2009-2019) of a) rabbitfishes and b) surgeonfishes, and coastal population per reef area (km^2) across the Indo-Pacific (darker colours) and Western Atlantic (lighter colours). Lines show the mean predicted fits from generalised linear models, shaded ribbons are the 95% confidence intervals. Note the y- and x-axes are on the log$_{10}$ scale in both cases and the r^2 value refers to the fit of the entire model. Also note that there is no plot for parrotfishes as the AICc scores suggested that coastal population did not have a substantial effect on parrotfish catch (Table C1).

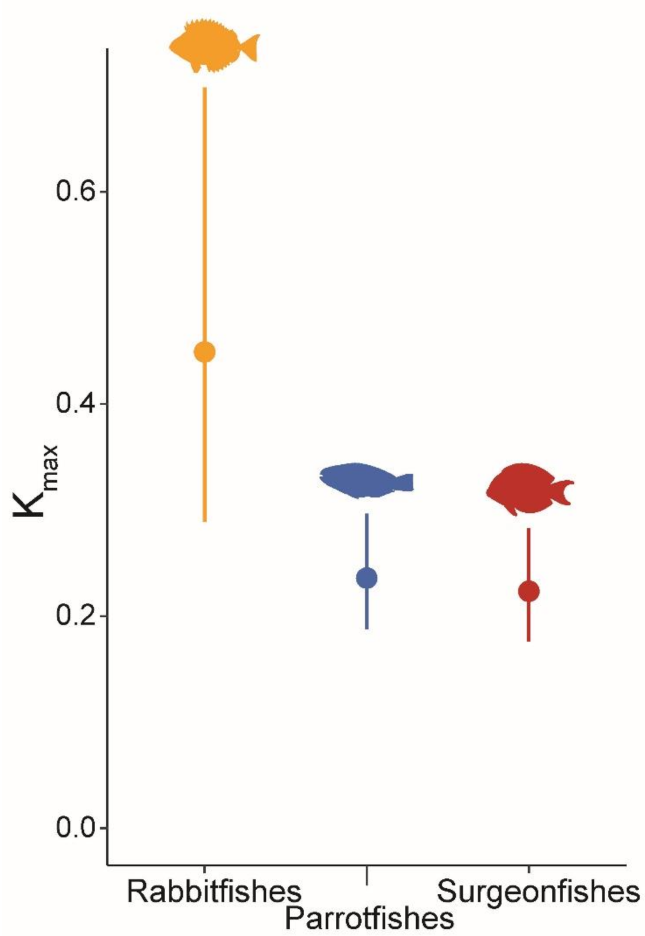

Figure C4. The theoretical growth rates (K_{max}) for each tropical herbivorous fish group. Points show the mean predicted value of generalised linear mixed effect model and ranges denote the upper and lower 95% confidence intervals.

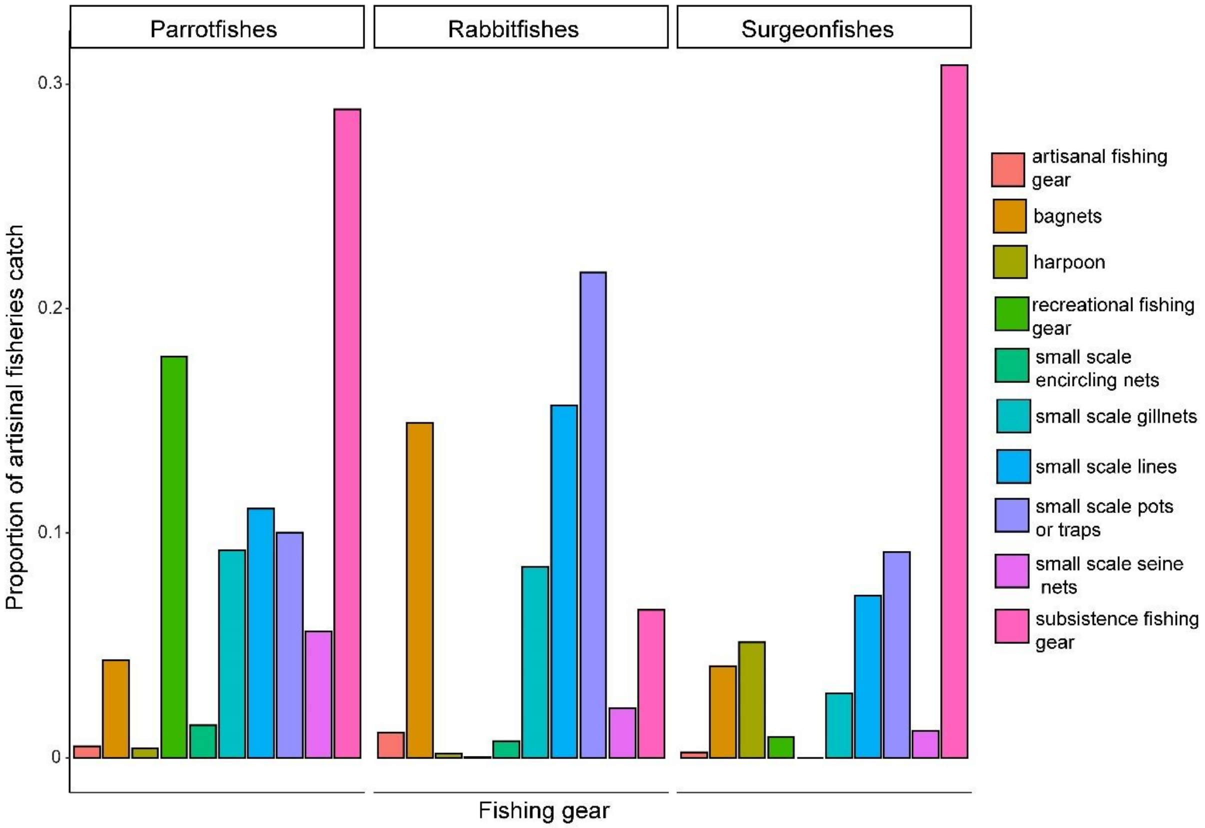

Figure C5. The relative distribution of total catch across each gear type for the three herbivorous fish groups.

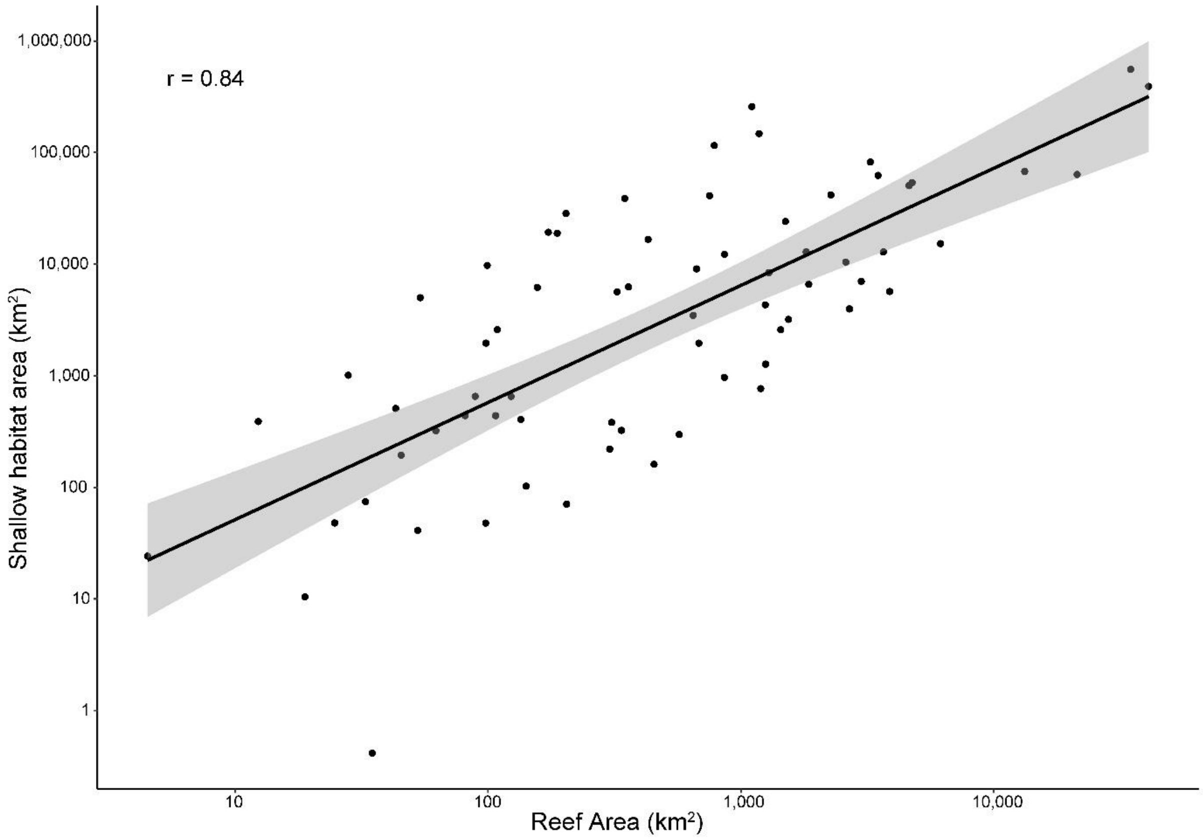

Figure C6. The relationship between shallow coastal habitat area (km^2) and reef area (km^2) (Pearson's r = 0.84). The line shows the mean predicted fit of a linear model, the shaded ribbon denotes the upper and lower 95% confidence intervals, and the points represent the raw data. Note the y and x-axes are on the log$_{10}$ scale.

Table C1. Comparison of models used to examine variation in average total catch across each herbivorous fish group, as well as average catch-per-unit-effort (CPUE) of all herbivorous fish groups both including and excluding the outlier (Niue). Models are compared using the corrected Akaike Information Criterion (AICc). Shown are degrees of freedom (df), model maximum log-likelihood (logLik), AICc, change in AICc (Δ), AICc weight (wAICc), and the conditional coefficient of determination (r^2). OHI = Ocean Health Index; CoastalPop = Coastal population; MDS = Marine Dependency Score.

Response variable	Variables	df	logLik	AICc	Δ	wAICc	r2
Rabbitfish catch	Reef Area+OHI+CoastalPop	5	-268.55	549.09	0.00	0.60	0.67
	Reef Area+CoastalPop	4	-271.05	551.38	2.29	0.19	
	Reef Area+OHI+MDS+CoastalPop	6	-268.52	551.94	2.85	0.15	
	Reef Area+MDS+CoastalPop	5	-270.85	553.71	4.61	0.06	
	Reef Area+MDS	4	-276.44	562.17	13.08	0.00	
	Reef Area+MDS+OHI	5	-276.42	564.83	15.74	0.00	
	Reef Area	3	-280.04	566.83	17.73	0.00	
	Reef Area+OHI	4	-280.01	569.32	20.23	0.00	
	Null	2	-286.23	576.82	27.72	0.00	
Surgeonfish catch	Reef Area+Realm+MDS+CoastalPop	6	-308.45	630.77	0.00	0.38	0.51
	Reef Area+Realm+CoastalPop	5	-310.39	632.09	1.32	0.20	
	Reef Area*Realm+MDS+CoastalPop	7	-308.24	633.03	2.26	0.12	
	Reef Area+Realm+MDS+OHI+CoastalPop	7	-308.42	633.38	2.62	0.10	
	Reef Area*Realm+CoastalPop	6	-310.15	634.17	3.40	0.07	
	Reef Area+Realm+OHI+CoastalPop	6	-310.39	634.64	3.87	0.06	
	Reef Area*Realm+MDS+OHI+CoastalPop	8	-308.24	635.84	5.07	0.03	
	Reef Area*Realm+OHI+CoastalPop	7	-310.14	636.82	6.05	0.02	
	Reef Area+Realm	4	-315.34	639.52	8.75	0.00	
	Reef Area+Realm+OHI	5	-314.31	639.92	9.15	0.00	
	Reef Area+Realm+MDS	5	-314.84	640.98	10.21	0.00	
	Reef Area+Realm+MDS+OHI	6	-313.82	641.50	10.73	0.00	
	Reef Area*Realm	5	-315.33	641.96	11.20	0.00	
	Reef Area*Realm+OHI	6	-314.12	642.10	11.33	0.00	
	Reef Area	3	-318.32	643.14	12.37	0.00	
	Reef Area*Realm+MDS	6	-314.81	643.49	12.72	0.00	
	Reef Area*Realm+MDS+OHI	7	-313.70	643.95	13.18	0.00	
	Realm	3	-319.51	645.53	14.76	0.00	
	Null	2	-326.08	656.41	25.64	0.00	
	Reef Area	3	-290.70	587.99	0.00	0.30	0.54

Parrotfish catch	Reef Area+Realm	4	-290.42	589.84	1.85	0.12	
	Reef Area+Realm+CoastalPop	5	-289.17	589.88	1.89	0.12	
	Reef Area+Realm+OHI	5	-289.39	590.31	2.33	0.09	
	Reef Area+Realm+MDS+CoastalPop	6	-288.17	590.55	2.57	0.08	
	Reef Area+Realm+OHI+CoastalPop	6	-288.72	591.65	3.66	0.05	
	Reef Area*Realm	5	-290.08	591.71	3.72	0.05	
	Reef Area*Realm+CoastalPop	6	-289.06	592.33	4.34	0.03	
	Reef Area+Realm+MDS	5	-290.41	592.35	4.36	0.03	
	Reef Area*Realm+OHI	6	-289.29	592.80	4.81	0.03	
	Reef Area+Realm+MDS+OHI+CoastalPop	7	-287.95	592.93	4.94	0.03	
	Reef Area+Realm+MDS+OHI	6	-289.39	592.98	5.00	0.02	
	Reef Area*Realm+MDS+CoastalPop	7	-288.08	593.19	5.21	0.02	
	Reef Area*Realm+MDS	6	-290.08	594.38	6.39	0.01	
	Reef Area*Realm+OHI+CoastalPop	7	-288.68	594.40	6.41	0.01	
	Reef Area*Realm+MDS+OHI	7	-289.29	595.62	7.63	0.01	
	Reef Area*Realm+MDS+OHI+CoastalPop	8	-287.92	595.84	7.86	0.01	
	Null	2	-300.18	604.65	16.67	0.00	
	Realm	3	-299.74	606.07	18.08	0.00	
CPUE	Reef Area*Realm+OHI+CoastalPop	7	235.81	-455.55	0.00	0.63	0.54
	Reef Area*Realm+MDS+OHI+CoastalPop	8	236.01	-453.31	2.24	0.21	
	Reef Area+Realm+OHI+CoastalPop	6	232.29	-451.06	4.49	0.07	
	Reef Area*Realm+CoastalPop	6	232.03	-450.52	5.03	0.05	
	Reef Area+Realm+MDS+OHI+CoastalPop	7	232.83	-449.58	5.97	0.03	
	Reef Area*Realm+MDS+CoastalPop	7	232.23	-448.38	7.17	0.02	
	Reef Area+Realm+CoastalPop	5	226.50	-441.93	13.62	0.00	
	Reef Area+Realm+MDS+CoastalPop	6	227.66	-441.80	13.75	0.00	
	Reef Area*Realm+MDS	6	219.77	-426.02	29.53	0.00	
	Reef Area*Realm	5	217.94	-424.82	30.73	0.00	
	Reef Area*Realm+MDS+OHI	7	220.26	-424.44	31.11	0.00	
	Reef Area*Realm+OHI	6	218.02	-422.50	33.05	0.00	
	Reef Area+Realm+MDS+OHI	6	217.43	-421.34	34.21	0.00	
	Reef Area+Realm	4	214.89	-421.08	34.47	0.00	
	Reef Area+Realm+MDS	5	215.68	-420.29	35.26	0.00	
	Reef Area+Realm+OHI	5	215.53	-419.99	35.56	0.00	
	Realm	3	213.04	-419.66	35.89	0.00	
	Reef Area	3	206.08	-405.74	49.81	0.00	
	Null	2	204.19	-404.18	51.37	0.00	
CPUE - outlier removed	Reef Area*Realm+MDS+CoastalPop	7	246.49	-476.86	0.00	0.23	0.43
	Reef Area+Realm+MDS+CoastalPop	6	245.08	-476.60	0.26	0.20	

Reef Area+Realm+MDS+OHI+CoastalPop	7	245.87	-475.63	1.23	0.12
Reef Area*Realm+MDS+OHI+CoastalPop	8	247.01	-475.24	1.62	0.10
Reef Area+Realm+MDS	5	242.91	-474.74	2.13	0.08
Reef Area*Realm+CoastalPop	6	243.68	-473.81	3.06	0.05
Reef Area+Realm+CoastalPop	5	242.42	-473.76	3.11	0.05
Reef Area*Realm+MDS	6	243.63	-473.71	3.15	0.05
Reef Area+Realm+OHI+CoastalPop	6	243.50	-473.45	3.41	0.04
Reef Area*Realm+OHI+CoastalPop	7	244.65	-473.18	3.68	0.04
Reef Area+Realm+MDS+OHI	6	242.98	-472.40	4.47	0.02
Reef Area*Realm+MDS+OHI	7	243.64	-471.16	5.70	0.01
Reef Area+Realm	4	232.16	-455.60	21.26	0.00
Reef Area+Realm+OHI	5	232.81	-454.53	22.34	0.00
Reef Area*Realm	5	232.18	-453.26	23.60	0.00
Reef Area*Realm+OHI	6	232.88	-452.20	24.66	0.00
Reef Area	3	229.30	-452.19	24.67	0.00
Realm	3	227.32	-448.23	28.64	0.00
Null	2	220.87	-437.52	39.34	0.00

Table C2. Summary of generalised linear model (GLM) and generalised linear mixed effects model (GLMM) results used to examine differences in average total catch across each herbivorous fish group, average CPUE of herbivorous fishes with and without the outlier (Niue), and variation in growth coefficients among herbivorous groups. Note that the significant interaction between reef area and Western Atlantic, as well as effect of OHI in the CPUE model appears to be primarily driven by a single outlying data point. This outlier was Niue, a single uplifted atoll island with limited shallow reef habitat and shelf are (Zylich et al. 2012). Niue is likely an outlier as its fisheries primarily target pelagic species with minimal near-shore effort (Zylich et al. 2012).

Response variable	Model used	Predictor variable	Estimate	SE	*z* value	*p* value
Rabbitfish catch	Gamma GLM	Intercept	6.60	0.22	29.67	<0.001
		Reef Area	1.50	0.29	5.25	<0.001
		OHI	0.77	0.35	2.22	0.03
		CoastalPop/ReefArea	1.54	0.22	6.90	<0.001
Surgeonfish catch	Gamma GLM	Intercept	5.63	0.27	20.93	<0.001
		Reef Area	0.85	0.28	3.05	<0.01
		Realm (W.Atlantic)	-1.27	0.51	-2.47	0.01
		MDS	0.54	0.26	2.03	0.04
		CoastalPop/ReefArea	0.89	0.23	3.90	<0.001
Parrotfish catch	Gamma GLM	Intercept	5.67	0.21	26.99	<0.001
		Reef Area	1.52	0.31	4.98	<0.001
CPUE	Gamma GLM	Intercept	-4.46	0.22	-20.71	<0.001
		Reef Area	-0.17	0.18	-0.95	0.34
		Realm (W.Atlantic)	-0.19	0.51	-0.37	0.71
		OHI	-0.65	0.22	-3.01	<0.01
		CoastalPop/ReefArea	-1.08	0.15	-7.10	<0.001
		Reef Area*Realm (W.Atlantic)	1.22	0.43	2.85	<0.001
CPUE – outlier removed	Gamma GLM	Intercept	-4.80	0.18	-26.61	<0.001
		Reef Area	0.29	0.17	1.68	0.09
		Realm (W.Atlantic)	-0.34	0.39	-0.88	0.38
		MDS	0.42	0.17	2.46	0.01
		CoastalPop/ReefArea	-0.40	0.17	-2.31	0.02
		Reef Area*Realm (W.Atlantic)	0.62	0.36	1.71	0.09

Kmax	Gamma GLMM	Intercept	-1.50	0.12	-12.51	<0.001
		FamilyScaridae	0.05	0.17	0.33	0.74
		FamilySiganidae	0.70	0.25	2.75	0.01

Table C3. Post-hoc pairwise comparisons of growth coefficients between herbivorous fish groups.

contrast	ratio	SE	df	asymp.LCL	asymp.UCL	z.ratio	p.value
Acanthuridae / Scaridae	0.95	0.16	172.00	0.64	1.40	-0.33	0.94
Acanthuridae / Siganidae	0.50	0.13	172.00	0.27	0.91	-2.75	0.02
Scaridae / Siganidae	0.53	0.13	172.00	0.29	0.95	-2.55	0.03

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Appendix D: List of publications arising from this thesis

1. **Lutzenkirchen, L. L.**, Duce, S. J., & Bellwood, D. R. (2023). The global biogeography of reef morphology. Global Ecology and Biogeography, 32, 1353–1364.
2. **Lutzenkirchen, L. L**., Duce, S. J., & Bellwood, D. R. (2024). Exploring benthic habitat assessments on coral reefs: a comparison of direct field measurements vs. remote sensing. Coral Reefs, 43, 265–280.
3. **Lutzenkirchen, L. L**., Tebbett, S.B., Yan, H.F. & Bellwood, D. R. (*Under revision*). Drivers of tropical marine herbivorous fish catches across the Indo-Pacific and Western Atlantic. Cell Reports Sustainability

Appendix E: Publications during candidature not arising from this thesis

1. Tebbett, S.B., Yan, H.F., **Lutzenkirchen, L.L.**, Siqueira, A.C., & Bellwood, D. R. (2024). Global patterns of herbivorous reef fish productivity: the role of Prionurus laticlavius in the Galápagos. Coral Reefs, 43, 299–305.